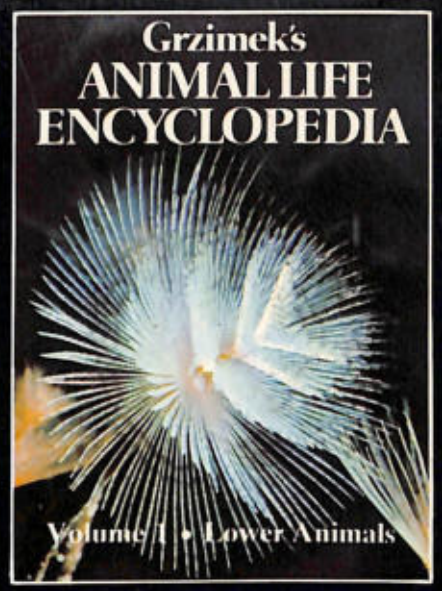
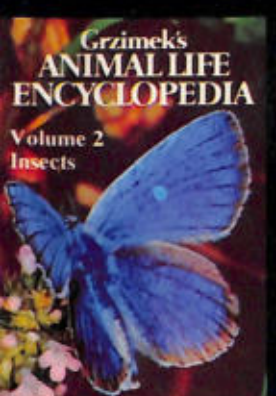
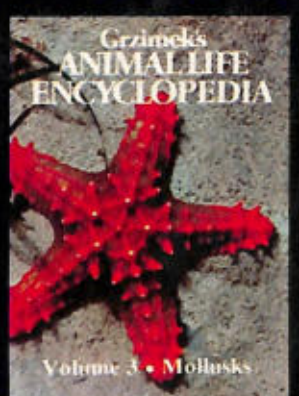
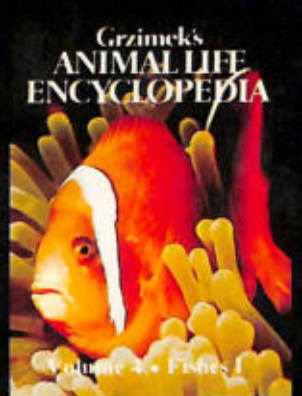
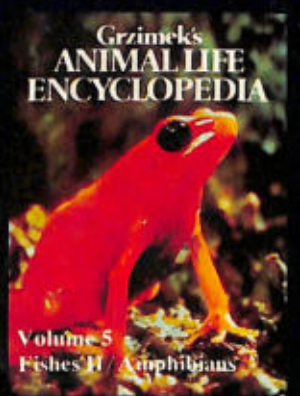
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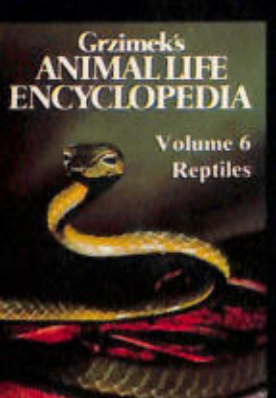


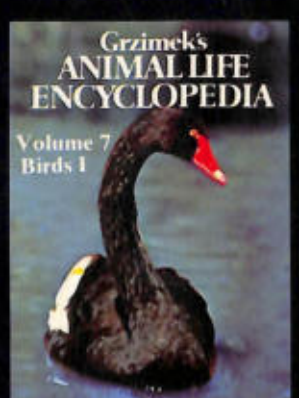


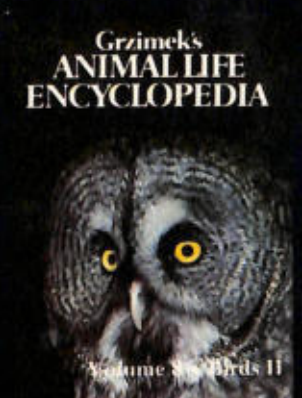


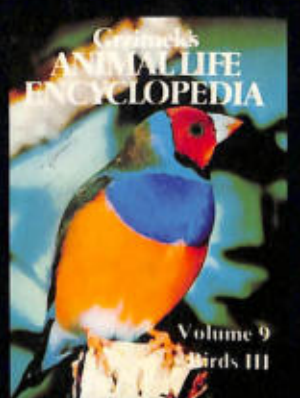


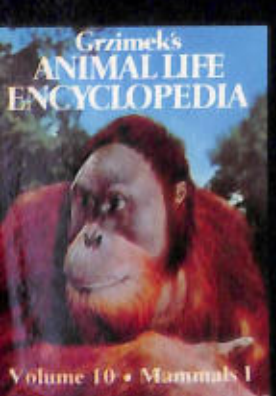


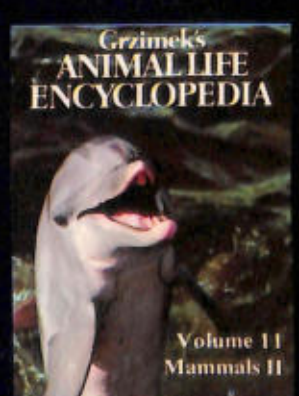


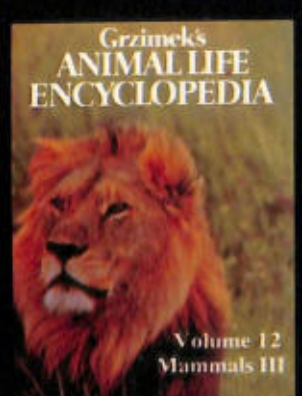


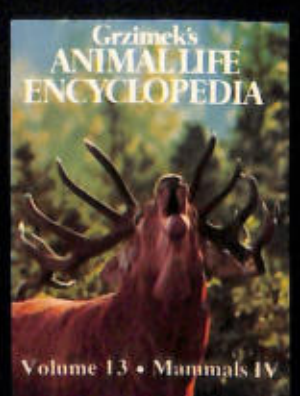


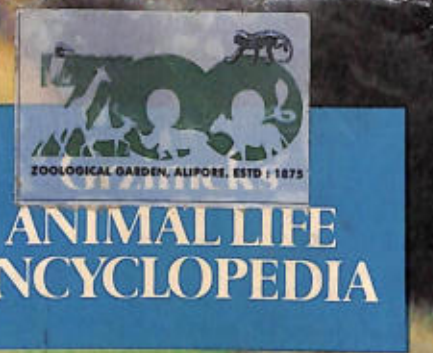












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Springtails
Two-pronged bristle tails
Bristle tails
Large-winged insects



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Volume 2

INSECTS

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1 The Insects

Class: Insecta, by P. Rietschel

By far the largest class in the entire animal kingdom, with more than three-quarters of a million species, is that of the insects (Insecta). The Latin word *insectum* means "notched"; this class of arthropods has earned its name because of the characteristic indentation in the body which separates the posterior "abdomen" from the more anterior "thorax." Usually only the three segments of the thorax of the adult bear well-developed walking legs. The limbs of the abdominal segments have more or less completely regressed, and where vestiges do remain, they have not retained the divisions characteristic of the thoracic limbs. It is this property which distinguishes the insects from the closely related millepedes, which have retained a uniform segmentation of the body.

Distinguishing characteristics

L (total length of head, thorax, and abdomen, without appendages) is 0.2–260 mm. Insects are distinguished from the other arthropods which breathe through tracheae (Tracheata, see Vol. I), the millepedes and centipedes, by the division of the body into thorax and abdomen. The thorax consists of three segments, each with one pair of legs. Primitive forms lack wings, while higher insects are winged or have lost the wings as a result of regression. Development is either direct or by way of divergent intermediate stages. Wingless insects have existed since the Devonian (ca. 400–350 million years ago), and winged, since the Carboniferous (ca. 350–280 million years ago).

There are three subclasses: A. the Myrientomata (with the order Protura); B. the Oligoentoma (with the Collembola); and C. the Euentomata with 27 extant orders. The section Apterygota, the true wingless insects, has two orders, Thysanura and Diplura. The winged insects (section Pterygota, see Chapter 3 and following) have five superorders and twenty-five orders, as follows:

1. Paleoptilota, with the Mayflies (Ephemeroptera, see Chapter 3) and the dragonflies and damselflies (Odonata, see Chapter 3). 2. Neoptilota, subdivision Exopterygota (=Hemimetabola), superorder Orthopteroidea, with the stoneflies (Plecoptera, see Chapter 4), grylloblattids

(Grylloblattodea), grasshoppers, katydids, crickets (Orthoptera), walking-sticks (Phasmida), mantids and cockroaches (Dictyoptera), termites (Isoptera), earwigs (Dermaptera), webspinners (Embioptera), and zorapterans (Zoraptera). 3. Superorder Hemipteroidea, with the barklice and booklice (Psocoptera), biting lice (Mallophaga), suckling lice (Anoplura), thrips (Thysanoptera), bugs (Hemiptera), cicadas, hoppers, whiteflies, aphis, scales (Homoptera). 4. Subdivision Endopterygota (=Homometabola), superorder Neuropteroidea, with the fishflies, lacewings, snakeflies, antlions (Neuroptera), beetles, weevils, stylopids (Coleoptera), caddisflies (Trichoptera), butterflies, skippers, moths (Lepidoptera). 5. Superorder Mecopteroidea, with the scorpionflies (Mecoptera), bees, wasps, ants (Hymenoptera), flies, keds (Diptera), and fleas (Siphonaptera).

Special position in the animal kingdom

The class Insecta occupies a unique position in the animal kingdom: the unmatched ability of the insects to adapt to a variety of living conditions has gained them entrance to the most diverse habitats. As descendants from relatives of the millepedes, the insects were originally land dwellers. But they developed wings at an early stage, and so became pioneers in conquering the air, which they alone ruled for more than 150 million years, into the Jurassic period. It was only then they were followed by the flying lizards, the birds, and, in the early Tertiary, the bats. Many insects left the land and adapted themselves to life in fresh water; of these, some spend only the larval period in water, and others, their whole lives. Insects also inhabit the coastal lagoons of the oceans, though they almost entirely avoid the high seas. Nevertheless, certain water bugs (see Chapter 10) have in fact chosen the oceans as a permanent dwelling place. Insects live in all climatic regions of the earth: we find them in the waterless and nutrient-poor deserts as well as in the polar latitudes. In the latter, the few summer weeks of the year are enough for swarms of billions of mosquitoes to develop; their eggs survive undamaged the cold of the long polar winter. On the other hand, larvae of some shore-flies in eastern Asia populate hot springs at over 55°C; other related larvae live in the brine near salt mines, highly concentrated by evaporation; and still others have actually selected the petroleum pools in California as their habitat. Some insects go through their entire development in the short-lived fruiting bodies of mushrooms, in the equally transient niche offered by the corpses of small vertebrates, and in other quickly perishable materials. A rich insect fauna is found in the soil, in both terrestrial and fresh-water plants, and not least as parasites on other animals. Among the latter, it is above all the insects themselves, their larvae, and even their eggs, which serve as a habitat for other insects. In short, insects are almost ubiquitous on the earth.

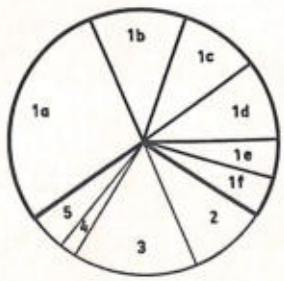


Fig. 1-1. The number of insect species compared with those in the rest of the animal kingdom; the species of insects are divided to show the proportions belonging to the major groups: 1a. Beetles; 1b. Butterflies; 1c. Bees and ants; 1d. Flies; 1e. Bugs; 1f. Other insects; 2. Other arthropods; 3. Other invertebrates; 4. Protozoa; 5. Vertebrates.

This unique ability of the insects to adapt themselves to the most varied and often extreme conditions is reflected in the large number of their species. Over a million species of animals which populate the earth today have been described and named by zoologists. Of these, seventy

percent are insects! Thus the number of their species exceeds that of all the other animal and plant species in the world. The insect world offers us a vast abundance of forms, which is still further increased by the fact that the insects which undergo complete metamorphosis (and these are in the majority) live as larvae in a completely different way, and look entirely different, than do the adults. Moreover, the true insects can differ between the sexes and even between generations.

Entomology, the study of insects

The science which is concerned with this greatest by far of all animal classes is called "entomology" (from the Greek ἔντομον, "notched," like the Latin word *insectum*). The description, naming, and classification of species is of course not the final goal of entomology, but rather only a prerequisite for extremely diverse research. Comparative investigation of the forms and of the development of insect species clarify, on the one hand, their evolutionary relationships to one another, revealing, on the other hand, the differences which have resulted from adaptation to varying conditions. It is precisely the diversity of insects which makes this interaction between structure and function an inexhaustible field for entomological research. Just as with the physical forms, so too are the forms of insect behavior adapted to their specific environments. The prerequisites for complex behavior are a highly developed nervous system and a variety of sense organs. Thus, studies of insect ethology and sensory physiology have produced informative results. Genetics is also closely tied to entomology: the fruit fly (see Chapter 16) became the preferred experimental animal for research in genetics, enabling discoveries which apply far beyond the insect class to humans and the entire realm of animals and plants. The branches of science dealing with the relationships of living things to their environment (ecology) and with their distribution over the earth (zoogeography) are extensively concerned with the insects.

Applied entomology

But entomological research is not done simply for its own sake. Insects, in their vast numbers of species and individuals, often directly or indirectly invade large areas of human life: some transfer pollen among cultivated plants and thus help them to set fruit, but others destroy harvests and stores. Other insects transmit diseases, even in epidemics, to man or his domestic animals, while yet others play an important role in the regulation of biological equilibrium in nature. Thus self-preservation demands that mankind came to terms with these "useful" and "destructive" insects, and explore thoroughly their ways of life. These are the manifold tasks of "applied entomology," the search for the most economical means of combating the destructive insects and increasing the value of the useful ones.

Entomology as a hobby

Moreover, entomology is not confined to the research laboratories; it is becoming a widespread and popular hobby. Nature lovers of all sorts have contributed a great deal to its present state of development. The large number of species represented by the beetles, butterflies, bees, wasps, ants, flies, and bugs makes it necessary for collectors of these

groups to limit themselves to subgroups or to collect only in restricted localities. The collector should not develop large series of rare species, in order not to endanger their continued existence. In no case should one collect only for the joy of possession; for one with this attitude, stamps —which are more likely to increase in value—are a better subject. From the prominence of beetle, butterfly, and moth students at annual meetings, it is clear that Coleoptera and Lepidoptera are studied preferentially; however, other groups of insects offer more unexplored territory.

The more experienced amateur student of insects is not content to collect them, but tries to learn the ways of life of his or her favorites and to rear them. In this way one often advances into unknown territory, even with the more common species. This prospect also holds for observations and experiments on the behavior of insects. The *Souvenirs Entomologiques* of the great amateur observer J.-H. Fabre (1823–1915) can still provide insight into the lives of insects. A low-power microscope, too, can be an unending source of discoveries for the amateur. With it the details of the exoskeleton and even the internal anatomy can easily be investigated, and one can find impressive examples of the correspondence between structure and the associated functions. In this approach, one can dispense with the quest for rarities; under the microscope even a honey bee, housefly, grasshopper, or water bug discloses an unsuspected world, and it is not uncommon for the careful observer of even such ordinary insects to make new discoveries. A prerequisite for any kind of insect study is, of course, that one knows the species of the animal being investigated. One identifies insects by using tables (or "keys"), which usually guide the lay entomologist who makes a serious effort, to the goal, the name of the species (for references see the Suggested Readings). An additional prize for the nature lover in this work is a view through a strong lens of the details, revealing things of beauty which remain hidden to the unaided eye and the fleeting glance.

Size and shape

The maximum size of the insect body is limited by the non-living exoskeleton that cannot grow, and by the limited circulatory system that does not permit a large size. It is far below the upper limit of size for mammals. The body mass (but not length) of a few tropical beetles, the Hercules and Goliath beetles, exceed by far those of the smallest birds and mammals. At the other extreme are certain tiny parasitic wasps, the fairyflies (Mymaridae), with body mass smaller even than that of some medium-sized protozoans, such as paramecia. To one who is acquainted with the highly intricate construction of the insect body, the fact that the whole can be housed in such a tiny space—about one-fifth of a millimeter long—may seem almost incredible.

The external form of an insect is determined entirely by the shape of its cuticle (from the Latin *cuticula*, "little skin"), which forms the supportive and protective armor of the animal. This is true for the hard "antlers" (mandibles) of the stag beetle, the transparent wings of the dragonfly,

the bright scales of the butterfly wing, and the metallic-green wing covers of the rose chafer. Only in a few insect larvae with thin, colorless cuticle can the interior organs be seen from outside. As with the other arthropods, the insect cuticle is composed of a protein—50–75%—and of chitin (a substance closely related to the cellulose of plants—25–75%. The hardness of the armor is a consequence of the tanning of part of the protein to form sclerotin. The hard parts of the exoskeleton are therefore not, as one often reads, strongly "chitinized," but "sclerotized." The membranes joining these plates, on the other hand, consist of untanned protein and chitin. The mandibles of insects can, by sclerotization, attain degrees of hardness greater than that of calcite. Thus some insects are capable of chewing through even lead, silver, zinc, and copper products with these hard jaws. Chitin and sclerotin are insoluble in water, but they do allow penetration of water through the cuticle. Therefore the cuticle, in contrast to the horny layer (keratin) in vertebrate skin, does not itself prevent desiccation. It is covered, however, with a series of protective layers, the epicuticle, which contains waxes and other fatlike substances and is impervious to water.

Among the insects alive today, the stoneflies (Plecoptera, see Chapter 4), which appear quite uniform as a group, have retained many primitive features with few adaptive changes. The higher orders of insects, on the other hand, have independently altered this basic plan in a great variety of ways. The whole body, or individual parts of it, may be stretched out, compressed, flattened, or enlarged, and frequently the surface is beset with spines, setae, horns, scales, and other projections. Anyone who has had the opportunity to examine a collection of beetles, bugs, or cicadas with a simple lens (or, better, with a binocular microscope) will be both aesthetically attracted and stimulated to ask, "What is it for?" Many such structures can be understood in terms of adaptation to certain modes of life, while others seem to have been produced by a capricious extravagance of Nature. In ignorance of their origin and significance, we call the latter "atelic" ("aimless," from the Greek ἀ, "without," and τέλος, "goal, target").

The colors of insects

The colors of insects are just as diverse as their shapes. Here nature has at its disposal a full palette of pigments to produce various hues: the most widespread are the melanins, which range from yellow-brown to black, and the white, yellow, or red pterines. Red carotenes are derived from plant foods, but the green pigments in the skin and blood of green caterpillars and grasshoppers are made by the animals themselves and are by no means the same as the green pigment of leaves. The red pigment in the blood of the so-called "bloodworm" (the larva of the midge of *Chironomus* species), like that in vertebrate blood, is hemoglobin. Many effects of color and luster are brought about not by pigments but by the fine structure, of the order of magnitude of the wave length of light, in the outer layers of the cuticle. Such effects include the splendid

metallic sheen of many beetles, as well as the iridescent colors (see Chapter 13) and the magnificent blue of many butterflies. All these "structural colors" vanish instantly from such a glorious collector's item if one sprinkles the cuticle with benzene, which penetrates into the fine structure of the cuticle and eliminates the optical effects. When the benzene evaporates, the colors immediately reappear.

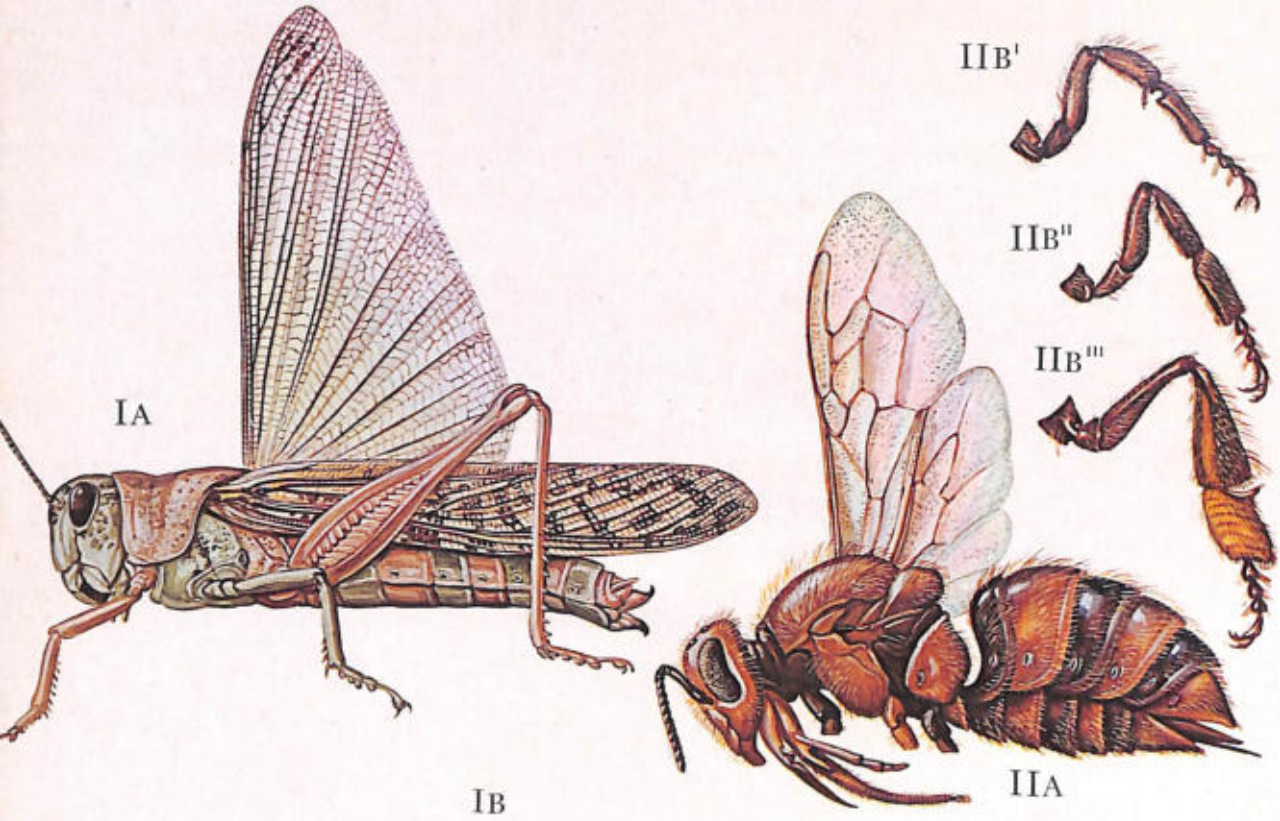
Patterns of coloration

Insect coloration is frequently arranged in patterns. As with body shape, so too the colors and patterns often impart no obvious advantage to the insects which bear them, but in other cases they are clearly of value. As a concealing costume, the patterning can allow the insect to simulate its surroundings just as though it wore a suit of camouflage (background coloration). By means of its coloration the insect can also imitate specific objects to which its predator is indifferent (mimetic protective coloration). The leaf-insects (see Chapter 5 and Color plate, p. 125), the dead-leaf butterfly *Kallima* spp. (see Chapter 15 and Color plate, p. 360), and other insects are practically indistinguishable from foliage; the buff-tip moth (*Phalera bucephala*) in its resting position looks like a small piece of wood with silvery bark, the broken end of which is beginning to molder; many inchworms (larvae of geometrid moths) imitate a thin branching twig, and a small butterfly, *Argyroploce variegana*, when at rest resembles a pile of bird droppings. In interpreting such mimicry, some caution is required. It is simply that the diversity possible, given nearly a million insect species, allows much opportunity for the vagaries of chance. Most of the striking patterns of coloration have a warning function. The pair of staring eyes on the posterior wings of the eyed hawk-moth (see Chapter 15 and Color plate, p. 327), which suddenly become visible when the moth adopts a defensive posture, are an example of "warning coloration." Stinging and supposedly bad-tasting insects often bear a striking warning pattern, usually black and yellow. These insects are said to be carefully avoided by birds which have once had a bad experience with them. This state of affairs is to the advantage of species which are similarly colored but defenseless, though should these imitators become more numerous than their dangerous models, the pattern would no longer afford protection. Recently this notion of bad-tasting insects in relation to mimicry has been seriously called into doubt, as has the deterrent effect of the poisonous sting, with which the birds can cope quite skillfully when necessary.

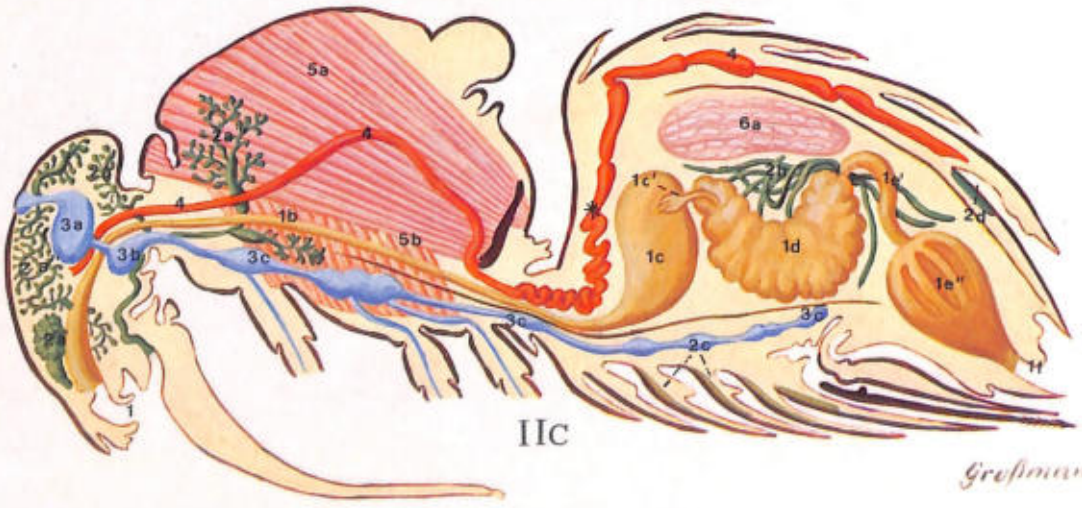
A puzzle which is still entirely unsolved is the "over-all patterning" of many butterfly wings (see Color plate, p. 25). Often the patterns of the front and hind wings fit together perfectly when the wings are in their natural position. The unnatural wing position of mounted butterflies disrupts this composite pattern. The partial patterns which eventually fit together to form the total pattern arise in the pupa at some distance from one another, and they are also separated in the newly emerged butterfly. Not until the wings are fully extended do they merge to form

▷
The wings of the butterfly *Iphiclides podalirius* (see Chapter 15) have a composite pattern; the black stripes of the front wings are continued on the hind wings so as to complete the design. The front and hind wings develop independently from separate wing-buds, but in spite of this their coloration matches exactly, producing a uniform pattern; the way this is done remains one of the unsolved puzzles of nature.

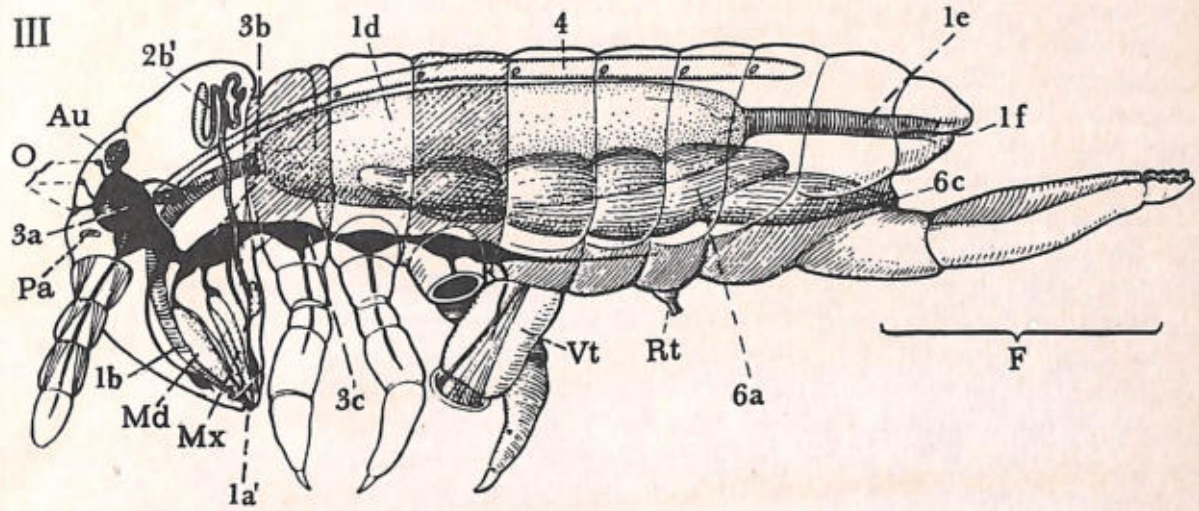



IIB'
IIB''
IIB'''
IA
IB
IIA


3a
1c
1b
3b
1d'
1d
2b
5a
6a
1e
1e'
6b
3c
1a


5a
6a
1c'
1e'
2d
3a
1b
5b
1c
1d
1e''
3b
3c
2c
IIC

Großmann



Examples of insect anatomy.

I: MIGRATORY LOCUST (see Chapter 5); IA, Side view, right hind wing unfolded; first and third thoracic segments as well as the first, third, fifth, and seventh abdominal segments distinguished by brown shading. IB, Diagrammatic longitudional section showing the internal organs (key to the numbers in the next column).

II: HONEY BEE (see Chapter 18), worker; IIA, Side view, right wings unfolded and left wings removed; only the basal segments of the legs are shown; first and third thoracic segments and second, fourth, and sixth abdominal segments distinguished by darker shading. IIB'-IIB''', Front, middle, and hind legs from the inner side. IIC, Diagrammatic longitudinal section showing the internal organs (key to the numbers in the next column).

III: SPRINGTAIL (see Chapter 2); drawn as though transparent, with the forked spring tail (furca) extended; left hind leg removed; first and third thoracic segments distinguished by darker shading. Pa, postantennal organ (a sense organ); Oc, ocelli (simple eyes); Au, compound eyes; Md. mandible; Mx, maxilla; Vt, ventral tube or collophore; Rt, retinaculum, which holds the folded furca in place; F, furca.

INTERNAL ORGANS (in I–III):
1. Alimentary canal (olive-green in I and II): 1a. Mouth; 1a'. Oral cone (in the springtail); 1b. Esophagus; 1c. Crop; 1c'. Proventriculus (in the honey bee); 1d. Midgut; 1d'. Midgut caecum (in the locust); 1e. Hindgut; 1e'. Anterior hindgut; 1e''. Posterior, expanded hindgut with rectal papillae; 1f. Anus.
2. Glands (green in I and II): 2a'. Mandibular gland; 2a''. Salivary gland; 2a'''. Labial gland (2a' to 2a'''. drawn only for the honey bee); 2b. Excretory organs; 2b'. Head kidney (only in the springtail); 2b''. Malpighian tubules (lacking in the springtail); 2c. Wax glands (only in the honey bee); 2d. Scent glands (only in the honey bee).
3. Nervous system (blue in I and II): 3a. Supraesophageal ganglion; 3b. Subesophageal ganglion; 3c. Ventral cord.
4. Circulatory system (dark red in I and II): * boundary between aorta (anterior) and heart (posterior).
5. Flight musculature (light red, only in locust and honey bee): 5a. Wing depressors; 5b. Wing elevators.
6. Reproductive organs (pink in I and II): 6a. Gonads (in the springtail); 6a. Ovary in the female (in locust and honey bee); 6b. Oviduct (drawn only for the locust); 6c. Genital aperture (drawn for locust and springtail).

the final pattern. In the dead-leaf butterfly *Kallima* spp. the two partial patterns join to form the system of "leaf ribs." But how could this match be developed with such precision? No bird would notice a slight misalignment (for example, a small discontinuity in the supposed midrib of the "leaf") and thus be able to see through the deception. And what advantage does the zebra swallowtail butterfly obtain from the exact overall matching of its stripes? Unsolved puzzles.

Segmentation of the insect body

The insect body, like that of other segmented animals, is divided into sections which lie in series one behind the other; associated with this segmentation is a serial repetition of certain elements of the body structure. These "segmental" (i.e., belonging to each segment) parts are as follows: (1) dorsal and ventral plates of the exoskeleton; (2) one pair of limbs; (3) the longitudional muscles which run between the boundaries of the segments; (4) one pair of ganglia of the ventral nerve cord, with transverse connections; (5) one pair of body cavities, which disappear at an early stage in the insects; and (6) one pair of openings (spiracles) of the breathing tubes (trachaea). The heart can also have segmentally arranged lateral openings for intake of blood from the body. This series of segments is terminated anteriorly by a pre-oral structure (the acron, or prostomium) and posteriorly by an anal structure (the telson): these lack the segmental parts listed above. The acron is no longer recognizable in any insect, as it has been incorporated into the head capsule; the telson has joined the last abdominal segment except in the proturans where it has remained distinct. Of the three divisions of the insect body, the head comprises the acron and at least four segments, the thorax, three segments, and the abdomen, eleven segments plus the telson. Usually the terminal segments of the abdomen are fused; only in the case of the springtails (see Chapter 2), which have only six abdominal segments, is it to be assumed that their ancestors did not have a greater number of distinct segments.

The abdomen

The exoskeleton of each segment consists of a dorsal plate (the tergum) and a ventral plate (the sternum), which are connected to one another and to the adjoining segments by membranes. Lateral plates of the thorax (the pleura) are in an evolutionary sense the parts of the leg nearest the body, which have been incorporated into the body wall. Therefore they are lacking in the legless abdomen. The connecting membranes permit extension of the abdomen in its circumference as well as in its length. This flexibility plays a role in breathing and also in feeding. The latter can readily be observed in a mosquito which is sucking blood. Similarly, the ripe egg masses of female insects can cause considerable swelling of the abdomen, as one can see in the leaf beetles. But the greatest distension occurs in the egg-filled abdomen of the queen termite (see Chapter 7 and Color plates, pp. 135/136 and 145).

In the thorax the freedom of movement of the skeletal plates relative to one another is limited, especially in the wing-bearing segments, where

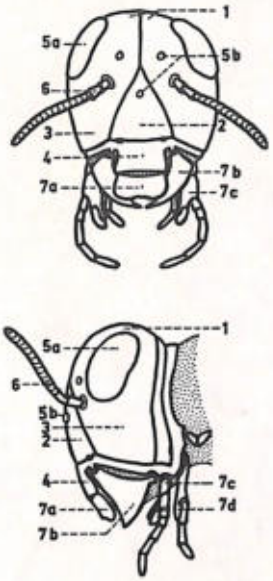


Fig. 1-2. Parts of the insect head: 1. Epicranial suture; 2. Frons; 3. Gena; 4. Clypeus; 5a. Lateral compound eyes; 5b. Medial ocelli; 6. Antennae; 7. Mouthparts: 7a. Labrum; 7b. Mandible; 7c. Maxilla; 7d. Labium.

The antennae

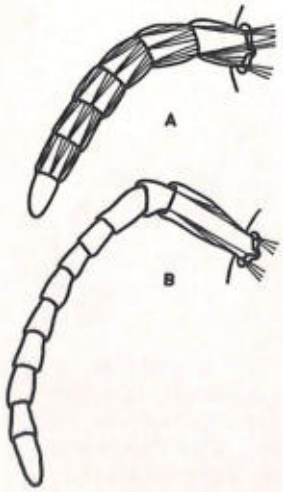


Fig. 1-3. Insect antennae: A. Articulated; B. Flagellate.

the plates must provide a firm support for the wings. Only structures outside this framework, the dorsal plate and with it the wings, may be moved by muscles. Even the parts of the legs nearest the body can be incorporated into the rigid framework of the thorax. In wingless larvae the thorax remains more flexible.

The skeletal plates of the head are so tightly fused to form the head capsule that there is a recognizable boundary only between the last segment of the head and the one immediately in front of it. For that reason, the number of segments forming the insect head is still debatable. An indication could be given by the number of pairs of appendages on the head, but here we are confronted with a difference of opinion over whether the antennae of insects (as well as the first antennae of crustaceans) arose from limbs or whether they correspond to the antennae on the acron of their ancestors, which were related to the segmented worms. It is certain that four true segments are represented posterior to the antennae. In the first of these, limb buds form initially but are resorbed early in development. These correspond to the second pair of antennae of the crustacea. The three following head segments bear the following limbs: (1) the upper jaws (mandibles), (2) the lower jaws (maxillae), and (3) the lower lip (labium).

The antennae of insects consists of a variable number of segments which can move with respect to one another. In the primitive springtails and diplurans (see Chapter 2) all the segments are identical, and each except the final one has muscles with which it can move the one distal to it (toward the tip). These articulated antennae are similar in structure to those of the millepedes, relatives of which were the ancestors of the insects. In the bristletails (see Chapter 2) and the winged insects (see Chapter 3), on the other hand, the antennae have become flagellate. The degree to which they can be moved by muscles is very limited: only the basal segment (the scape, from *scapus*, Latin for "shaft") has muscles which can move the next segment (the pedicel) and with it the rest of the antenna, the flagellum. If the flagellum itself is to be moved, as in the spreading of the antennal lamellae of the scarab beetle, the action is accomplished entirely by means of the blood pressure; when the pressure is subsequently reduced, the elasticity of the joints returns the segments to their resting configuration. In the simplest case, which we find in the stoneflies, cockroaches, and primitive Orthoptera, the antennal segments are shaped like bristles or threads and are composed of a large number of identical segments. This type of antenna is termed filiform. If each of these segments bears a tooth on the same side, as in some click beetles, the antenna is termed serrate. If these projections are longer, the antenna is called pectinate, and if they are in two opposed rows it is bipectinate. An intermediate stage between the serrate and pectinate antennae is represented by the serro-pectinate antennae. The lepidopteran families in which the larvae spin cocoons (e.g., the silkworm) offer

examples of these antennal forms. In many beetles and butterflies the terminal segments of the antennae are thickened to form clublike heads. In the scarab beetles and their relatives, on the other hand, the terminal segments are drawn out into leaflike plates, densely covered with sense organs; these antennae are lamellate. There are whorls of hairs on the antennae of mosquitoes. Not infrequently the flagellum is shortened and lacks segmentation, as in the flies and cicadas. The nimble insects which live in fur and feathers would be hampered by long antennae; therefore those of the flea can be laid into grooves in the head capsule, while those of louse flies are shortened, with the third segment recessed into the second.

The antennae have many different functions. As tools for the sense of touch, they are provided with tactile sense organs, which are also found on many other parts of the body. Primarily the antennae bear organs of smell. Male Lepidoptera, which find the females by means of their olfactory sense, therefore often have the more strongly pectinate or plumose (feather) antennae. Similarly, the seven large antennal lamellae of the male scarab beetle provide a larger expanse of odor receptors than do the six small ones of the female. The whorls on the antennae of mosquitoes are also much larger in the males than in the females, but here the antennae are above all organs of hearing! With them the males, dancing in swarms, perceive the flight tone of approaching females, but not their own tone. The same organ in the second antennal segment of water bugs serves to maintain equilibrium. In still other cases it detects air currents.

Although according to their evolutionary origin the mandibles, maxillae, and labium are pairs of legs, they are no longer used for locomotion but rather for feeding, and therefore they are called "mouthparts." The mandibles are basically biting tools; for this purpose they have teeth (incisors) and a grinding surface (the molar area) on the ends which are turned toward one another. They are usually articlated by means of two ball joints, one with the ball on the mandible and the socket on the head capsule, and the other with the reverse arrangement. Between these two joints there arises a powerful tendon of the muscles which closes the mandible and, opposite this, a less powerful one for the extensor muscle. The sizes of the tendons and their muscles correspond to the amount of work that the closing and opening of the mandible must perform. The teeth and grinding surfaces of the biting mandibles take very different forms, according to the manner of feeding. Compare the mandibles of the vegetarian June beetle with those of a predatory ground beetle, which serve not as cutting and grinding teeth but rather as grasping teeth. The mandibles of some predatory insect larvae (the giant water beetle and the firefly, see Chapter 13; the antlion, see Chapter 12) have become actual injection cannulae. They inject digestive juices into their prey and thus dissolve it from within; then the solution is sucked back through the same cannulae. The licking/sucking mouthparts of the caddis fly (see Chapter 14), the sucking proboscis of Lepidoptera (see

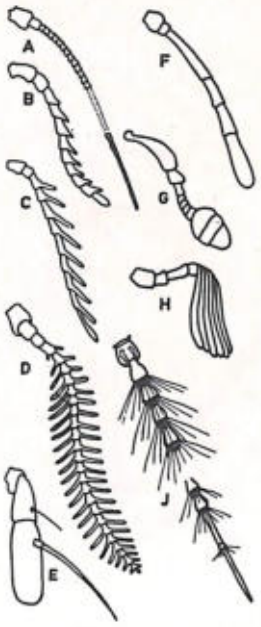


Fig. 1-4. Types of flagellate antennae. A. Filiform; B. Serrate; C. Pectinate; D. Bipectinate; E. Aristate; F. Clavate; G. Capitate; H. Lamellate; J. Whorled plumose.

The mouthparts

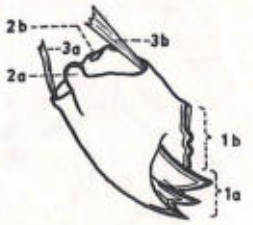


Fig. 1-5. Mandible (cockroach): 1a. Incisor area; 1b. Molar area; 2a. Ball of posterior joint; 2b. Socket of anterior joint; 3a. Tendon of the extensor muscle; 3b. Tendon of the flexor muscle.

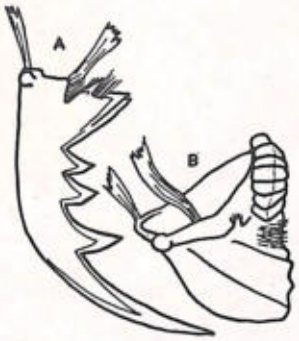


Fig. 1-6. Mandible of a predatory tiger beetle (A) and of a vegetarian scarab beetle (B).

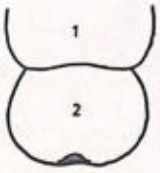


Fig. 1-7. Preoral sclerites of a primitive insect (cockroach): 1. Clypeus; 2. Labrum.

Chapter 15), and the sponging proboscis of many flies made the mandibles superfluous; they underwent regression. In the juice-sucking insects (the true bugs, see Chapter 10), blood-sucking mosquitoes, and horse flies (see Chapters 19 and 20), on the other hand, the mandibles are incorporated in the piercing apparatus and have been converted into long, thin stylets.

Since the biting mandibles themselves are not segmented and can only carry out simple rotational movements, they are capable only of grasping, cutting, and crushing food, and cannot send it on into the gullet. This function is served by the next two pairs of limbs; these are made up of a number of parts hinged together so that they can move in several ways. Like the mandibles, these too are most primitively constructed in the insects with biting mouthparts. Here they consist of two basal segments, the second of which bears a multisegmented extension, the palpus. The palpus and the two basal segments correspond to the chain of segments in a leg. In addition, two projecting lobes which turn toward one another have been elaborated from the second basal segment; the inner one is called the lacinia and the outer, the galea. The maxillae on the two sides are, like the legs, completely separate, whereas the labium consists of a pair of appendages which has fused at the midline. This fusion extends to both basal segments and often to the laciniae as well, which in that case form an unpaired tongue, or glossa. By extension of the two basal segments, the labium of the dragonfly larva (see Fig. 4–4), like that of the rove beetles of the genus *Stenus* (see Fig. 10-6), has become a "mask" used in the capture of prey. It is normally folded up, but in use it is unfolded and extended with lightninglike rapidity. The mask of the dragonfly larva is extended by muscles, and that of the beetle, by blood pressure.

Like the mandibles, the maxillae are greatly modified in the mouthparts which are adapted for licking and sucking. Thus the tongue of the honeybee was formed from the fused laciniae of the labium, the tongue of the butterfly from a folding together of the galeae of the maxillae, and the proboscis of the fly from the entire labium. In the juice-sucking bugs and midges the maxillae, as well as the mandibles, have become long, thin stylets, while the labium has taken the form of a protective sheath, surrounding the whole bundle of stylets when they are in the resting position. When the stylets are in use, the labium serves as a guide for them, but its tip does not penetrate the tissues of the host.

In addition to these mouthparts, formed from paired legs, there are two unpaired structures which participate in feeding: the upper lip (the labrum) and the inner lip (the hypopharynx). In the basic (biting) form the labrum is a broad, flat, flexibly jointed flap adjoining the upper border of the mouth. In the beaks of bugs (see Chapter 10) the labrum serves to close the upper side of the base of the stylet sheath formed by the labium. In the piercing mouthparts of some Diptera (mosquitoes, horse flies, and

other blood-sucking flies), on the other hand, the labrum itself has become a stylet. In the biting type of mouth the hypopharynx forms the floor of the mouth cavity; here it takes the form of a peg, the upper side of which is continued into the floor of the gullet, while its lower side forms the roof of the saliva-containing chamber, the salivarium. The salivary glands open at the base of the hypopharynx. In some higher insects the hypopharynx has been transformed into a pump for saliva, and it serves as a spinning device (the silk press) in insects with salivary glands that have become silk glands. In the field and house crickets and their relatives (see Chapter 5) the lower side of the hypopharynx (that is, the roof of the salivarium) may protrude to form a massive "sponging" proboscis (see Color plate, p. 126). On the other hand, the hypopharynx of the stinging Diptera (like the labrum, mandible, and maxilla) has become a stylet. The alimentary canal and the salivary canal are like a pair of one-way streets running in opposite directions; the former lies between the hypopharynx and labrum, and the latter, within the hypopharynx.

Despite the variability in their forms, the mouthparts of the insects are always composed of the five elements just named: the labrum, the hypopharynx, the mandibles, the maxillae, and the labium. Their modifications can be understood only in connection with their function, and even then it is not enough to consider the individual parts. The key to understanding lies in the way they work together. With nothing more than a good lens—the constant companion of the amateur entomologist—one is sure to make intriguing observations: the wasp on a fruit pie, the honeybee at a bowl of sugar water, the mosquito on the back of one's hand, the butterfly on a flower or a drop of honey, and the housefly among scattered grains of sugar—all of these reward quiet study.

The three thoracic segments of the insects bear three pairs of legs, which is why the insects have also been called Hexapoda (from the Greek word for "six-footed"). These legs, as in all the arthropods, are divided into movable segments. The segments, from the body outward, are (1) the coxa, (2) the trochanter, (3) the femur, (4) the tibia, (5) the tarsus, which represents the foot, and (6) the pretarsus, or claw. Of these, the trochanter is sometimes subdivided into two parts, while the tarsus usually has up to five subdivisions. Though the tarsal segments are flexibly jointed, they are not provided with muscles. The pretarsus usually bears two claws and often also has one or two adhesive pads. The claws are flexed by a long tendon which runs through the foot; the muscles of the tendon originate in the tibia and the femur. Extension of the claws, however, is done not by muscles, but by the elasticity of the joints. The way in which these various clinging devices are selected to suit different conditions can be well observed in honeybees. When walking on a rough surface they use their claws, while on a smooth surface (for example, on the cleaned glass wall of an observation hive) the claws are bent inward so

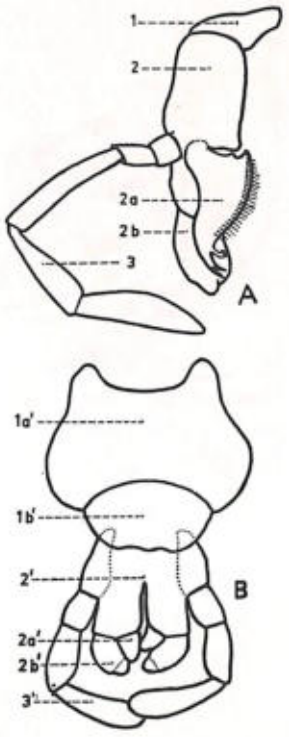


Fig. 1-8. Maxilla (A) and labium (B) of a primitive insect (cockroach) (corresponding parts of the two mouthparts bear the same number): 1. Cardo; 1a'. Submentum; 1b'. Mentum; 1a' & 1b', Postmentum; 2. Stipes; 2a. Lacinia; 2a'. Glossa; 2b. Galea; 2b'. Paraglossa; 2'. Prementum; 3. Maxillary palp; 3'. Labial palp.

The thoracic legs

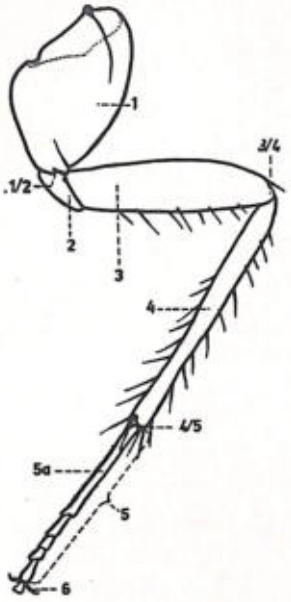


Fig. 1-9. Walking leg of a primitive insect (cockroach): 1. Coxa; 2. Trochanter; 3. Femur; 4. Tibia; 5. Tarsus or foot; 5a. First tarsal segment (basitarsus); 6. Pretarsus; 1/2, Coxal joint; 3/4. Femoral joint; 4/5. Tarsal joint.

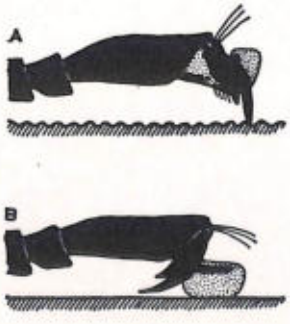


Fig. 1.10. How the pretarsus of the honey bee adheres to a rough (A) and a smooth (B) substrate.

that the adhesive pads stand out in front of them and can come into action. The basis of their adhesiveness is still unknown. There are also adhesive cushions on the soles of the tarsal segments in many insects (cockroaches, grasshoppers, phyllids, and leaf beetles). Insects often stand with the legs supported not only on the tarsus, but also on the end of the tibia, which may have strong spurs or rows of bristles.

The thoracic legs of the insects are primarily organs of locomotion, but they play a number of other roles. The basic form is represented by the walking (ambulatorial) leg. From this, the most widespread form of leg, the jumping (saltatorial) leg has developed by acquiring the ability to extend in a rapid jerk. In the leafhoppers the joint which produces the jumping movement is that between coxa and trochanter, whereas in the grasshoppers it is the "knee" joint between femur and tibia. The jumping musculature of the leafhoppers, therefore, is located in the coxa and the thorax, while that of the grasshopper is in the femur. These segments of the legs are correspondingly thickened in a characteristic way. The jumping legs of the flea occupy an intermediate position: they extend during a jump by means of both the coxal joint and the knee. The springtails (see Chapter 2), though, jump by means of posterior abdominal appendages, and the legless maggots of the cheese skipper jump by extension of the whole body. Swimming (natatorial) legs are found in many water insects. They move like oars, in only one plane, and in the whirligig beetles (see Chapter 13) they are widened into leaf-like paddles; but even the narrow swimming legs of the back-swimmers (see Chapter 10), the water boatmen, and the giant water beetle are effective oars, because they have a border of hairs which spreads out during the rowing stroke, enlarging the rowing surface. When the oar is pushed forward, however, the hairs are pressed tightly against the leg, so that they present no resistance to the water. Legs may be broadened in various ways to form digging (fossorial) legs, as in the dung beetle and its relatives (see Chapter 13), the mole-cricket (see Color plate, p. 125), the cricket *Cylindrachaeta* sp. (see Color plate, p. 116), and the cicada nymphs (see Chapter 11). The processes by which these "shovels" were formed are different in the various groups listed, but particularly in the last three groups astonishingly similar digging tools have evolved. The clasping (scansorial) legs of the biting lice found on birds and mammals (see Fig. 7-1), and those of other animal lice, serve more to anchor the insect than to move it. They stand out to the side of the body and are bent toward the midline at the knee. The shortened tarsus, with only one or two segments, bears large claws—usually two in the biting lice but only one in other lice. The tip of the claw is pointed backward toward the tibia to form a powerful gripping hook which anchors the insect in the feathers or pelt of its host.

Besides locomotion, insect legs often perform other tasks which are apparent from their specialized construction: the front legs of the embiids

(see Chapter 7) have a spinning gland built into the first, thickened segment of the tarsus; groups of embiids cooperate in using these to construct the tubes in which they live. The front legs of the hymenoptera often bear a toilet organ, used to clean the antennae. There is a notch in the first tarsal segment which contains comblike hairs and can be closed by the fibula, a large spur of the tibia, when the tarsus is bent. The insect draws its antennae through this apparatus; thus the antennal surface, covered with thousands of sense organs, is wiped free of dirt. The front legs of the male water beetle (*Dytiscus* sp.) bear suction cups and hairs with which they cling to the back of the female during copulation. The front legs of the praying mantis (see Chapter 6) and the predatory lacewings (see Chapter 12) are grasping (raptorial) legs, as are those of the water scorpion, the water stick-insect, and the ambush bug (see Chapter 10); the tibia can be folded back against the femur like the blade of a pocketknife. The hind legs of the honey bee and bumble bee have become collecting legs which bear pollen baskets on the tibiae; the legs are used to brush pollen from the hairs on the body into the basket so that it can be carried home. The jumping legs of the grasshoppers also serve for the production of sound; in one species, the South African *Methone anderssoni*, this has actually become their only function. Sense organs, too, are often located on the legs; the organs of hearing of the bush crickets (see Chapter 5) are on the anterior tibiae, and the taste organs of many butterflies are on their tarsae.

The wings

In contrast to the legs, which all arthropods possess, the wings are an achievement of the insects alone. Of course, not all insects have wings:

1. The juvenile stages are wingless, or they bear only incomplete wing rudiments (the so-called pterotheca). Only after the last molting do the fully developed wings unfold. The only exception to this rule is in most Mayflies (see Chapter 3), which have an additional molt after reaching the adult stage.

2. The "primitive insects" (Apterygota) diverged from the main lines of descent before wings had been developed; thus they remain wingless even today.

3. Among the winged insects (Pterygota), many have sacrificed their wings in the course of adaptation to particular ways of life. Thus, many of the parasitic insects which inhabit feathers and fur are completely wingless (the biting and other animal lice, the sheep tick, and some bird flies); further, most of the insects on stormy oceanic islands are without wings. Within a species it often happens that some individuals have wings and others do not. In the ants and the termites the reproductive individuals are initially provided with wings for the nuptial flight, but the workers and soldiers are not. Among some butterflies, mealy bugs, and stylopid insects it is only the males which have wings, wile among the fig insects (see Chapter 17) it is only the females. In the bisexual generation of aphids (see Chapter 11) usually only the males have wings; in the purely female

generations both winged and wingless individuals occur simultaneously in a ratio which varies from generation to generation. In many species of insects, particularly among the grasshoppers and the bugs, there are many transitional stages between the full formation and the complete absence of wings.

4. Quite a few winged insects have developed only one pair, either the forewings or hindwings, for flight, while the other pair has been assigned a new task (see below).

5. The reproductive individuals among the termites, as well as the queen ants, initially possess wings; once a colony has been established they break off these now unnecessary structures at preformed break points near the roots. Similarly, the deer ked (see Chapter 20) and some of its relatives, which after emergence seek their future hosts in flight, lose the wings after they have reached their goal.

It is true of most insects that the second and third thoracic segments each bear a pair of wings. Since these segments also possess legs and each segment is allocated only one pair of limbs, the wings cannot be transformed limbs. Some indication of their origin is given by the silverfishes (see Chapter 2), primitive insects in the subclass of the bristletails, which are most closely related to the ancestors of the winged insects. In the place of wings, the thoracic segments of the silverfish have formed lateral lobes (paranota) into which the breathing tubes (tracheae) extend. The tubes are branched in the same way as the tracheae in the wings of the winged insects! One may conclude from this that insect wings arose from these paranota. The oldest winged insects of the Carboniferous possessed large paranota on the first thoracic segment; in the course of evolution these failed to develop into wings. It would be very disadvantageous aerodynamically to have wings on all three thoracic segments, and even the two pairs are not an ideal design, since the air turbulence created by each pair affects the other. The damselflies (see Chapter 3) and the stoneflies (see Chapter 4) are therefore quite poor flyers. The dragonflies, however, which are extremely adept at flight, coordinate the strokes of the forewings and hindwings by means of their highly developed nervous system. Occasional alternating strokes of their wings during some flight maneuvers are accompanied by a loud rustling noise. The simultaneous stroke of both wing pairs is made more effective by devices which unite the leading edge of the hindwing with the trailing edge of the forewing. In the book lice, bugs, Hymenoptera, and Lepidoptera this technical problem has been solved in various ways, but in all of them the result is the same: the forewings and hindwings operate as a single surface. Other insects have achieved the same aerodynamic effect by flying with one pair of wings. Beetles and earwigs fly with only the hindwings; their forewings have become wing covers (elytra), which protect the delicate hindwings from damage when they are folded. The male stylopid insects also fly with the hindwings alone (see Chapter 13). The Diptera, the males of the

mealy bugs, and many Mayflies, on the other hand, fly with only their forewings. In the Mayflies the hindwings have more or less regressed. The hindwings of the male mealy bugs have also become tiny lobes, but their connection with the forewings has been preserved. The forewings of the stylopid insects and the hindwings of the Diptera are no longer organs of flight, but have been transformed into little oscillating clubs (halteres) which stabilize flight through a gyroscopic action. If these small structures, covered with numerous sense organs, are put out of action, the insect is incapable of maintaining equilibrium in flight.

Insect flight

The upstroke and downstroke of the wings are brought about by changes in the shape of the thoracic exoskeleton. Dorso-ventral "indirect flight muscles" draw the tergum (the dorsal plate) downward and thus raise the wings. Longitudinal muscles restore the original configuration, depressing the wings. These muscles represent a considerable fraction of the body weight: 11% in the housefly, 13% in the honeybee, and as much as 24% in certain dragonfly nymphs (see Chapter 3). "Direct flight muscles," which exert force on the wings directly, operate the forewings and hindwings of lower insects, which do not beat in synchrony; these are also present in the higher insects, but here they serve to set the position of the wings during turns, hovering, backward flight, and other special maneuvers. The most amazing thing about the performance of some flight muscles (those called myogenic) is the rapid sequence of their contractions: a fly with 200 wingbeats per second must contract and relax its flight muscles 200 times per second. However, it has been shown that in these muscles a very much slower sequence of nerve impulses suffices to maintain this high rate of contraction and relaxation, i.e., individual contractions are induced not by individual nerve impulses (as in neurogenic muscle) but by cyclic stretching that occurs at the resonant frequency of the thorax-wing system. The wingbeat frequency varies within a wide range, from more than 1000 beats per second in the gnat *Forcipomyia* spp. (with myogenic flight muscle) down to about six per second in the neurogenic flight musculature of butterflies. The flight velocity also varies within a wide range. Thus, hawk moths travel up to 15 m in a second (about 30 mph), but in the same time the white cabbage butterfly covers only about 2 m (4.5 mph). The speed record is perhaps held by the male of a bot fly *Cephenomyia pratti*; the velocity claimed for it, 818 mph, would be faster than that of sound. It is hardly likely that an insect exoskeleton could manage this, nor is it apparent how such haste would be of advantage to the animal. But a genuinely astonishing thing about some good insect flyers is their endurance: hawk moths and migratory locusts can fly for hours without a pause and, if the wind is with them, cover hundreds of miles. Houseflies can maintain uninterrupted flight for almost two hours, and a small fruit fly forced to fly constantly is provided with enough fuel (glycogen) to fly as long as four or five hours.

In flight, the wingtips describe a figure-of-eight, with the turning

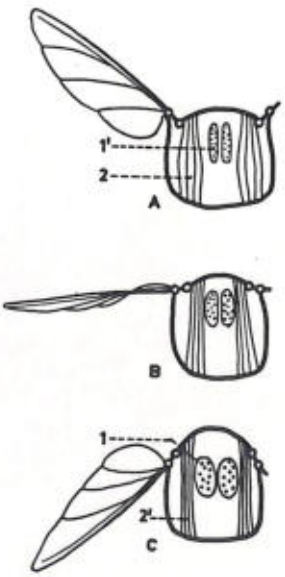


Fig. 1-11. Wingstroke caused by the indirect flight muscles, schematic cross section of the thorax including the wing: wing elevated (A), horizontal (B), and depressed (C). Longitudinal muscle (wing elevator) contracted (1) and relaxed (1'); dorso-ventral muscle (wing depressor) contracted (2) and relaxed (2').

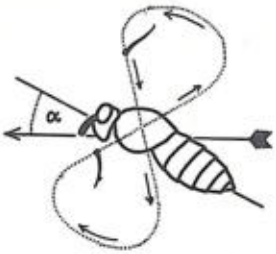


Fig. 1-12. Figure-of-eight path of the wingtip (dotted); flight path (arrow); α, angle of the body axis to the flight path.

points slanted above-back and below-forward. The front edge of the wing always leads the back edge, as a consequence of the stiffening of the front edge by the sturdy costal vein. In addition, the angle of the wings is set by the direct flight muscles, so that the level forward flight of some insects can be converted into flight in one spot (hovering) or even to backward flight. The flower flies (see Chapter 20) which are found at the edges of woods in summer, and the hummingbird hawk moth (see Chapter 15) at a flower bed offer the most impressive examples of such aerobatic tricks. Flight performance is also largely dependent upon the shape of the wings. Compare the broad wings of a fluttering butterfly with the narrow, sharp wings of a swiftly flying hawk moth; these differences are like those in the wing shapes of slowly and rapidly flying birds (compare, for example, the lapwing and the tern).

The wings represent lateral outfoldings of the thorax and thus consist of a double membrane of cuticle, within which nerves and tracheae are imbedded. These run in the wing veins, which are formed by local strengthening of the two membranes and which reinforce the wings. Between the bars of this framework the membranes form thin-skinned wing cells. Longitudinal veins run from the base of the wing to its outer margin. In primitive insects (the Palaeodictyoptera of the Carboniferous, present-day dragonflies, and many Orthoptera) cross veins run between the longitudional veins to form a dense network. In higher insects the number of cross veins is much decreased. The longitudinal veins are formed alternately by the upper and lower membranes, and the membranes of the wing cells between them run in a zig-zag manner as seen in longitudinal section. The well-known aircraft designer and aeronautical scientist Prof. H. Hertel says of this design, "The structure and dimensions of such membranous wings are of great interest to the engineer concerned with finding new ways of designing light structures." The wing construction of the smallest insects is very much simplified. In the tiny proctotrupoid wasps (see Chapter 17), the costal vein alone, with one small side branch, is enough to support the delicate little wing. The wings of the thrips (see Chapter 9) and the hindwings of the smallest beetles of the family Ptiliidae consist solely of one longitudional vein which forms the shaft for a plume of marginal hairs. Several such shafts form the wings of the plume moths; the spaces between the shafts have lost all traces of a connecting membrane. The surface area of these tiny creatures is very large in proportion to their mass, which permits wing designs quite unsuitable for larger animals.

Abdominal appendages

In the early ages of the earth the insects developed from ancestors of the millepedes, which had legs on all segments of the trunk. When the trunk was divided into thorax and abdomen, the walking legs of the thorax were retained and even further developed. The legs of the abdomen have more or less regressed, but remnants are commonly found even in present-day insects. Thus, the first three abdominal segments of

the proturans (see Chapter 2) still bear pairs of leg stumps; those of at least the first pair always consist of two segments. The jumping appendages of the springtails (see Chapter 2) developed from abdominal legs. Even the larvae of many flying insects (for example, the caterpillars of butterflies and of sawflies) still have abdominal feet. Here they actually function in locomotion, whereas in the aquatic larvae of the Mayflies and the fishflies they have been converted into gills. And even in the adult winged insects the legs of the eleventh abdominal segment have frequently been retained as cerci (singular, cercus). These appendages, usually composed of many segments, are particularly noticeable in the Mayflies, stoneflies, crickets, and cockroaches. The massive unsegmented forceps of the earwigs also represent cerci. In females, the leg vestiges often retained on the eighth and ninth abdominal segments are used as an ovipositor, as in bush crickets, cicadas, and Hymenoptera. In numerous wasps the corresponding structure has been made into an injection needle which they use to paralyze animals they capture as food for their young. In many social Hymenoptera what once was an ovipositor has become an extremely effective defensive sting. Thus these abdominal legs have changed their function and, correspondingly, their structure several times in the course of evolution.

A number of appendages of the insect body arose without the participation of ancestral legs, such as the gills of certain aquatic larvae (midges, beetles, caddisflies, and Lepidoptera), the abdominal suction cups of the larvae of net-winged midges (see Fig. 16-3), the walking ridges of the long-horned beetle larvae, the dorsal horn of hawk moth caterpillars, and others.

Food and feeding

The ways in which insects feed are as varied as the other aspects of of insect life. Some insects are omnivorous; according to Kemper, the cockroach's menu reads, "cooked potatoes, vegetables, flour pudding, dough and the like, dead and sick members of their own species, chocolate, honey, butter, vaseline, bread, flour, sugar, leather, wool items, rayon, shoe polish, book bindings, fruit, and other items according to season." Other insects are definitely specialists in their feeding: some aphids suck the juice from only a single species of plant, and certain lice live only in the feathers of a single species of bird. Between these extremes one finds many interesting cases. Some plant-eating or juice-sucking insects are host-specific to certain species, genera, or families of plants, and the mothers, in laying their eggs, make this choice for their progeny. The Mediterranean oleander hawk moth lays its egg on oleanders, but females who have strayed to the north, for lack of this plant, lay theirs on the myrtle, which is the only plant of the same family to be found there! The botanist may well envy the moth for its ability to tell by smell the family to which a plant belongs. Just as they have specialized in certain species of plants, insects have also chosen certain parts of these plants as food. Thus, most termites live on dead wood and in fact are satisfied

even with pure cellulose. Other wood-dwellers demand living wood, and still others bore tunnels in wood but feed on the coatings of fungus which grow in them. Insects with piercing and biting mouthparts drill into the sieve-tubes of plants and let themselves be filled with food by the pressure of the sap; other plantsucking insects pierce the parenchymal tissue and with their saliva disintegrate its cells. It is only a short step from the sucking of plant juices to the sucking of the blood of animals; juice-sucking bugs became hunters of small prey that do not survive the attacks, and parasites of the larger ones. Another route to parasitism was by way of life in rotting materials. From the fly larvae which feed on pus in wounds it is again only a short step to those which also attack the healthy tissue at the edge of the wound. Yet another path of development led from the feeding behavior of chewing lice, which live in feathers and fur and eat scales that fall from the skin, to the blood-sucking of the true lice. Parasitism, whether on the host (ectoparasitism) or in the host (endoparasitism), is very widespread in the insect groups. A special form is the predatory endoparasitism of the larvae of the parasitic Hymenoptera and flies. At first, the young larvae of these animals inside their hosts obey the motto "live and let live"; a too-early death of the host would mean their own as well. But shortly before pupation they begin to devour it voraciously, behaving like genuine predators. The strangest mode of feeding, though, is that of the larvae of the tsetse fly (see Chapter 19) and the pupiparous flies. They are carried in the body of the mother until pupation, and during this time are completely supplied with food by the glands in the womb! During the pupal period, while the whole organism is transformed, all insects do without food; in fact, they usually stop feeding some time previously. But even as adults many insects do not eat: these include, for example, the Mayflies, males of both the stylopid insects and certain mealy bugs, and the emperor moth. The larvae of these insects lay up a sufficient reserve for the sole task of the adult insect—reproduction.

Digestive system

There is corresponding diversity in the digestive organs. However, in the alimentary canal of all insects the same divisions are repeated. The mouth cavity, surrounded by the mouthparts, is divided by the hypopharynx into an upper food chamber (the cibarium) and a lower salivarium into which the salivary glands open. The cibarium opens into the pharnyx and this, in turn, into the esophagus. The escophagus expands to form a crop, which is followed by the anterior stomach (the proventriculus). All of these divisions make up the foregut, which, like the body surface, is covered by cuticle. When the insect molts, the shed exoskeleton extends all the way to the proventriculus. The pharynx is surrounded by swallowing muscles, and the proventriculus, by chewing muscles. The proventriculus is often provided with powerful teeth which enable it to carry on the work of breaking up the food, begun in the mouth. The esophagus and crop have only a thin covering of muscle; they are usually

folded longitudinally so that they can expand when food is passing through. In the Diptera the crop is a closed sac and serves as a storage place for food, while in the social Hymenoptera it receives the food which is meant for the community; therefore it is called the social stomach.

The proventriculus is followed by the midgut, the wall of which arises from the endoderm and has no cuticle layer. The cells of the midgut wall have a dual function: they secrete the digestive enzymes which dissolve the food, and they take up the digested food in order to pass it on to the blood. But almost every kind of food contains indigestible elements; often these are hard, sharp particles which could damage the delicate wall of the midgut. As soon as they enter the midgut these are surrounded by a tubular membrane through which the digestive enzymes and the digested food can pass, but which protects the intestinal wall from harm. This peritrophic membrane is produced continuously at the entrance to the midgut and proceeds towards the anus with the bits of food which it surrounds. Because of this activity the cells of the midgut wall are used in a short time, so they are constantly being replaced by the division of special formative cells.

The midgut is followed by the hindgut, which, like the foregut, is lined with cuticle. Usually, the boundary between midgut and hindgut is clearly demarcated by the openings of the excretory organs (the Malpighian tubules). Several divisions of the hindgut can often be recognized; the last division usually has distinctive groups of cells which protrude into the interior of the gut. These rectal papillae are supposed to be organs which reclaim water from the gut contents; for many insects, water is a particularly scarce commodity.

Malpighian tubules

Like the other parts of the digestive system, the Malpighian tubules, which serve to eliminate the waste products of metabolism, were inherited by the insects from their millepede ancestors. But the millepedes possess only two of these organs, whereas their number is increased in most insects; the honeybee, in fact, has about 150. Wherever they are so numerous they generally remain short, and where there are only a few tubules they usually make up in length what they lack in number. Since the tubules are as fine as threads, they have a surface area which is very large in relation to their mass; for the sixty tubules of the cockroach *Periplaneta americana* the area amounts to one-seventh m^2 and for the tubules of the lappet moth *Epicnaptera americana*, of which there are only six, to as much as one-fifth m^2 ! Since the performance of these organs is directly dependent upon the the area of their surface, these measurements suggest a high degree of efficiency. Oddly, Malpighian tubules are altogether lacking in the springtails (see Chapter 2) and the aphids (see Chapter 11).

Symbiosis with microscopic organisms

It is very common for insects to have tissues or organs that have been colonized by bacteria or by some lower fungi. In the simplest cases these lower forms of life inhabit the space within the gut, and in other cases, the blood or the fat bodies. But usually the insect has special organs, the

mycetomes, which serve to house these organisms; it also has particular devices to ensure that these indispensable guests are handed on to its progeny. It is quite evident that both partners find this association to their advantage, so we refer to the relationship as symbiosis (the situation in which two different species live together to their mutual advantage; cf. Vol. I). Since in this case one partner lives not next to, but within, the other, this communal situation is called endosymbiosis. We find this arrangement primarily in insects that eat only one kind of thing: the plant-juice feeders and blood-suckers. Evidently such an insect's guests provide substances which it requires for life but which it can neither obtain in food nor synthesize for itself. Accordingly, endosymbionts are not found among those blood-suckers which as larvae have a more varied diet (fleas, mosquitoes, horseflies, stable flies). In other cases the advantage to the insect must be of another sort—for example, in the cockroach, whose diet is as varied as one could possibly wish. Weevils that feed on bread have been raised experimentally without their symbiotic yeasts; they showed signs of a deficiency which could be relieved if they were given vitamins, an indication that the symbionts produce vitamins which the beetle larva itself cannot synthesize and which are also lacking in its normal food.

Respiratory organs

In the structure of their respiratory organs the insects are similar to the millepedes, but they have developed the system to a much higher level. They breathe by means of tubes, the tracheae, which open at the body surface in spiracles. Inside the body the tracheae divide into very fine branches which lead to all the organs and often even into their cells. In this way they conduct air to these organs, providing them with the oxygen they require. The carbon dioxide produced by cellular respiration is disposed of only in part through the tracheae; most of its escapes through the body surface. The spiracles frequently have closing devices and chambers (atria) containing little hairs which prevent dust from entering the tracheae. The spiracles are water-repellent but they can be wetted by oils. Thus water can be kept out of the tracheae but oil enters the respiratory system easily, with a fatal effect, as was known to Aristotle over 2400 years ago. This knowledge used to be employed in eradicating mosquitoes by spreading a film of oil on the surface of the water where they live.

The basic arrangement is a pair of spiracles on each of the segments from the second thoracic to the eighth abdominal. Sometimes the first pair is found on the first thoracic segment, and some or even all of the spiracles may have closed or regressed. In many fly grubs only the most anterior and posterior pairs remain open, in midge larvae only the last, and in midge pupae only the first pair. Those spiracles which ordinarily are closed are open during each molt, since the exoskeleton which is shed includes the lining of the tracheae (the intima); the old intima is shed through the spiracles, which then close again. Aquatic insect larvae with permanently closed spiracles cannot, of course, breathe atmospheric air,

but they do possess gas-filled tracheae which are very numerous in the tracheal gills formed by extension of the body wall. Such larvae include those of the Mayflies, dragonflies, stoneflies, some Neuroptera, most caddisflies, and some water beetles, as well as the aquatic caterpillars of certain Lepidoptera. This form of respiration has thus arisen quite often, and independently, throughout the insect groups as an adaptation to life in the water. Finally, in some parasitic larvae the spiracles and tracheae have altogether disappeared. In contrast to this regression, the spiracles of some beetle larvae (scarab larvae and wireworms) have atria which are built in a very complex way. The spiracular atria of fly grubs even form new openings to the exterior, whereas the original spiracles close and only reopen transiently when the intima of the tracheae is shed.

In some primitive insects, as in the millepedes, the tracheal cluster within each segment is quite separate from those within adjacent segments. But in the great majority of insects they combine over all the segments to form longitudinal trunks with transverse connections between the two sides. Often these develop into large air sacs which, in many flies and the male cicada, fill up almost the whole abdomen.

The tracheae of insects serve not only for respiration, but also as a framework upon which the viscera in the abdominal cavity are hung. The air sacs of the phantom midges (Chaoboridae) larvae act as floats (see Chapter 19), those of the drum organ of male cicadas act as sound amplifiers (see Chapter 11), and those in the tympanum of grasshoppers form part of the organ of hearing. Air sacs are also found inside the heavily armored parts of the body such as the mandibles of the male stag beetle (its "antlers," see Chapter 13). Whether and in what way these air sacs have to do with respiration is still in dispute.

Neither the direction of air flow nor the manner in which the air is exchanged within the tracheal system is uniform among insects. Grasshoppers expel oxygen-depleted air by pulling in the sterna (the ventral plates), whereas wasps achieve the same thing by telescopic shortening of the abdomen. Aquatic insects without gills (water bugs and beetles) take an air bubble with them when they submerge, to serve as a reserve supply for breathing. This small supply would of course soon be used up, except that the vapor pressure of the oxygen dissolved in the water causes a continual replacement of oxygen within the bubble. This aqualung works as long as the nitrogen in it has not dissolved in the surrounding water. Such a loss of nitrogen can be prevented by providing the bubble with a border of little water-repellent hairs which are bent at the tip, or by covering it with a layer of cuticle which repels water but is permeable to gas. An insect equipped with such a permanent layer of air, a plastron, need never bother to fetch air from the surface. Thus we find plastron respiration in midge pupae which are firmly attached to the bottom, and in the small water bug *Aphelocheirus* spp. (see Chapter 10). Recently plastron respiration has also been demonstrated for many insect eggs;

without the plastron they would suffocate when wetted by the rain.

Many insects, for a limited time at least, can even fulfill their energy requirements without oxygen (that is, anaerobically) by means of other chemical processes. In this way the insect larvae which live in the ground can survive the spring floods, even if the underground water, which surrounds them for weeks, becomes depleted of oxygen. The bot fly larvae which live in the stomachs of horses are also dependent on anaerobic metabolism (see Chapter 20), as are some of the non-biting midges, whose larvae colonize the decaying mud under bodies of water which are poor in oxygen.

Body cavity and circulatory system

The body cavity of an insect is formed early in development by a fusion of parts of the circulatory system with the true body cavity. Within the cavity thus created the blood flows freely, and is not confined to particular channels. This space is divided into three layers by two horizontal diaphragms: the middle, largest layer contains the gut together with the excretory and reproductive organs; the upper one contains the tubular heart; and the lower one, the ventral nerve cord. The heart is the only remnant of the vascular system of the ancestral insects. It extends along the back from the rear end to the head, which is the direction in which the waves of contraction travel. These waves continuously push the blood forward within the heart, while new blood flows in behind through lateral openings. One-way valves prevent the blood from flowing back out of the heart through these inlets. The anteriormost section of the heart, in which the lateral openings are lacking and the waves of contraction die out, is called the aorta. The blood is usually colorless, but in the midge larvae, which are valued as food for aquarium fish, it is colored red by hemoglobin. This red pigment is not confined to the blood cells as it is in vertebrates, but is dissolved in the blood fluid. One function of vertebrate blood is to supply all organs and tissues of the body with oxygen; the blood of insects does not serve this function, which has been taken over by the tracheae.

The working respiratory and circulatory organs can be observed in many living insect larvae which are thin-skinned and lightly colored, most impressively in the transparent larvae of phantom midges, Mayflies, and stoneflies, viewed at low to medium magnification through a microscope. The heartbeat and the blood flow, which can be seen by the movement of the blood cells, can be followed in great detail. A fascinating experience!

Endocrine glands

The molting and metamorphosis of insects are governed by a highly developed system of hormones, under the control of certain nerve cells in the brain called neurosecretory cells. These cells produce a hormone which is carried along the nerve fibers and by way of the blood to endocrine glands, the ecdysial glands, which may be located on the underside of the head or in the anterior thorax. The hormone from the ecdysia glands causes three types of molting: larval molting, pupation, and the

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emergence of the adult, sexually mature insect (the imago). The type of molt which occurs at a given time depends on the amount of hormones being produced by another endocrine gland, the corpus allatum, a paired structure at the back of the brain near the dorsal blood vessel. In addition to the rhythmic processes of molting, these hormones control sexual maturation, behavior, the patterns of coloration, and several other things. The governing position of the neurosecretory cells of the brain is in remarkable correspondence to the situation in vertebrates, where just such dominant cells are found in the floor of the midbrain.

Within an individual animal, these hormones are a means of communication from one organ to another; similarly, other glandular secretions make possible an external communication from one member of a species to another. They regulate the communal life of animal societies and therefore are called social hormones, or pheromones. In this category is the "queen substance" produced by the mandibular glands of the queen bee, which suppresses the maturation of the ovaries of the workers. Insects other than the social ones also have pheromones: scent substances from the glands of males or females serve to attract the sexual partner, and the species-specific smell of the caterpillars of the white cabbage butterfly helps them to congregate.

Sense organs

Throughout their lives insects are constantly receptive and responsive to environmental events: in seeking the most favorable microclimate, in the search for food and protection from their enemies, in reproduction, and frequently in caring for the young. The remarkable variety of insect behavior demands highly developed sense organs and an equally developed nervous system. Both of these are of course built quite differently than ours, so that it is impossible to empathize with the experiences of an insect. Nevertheless, the experimental methods of behavioral analysis and more recently of electrophysiology have given insight into the sensory experience of the insect.

Light receptors

Light is primarily sensed with the eyes, but in some insects the surface of the body is also sensitive to light; cockroaches and mealworms with eyes covered by lacquer so that light is excluded still respond to light stimuli. The larvae of the giant water beetle have a similar sensitivity to light, particularly in the region of the spiracles near the tip of the abdomen; they use this sense to find the way to the surface of the water to obtain air. Three kinds of eyes may be distinguished on the insect head: (1) dorsal ocelli, (2) lateral ocelli, and (3) compound or facet eyes. The dorsal ocelli are typically three in number, and are found only in winged forms. Their structure indicates that they are definitely lightsensitive organs but probably not organs of vision, in the sense of image interpretation. Experiments have shown that when they are illuminated the excitability of the nervous system is increased, and when they are darkened it is diminished. Since they act to produce a general excitation they are sometimes called stimulatory organs. The lateral ocelli (or stemmata) are the

embryological predecessors of the compound eyes; one or a small number of them is found on each side in larvae and pupae, in the position which the compound eyes eventually occupy. In structure, the lateral ocellus is like a single element (ommatidium) of the compound eye; the compound eye of insects is very similar to that of the crustacea (see Vol. I). The cup-shaped cuticle over the compound eye is divided into regions like a honeycomb; each of these facets consists of a lens-shaped cornea (so named after the cornea of the human eye). Behind each corneal lens there is usually a crystalline cone consisting of four cells, and behind this, a bundle of seven or eight receptor cells. Along with their covering of dark pigment cells, which are also regularly arranged, the cornea crystalline cone, and receptor cells constitute the ommatidium; many ommatidia—several thousand in the honey bee—make up a single compound eye. Although in its basic structure the compound eye is quite different from the vertebrate eye, it is comparable in its function: the light-sensitive visual pigment of both eyes is retinene, a derivative of vitamin A, and the color vision of both eyes is based on the presence of sensitivity maxima associated with three spectral colors. In humans these are blue-violet, yellow-green, and red, whereas in the worker bee they are ultraviolet, violet, and green. In the long-wave (red) part of the visual spectrum the bee is color-blind, but it sees as a color the ultraviolet light which is invisible to us. The insect eye is also superior to ours in its ability to resolve a very rapid temporal sequence of individual events, as well as in its ability to distinguish the plane of polarization of light from the sky. The latter makes it possible for the honey bee to orient itself according to the position of the sun, even when the sun is covered by clouds.

Sensilla

The various insect sense organs which transmit mechanical and chemical stimuli are called sensilla; they have been developed from hairs in the course of evolution. For a long time futile attempts were made to associate their varied forms with the reception of particular stimuli. It is only in recent years that electrophysiological research has begun to clarify the problem. With extremely delicate techniques one can measure the electrical potential at the surface of the sense cells and observe its change (the action potential) in response to a particular stimulus; thus one can determine which kind of stimulus (chemical, mechanical, etc.) is the "adequate" one for the cell, the one which it is specialized to receive. Such investigations have shown that in a sensillum with several sense cells, both chemical and mechanical receptors may be present.

Sensilla are distributed over the entire insect body, but tend to be concentrated in certain places such as the antennae, the mouthparts, and the tarsi. At the joints they detect the relative position of parts of the body, and at oscillating membranes (the tympana) or on the antennae they respond to the oscillations produced by sound waves and thus function in hearing. Among insects which produce sounds themselves, the auditory sense serves for the detection of the sexual partner or a rival of the same

sex, whereas in dumb insects (nocturnal moths) it allows them to tune in on the ultra-high-frequency calls of their enemies, the bats (cf. Vol. XI).

The nervous system of insects, like that of the other segmented animals, has the shape of a ladder (see Vol. I). But this characterizes only its basic structure, not the degree of its development. Organisms like the insects, equipped with so many and varied sense organs and responding to their environment with such diverse forms of behavior, must have a correspondingly sophisticated nervous system. Unfortunately, insect neurology, though no less deserving an area of research than that of the vertebrates, is still in its infancy. The part of the central nervous system which is equivalent to a brain and lies above the esophagus, the supraesophageal ganglion, consists of three divisions lying one behind the other: the protocerebrum, deutocerebrum, and tritocerebrum. The protocerebrum is associated with the ocelli and compound eyes and also contains the neurosecretory cells which control the hormonal system. Further, in the insects with the greatest behavioral capacity the protocerebrum contains a pair of stalked, mushroom-shaped formations, the "mushroom bodies," regarded as the seat of complex behavioral and learning ability. The deutocerebrum sends out a pair of antennal nerves, and the tritocerebrum, the nerves which supply the labrum. Although the tricocerebrum lies above the esophagus, the commissure connecting its right and left sides runs below the esophagus, thus revealing that the tritocerebrum was originally a paired ganglion belonging to the ventral nerve cord, and only later in evolution migrated up to join the brain. Originally it supplied the first segment of the trunk, which bore as limbs the second pair of antennae. In present-day insects these limbs have disappeared, though they can be shown to be present transiently in the earliest stages of development of some insects. The subesophageal ganglion is formed by the fusion of the paired ganglia of the last three head segments. It sends nerves out to the three limb pairs of these segments; that is, to the mandibles, the maxillae, and the labium. The thoracic portion of the nervous system consists of three pairs of ganglia, one pair for each segment. In the abdomen, as a rule, only the first seven segments have ganglia of their own, while the four following pairs of ganglia have fused to form the eighth abdominal ganglion. The actual form of the insect ventral cord in various species is altered in many different ways by additional fusion of certain of these ganglia.

Nervous system

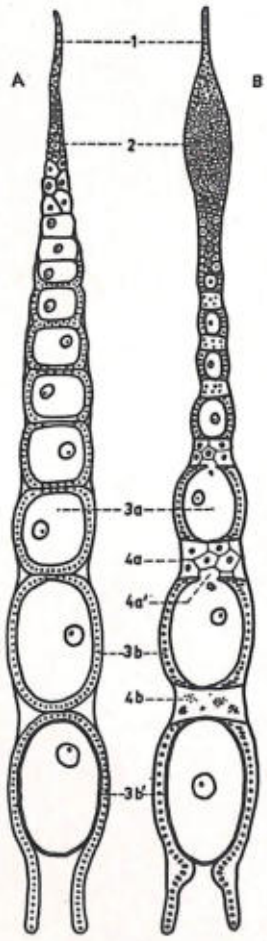


Fig. 1-13. Egg tubes (ovarioles) of a female insect without (A) and with (B) nutrient cells: 1. Terminal filament: 2. Germarium; 3a. Egg; 3b. Follicle of egg; 3b'. Chorion; 4a. Nutrient cells; 4a'. Nutrient cell penetrating the egg; 4b. Exhausted nutrient cells.

Reproductive organs

The external genitalia of female insects are formed from limb derivatives of the eighth and ninth abdominal segments. Internally, the paired ovaries are composed of a variable number of egg tubes or ovarioles, at the tips of which are the immature germ cells. In primitive insects (Mayflies, dragonflies, stoneflies, cockroaches, grasshoppers, and others) these all become eggs through growth, nourished by the follicular cells which surround them. But in higher insects most of the primary germ cells become nutritive cells, the contents of which enter the egg cells so

as to nourish them. Once the egg has attained its final size, the follicular cells surround it with an eggshell, the chorion. At one pole of the shell a tiny opening (the micropyle) remains for penetration by the sperm at fertilization. Often the shell is covered with a delicate pattern of ribs or ridges, as in many Lepidoptera and bugs. Often, too, there is a thin layer of air enclosed in the shell wall, which acts as a plastron.

The reproductive organs of male insects open on the underside of the ninth abdominal segment, at its hind edge. The forms of genitalia are diverse and often of intricate design. Since they differ from species to species, they are often the most important characteristics used by systematists in classifying species. The paired testes, like the ovaries, are composed of tubes, which open into the vas deferens. The vasa deferentia on the two sides join to form an unpaired canal, which may be expanded to form a seminal vesicle, though it is not uncommon for the vasa deferentia themselves to swell into seminal vesicles. The sperm is transferred either free in liquid form or enclosed in a spermatophore produced by accessory glands.

Development

Insects almost always reproduce sexually. One asexual mode of reproduction is by disintegration of young embryos into single cells, each of which then develops into an individual animal. This process, "polyembryony," has been observed in parasitic Hymenoptera and the stylopid insect *Halictoxenos* spp. (see Chapter 13), also a parasite. Unisexual reproduction via unfertilized eggs (parthenogenesis) is common, but bisexual reproduction is more frequently found. The larvae which emerge from the eggs are always wingless; as they grow, they molt several times. The wing buds may appear in the larva at an early stage or not until the last stages, but only the imago (the fully formed adult) is able to fly. Only the Mayflies are an exception to this rule, since here the stage just preceding the last one, the subimago, already has functional wings. Larvae with wings not fully developed, but which resemble the imago, are called nymphs. In lower insects the nymph continues to grow until its last molt, whereas in higher insects the stage between the last molt and that just preceding it is devoted entirely to an internal transformation; the insect becomes a dormant pupa. Such a complete metamorphosis (holometabolism) occurs in the Neuroptera (see Chapter 12) and in all the insects which come after them in this volume. This transformation is associated with a drastic change in both the animal's structure and its way of life, as is apparent if one compares a plant-eating caterpillar with a nectar-sipping butterfly. But even in incomplete metamorphosis (hemimetabolism) the alteration can be significant; for example, compare a dragonfly nymph, stealthily lying in wait to snatch its prey in its prehensile mask, with the adult dragonfly, flitting precipitiously about and catching prey in a basket formed by the legs (see Fig. 4-1).

Many insects can interrupt their development temporarily at a certain stage (egg, larva, pupa, or imago). Such a diapause may either be a

regular aspect of development or be caused by particular environmental conditions. The diapause is a peculiarity of some species or (as in the silk moth, see Chapter 15) of some subspecies, or even of individual animals, as every breeder of Lepidoptera has experienced when a few of his pupae delay their emergence. The interruption of development is caused by various factors, such as day length or temperature; it is primarily controlled by the neurosecretory cells of the brain. Cessation of development helps the insect withstand periods of famine, cold, heat, or desiccation; the diapause also helps it coordinate the timing of its temperature-dependent period of development with the annual rhythm of its environment. For example, in the cooler latitudes or in cooler years the Colorado potato beetle (see Color plate, p. 255) manages only one generation a year, but in warmer latitudes or years it has two. At intermediate temperatures there could be one and a half generations, so that the larvae of the second generation would come into being when their food, the leaves of the potato plant, was hard or wilted. All the progeny would therefore be condemned to death were it not for the fact that a majority of the beetles bury themselves in the ground in summer, when food is abundant, and there enter diapause. They re-emerge only in spring, and lay their eggs on the young potato plants. Now the young larvae have been brought into synchrony with the young plants.

Population dynamics

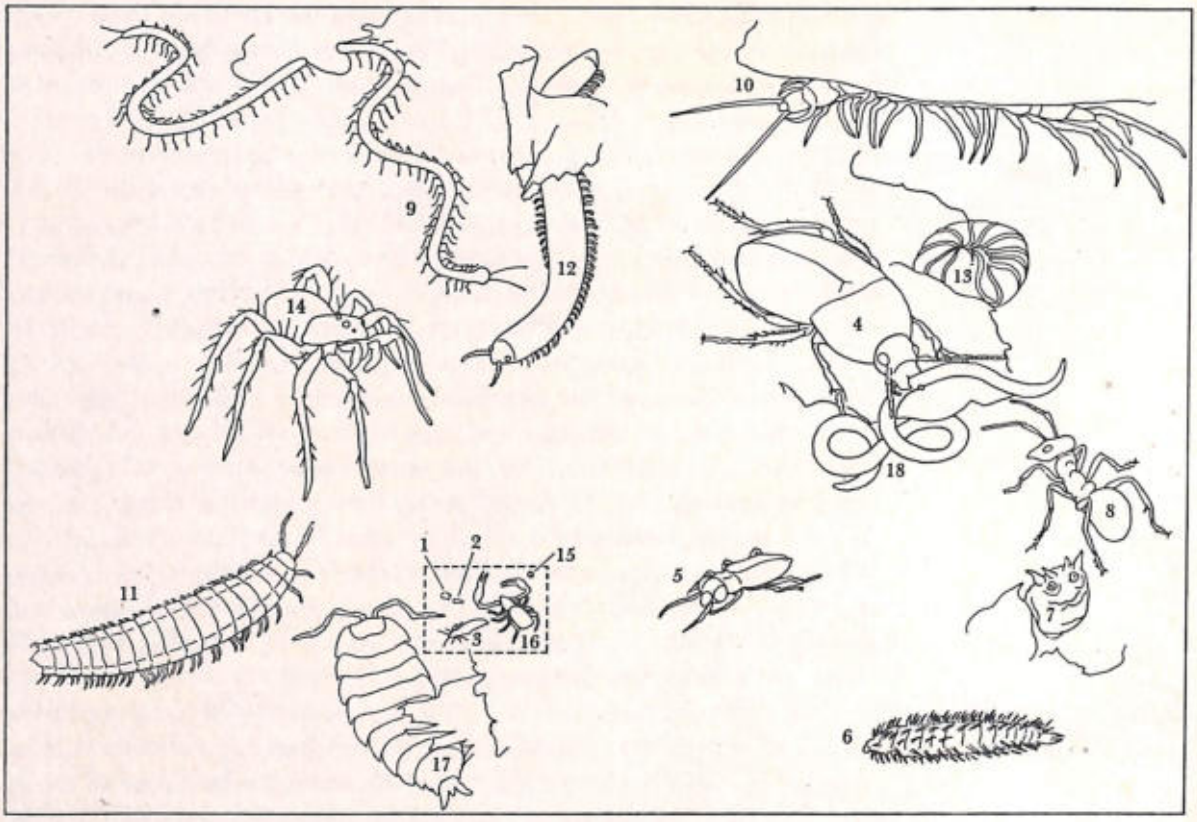
The ubiquity, the profusion of species, and the occasional outbreaks of vast swarms of insects have caused widespread invasion of the regions inhabited by humans; hence, insects can cause considerable damage to agriculture, forestry, stored provisions, and, not least, the health of man and domestic animals. An individual insect rarely does perceptible harm; usually the damage is done when a species appears in massive numbers. To recognize such a plague when it is just beginning, and put an early end to it, is more economical than to carry out a campaign of eradication after the damage is apparent. Research into the regularities governing outbreaks of insect infestations (population dynamics) is therefore an important element of applied entomology.

Some insects appear in about the same numbers year after year; the white cabbage butterfly is typical of this stable category. In contrast to this, other insects are so rare, for several years, that they are scarcely to be seen, and then quite unexpectedly they appear in multitudes—only to become rarities again after one or a few years. This kind of population cycle is typified by the snout butterfly (*Libytheana bachmannii*). This category includes some moths (for example, the eastern tent caterpillar, forest tent caterpillar, gypsy moth, and brown-tail moth) which, at long intervals, destroy whole forests. The large number of eggs which a female of these species can produce in a year enables a population explosion of enormous extent, unless an unfavorable environment happens to contain it. With 125 female and 125 male offspring in a year, a pair of black arch moths could have 31,250 grandchildren and almost a quarter-billion great-

great-grandchildren! If, as usually happens in the course of many years, the number of black arch moths neither increases nor decreases, it must be the case that, on the average, of the progeny of each pair, only one pair survives, while all the other individuals (in our example 99.2%) die before reaching maturity. This proportion—which can be computed for each species from the average number of eggs, the ratio of males to females, and the number of generations annually—may be called the normal mortality quotient. If the mortality quotient sinks below this norm, the species increases, and if it exceeds the norm, the species declines. Many factors influence the mortality quotient, such as climate, competitors for food, availability of food itself, and, above all, predators and parasites. Among the latter the innumerable parasitic insects play a major role, and their population cycles are dependent in turn on the population cycles of their hosts! If an insect species increases in numbers because of favorable conditions, there is immediately thereafter an increase in its parasites which brings the increase of the hosts to a halt, sometimes so quickly that it never becomes apparent at all. Thus, in the natural community of plants and animals, new states of equilibrium are continually being approached. As long as nature is undisturbed, it is governed by control systems like those in modern automation technology.

Disturbance of equilibrium by man

But when humans intervene, these systems are disturbed or even destroyed. Extensive cultivation of a single useful plant produces a population increase of the plant which must automatically be followed by an increase in the population of those animals whose lives depend upon it. From the human point of view these natural controllers are pests which cannot be tolerated. In the natural course of events the army of parasites which infests these pests would, by its own population increase, limit the increase of the pests; but while this stage is being approached the damage steadily increases. Therefore the poisoning of animal life is begun, which interferes crudely with the regulating system and destroys it entirely, for not only the pests fall victim to the poison but all their natural enemies as well. This makes the cultivated plants even more vulnerable and forces a continual repetition of the poisoning. In this way the highly developed orchard and vineyard regions which once, because of their warm climate, were an El Dorado for the insect researcher, have become wastes devoid of animal life, in which only the poison-covered crops have the right to live. In forestry, many more areas have been preserved, to which the controlling parasitic insects and their alternative hosts can withdraw; these include mixed woods with undergrowth and ground cover, hedges at the edges of the woods, and clearings rich in plant growth. Such practices of foresters also leave room for the birds as well as the large red ant (see Chapter 18). These measures probably cannot bring to a sufficiently rapid end a plague which has already broken out, but they contribute toward preventing such an outbreak in the first place. Here, too, prevention is better than a cure.



ANIMALS OF THE FOREST FLOOR IN CENTRAL EUROPE (I)

Along with bacteria and lower plants, the small animals which live in the earth are essential for its fertility: earthworms loosen the soil and pull fallen leaves into their tubes, where they rot more quickly; medium-sized insects and millepedes eat the dead parts of plants which have been partially decomposed by bacteria and pass them out again as smaller pieces, half digested and with a greater accumulation of bacteria; this enables the smallest arthropods, such as the primitive insects, to break up the bits of humus still further so that they are open to the action of single-celled animals and plants. Hunting beetles, ants, and other small animal predators contribute to the maintenance of biological equilibrium in these habitats. Whenever humans use chemical agents to combat the "destructive" insects of forest, field, meadow, and garden (that is, those plant-eating insects which have multiplied excessively as a result of the massive cultivation of certain plants), they also unwittingly destroy part of the animal world of the ground. In so doing they interfere, not infrequently to their own disadvantage, with this delicately balanced system of natural interactions.

Insects: Springtails (cf. Chapter 2): 1. *Orchesella cincta*; 2. *Onychiurus* sp. Diplura: 3. *Campodea staphylinus* (cf. Chapter 2). Beetles (two predatory carabid species; see Chapter 13): 4. *Abax ovalis*; 5. *Notiophilus rufipes*. Diptera (see Chapter 19): 6. Larva of the midge *Penthetria holoseriacea*; 7. Hind end of the larva of a crane fly, *Tipula scripta*, with the appearance of a grimacing mask (cf. Chapter 19). Hymenoptera: 8. The large red ant (*Formica rufa*, see Chapter 18).

Other arthropods (see Vol. I): Myripods: 9. The centipede *Geophilus* sp.; 10. The centipede *Lithobius forficatus*; 11. The millepede *Polydesmus complanatus*; 12. The millepede *Julus* sp.; 13. The millepede *Glomeris marginata*. Arachnids: 14. A wolf spider (*Pardosa palustris*); 15. The mite *Nothrus silvestris*; 16. The pseudoscorpion *Neobisium simoni*. Crustacean: 17. The pillbug *Porcellio scaber*.

Annelids (see Vol. I): 18. Earthworm (*Lumbricus* sp.) The section of the above sketch set off in a dashed square is enlarged in the Color plate, pp. 97–98, and shown as it might appear at a somewhat later time.




Großmann

Insects have proved to be particularly damaging when they are introduced from foreign countries. Often they find that their new home offers a much less inimical environment than the old, for their previous predators and parasites are absent. Examples include the arrival of the European gypsy moth, the Hessian fly, and the Japanese beetle in America, and the vine louse, the San Jose scale, and the Colorado potato beetle in Europe. In some cases it was possible to keep these immigrants in check by importing their enemies, culturing them in large numbers, and then setting them free in the infested areas.

Blood-sucking insects

Blood-sucking insects can seriously affect man and his domestic animals, actually making some regions uninhabitable. Severe deterioration of health, even death by loss of blood, can be caused by swarms of black flies (see Chapter 19). Some parasitic fly larvae are also the direct cause of illness (see Chapter 20).

Insects as disease transmitters, by R. Geigy and D. Heinemann

Transmission of disease by insects, however, is incomparably more dangerous to man and his beasts than the drawing of blood, and sometimes leads to epidemics. Yellow fever, malaria, typhus, sleeping sickness, the horse- and cattle-disease nagana, and the plague are predominantly or exclusively transmitted by blood-sucking insects; an insect, the house fly, is suspected of playing a role even in the spread of infantile paralysis (poliomyelitis).

Malaria

The participation of certain species of the mosquito genus *Anopheles* (see Chapter 19) in the transmission of malaria is particularly well known. This intermittent fever is caused by single-celled animals of the genus *Plasmodium* (class Sporozoa, see Vol. I). They are parasitic in the red blood cells of humans and many other vertebrates. The development of the plasmodia is described in detail in Volume I. Part of their development takes place not in the infected vertebrate (the carrier), but in the body of the mosquito (the transmitter). It is this alternation of hosts, and the development of the plasmodia while in the mosquito, which will be discussed here.

The earliest forms of the plasmodia, both male and female (the microgametocytes and macrogametocytes, respectively), as described in Volume I, cannot develop further in the vertebrate host. However, if an anopheline mosquito draws blood containing these mature gametocytes from a human or other vertebrate, development can proceed in the mosquito.

When the female mosquito bites (the male sucks only the juices of plants), blood is drawn through the sucking proboscis directly into the midgut. The asexual stages of the plasmodium which are taken in along with the blood quickly degenerate and are digested. The mature gametocytes, however, can withstand the digestive juices of the mosquito gut and, within the first ten or twenty minutes after ingestion of the blood, have transformed themselves into fertilizable cells: the female sexual cell, the macrogametocyte, becomes a macrogamete, which corresponds to

the ovum of multicellular animals. The male microgametocyte produces four to eight small, highly motile microgametes. These correspond to the sperm cells of the Metazoa, and swim about in the mosquito gut with rapid, snakelike movements. As a rule, fertilization occurs within twenty minutes to two hours after blood ingestion: each macrogamete is penetrated by one microgamete. About thirty minutes later the fertilized cell (the zygote), which initially is rounded and immobile, transforms itself into a motile, long-drawn-out body, the oökinete (from the Greek *ὠόν*, egg, and *κινέομαι*, to move), within which the gamete nuclei fuse after several hours.

All these processes can occur within the gut of any blood-sucking insect or even outside the insect body, on a slide under a researcher's microscope. But with respect to the further development of the oökinete, this is not at all the case. The actual formation of spores (sporogony), which occurs on the gut wall of the transmitter, can take place only in the particular species of mosquito which acts as the transmitter of the plasmodium concerned. For example, human plasmodia can be transmitted only by certain mosquito species of the genus *Anopheles*, whereas bird plasmodia are necessarily associated with species of the genera *Culex* and *Aedes* (see Chapter 19).

Approximately twenty-four hours after blood ingestion, the oökinete begins to migrate through the contents of the gut to its wall. It bores through the lining of the gut (the peritrophic membrane) and passes between the gut cells into the space separating the mucous layer and the elastic membrane which covers the outer surface of the gut; there it becomes round, forming a capsule, the so-called oöcyst. This capsule gradually grows to about 100 times its original size, and after several days (after about eight to ten days in *Plasmodium vivax*, at an average temperature of 21°C) it bursts, releasing thousands of freely moving daughter cells, the sporozoites. Depending upon how many gametocytes the mosquito has taken in, 100 or more oöcysts may be ripening simultaneously. Therefore, hordes of sporozoites spread through the entire body of the mosquito; they move under their own power through the insect's blood, and are also carried everywhere by the circulation of the blood. If the mosquito is severely infected, the sporozoites penetrate all the organs—even between the muscles of the heart—but they never appreciably damage the transmitter. Most of the sporozoites, however, migrate into the mosquito's salivary glands. At the earliest, they begin to appear there eight to ten days after blood ingestion (for *Plasmodium vivax* with ambient temperature 24°–30°C); later, up to 60,000 sporozoites may lie bundled up inside the gland cells and embedded in the fine salivary ducts.

If such a mosquito again bites a human, the bundles of sporozoites of the malaria-causing organism are carried out of the gland in a flood of salivia and injected through the stylet (see Chapter 19) directly into, or

into the vicinity of, the pierced capillary. In the human body the plasmodia then proceed with their cycle of development, in the course of which the carrier falls ill with malaria.

Sleeping sickness and nagana

The role of the mosquitoes in transmission of malaria is played by the blood-sucking tsetse flies of the genus *Glossina* (see Chapter 16) in transmission of sleeping sickness and nagana. Pathogens of these sicknesses, as with malaria, are Protozoa; they are flagellates of the genus *Trypanosoma* (see Vol. I). The cycle of development of the trypanosomes is less distinctly divided than that of the plasmodia, and there are great differences between the individual species of trypanosomes. The association of these parasites with specific hosts is not as obligatory as for the malaria parasites. Among the trypanosomes transmitted by tsetse flies, the species *Trypanosoma rhodesiense*, *T. gambiense*, and *T. brucei* have about the same developmental cycle; therefore they are called the *brucei*-group. We shall use this group to illustrate the role of the tsetse flies as transmitters of disease.

The three species cannot be distinguished by their appearance, but rather by the differences in their relationships to their warm-blooded hosts. *Trypanosoma gambiense* is limited to western and central Africa, where it produces the western form of human sleeping sickness. This species usually does not occur in domestic cattle or wild animals. *T. rhodesiense* occurs only in eastern and southeastern Africa, and there it is responsible for the eastern modification of human sleeping sickness; this species does attack cattle and wild animals, which thereupon show symptoms similar to those of nagana. The third of the species listed, *T. brucei*, is an important cause of nagana; it attacks only horses, sheep, domestic cattle, and wild mammals, and cannot live in humans.

Along with the blood of a human suffering from sleeping sickness, or of an animal with nagana, the tsetse fly takes up the trypanosomes which are swimming freely in the blood. After a short stay in the fly's crop, these small flagellates pass through the proventriculus into the tubular peritrophic membrane which lines the midgut; at this time they divide and assume a long, thin shape. From the hindgut they migrate forward again, through the space between the peritrophic membrane and the gut wall. Then they break through the membrane and gather once again in the proventriculus and in the blood-sucking tube of the proboscis. During this process certain rearrangements of the cell organelles within the trypanosomes are made (see the crithidia form, Vol. I). But they still have not reached the final stage: experiments have shown that these tsetse-gut forms multiply in the blood of warm-blooded animals but are not yet capable of producing illness. It is only in the salivary glands of the fly that they complete their development into infectious trypanosomes. But how do the parasites assembled in the foregut reach the salivary glands? The openings of the tubes for blood sucking and saliva injection lie, as we know, next to one another at the tip of the proboscis. Since hungry tsetse flies often produce some saliva even before biting, the tip

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of the piercing proboscis is usually wet with a drop or a thin layer of saliva. This fluid film is enough for the trypanosomes to slip through into the opening of the saliva-injection tube and from there through the salivary duct into the tubules of the gland itself. Here they continue to multiply and transform themselves into the final, infectious form. Finally they come to lie at the front of the salivary gland, ready to be injected into the bloodstream of the next warm-blooded animal the fly bites.

The entire portion of trypanosome development taking place in the tsetse fly lasts about eleven to eighteen days in the three species mentioned above; the fly then remains capable of transmitting infection for the rest of its life. In the sleeping-sickness and nagana regions, at most five tsetse flies in 1000 are infected. If one does the scientific experiment of setting tsetse flies on mice, rats, monkeys, sheep, or other warm-blooded animals which have previously been infected with trypanosomes, then one can succeed in infecting at the very most about ten percent of the experimental flies (in the case of plasmodia and mosquitoes it is ninety-five per cent!).

Like all blood-suckers, the tsetse flies are closely dependent upon the hosts which give them blood—humans and other mammals like monkeys, ungulates, and rodents, as well as various birds and certain reptiles. Where these blood donors are lacking, there are no tsetse flies. In a few regions of eastern Africa, therefore, it was proposed that all wild animals be exterminated in order to deprive the tsetse flies of the basis of their nutrition (cf. Vol. XIII)! At the same time it was hoped that the reservoir of nagana and sleeping-sickness organisms living in the wild animals would be destroyed. Even though all the large wild animals were shot over wide areas, the project was doomed to failure because the tsetse flies could still survive upon dik-diks, duikerboks, and other small mammals, which the hunters could not get at and which also harbored trypanosomes.

Chagas's disease

Another form of trypanosome (*Trypanosoma cruzi*), the cause of Chagas's disease, is transmitted to humans by bugs of the genera *Triatoma*, *Rhodnius*, and others (see Chapter 10). Just as the tsetse flies, and with them sleeping sickness and nagana, occur only in Africa, these bugs and therefore Chagas's disease are found only in South America. There a very large number of mammalian species serve as a reservoir for the disease: among the wild animals the main carriers of trypanosomes are the opossum and armadillo, along with rodents and other small mammals; among domestic animals the carrier is the dog. The course of development of the Chagas pathogen in the bug is less complicated than that of the *brucei*-group in the tsetse fly. The infectious organisms are not injected into the blood by the bug, but simply deposited on the skin of the victim along with the bug's feces and then usually rubbed or scratched into the itching area of the bite by the host itself.

In all of the cases so far described, the disease-causing organism spends a certain indispensable part of its life cycle in the body of the transmitter. We call this sort of transmission, with a true alternation of hosts, cyclic.

But even within the genus *Trypanosoma* there are forms whose entire life cycle occurs in the carrier alone. Here the transmitter often plays the role simply of a means of transport; it takes up the trypanosome from the host along with the blood or at some other opportunity and conveys it onto or into the next host. Since no (or at least no indispensable) part of the cycle takes place in the transmitter, this form of transmission is called acyclic.

The means of multiplication of bacteria, spirochaetes, rickettsiae, and viruses is much less complicated than the course of development of the insect-transmitted pathogens discussed so far, all of which are unicellular animals. These other organisms show no sequence of developmental stages which differ in form—at least none which we can demonstrate with present-day experimental methods. Whether the organism undergoes physiological changes while it is in the body of the transmitter has not yet been clarified. The view that cyclic processes are also involved here, however, receives a good deal of support from the finding that bacteria, spirochetes, rickettsiae, and viruses also multiply both in the carrier and in the transmitter; moreover, it is not uncommon that they occupy special locations in the transmitter which facilitate transmission.

Bubonic plague

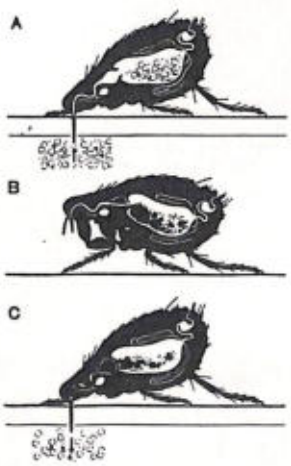


Fig. 1-14. The Oriental rat flea as a transmitter of plague: A. The flea takes up blood infected with plague bacilli; a brushlike coating of bacilli is formed in the proventriculus. B. Multiplication of the bacilli, which fill up the anterior midgut and the proventriculus. C. When the flea next sucks blood, some of the bacilli crammed into the proventriculus are squeezed out into the blood of the host.

One of the diseases caused by bacteria and transmitted by insects is bubonic plague. The main hosts of the plague bacillus (*Pasteurella pestis*) are rats and various other species of rodents. The transmitters are fleas (see Chapter 21), primarily the Oriental rat flea (*Xenopsylla cheopis*); the human flea (*Pulex irritans*) is also involved as a transmitter among humans.

When a flea takes blood from a plague-stricken rodent or human, it sucks into its midgut the plague bacilli contained in the blood. In some species of flea, particularly the rat flea, the bacilli multiply in the new environment at a striking rate, so that masses of these organisms soon accumulate, primarily in the foregut. Eventually the swarms of bacilli can completely stop up the proventriculus, occasionally even causing the death of the flea. But usually it does not come to that, and the plug of bacteria is loosened somewhat during the next sucking action. Nevertheless, as a consequence of the blockage the first attempts of the flea to pump blood are unsuccessful; in its efforts it squeezes whole groups of bacilli out through the sucking proboscis into the blood of the new host. In this way a new infection is brought about.

Each species of flea is more or less specialized to a certain species or other group of animals as a host (cf. Chapter 21). But here it is more a matter of a pronounced preference than of an obligatory association with the host. Epidemics of plague would take quite a different course if the fleas could not occasionally exchange their hereditary host for another. That such an exchange can occur is clear to everyone who has been bitten by cat or dog fleas. Great numbers of rat fleas leave the cooling bodies of rats which have died of plague and—where men and rats live close together—jump onto people, transmitting the plague to them. The role

of rodents other than rats—in Asia primarily the bobac and ground squirrel—as carriers and thus reservoirs for the bubonic plague is discussed extensively in Volume XI.

Typhus

The typhus pathogen, *Rickettsia prowazeki*, belongs to a group of peculiar organisms intermediate between the bacteria and the viruses. The main transmitter of typhus is the body louse (*Pediculus humanus humanus*; see Chapter 7), and a secondary transmitter is the head louse (*P. humanus capitis*); the crab louse (*Phthirus pubis*), on the other hand, plays hardly any role in transmission.

The organisms causing tyhpus live primarily in the interior of their host's cells. After blood is drawn they begin to multiply in the gut cavity of the louse, but they soon penetrate into the cells of the gut wall and continue to multiply there until the cells are densely packed with rickettsiae and distorted by swelling. Finally they burst open or disintegrate and free the masses of rickettsiae, so that they pass out with the feces of louse. In this way the pathogen can easily invade the human through small wounds or scratches in the skin. If during this time the louse has transferred from a human who is sick with spotted fever to a healthy one, a new victim becomes infected. But the dried-up louse feces disintegrate into dust and can also be carried through the air to the mucous membranes of the nose, the eyes, and the mouth, or be inhaled into the lungs, producing infection in this way.

While most insect transmitters are not harmed by the infectious organisms, a louse infected with rickettsiae eventually does perish because of it. This is because the louse is not capable of replacing rapidly enough the groups of cells in the gut wall which have been destroyed by bursting during the progressive multiplication of the rickettsiae, so that after ten days or more it dies.

Diseases caused by worms

A number of "worm" diseases are transmitted by insects; here we shall mention only elephantiasis, a disease caused by nematodes which are transmitted by mosquitoes. Since many illnesses caused by worms involve other animal groups besides insects as intermediate hosts or transmitters (for example, crustaceans and snails) we shall confine ourselves to this reference; more details are given in Volume I in the chapters about the trematodes and parasitic nematodes.

Significance in human history

Some of the epidemics spread by insects have influenced human history. The devastating role of the plague in Europe, particularly in the Middle Ages, is only too well known. But malaria also has intervened repeatedly in history. In 1166 Friedrich Barbarossa's chancellor, Rainald von Dassel, and almost the entire court of the emperor, died in Italy of malaria; because of this weakening of his power, Friedrich had to give up for many years his hope of occupying the city of Rome. In 1227 Emperor Friedrich II wanted to start a crusade from Italy, and this project also failed because of malaria; Friedrich himself became ill and was excommunicated by the Pope because he had broken his vow to undertake a

crusade. During the withdrawal of Napoleon I from Russia in the winter of 1812/13, typhus caused more devastation among the flood of retreating French troops than did the attacks of the pursuing Cossacks. Fleas, mosquitoes, and lice have contributed again and again to the failure of army campaigns and have frustrated the highest political ambitions.

The value of insects, by P. Rietschel

But one must not overlook the fact that set against all the dangers with which insects threaten humanity, insects perform many useful functions. As food, insects are only rarely useful; although migratory locusts are dried, ground up, and baked into bread, this fare is a poor compensation for the damage they have caused. It is difficult to evaluate the relative usefulness and destructiveness of some aphids, whose sweet excretions (honeydew) are the basis of the highly prized leaf and pine honey. On the other hand, the usefulness of the honey bee is unquestionable: it produces honey and wax, and in addition its poison is an effective medication for rheumatism. Bee poison is extracted commercially, as is another bee product, the royal jelly fed to the queens, which is sometimes regarded as a "cure-all." Much more significant is the activity of honey bees in carrying pollen from one food plant to another, thus aiding the setting of many kinds of fruit. In this role the higher insects have decisively influenced the appearance of the face of the earth: without the insects we would live on an earth without flowers! The shape, colors, and scents of flowers are specifically evolved to attract the visits of insects, just as the structure, senses, and behavior patterns of many higher insects are designed to facilitate visiting the flowers. Thus the flowering plants and the insects have, since the earth's middle ages, evolved hand in hand.

The economic significance of the silkworm has declined since the invention of synthetic fibers. On the other hand, the breeding of the parasites of destructive insects for use against their hosts is growing in importance. It is still not widely recognized that many an insignificant insect can serve as a reserve host for those parasites one wants to have available to prevent outbreaks of destructive insects. Finally, the red ant *Formica* spp. must be mentioned; it is valued as a "policeman" of the forests. But we should be careful not to think of insects strictly as either "useful" or "harmful." A future world which housed, besides man, only "useful" animals and plants would be a melancholy one.

In the chapters to follow, the insects will be treated in a systematic sequence, beginning with the most primitive, so that after the four subclasses of fundamentally flightless insects there follows the fifth, the winged insects. Since the class Insecta comprises seven-tenths of all animal species, whereas only one-thirteenth of this Encyclopedia could be devoted to them, the authors have had to restrict themselves—even more so than in the other volumes—to discussion of a limited selection of species. Those who wish to deepen and extend their knowledge of one or another group will find a guide in the list of references at the end of this volume.

Nearly a million insect species have that many scientific names, each

of which consists of a generic and a specific name. But only a few insects also have a common name. These are primarily insects of striking appearance or economic importance which are familiar to many people. Common names may also be of recent invention; for example, those applied to native American forms of the dragonfly by the Committee on Common Names of Insects of the Entomological Society of America are particularly concise and appropriate, and follow certain rules. All of those names used in this volume follow this standard system. Less successful are the names which have been created to try to describe an insect as precisely as possible. In German, this can lead to such prodigies as the "Mittelrippenbeutelgallen-Schwarzpappelblattlaus" (the "black-poplar midrib-pocket-gall aphid"); some English descriptive names are cumbersome, too. The majority of insects will have to get along without common names, since such names are needed only for insects which are commonly known. For the hordes of parasitic wasps, beetles, and flies, the species of which are known only to the specialist—and even he can distinguish them only under the microscope—common names will never arise naturally, and to invent names for them would be a thankless task.

2 The Primitive Insects

The primitive insects, by F. Schaller

Only a few groups, particularly many arthropods and vertebrates, have achieved independence of water as a place to develop and live. The peak of structural and functional development is represented in the first of these groups by the insects and in the other, by the birds and mammals. These animals have the most efficient sensory apparatus and the most adept nervous and motor systems; being air-breathers, they rule the land and the air. Within the vertebrates, these highly successful forms evolved from the fishes by way of the amphibia and reptiles. Among the arthropods, on the other hand, we do not know for certain how the land-dwelling arachnids, myriapods, and insects evolved from their aquatic wormlike ancestors, the annelids. But there are some groups of animals which can be considered "living models" of those unknown intermediate forms. These include the insects described in this chapter.

The term "primitive insect" may suggest to the non-zoologist the fossil insects of the Carboniferous. At that time, though, the evolution of this class of animals was already in full bloom; insects inhabited the hot, humid forests in great numbers and in many forms. There were giants among them with wingspans up to 70 cm. But these were awkward flyers—the wings were rigid and could not be folded, and the joints permitted movement in only one plane.

What are primitive insects?

When the zoologist speaks of PRIMITIVE INSECTS, he does not mean these clumsy forms from the Carboniferous. Instead, he applies the term to much smaller, humbler six-legged arthropods which look like insects but lack an essential characteristic of the winged insects—the wings. Accordingly, these animals are referred to as Apterygota (wingless); many insect researchers classify these primitive insects as a systematic unit under this name, to contrast them with the winged insects (Pterygota). In any case, the primitive insects are older than the above-mentioned winged insects of the Carboniferous; even today they are a living proof that the basic divisions of the insect body evolved before protrusions of the skin were developed to form the wings.

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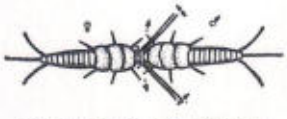
Besides their fundamental lack of wings, other aspects of the body structure are characteristic of the primitive insects: the body is divided into head, thorax, and abdomen, each with a fixed number of limbs, as in the winged insects; there are always three pairs of legs on the thorax, but there are several paired abdominal appendages, which may be small stumps (styli) or may form a curious jumping apparatus. These are generally interpreted as vestiges or modifications of limbs which, early in evolution, were well developed all along the body. (The embryological development of the higher insects still indicates that their ancestors must in fact have had legs on the abdomen, as do the myriapods, for on each abdominal segment there appears transiently, at a certain stage of development, a distinct pair of limb buds.) Furthermore, there are small, protrusible "blisters" of skin at the base of the abdominal appendages (so-called "coxal vesicles"); they are found elsewhere only in the myriapods, which are regarded as predecessors of the insects. Several other distinguishing characteristics are as follows: the tracheal system is simplified or absent; reproductive organs and embryological development are very primitive; excretory organs are much more simply constructed than in the winged insects; the skin is entirely thin, soft, and permeable to water; and finally, there is as a rule only a very moderate development of the sense organs.

The four orders

Although they have all these properties in common, the four clearly distinguishable orders of primitive insects have been judged by many systematists to belong to three separate subclasses. These separate entites are: (1) The springtails (Collembola) in the subclass Oligoentoma. (2) The proturans (Protura) in the subclass Myrientomata. In members of these first two groups the mouthparts are buried in the head, and there are no external genital appendages. (3) The bristletails (Thysanura). (4) The two-pronged bristletails (Diplura). The bristletails have the unusual external chewing mouthparts and reproductive organs which are characteristic of other insects, but the two-pronged bristletails have retained the primitive type of mouthparts characteristic of the first two orders.

On account of these characteristics, the bristle tails and diplurans are generally placed nearest the flying insects in zoological systematics, while the springtails and proturans stand near the base of the tree of relationships, being both more primitive and more divergent. Some entomologists even think that the springtails, at least, should not be counted as insects at all, since these arthropods continue to molt after reaching sexual maturity. But if one were to assume that the springtails evolved from the annelid ancestors quite independently of the insects, then it would follow that the possession of six legs had evolved independently in the two cases as well. But this would be inconsistent with the principle of the "most economical explanation," which states that in the natural sciences, when there are several possible explanations which cannot be tested experi-

Fig. 2-1. Courtship of the silverfish:



Male and female vibrate one another with their antennae (arrows).

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Order: Thysanura

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The silverfish

One member of the bristletails is the SILVERFISH (*Lepisma saccharina*; see Color plate, p. 73), the only primitive insect known to many nonzoologists, because it is relatively large and is often found in houses and apartments. It is a nimble animal, about 1 cm long, covered with glistening scales. Frequently it can be seen scuttling about in pantries and nibbling the groceries stored there; for this reason it is also called the "sugar-mite." Sometimes silverfish are found in libraries. A close relative, the somewhat larger FIRE-BAT (*Thermobia domestica*), is also a house-guest of humans. It prefers rooms which are constantly heated, thus betraying its southern origin. About 400 species occur in the world.

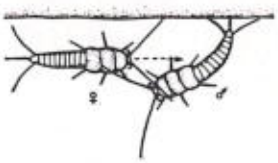
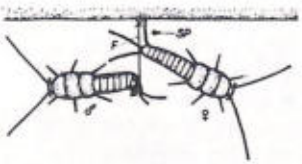


Fig 2.1 (cont.) Then the male stands in the way of the female and swings his tail back and forth against a wall or other elevation. He spins a few threads and deposits a packet of sperm on the ground.



The female runs under the the threads (F) and strikes them with her raised abdomen. She then stops and searches for the packet of sperm (SP) with her genital opening.

The natural history of the silverfish, with its furtive, nocturnal life, was practically unknown until a few years ago. Since then, however, much has been discovered, in particular its peculiar reproductive behavior; this is so complicated that it seems at first to be incompatible with the primitive nature of the animal. It begins with the performance by the male of a lively and varied "dance," which involves a good deal of contact with the partner to determine her readiness for mating. A particularly pretty phase of these preliminaries is shown in Fig. 2-1. Then the male very rapidly spins a few threads with his penis between two elevations of the ground, and under the threads he deposits a membranous capsule which contains sperm. As the courtship progresses, the female eventually touches, with her bristlelike abdominal appendages, the threads which the male has spun; she then stops in her tracks, lowers her abdomen so as to search for the sperm packet with the genital opening, and finally takes it up. All the patterns of behavior of the two partners are so well coordinated that successful transfer of the sperm into the female reproductive system is assured.

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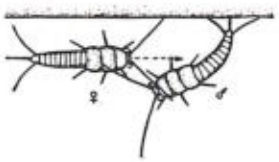
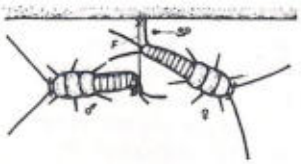


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the fact that the sperm is left for some time in the open, outside the bodies of both the male and the female. This behavioral trait expresses most clearly the primitive nature of the bristletails, for it reminds us that the wormlike ancestors of the insects simply let loose their eggs and sperm into the water. With the transition to air breathing and to life on land they have had to change their reproductive behavior in order to prevent dessication of the egg and sperm cells. Of course, as always in nature, the result was not achieved overnight, but by way of many transitional stages. In this connection, it is particularly noteworthy that indirect methods of sperm transfer, similar to those of the bristletails, are found not only in the other primitive insects but in many myriapods as well. Many zoologists consider the myriapods, especially the Symphyla (see Vol. I), to represent possible evolutionary stages of transition between the annelids and insects.

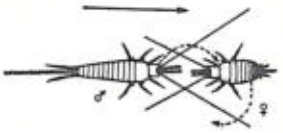
In a sense, the silverfish and other bristletails, like all the primitive insects alive today, also represent transitional forms with respect to their adaptation to the environment. They almost all live in damp places, since their skin provides a poor barrier against evaporation. In particular, their manner of sperm transfer appears practicable only in a humid environment.

This last point is even more applicable to the relatives of the silverfish which live in the open. These are the JUMPING BRISTLETAILS (family Machilidae, type genus *Machilis*; see Color plate, p. 73), with scales partly gray and partly brown, which prefer to live near and under stones. There they graze on algae or gnaw at lichens or fallen leaves. Using their caudal appendages, they are proficient jumpers. Like the silverfish, they are sensitive to dryness.

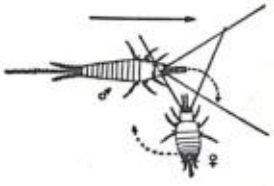
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Thus the seminal fluid of the jumping bristletails is temporarily quite open to the air. If it were not for the complicated behavior of the mating pair it would hardly be possible for the eggs to be fertilized with the necessary speed. Here one has an obvious comparison with the lower vertebrates, where absence of special copulatory organs in the male is very often accompanied by particularly long and varied preliminary court-

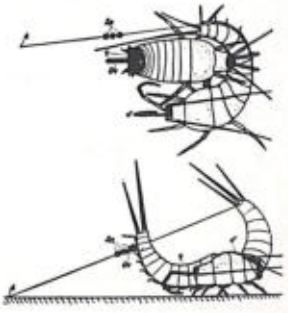
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Final position as seen from above (upper picture) and from the side (lower picture): the male has fastened to the ground a thread from which sperm droplets (black dots) are hanging; he then shoves the female toward it in such a way that she can take up a sperm drop with her ovipositor.

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The bristletails have no special means of caring for the young; they simply glue their eggs in protected, damp places. The young have the appearance of adults from the start, and they live in just the same way.

Other bristetails

There are some other species of bristletails, but we know very little about their natural history. Particularly noteworthy among them are certain relatives of the silverfish which live as guests in the hills of ants or termites. Details of their relationships to their hosts have not yet been discovered; presumably they roam about the nests as clever thieves. In 1893 the French entomologist Janet observed one such ant-guest (genus *Lepismina*) nibbling at a drop of food that was being handed from one ant to another. Among the Machilidae one especially large example should be mentioned, the SHORE BRISTLETAIL (*Halomachilis maritimus*). It lives on rocky coasts just above the spray zone, where it grazes on algae.



Fig. 2-3. A silverfish *Lepismina* sp. stealing a drop of food from an ant.

Various aspects of the body structure and behavior of bristletails can be considered as primitive insect characteristics. It is even possible to discern a trace of the later wing structures of higher insects: the dorsal plates are widened precisely at the places where the wings of winged insects are found.

This ancestral quality has not been preserved in all the other so-called "primitive insects." They are fundamentally wingless and very primitive in certain other aspects of their body structure, but in addition they bear traits which indicate that they have gone their own ways in the course of an especially long evolutionary history.

Order: Diplura

Closest to the bristletails are the TWO-PRONGED BRISTLETAILS (Diplura). They are blind ground-dwellers, of a pale color, and with almost wormlike movements; posteriorly they have, as a rule, two caudal appendages. The mouthparts are not visible externally but are recessed into the head, though they are formed from the same three pairs of limbs as in all insects. There are no external genital or copulatory organs.

The three families of diplurans are easily distinguishable by the differences in the form and function of their caudal appendages. In the CAMPODEIDS (Campodeidae, type genus *Campodea*; see Color plates, pp. 51/52 and 73) the appendages look like antennae and are nearly the same length. The 190 species of these animals live in humus, and consume all sorts of rotted materials. The family Anajapygidae, with very short caudal appendages, has only 20 species in the world, and only one rare species in the U.S.A., confined to California. In the JAPYGIDS (Japygidae, type genus *Japyx*; see Color plate, p. 73) the caudal cerci have been converted into pincers, so that at first glance these diplurans look like blind, colorless earwigs. They are predators which attack preferentially small-insect larvae as well as other primitive insects (diplurans and springtails); as soon as they detect prey with their incessantly moving antennae, they take it in their jaws or grasp it with a quick movement of the

the fact that the sperm is left for some time in the open, outside the bodies of both the male and the female. This behavioral trait expresses most clearly the primitive nature of the bristletails, for it reminds us that the wormlike ancestors of the insects simply let loose their eggs and sperm into the water. With the transition to air breathing and to life on land they have had to change their reproductive behavior in order to prevent dessication of the egg and sperm cells. Of course, as always in nature, the result was not achieved overnight, but by way of many transitional stages. In this connection, it is particularly noteworthy that indirect methods of sperm transfer, similar to those of the bristletails, are found not only in the other primitive insects but in many myriapods as well. Many zoologists consider the myriapods, especially the Symphyla (see Vol. I), to represent possible evolutionary stages of transition between the annelids and insects.

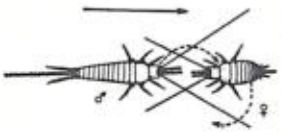
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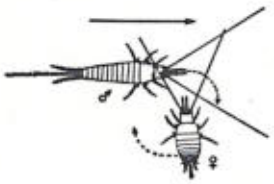
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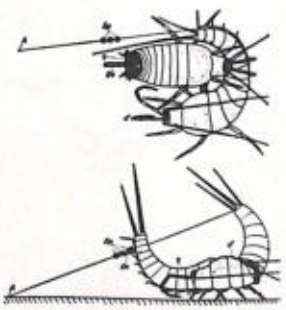
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abdominal pincers. Japygids are primarily tropical. Only about 20 species have been found in North America, but more than 200 occur in subtropical and tropical regions. In the tropics there are giant japygids, up to 4 cm in length, which can overcome even large ground-dwelling insects with their pincers.

The reproductive behavior of the diplurans is considerably more primitive than that of the bristletails. As soon as a male has detected a mature female in the vicinity, he proceeds with characteristic movements to deposit on the ground some drops of sperm mounted on short stalks. He pays no further attention to his partner, but leaves to her the responsibility for finding the seminal drops and taking up the sperm.

This means that the seminal fluid of the diplurans often remains in the air for a considerably longer time than that of the bristletails. This is only possible because the diplurans always live in the deeper layers of the ground which are saturated with moisture; there this primitive form of sperm transfer has been feasible. The female dipluran bores a hole in the ground and hangs from its roof a number of eggs on a common stalk which is produced by a glandular secretion. Until the young hatch, the japygid mother remains in the nest; she guards and defends the brood by curling her body protectively around the ball of eggs or the young.



Fig. 2-4. A dipluran *Japyx* sp. catching a *Campodea* sp. in its caudal pincers and eating it.

The PROTURANS (Protura) are the most puzzling of all the insects. These ground-dwellers are hardly more than 1 mm long, colorless, and lack not only eyes but also antennae. They use the forelegs, which are constantly held up like antennae, as organs of touch, and therefore walk on only four legs. They are unique among insects in having the full number of abdominal segments, eleven, in the sexually mature stage. External sexual characteristics are entirely lacking. The mouthparts are certainly not primitive; they have not only become recessed into the head capsule but have been converted into stylets, so that the proturans can obtain their food only by sucking.

Order: Protura

Until most recently it was not clear what the proturans eat; no one had succeeded in keeping these extremely sensitive creatures, which normally live well hidden in the ground, in the laboratory long enough to observe them. Most zoologists believed that, using their forelegs (which are held up in such a threatening posture), they would be capable of capturing other soil-dwellers so as to suck out their body contents. But a short while ago the German zoologist H. Sturm refuted this myth. He discovered that the proturans pierce certain fungi which grow as masses of threads (mycelia), and suck out their contents. These mycelia are generally associated with the rootlets of many higher plants. The reproductive behavior of the proturans, however, still remains a completely blank chapter in biology. The color plate on page 73 shows one of these singular animals.

Order: Collembola

The fourth and last group in this chapter, the SPRINGTAILS (Collembola) is probably the most interesting in every respect. Because of their

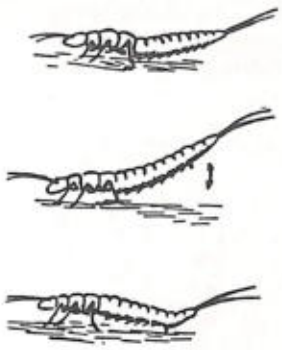


Fig. 2-5. With up-and-down movements of the abdomen, a male *Campodea* sp. deposits a sperm packet.

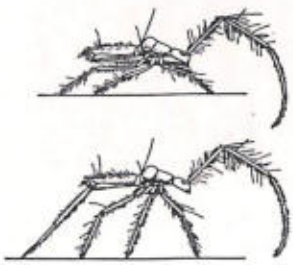


Fig. 2-6. The tree-dwelling tropical springtail *Campylothorax* sp. (below, with furca extended).

worldwide and unbelievably versatile distribution, the springtails are considered by many zoologists to be the insect group containing the greatest number of individual animals. Most of these tiny creatures are surface-dwellers hardly 5 mm long, and the subterranean forms often barely reach 1 mm in length. The largest example is the genus *Tomocerus*, which occupies a niche similar to the wood louse and lives in leaf litter in many parts of the world. In numbers of species (perhaps as many as 4000), as well, the springtails far exceed the other primitive insects. There is hardly any habitat on continental land masses which is not occupied by springtails; from the flowerpot in the window to the eternal snow of the glaciers, from the hollows within the earth to the nests of birds, from tree bark to the surfaces of lakes and ponds, from the alpine meadows to shores of the oceans, springtails abound.

The forms taken by the bodies of the springtails are correspondingly varied, though they all have the same fundamental structure. As with all insects, the body is divided into head, thorax, and abdomen, with two antennae on the head and six legs on the thorax. Wings and external reproductive appendages are lacking. The mouthparts, like those of the diplurans and proturans, are recessed within the head capsule. It is particularly characteristic of the springtails that they have only six abdominal segments (see Chapter 1). A further characteristic is the presence of three peculiar appendages of the abdomen which occur nowhere else among the insects. The most striking abdominal appendage is the so-called "furca" on the fourth abdominal segment; this is a two-pronged projection which can be unfolded so as to extend downward and backward, enabling certain springtails to perform quite notable jumps. In the resting position the furca is folded against the ventral side of the body, with the tip pointing forward, and held there in another appendage which is likewise two-pronged but much smaller—the so-called retinaculum. Strong muscles within the abdomen can propel the furca rapidly and powerfully against the ground, producing a jump.

On the first abdominal segment, the springtails have a third appendage, the significance of which has long been a matter of debate among zoologists. It is a sort of tube from which either a membranous double sack or two single hoselike tubules can be extended. It was believed that springtails could use this ventral tube, or "collophore," either to stop themselves after a jump or for attachment when walking on smooth surfaces. Other researchers thought that the animal might breathe or drink with it. Now we know that all these guesses are right: the springtails do use the collophore for attachment and they also take up oxygen through its especially thin skin; under dry conditions they can suck up water with it. Some species which have particularly long collophore tubules can even use them to clean themselves. Thus this queer appendage is truly a multipurpose organ.

These structural peculiarities of the springtails are of course not

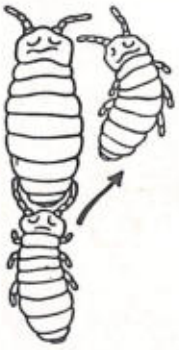
developed in the same way in all species. As a consequence of adaptation to widely varying habitats, certain springtails can become so altered as to be almost unrecognizable. In the first place, there are two fundamentally different "life-style" types: (A) the normal extended forms, in which thorax and abdomen, as is usual in insects, are clearly demarcated externally, and (B) forms in which the trunk is swollen like a balloon. These "rounded" springtails, as a rule, live above ground, often on the higher plants, where they can make particularly high and broad jumps;they always have powerful furcae and collophore tubules which can be considerably extended.

Among the normal extended forms, the species which live above ground are quite distinct from those living deeper in the ground or in holes. The former are larger and have long antennae, legs, and furcae; their skin is often brightly colored, with hairs or scales. On each side of the head they bear the full number (eight) of well-developed eyes. They are always very adept at running and jumping. The subterranean species, on the other hand, are progressively smaller, the deeper the region in which they live; they have shorter antennae, legs, and furcae, and they are pale in color and have fewer eyes. In the extreme case, those which inhabit the deepest levels of the soil have no furcae at all; they are completely blind and colorless and propel themselves forward on their short legs more like worms than insects. Actually, these light-shy creatures no longer deserve the name "springtails."

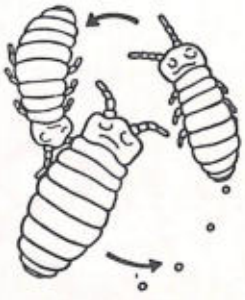
The remarkable variety of springtail shapes is matched by that of their menu. Basically they are omnivorous and can consume both vegetable and animal food in various degrees of freshness. But there are also many among them which depend upon quite specific foods. Some prefer algae or fungi, while others chew up the litter of leaves and needles or the fallen wood in the forests, and still others are at work in compost heaps and the soil of gardens, fields, and meadows—processing the waste material into humus. One community of springtails which shares similar eating habits is found at the so-called "corpse level" in cemeteries, about six feet deep; only small, blind, wormlike forms live there, mainly those of the genus *Onychiurus* (see Color plates, pp. 51/52 and 73).

Other springtails chew green plants and can thus become "destructive." The best-known of these is the LUCERNE FLEA (*Sminthurus viridis*; cf. Color plate, p. 73), a brightly colored rounded springtail which often appears by the millions in alfalfa fields. In the southern U.S.A., Jamaica, and a few other regions, springtails have been found as pests on sugarcane or tobacco plants. In mushroom cultures, springtails of the genus *Hypogastrura* (see Color plate, p. 73) often appear in masses and are a great annoyance to the grower. As particularly interesting food specialists, the little rounded springtails of the genus *Sminthurides* should be mentioned; they live on the surfaces of ponds and prefer duckweed as food. A mountain springtail, *Isotoma viridis*, feeds preferentially on pollen grains

Fig. 2-7. Mating of the springtail *Podura aquatica* (unilateral pair formation):



Testing with the antennae.



Shoving with directed pushes.



Stalked sperm droplet.

which the wind blows onto the surface of the ice and snow. Finally, there are springtails with piercing mouthparts which prefer to slit open and suck out the mycelia in decayed wood. One species of these, *Anurida maritima*, has other tastes; it lives on the shore and sucks the washed-up corpses of animals.

Like the other primitive insects, the springtails are almost all limited strictly to habitats of high humidity; their skin is also very thin and soft, so that it offers no effective barrier against evaporation. Again, their ancient status is betrayed most clearly by their primitive reproductive behavior. Although it is quite simple to keep springtails in the laboratory and to raise them, their mating behavior was described only quite recently. The great age of the group, from an evolutionary point of view, is demonstrated on the one hand by the fact that most species practice a particularly simple method of indirect sperm transfer, and on the other hand by the considerable further development of reproductive behavior, which is designed to assure the safe transmission of sperm, in certain species of springtails. It is not an exaggeration to claim that the reproductive behavior of these primitive insects is one of the most attractive chapters in behavioral analysis, although so far many of its modifications remain unstudied.

With most of the springtails, one cannot even speak of pair formation; the sexual partners take no notice of one another, even in the process of reproduction. Regardless of whether females are in the vicinity, the males deposit a number of stalked droplets of sperm on the ground. The females, just as independently, find these droplets and sweep them away with their slitlike genital openings. Only rarely does one see that springtails of opposite sexes are interested in one another; they show this by conspicuously touching each other. These springtails, then, exhibit reproductive behavior which is about as primitive as that of some marine animals (for example, worms and echinoderms) which simply discharge their reproductive cells into the water. But at least the female springtail must show behavior which is "directed" to some extent, if she is to be sure of fertilizing her eggs.

Certain species of springtails have gone a step further in the direction of pair formation. For example, there is a forest-dwelling rounded springtail called *Dicyrtomina labellei*. The males of this species have such sharp eyes that they can detect their females, which are only the size of a pinhead, at a distance of 2 cm. The male then runs to the female to test with his antennae whether the potential partner is sexually mature. If that is the case, he refuses to leave the "chosen one," although she never takes the slightest notice of her "admirer." Finally, he plants several stalked sperm drops like a picket fence in a semicircle around the partner, so that as she walks along there is a high probability that she will bump into them. If she is carrying eggs which are ready to be laid, she promptly sweeps off one of the sperm droplets, which ensures fertilization.

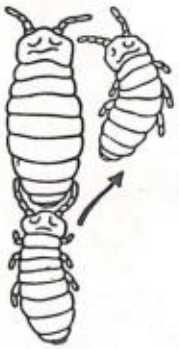
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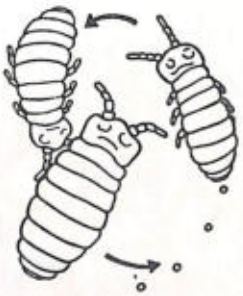
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Stalked sperm droplet.

which the wind blows onto the surface of the ice and snow. Finally, there are springtails with piercing mouthparts which prefer to slit open and suck out the mycelia in decayed wood. One species of these, *Anurida maritima*, has other tastes; it lives on the shore and sucks the washed-up corpses of animals.

Like the other primitive insects, the springtails are almost all limited strictly to habitats of high humidity; their skin is also very thin and soft, so that it offers no effective barrier against evaporation. Again, their ancient status is betrayed most clearly by their primitive reproductive behavior. Although it is quite simple to keep springtails in the laboratory and to raise them, their mating behavior was described only quite recently. The great age of the group, from an evolutionary point of view, is demonstrated on the one hand by the fact that most species practice a particularly simple method of indirect sperm transfer, and on the other hand by the considerable further development of reproductive behavior, which is designed to assure the safe transmission of sperm, in certain species of springtails. It is not an exaggeration to claim that the reproductive behavior of these primitive insects is one of the most attractive chapters in behavioral analysis, although so far many of its modifications remain unstudied.

With most of the springtails, one cannot even speak of pair formation; the sexual partners take no notice of one another, even in the process of reproduction. Regardless of whether females are in the vicinity, the males deposit a number of stalked droplets of sperm on the ground. The females, just as independently, find these droplets and sweep them away with their slitlike genital openings. Only rarely does one see that springtails of opposite sexes are interested in one another; they show this by conspicuously touching each other. These springtails, then, exhibit reproductive behavior which is about as primitive as that of some marine animals (for example, worms and echinoderms) which simply discharge their reproductive cells into the water. But at least the female springtail must show behavior which is "directed" to some extent, if she is to be sure of fertilizing her eggs.

Certain species of springtails have gone a step further in the direction of pair formation. For example, there is a forest-dwelling rounded springtail called *Dicyrtomina labellei*. The males of this species have such sharp eyes that they can detect their females, which are only the size of a pinhead, at a distance of 2 cm. The male then runs to the female to test with his antennae whether the potential partner is sexually mature. If that is the case, he refuses to leave the "chosen one," although she never takes the slightest notice of her "admirer." Finally, he plants several stalked sperm drops like a picket fence in a semicircle around the partner, so that as she walks along there is a high probability that she will bump into them. If she is carrying eggs which are ready to be laid, she promptly sweeps off one of the sperm droplets, which ensures fertilization.

This "one-sided" pair formation is carried even a bit further in another small, blue-black springtail, *Podura aquatica*, thousands of which can inhabit the water surface of weedy pools. Here the male is not satisfied simply to test the female with his antennae and, judging her "ripe," to build a fence of sperm droplets next to her; he actually proceeds to shove his chosen mate with well-directed pushes toward the fence so that she is quite certain to find it and put it to its intended use. But even with this species one has the impression that only the male considers himself "paired," while his partner does not participate at all.

Finally, there are also springtails which form true pairs. The best-known species is the tiny (1 mm) rounded springtail *Sminthurides aquaticus*, a small yellow ball to be found on the surface of ponds overgrown with duckweed. Here the males and females are clearly different, which is rarely the case among springtails. The males are much smaller than the females, and their antennae have developed into clasping organs. With these, they cling to the antennae of mature females and often allow themselves to be carried about by them for days. In this process it frequently happens that the relatively giant females swing their "dwarf" males up so that they lie back-to-back on their partners and wave their legs helplessly in the air. For a long time it was a puzzle, what significance this apparently nonsensical copulatory position might have, but eventually the zoologist Helmut Mayer realized that it is only a preliminary to the actual transfer of sperm. From time to time, the male gives up his passive role and makes such violent movements that he forces his partner to put him down. As soon as he feels ground—that is, the water surface—under his feet, he begins a tug of war with her which is evidently very strenuous; he pushes her back and forth and from side to side. If she follows him willingly, he quickly deposits a droplet of sperm and pulls her with great effort, staggering backwards or in an arc to the side, far enough along so that she can contact the sperm with her genital opening and take it up.

According to old reports, some researchers even claimed to have observed the males of certain species of rounded springtails depositing the sperm on the ground and then picking it up in the mouth in order to transfer it actively to the genital opening of their partners. Even if this observation is not confirmed, one may well say that the reproductive behavior of the springtails is unusually "inventive." That is also true for those male springtails which simply plant a few hundred sperm drops in an area, because even they display a remarkable auxiliary behavior. When they happen upon a droplet from a member of their own species, they do not simply ignore it but rather test it with a characteristic shaking movement of the head, holding it between the basal segments of their antennae. If the droplet is more than eight hours old they eat it and place a new one just next to it. Drops which are not so old are allowed to remain. The biological significance of this behavior is quite clear: it ensures that the

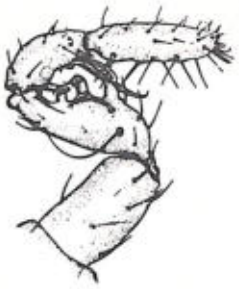
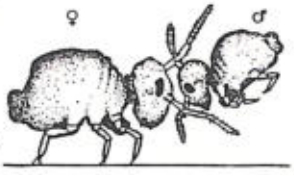


Fig. 2-8. In the male of the aquatic rounded springtail the antenna is developed into a clasping organ . . .



. . . which he uses to cling to the antennae of the female.

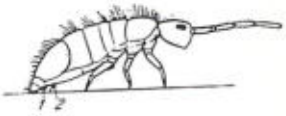


Fig. 2-9. A female springtail of the genus *Orchesella* sweeping up a sperm packet (2); at the genital opening there is a drop of fluid (1) which facilitates uptake of the sperm packet.



Fig. 2-10. A male *Orchesella* sp. tests a sperm packet (1) by head shaking (arrow). Cf. Color plates, pp. 51/52 and 73.

female springtails find only fresh sperm in their "garden of love." We do not yet know how the males can tell the age or the freshness of the sperm drops.

Another extraordinary aspect of springtail life is the rate of reproduction and the consequent density of population. They can reproduce almost all year long. In normal soils, rich in humus, it has been calculated that there are on the average 2000 springtails in every liter of earth; in each cubic centimeter, then, one can expect to find on the average two of these little animals crawling about. Some soil-dwelling species appear primarily in spring, on the snow or after the thaw, in such massive numbers that they are occasionally mentioned in the newspapers. As early as the 17th Century the springtails were mentioned as *vermes nivales* (snow worms). At that time, of course, most people believed that these millions of animals had fallen to earth along with the snow. In more recent times E. Handschin described a great outbreak in Germany, near Basel, particularly graphically:

"A massive multiplication of *Hypogastrura longispina* on the Isteiner Klotz (27 January 1924) went on for fourteen days on the slopes overhanging a small sunken path. The bank at the side of this path was about 50 cm high, and along the bottom trickled a brooklet of snow water from a vineyard. For about 150 m, the bank was completely covered with the little animals, and they dropped continually like poppyseeds into the rivulet, forming a layer about 5 to 8 cm deep. One could gather the animals by the kilogram and, forced by the hardship of the times, some people even tried to extract oil from them. If one estimates that there were about 4 million individuals per l, there might have been roughly 5 billion animals involved in this migration. That these figures are not too high is indicated by the estimates of other authors who arrived at similarly fantastic numbers. According to reports from Mühlberg it is even supposed to have happened that the hordes of Collembola crawling on the railroad tracks caused a train to skid temporarily, since the crushed bodies of the animals reduced the friction between the wheels and the rails."

Mountain climbers in the high Alps are familiar with the fact that springtails which live on glaciers can often appear in such density. The fields of ice freshly blanketed by new snow then appear as though covered with soot. An outbreak of springtails almost became an event in world history when it happened to occur during the Korean War in a region of North Korea where American planes had just been operating. The Chinese press had the idea of playing up these harmless arthropods in words and pictures, describing them as disease transmitters which had been dropped by the Americans. Many a zoologically naive person may have thought that these springtails were among the first modern biological weapons.

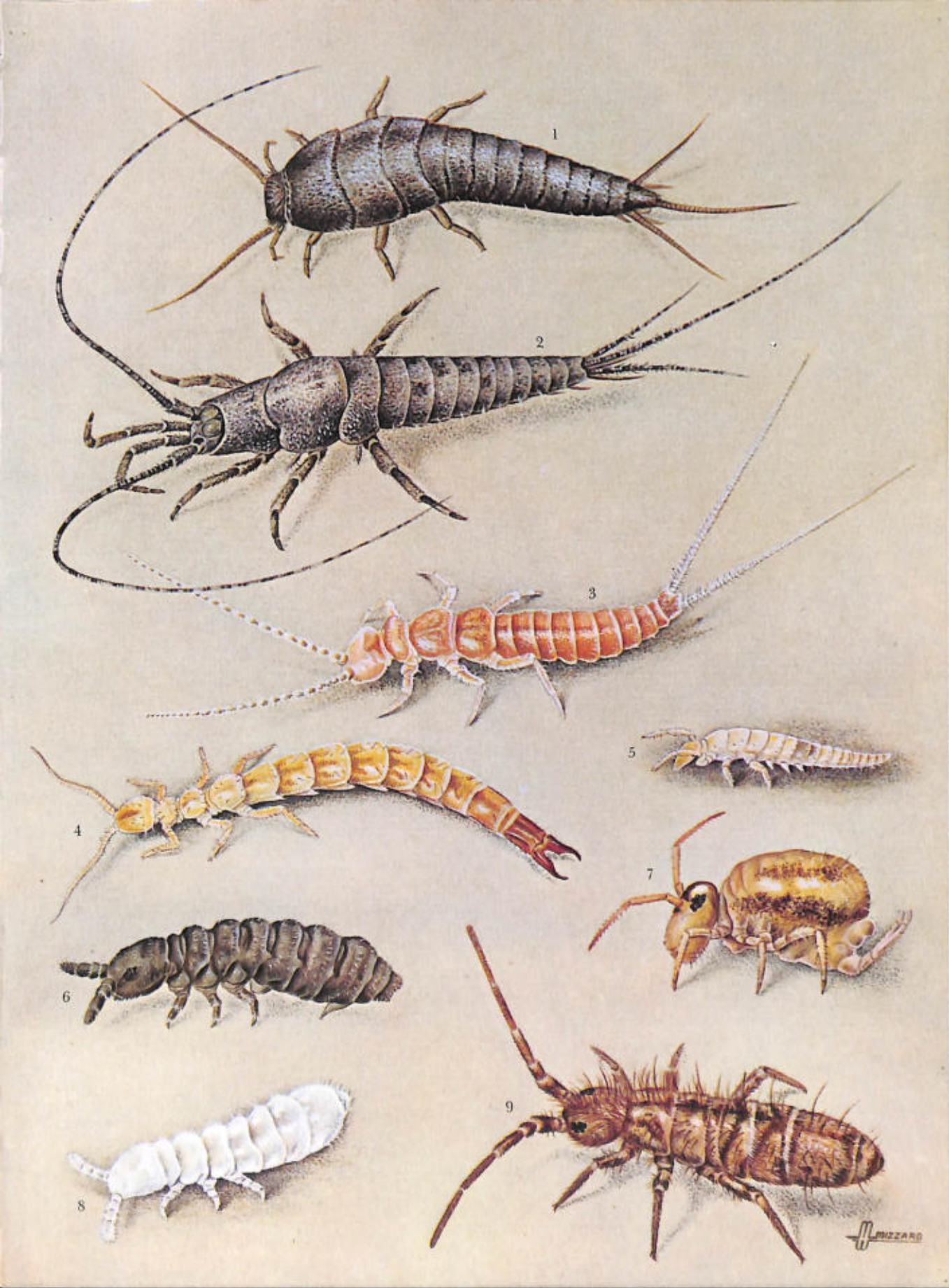
Since the springtails can appear in such great numbers, it is not surprising that in spite of their small size they play an important role in the natural food chain. They are eaten by countless other animals, above all spiders,

myriapods, and ground beetles. The excretions of springtails are an important component of the fine brown particles which make up the fertile humus of natural soils. It is for this reason that modern zoological research has been particularly concerned with these primitive insects. Numerous papers deal with their systematics, their ecology, and their nutrition. Nevertheless, we still know very little about important aspects of their lives. In particular, their sense organs have hardly been studied at all. The soil-dwellers among them naturally orient themselves through the senses of smell and touch, while those living above ground and on plants probably rely more upon their eyes. But it is very difficult to do the desired experiments; because of their softness and delicacy one cannot hold them like other insects. Most springtails shy away from light, and almost all of them require and search out high humidity. In an experimentally arranged temperature gradient they run to the cooler areas, except in the cases of the tropical species.

Otherwise there are only sparse observations which give some indication of the sensory capabilities of the springtails. For example, it was debated for a long time whether they could distinguish only light from dark, or whether they could detect outlines and thus shapes. Now we know of two cases of unquestionable "form vision." The first, as was already intimated in the description of reproductive behavior, is in the small forest-dwelling rounded springtail *Dicyrtomina minuta*. Here the males can detect their females at a distance of 2 cm, as could be demonstrated by experiments with "dummies," little balls of the same size as the animals. Members of this species also find the way to tree trunks about 30 cm in diameter and 2 or 3 m away. When they are blown down by a gust of wind from the trees where they feed on algae, they find their way back by walking in a nearly straight line, even over sticks and stones.

Such visual orientation is demonstrated even more clearly by certain springtail species of the genera *Lepidocyrtoides* and *Mastigoceras*, which live in leaf litter in the forests of the flood basins of the Amazon. If in their flight from the rising floodwaters they accidentally fall in the water, they show a surprising ability to find their way back to the land. Experiments in a water arena have shown that they definitely orient to dark silhouettes on the horizon, toward which they steer in zig-zag runs and finally even in well-directed jumps. Before or during these dashes toward the shore, they frequently turn around in a circle or swing back and forth—evidently to sample the horizon for outlines with their low-resolution eyes. These characteristic orienting movements are done up to twenty times in succession, even when the dark object on the horizon is so narrow that it is at the limit of visual resolution. Such experiments have demonstrated that the springtails can recognize and find only dark visual objects occupying at least eight to ten angular degrees of the visual field. Their sixteen single ocelli each have receptive fields of about forty degrees, but the regions seen by each of them overlap to such an extent that the measured ten-

▷
Bristletails: 1. A silverfish *Lepisma* sp., 2. *Machilis* sp
Diplurans: 3. *Campodea* sp. 4. *Japyx* sp.
5. A proturan.
Springtails: 6. *Hypogastrura* sp., 7. *Sminthurus* sp., 8. *Onychiurus* sp., 9. *Orchesella* sp.


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1a
1b
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degree resolution appears compatible with the visual apparatus. Note too that these springtails of the Amazon are capable of quite well-directed jumps on the water; there have been long arguments over whether springtails were capable at all of "aiming" their jumps.

Another special sensory achievement has been discovered in the white, blind *Onychiurus fimetarius*, which lives in the soil and cannot jump; these springtails can detect the slightest trace of carbonic acid in the earth. They are so strongly attracted by it that hundreds of them often gather at such spots. This special ability probably facilitates their search for food, since wherever organic materials are decaying, the activity of bacteria results in the production of carbon dioxide. The location of the sense cells for the detection of carbonic acid has not yet been investigated, but it may be assumed that they are in the complex sensory clubs on the fourth antennal segment, which are found only in these exclusively soil-dwelling springtails.

The mechanism of the fine sense for humidity which many springtails possess has likewise not yet been established. It is assumed that the remarkable "postantennal organs" of many species, particularly those which live in the soil, are responsible. These cell complexes, which may be shaped like a simple oval or a rosette, or may have elaborate lobes, are buried in pits behind the antennae and are hygroscopic.

There remain many remarkable aspects of the structure and behavior of springtails for the curious zoologist to investigate, and this opportunity exists with the other primitive insects as well. It is not only the reproductive behavior which presents us with intriguing puzzles. A 1-mm-long springtail, the species *Subisotoma variabilis*, occupies itself with structural engineering, as the French investigator Poinsot has recently discovered. The animal glues its own cylindrical fecal balls together in such a way as to build solid and often nicely symmetrical galleries in which, finally, the little engineer himself is enclosed. Evidently these springtails employ their building talents primarily when conditions become too dry for them. Like all primitive insects, they must guard against the danger of desiccation. In their nearly enclosed individual houses, moisture can be retained longer than in the open or even in large hollows under the surface.

But researchers other than sensory physiologists and students of behavior will also find pleasant surprises in the study of the springtails. Interesting questions arise for the physiologist concerned with metabolism. For example, it would be nice to know more about the mechanics and energetics of the jumping performance. A more detailed investigation of the respiratory metabolism would also be desirable, though we do already know a little about it. Oxygen consumption may be taken as a measure of the "biological productivity" of an animal species. This is a particularly useful measure for springtails which form humus in the soil. Measurements of respiration have shown that the small soil-dwelling species have a higher metabolic rate than the larger species which live on

◁ 1. A common Mayfly (*Ephemera vulgata*; L 14–22 mm): a, flying; b, resting; 1, naiad. 2. The stonefly *Perla marginata* (L 15–25 mm): a, flying; b, resting; 1, naiad.

the surface. That is, the soil-dwellers have a greater need for food, and in this lies their special importance in the formation of humus, as already discussed.

These investigations in respiratory physiology, which were recently published by the German zoologist D. Zinker, also included a study of the black springtails which live on glaciers. It turns out that these animals can breathe normally (that is, as their relatives do at 10–15°C) only when the temperature is below 8°C. At temperatures above 8°C the oxygen requirement of these springtails is so enormously increased that they are no longer capable of ordinary life. On the other hand, their respiration is normal at and below the freezing point; as a consequence, they are capable of carrying out all their ordinary functions perfectly well in snow and ice. If one stimulates them strongly they can jump even at —3°C.

Research on certain springtails may soon illuminate still another area of general biological importance. These studies concern species with sucking mouthparts (for example, the genus *Neanura*). Their salivary glands are much enlarged, and French researchers have recently demonstrated that they contain giant chromosomes. Such giant chromosomes have long been known in the famous experimental animal of genetics, the fruit fly genus *Drosophila* (see Chapter 19); it was possible to use those salivary-gland chromosomes to set up precise plots of the chromosomal sites responsible for heritable characteristics (genetic maps). Since the springtails, like the fruit fly, are easy to raise, reproduce quickly and in large numbers, and show conspicuously variable characteristics, they may in the future become important experimental animals in the science of genetics. Furthermore, occasional differences in the ratio of males to females have been demonstrated, suggesting that springtails have alternative means of sex determination, which would provide a further incentive for their investigation. Altogether, one may predict a promising future for the springtails as experimental animals in zoological research.



Fig. 2-11. Nest of *Subisotoma variabilis*.

3 The Mayflies, Dragonflies, and Damselflies

Subclass: Pterygota

The WINGED INSECTS (subclass Pterygota) comprise the great majority of all insects. In this chapter, we begin their description with two primitive orders, Mayflies (Ephemeroptera) and the Odonata, the dragonflies and damselflies.

Order: Ephemeroptera

Distinguishing characteristics

The MAYFLIES (order Ephemeroptera; see Color plate, p. 74) are fragile insects; the range of L is 1–6 cm, the largest American Mayfly being about 3 cm long. The body has no hairs, is yellowish to gray-brown, and may be of a single color or inconspicuously patterned. The wings are transparent and held erect when the animal is at rest; the forewing has the form of a rounded triangle, while the hindwing is smaller, ovoid, and sometimes regressed. There are three (less commonly, two) long caudal appendages. The last juvenile stage (the subimago) already has wings. The naiads have many forms, but all are aquatic and breathe with tracheal gills. They have existed since the Carboniferous (about 350–280 million years ago), and today there are about 1500 species.

As their name implies, the Ephemeroptera are noted for their brief existence, but actually it is only the winged stages which are short-lived; before the imago develops the naiad stage is aquatic and takes a period of several months or even one to three years to develop! Following that, to be sure, their life in the air usually lasts only a few hours to a few days; these are dedicated exclusively to reproduction. The name Mayfly is also misleading, for one may encounter the various species of Mayflies near bodies of water from April on into October, or, in warm regions, the year around.

Thus the Mayflies spend by far the greatest part of their not-so-short lives as aquatic animals, and it is in the water that their existence begins, as eggs. In the species which live in still water, the females hover over the water and drop the balls of eggs from their paired genital openings; they may also fall dying onto the water surface and release the eggs there. The females of species with naiads which live in flowing water must proceed differently, so that their eggs are not carried by the currents into quiet

pools. These females descend into the water when they are ready to lay, and attach the eggs to stones, moss, fallen leaves, or some other substrate. One of America's most common Mayflies, the two-winged *Callibaetis floridanus*, has given up egg-laying altogether and gives birth to six or seven hundred little naiads while flying over the water. For these to develop in the mother's body from the fertilized egg to the stage when they are ready to be born requires about two weeks, which the mother spends without moving or feeding, in the vicinity of the water.

The Mayfly imagos are quite uniform, so that only a very few species have acquired common names of their own. The naiads, on the other hand, being adapted to many different habitats, are quite variable; four main naiad types can be distinguished by shape and way of life:

1. The free-swimming naiads are inhabitants of standing or very slowly flowing water having an abundance of plant life. Their narrow bodies are not flattened; they have three sturdy caudal appendages, of which the outer ones have hairs on the inside, and the middle one, on both sides. Together they form a fan which aids in swimming, as do the little leaflike gills which arose in evolution from abdominal legs. The latter are simultaneously respiratory organs which in most species oscillate constantly, maintaining a flow of fresh, oxygenated water. The gills are lacking in the youngest naiads, which obtain enough oxygen through the body surface. Only as the animal grows (remember that volume increases as the cube of linear dimensions, and surface area, only as the square) does it become necessary to provide additional respiratory surfaces. The naiads also have a third means of propulsion; they eject water from the hindgut, which drives them forward. Free-swimming naiads of this type are primarily to be found in the families Baetidae, Leptophlebiidae, and Siphlonuridae.



Fig. 3-1. Crawling naiad of a Mayfly (*Ecdyonurus* sp.).

2. The crawling naiads live on the bottoms of muddy bodies of water. They vary quite a bit from species to species, but are all heavily endowed with body hairs which collect a great deal of mud, so that they are very well camouflaged. The gills of these naiads are adapted to life in the mud in several ways. The naiads of the Caenidae have rod-shaped vestigial gills on the first abdominal segment and on the second, a pair of gills which lies protectively, like wingcovers, over the remaining very delicate gills. The gills of *Potamanthus verticis*, on the other hand, look like feathers with two branches, which stick out to the sides of the animal and serve to keep it in place under stones. The naiads of *Ephemerella simulans* also have two-branched gills; one of the branches is a convex plate covering the other, which is provided with lateral lamellae and serves as the actual respiratory organ.

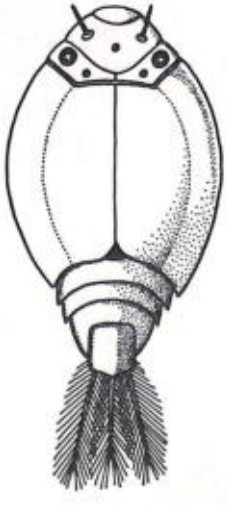


Fig. 3-2. Stream-dwelling naiad of the Mayfly *Prosopistoma foliacea* (L 5–6 mm).

3. The burrowing naiads have gone one step further. These naiads inhabit U-shaped tunnels in the bottom and the underwater banks of still or slowly flowing bodies of water. They construct the tunnels with their legs and the powerful mandibles, which tower far above the head. The

naiads of America's largest and most beautiful Mayfly, *Hexagenia munda*, have large tusks on the outer edge of their shovellike mandibles and on the tibiae of their digging forelegs. In the CARRIONFLY (*Ephoron leukon*) on the other hand, the mandibles are long sabers with the tip pointed inward; both the first and the third pairs of legs are digging legs. In the species of the genus *Ephemera* the mandibular tips are pointed outward and all three pairs of legs are for digging.

4. The naiads which live in fast-flowing mountain brooks have a flat ventral surface which allows them to lie close to the stones on the bottom. Correspondingly, the legs are attached at the sides of the thorax; neither the legs, with their broad, flat trochanters, nor the gill lamellae, which overlap like shingles, offer much resistance to the water. The upper side of the body is arched in such a way that the water flowing over it only presses the animal more firmly against the stone. The compound eyes on the flat, broad head look forward. These adaptations are to be found in the naiads of the Oligoneuriidae and, in somewhat modified form, in those of *Oligoneuria ammophila*. The abdominal gills of the latter are small, but the maxillae bear large tufted gills. These naiads can also anchor themselves with a special device shaped like a suction cup, which is formed from the galea of the labrum. The naiads of *Baetisca rogersi* have gone the furthest in adaptation to flowing water. The tergal plates of the thorax and those of the first six abdominal segments together form a solid dorsal shield, the oval shape of which is completed by the flat head (compare Fig. 3–2). Behind the equally flat last four abdominal segments is a plumed, tripartite caudal fan. This strange and rare animal lives in pebbly riffles in streams in the eastern U.S.A.; when disturbed it swims very rapidly with its caudal fan. It breathes with five pairs of gills which lie hidden in a gill chamber covered by the dorsal shield.

Naiad feeding

The naiads of the Mayflies obtain their food in part from decaying remains of leaves and other floating or sinking materials, and in part from green algae and diatoms, organisms which produce organic materials. The naiads themselves make up a large proportion of the food of fish, both directly and indirectly by way of the predatory insects which eat them. The imagos themselves no longer eat. Many of them become the prey of songbirds, swallows, spiders, and not least of dragonflies. In terms of the trophic levels in freshwater communities, then, the Mayflies are primary consumers, which feed on the producers and on which in turn the secondary and higher-level consumers feed. Together with various midge larvae, they constitute the greatest proportion of the organisms at their level and thus play an essential role in the biotic balance.

Subimago and imago

The Mayfly naiad metamorphoses, in the molt just preceding the final molt, to a winged subimago. Its wings are translucent, bear fine hairs, and are water repellent, so that after hatching, the animal can emerge from the water dry. Even the subimago no longer takes food; its mouthparts are stunted and its gut is filled with fluid. This stage lasts only a short

time; then, at the final molt, the imago emerges. However, for the females of the genus *Tortopus* the subimago is the final stage in their three-year lifespan. In this form they mate, in the air or on the water, deposit their eggs, and die.

As a rule, though, the subimaginal stage lasts only for six to thirty-six hours and then is followed by the molt which produces the imago. The imago devotes the few remaining hours of its life entirely to reproduction. In the hours near sunset one can observe the unique nuptial dance of the males, which collect in dense swarms above the water or at its surface. Witlf a fluttering wingbeat they rise vertically and then, with wings spread out, let themselves fall again. Now the females fly into the swarm of dancing males, which detect them and sieze them from beneath. The males are specially equipped for both of these activities. The upper halves of their eyes are constructed less for sharp image formation than for vision in twilight. Often they are completely separate from the lower compound eyes, sitting on them like a turban, so that they are sometimes called "turban eyes." Furthermore, the male is adept at grasping the female because of his elongated forelegs, which he throws around the thorax of his partner. At the same time, the claspers on his ninth abdominal segment close around the end of her abdomen. Thus the smaller male, holding his wings together, hangs beneath the female as she sinks slowly through the air with wings outstretched. Just above the ground or the surface of the water the partners separate and the female begins depositing the eggs, the last task of her brief aerial life.



Fig. 3-3. Head of a male Mayfly (*Baetis* sp.) from the front, with "turban eyes."

Mayflies inhabited the swamps of the Carboniferous over 300 million years ago. The hindwings of these ancient insects were the same size as the forewings, and at rest they were carried stretched out at either side; this arrangement was like that of their contemporaries, the Palaeodictyoptera, and of the present-day dragonflies as well. Therefore we distinguish them from our present-day Mayflies by calling them primitive Mayflies or Negasecoptera. But true Mayflies have been discovered as early as the period following the Carboniferous, the Permian (about 250 million years ago), so that we may regard this peculiar insect group as genuine survivors from the earth's antiquity.

Order: Odonata, by P. Rietschel

In contrast to the Mayflies, the DRAGONFLIES and DAMSELFLIES (order Odonata) are among the most conspicuous animals in the whole insect class. They hunt, mate, and lay their eggs in the bright sunshine, and are a delight to observe. The poet and zoologist H. Löns wrote a perceptive and delicately expressive book about their natural history in which he called them "messengers of summer and heralds of the sun." The pre-Christian Teutons regarded them as the animals of the goddess Frigga. Later, when the new teaching turned what was previously holy into works of the devil, Wotan's raven and Frigga's day (Friday) became associated with bad luck—the dragonflies became "devil's arrows," "devil's darning needles," and "eye piercers." Even today it is a popular superstition that they can

sting with a very dangerous poison. It is not without reason that H. Schiemenz introduces his book on dragonflies with the words, "Dragonflies do not sting! Don't be afraid to take them in your hand; nothing will happen to you."

Distinguishing characteristics

The dragonflies and damselflies are predatory insects. Structurally, they combine primitive characteristics with those of extremely specialized development. They range in size from medium to large (L 2–13 cm). The head is movable and bears biting mouthparts, short antennae, and very large eyes (dragonflies are the most emphatically "visual" animals among the insects). The thorax has only weak legs but two pairs of large wings which may or may not be similar and are richly supplied with longitudinal and transverse veins. The abdomen is long and may be either cylindrical or flattened. The body, which is without hairs, usually has lively and varied patterns of coloration. Metamorphosis is incomplete (hemimetabolous); the naiads are aquatic, rapacious stalkers with biting mouthparts, the labium having been transformed into a prehensile mask. Dragonflies have existed since the Permian (about 280–230 million years ago); there are now about 4500 species, of which 412 are native to North America.

Suborders: Anisozygoptera, Zygoptera, and Anisoptera

Apart from the PRIMITIVE DRAGONFLIES (suborder Anisozygoptera), two species of which have survived from the Triassic and now inhabit eastern and southeastern Asia, the present-day Odonata are divided into the two suborders DAMSELFLIES (Zygoptera; see Color plate, p. 83), and DRAGONFLIES (Anisoptera; see Color plate, p. 84). The former includes primarily medium-sized species and the latter, large species, but the sizes in the two suborders overlap somewhat. The smallest American dragonflies, the wet-meadow genus *Sympetrum* and the delicate white-face dragonfly *Leucorrhinia glacialis*, are only about 3 cm long, while the largest damselflies, the black-wing (genus *Calopteryx*) measure 5 cm.

Manner of flight

Therefore shape is a better criterion than size for classification of the Odonata: the damselflies have almost identical forewings and hindwings, which they hold together like the Mayflies when at rest, whereas the dragonflies spread their dissimilar wings away from the body in the resting posture. The damselflies are slow and awkward flyers, the forewings and hindwings beating differently. The extremely skilful flying of the dragonflies involves synchronization of the beat of the forewings and hindwings by means of the nervous system, and it is only during turns and other flight maneuvers that the edges of the wings touch. The rustling noise then produced is familiar to all who have observed these aerial artists.

Body structure of the imago

All adult Odonata are hunters, catching their prey in flight, a feat for which they are excellently prepared by certain peculiarities of their structure. The enormous eyes occupy the greater part of the surface of the head. With the damselflies, which in addition capture non-moving prey, the eyes are widely separated, so that the head has rather the shape of a cylinder at right angles to the body. In the dragonflies, with the exception of the

clubtails (family Gomphidae), the two eyes meet in the midline, either at one point or (in the aeschnids) over some distance along their margins. Their marked convexity provides a wide field of vision, which is further enlarged by the mobility of head and thorax. The small antennae, only sparsely supplied with sense organs, play a subordinate role in the sensory life of the Odonata.

The most highly specialized of the mouthparts is the labium. Bowl-shaped, with hooks around its rim, and framed at the sides by the jaws, it forms the dish on which the prey is torn apart while its captor continues to fly. The thin legs, covered with spurs, are used by the resting dragonfly for holding on to things, but only rarely for walking. In flight, they are laid against the body and thus offer only slight resistance to the air. But as soon as the flying dragonfly happens upon a victim, it spreads the legs to form a basket, open toward the front (see Fig. 3–4), in which the prey is caught. Since the dragonfly is flying at an air speed of about 40 to 50 km per hour, this involves a violent impact, not only for the surprised prey but equally so for the dragonfly. The dragonfly absorbs the force of the collision in its thorax, the segments of which are oriented obliquely; thus the impact is in line with the center of gravity and does not throw the flying dragonfly off balance. A hunting dragonfly does not detect its prey until it is quite close, and therefore has only fractions of a second for the final maneuver. The precision of this approach demands rapid visual analysis as well as quick reactions of the nervous system and flight musculature.

Like the capture of prey, the reproduction of Odonata is carried out largely in flight. The copulatory organs of the males are peculiarly adapted to this behavior; the posterior end of the tenth abdominal segment bears two "superior appendages" below which, on the terminal segment above the anal opening, there are one (in the dragonflies) or two (in the damselflies) inferior appendages (see Fig. 3–5). None of these serves as a device for sperm transfer; that organ is located far anteriorly on the ventral side of the abdomen, and next to it there are paired pockets which serve as seminal vesicles. The females lack the inferior appendages of the abdomen. In species which deposit their eggs upon plants, the eighth and the ninth abdominal segments form a ventral sheath for oviposition.

Damselflies: 1. Banded blackwings (*Calopteryx splendens*); 1, naiad. 2. Bluewing (*Calopteryx virgo*). 3. *Pyrosoma nymphula*, mating chain with female depositing eggs.

Mating and egg-laying

The courtship of the Odonata occurs in several steps. (1) The male bends his abdomen ventrally while flying so that the genital opening can reach the seminal pockets anterior to it and empty sperm into them. This transfer may occur either before or after the preliminary courtship. (2) As a preliminary to copulation, the male flies down to the female from above and then, with the abdominal appendages, grasps her head (in the case of the dragonflies) or her head and anterior thorax (damselflies). The shapes of the appendages are in each case exactly matched to those of the head and neck region of the female of the same species. Because of this lock-and-key system, matings between members of different species are


2♂
1♂
3♂
11
3♀


1
1a
2♂
1l
3l

largely avoided. (3) Now the partners, still in flight, form the mating chain, with the male flying in front and the female, behind him. The female bends her abdomen down and forward until her genital opening reaches the male's copulatory apparatus and the sperm-filled pockets next to it, so that the mating chain becomes a mating wheel (see Fig. 3–6). After this copulation the male and female genital organs become separated, but usually the partners do not separate immediately. (4) Most damselflies and some dragonflies now assume the mating-chain position again and remain in that postcopulatory arrangement while the female lays her eggs.

Egg deposition proceeds differently among the various Odonata. The female blackwing, America's largest and at the same time most primitive damselfly, first separates from her partner and climbs backward down the stalk of a plant standing in water, using the ovipositor to bury the eggs one by one within the stalk tissue. The females keep this up even after the abdomen has gone underwater, and sometimes until they have completely immersed themselves. Some dragonflies do this as well, but without submerging. Most of the damselflies deposit their eggs while in the mating chain position, since the male does not release the female after copulation. This means that the male, holding his partner's head and thorax with his caudal appendages, must go underwater with her. What possible advantage can this behavior confer on the species? Perhaps it is only to provide a fifty-fifty chance that an underwater predator would catch the male and not his egg-laying spouse, her activity now being the crucial link in the continuation of the species. Among the dragonflies, the females of the grayback dragonfly (*Tachopteryx thoreyi*) seek out shallow parts of the swampy areas in open woods. There they fly up and down with the body held vertically, repeatedly jabbing the two stylets which form the ovipositor into the soft ground; in this way they lay the eggs directly in the future home of the larvae. The clubtail dragonflies (Gomphidae) and others also avoid the predators lurking under water; they fly in an undulating path over the water and when the tip of the abdomen just skims the surface, they let the eggs fall. It sometimes happens that the eggs are cast down from a greater height; with some dragonflies the egg-depositing flight is performed in the mating chain arrangement, with the male leading the way.

The eggs which the damselflies insert in aquatic plants are deposited in a number of ways. The eggs may be laid singly or in pairs, and the laying positions may be scattered at random, in rows, or in a zigzag pattern. One damselfly, the blackwing (*Calopteryx maculata*), coenagrion, actually lays its eggs through a hole in a water-lily leaf. The eggs form three concentric circles on the underside of the floating leaf. This curious arrangement is achieved as follows: the female, in the mating-chain formation, lands on a leaf next to a hole which has been chewed out by a beetle, puts her abdomen through the hole and, turning continually, lays

◁ Dragonflies: 1. Blue-green darner (*Aeschna cyanea*): a, emerging imago, 1, naiad. 2. *Orthetrum* sp. 3. Broad-bodied libellula (*Libellula depressa*) : 1, naiad.

a circle of eggs on the underside of the leaf. For the second, larger circle she inserts the abdomen somewhat further and with the third, only the head, wings, and part of the thorax can be seen above the hole. During all this circling, the pincers of the male are fastened around the female's neck, and he follows the three full revolutions of his spouse. Other Odonata, which eject the eggs free into the water, encase them while they are in the oviduct with a substance which swells in the water, so that the eggs form thick spherical or elongated masses. Others simply drop the eggs one at a time.

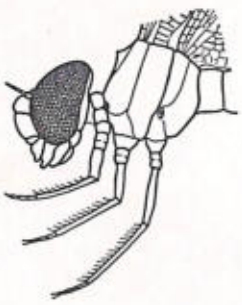


Fig. 3-4. Predatory basket position of the legs.

After a few weeks, or when the winter is past, a prenaiad stage emerges from the egg; it has no external limbs, both the legs and the mouthparts still being covered. A caudal spine consisting of three sharp bristles enables it to break open the egg case. Those prenaiad which hatch from gelatinous eggs use a hard ridge on the front of the head to cut open the case of the egg. A few seconds or minutes later the naiad has freed itself from the confines of the prenaiad case and begins its life as a naiad, which forms by far the largest fraction of the animal's existence.

Larval development

Like the imagos, the naiads are hunters, though they hunt in other surroundings and in quite a different manner. In contrast to the behavior of the imago, which is a prime example of deft and rapid pursuit in flight, the naiads use what is better described as a "deer-hunter's technique"—stalking slowly or lying in wait for the prey. The fields of vision of their forward-protruding eyes overlap widely in front of the animal, enabling good judgment of distance in this area. The prehensile mask does not strike out until the prey is just the right distance away. This mask is the specially modified labium, the long basal segments of which, when not in use, are folded together and cover the underside of the head. On the free end the mask bears sharp pincers which grasp the prey when the mask is unfolded and extended, which happens with incredible speed. The naiad uses its legs for walking much more than the imago does. Dragonfly naiads can also swim by jet propulsion, expelling water from the hindgut, while the damselfly naiads swim by bending the abdomen from side to side, with the three leaflike caudal appendages acting as oars. These appendages of damselfly naiads may have a secondary function as respiratory organs; the dragonfly naiads, however, have very effective intestinal gills, well supplied with tracheae, in the hindgut.

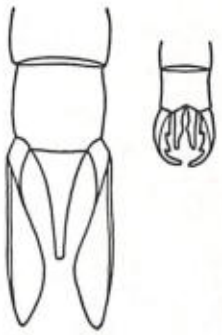


Fig. 3-5. Posterior end of abdomen of a male dragonfly (left) and damselfly (right), showing caudal appendages.

The metamorphosis of the naiad into the winged adult is a drastic change in the insect's life, and involves an extensive reconstruction of the organs. The transformation requires the animal to spend a period of dormancy comparable to the pupal period of higher insects, even though in the case of the Odonata the winged insect emerges directly from the naiad. This process occurs on land, and according to E. Straub, who has done the most thorough investigations of the act of emergence, it can be divided into six stages: (1) The naiad comes out of the water by climbing up a plant. (2) The dorsal part of the thorax bursts open, developing an X-shaped

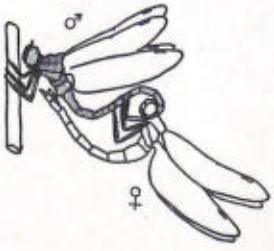


Fig. 3-6. Mating wheel of the blue-green darner (♂ shaded).

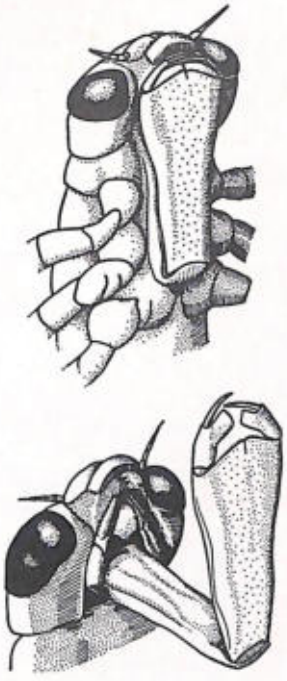


Fig. 3-7. Prehensile mask of a dragonfly naiad in the resting position (above) and extended (below).

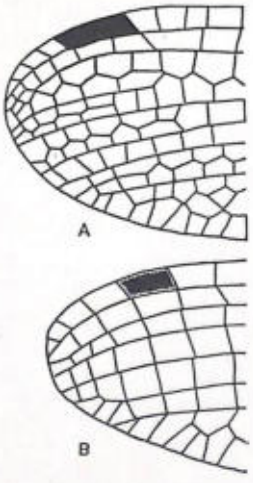


Fig. 3-8. Wingtips of two damselfly families: A, Lestidae, with stigma covering two cells and most cells roughly pentagonal. B, Agrionidae, with stigma in one cell and cells primarily rectangular.

tear through which the imago emerges. (3) The legs are the last to be pulled out of the larval skin, and the imago rests. (4) The wings extend as they are filled with blood. (5) The abdomen also extends, taking in air. (6) The abdomen expels drops of liquid and air through the anus, as it assumes its final form (see Fig. 3–9).

Most damselflies require a year for complete development, but the black-wings which live in cold, running streams spend two years. Two to three years is the normal development time for dragonflies, but the grayback dragonflies, which grow up in the cold, swampy areas around mountain springs, presumably take as much as five years.

Only a few of the great variety of Odonata found in America can be mentioned here by name. The largest and most beautiful damselflies, also the most primitive, are the BLACKWINGS (*Calopteryx* spp.; see Color plates, pp. 83 and 89). Poor flyers, they are always found near the places where they lived as nymphs: flowing waters rich in oxygen. The nymphs attach themselves among the tangled water plants so as not to be swept into still pools. The winged forms congregate in sleeping groups at night, although during the day each male occupies his own territory. If a male fails to find a partner in one territory, he soon chooses another. In this way, mating and egg deposition are limited to places where the species had developed successfully in the past. Among the other, much smaller damselflies, those of the family Lestidae may be recognized by the large marginal wingspot (stigma), which extends over two or three wing cells (the areas enclosed by the veins of the wing), and by the fact that most of the wing cells are five-cornered. Members of the genus *Sympecma*, which also belong to this family, spend the winter as imagos and thus are the only damselflies to be seen in the springtime. Another damselfly of the same family, *Lestes rectangularis* lays eggs in the bark of trees which stand by the water. The prenaiads that emerge either fall into the water or try to make their way to it from the dry shore with jerky movements. The BROAD-WINGED DAMSELFLIES (family Calopterygidae), include animals of remarkably variable coloration, which may be identified by the usually rectangular wing cells and the small stigma, often limited to one wing cell.

Among the dragonflies, those of the family Aeschnidae are the largest and most beautiful. The genera *Epiaeschna* and *Aeschna* (see Color plates, pp. 84 and 91), are called the DARNERS because they are thought to sew children's mouths closed! The BIG GREEN DARNER (*Anax junius*), an American species found throughout North America from Alaska to the Greater Antilles and on Hawaii and the eastern coast of Asia. It flies year-round in the south, and is even swifter and more beautiful than the large dragonflies of the woods. Its wings are hyaline, often tinged with amber; emerald-green jewels are on its brow, and its abdomen seems clothed in a robe of azure silk bordered in black. The family of the CLUBTAIL DRAGONFLIES (Gomphidae) is recognizable by the eyes, which do not join at the midline.

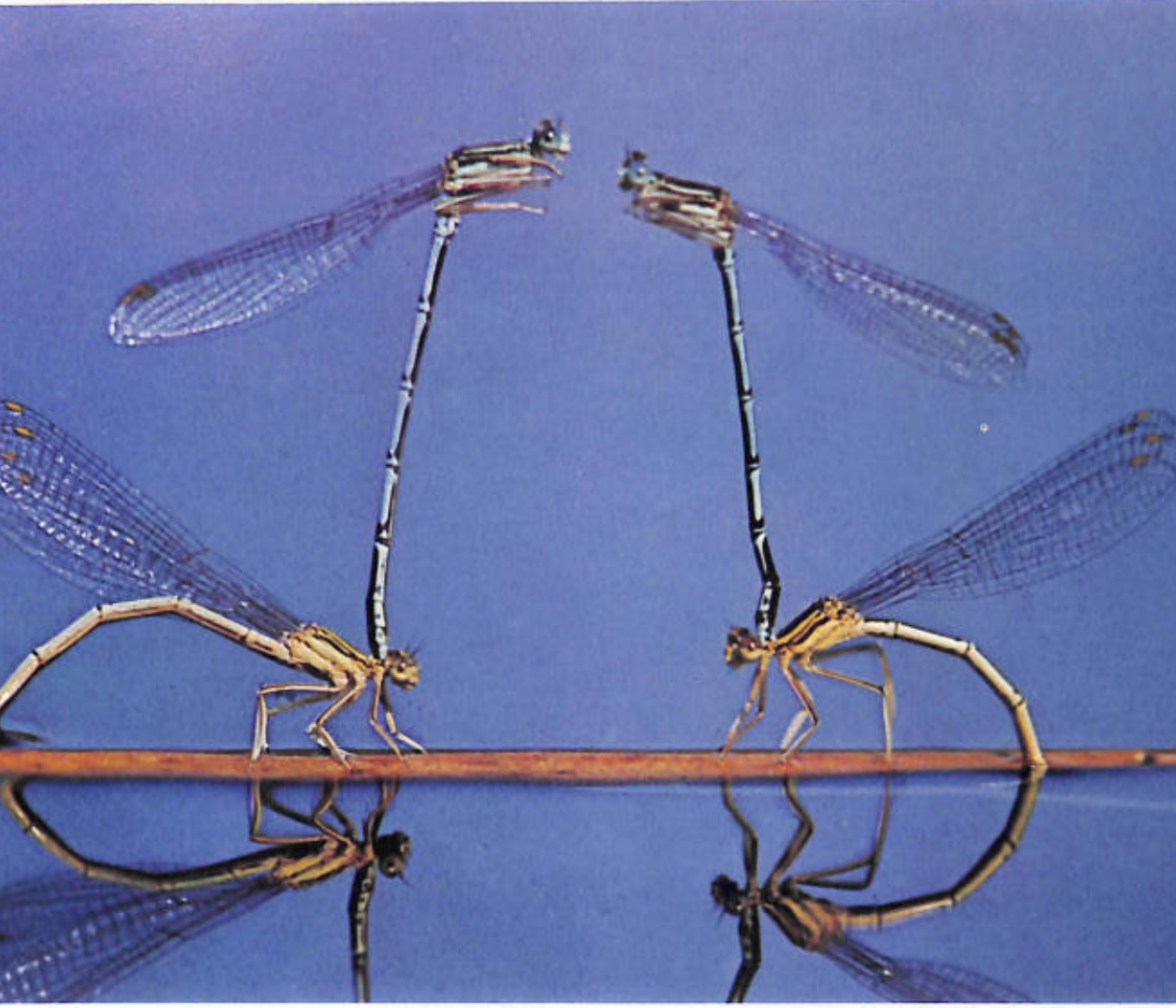








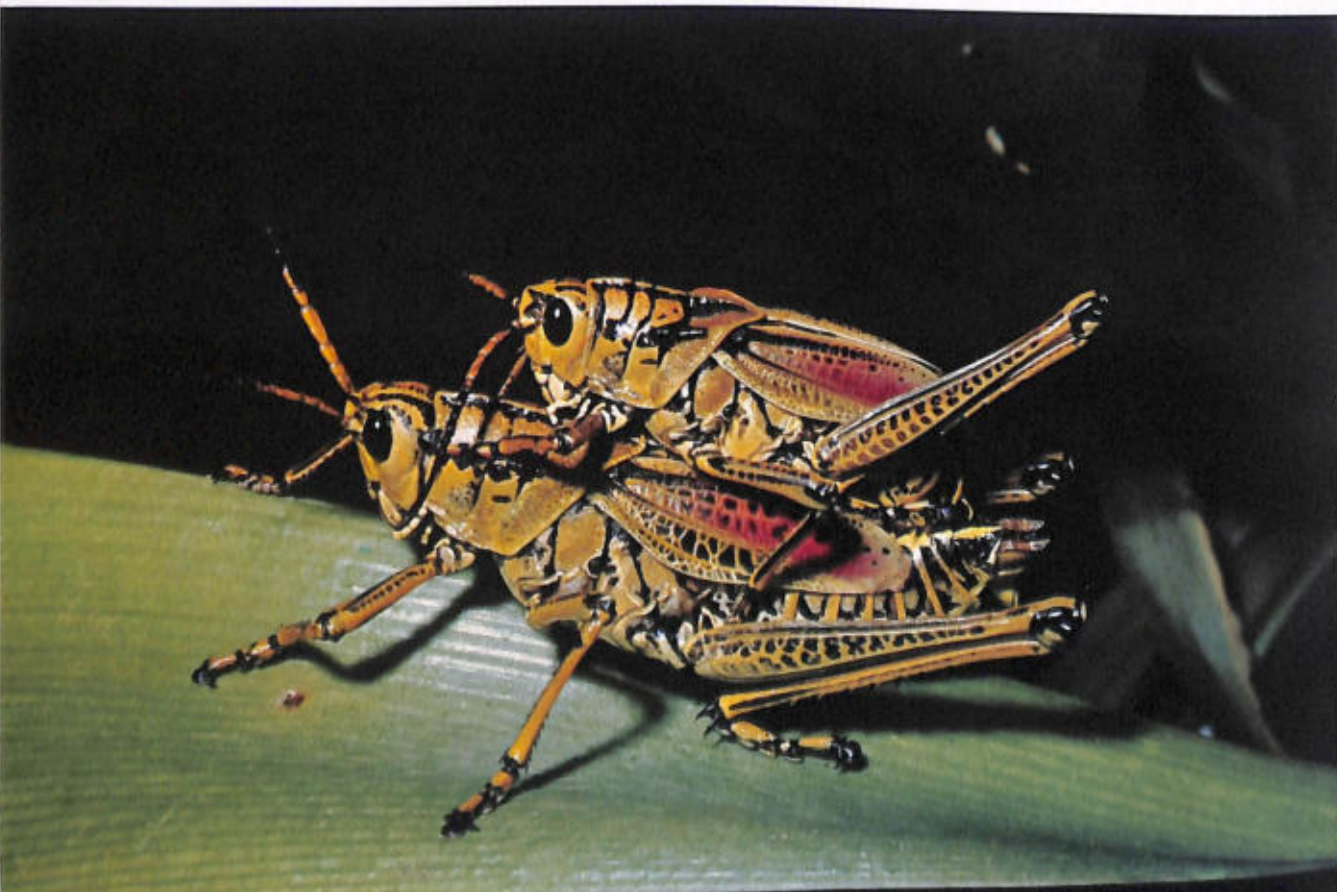












4 Stoneflies

Order: Plecoptera, by P. Rietschel

The STONEFLIES (Plecoptera; see Color plate, p. 74) are delicate insects with a wide range of sizes (L ranges from 4 to 30 mm). The body is without hairs, of a dusky color, and occasionally patterned. The almost identical forewings and hindwings are laid horizontally, one above the other, when at rest. The abdomen bears two long caudal appendages. The aquatic naiads are similar to the adults but are wingless, only the more mature ones having short wing-sheaths. They have tracheal gills on various parts of the body but never on the sides of the abdomen (in contrast to the Mayfly naiads). They have existed since the Permian, and today there are about 1600 species, of which slightly more than 400 are found in the U.S.A. and Canada.

◁ Above: the grasshopper *Truxalis nasuta*. Below: Short wings do not always designate a nymph. Here two adults prove it by mating.

Although the stoneflies are quite common in the vicinity of the flowing streams where their naiads live, they are much more difficult to observe than the Mayflies. Like the Mayflies, they move the forewings and hindwings independently, and since the two pairs of wings are of almost the same size the flight is very awkward; accordingly, the animals tend not to fly. Thus the imagos usually remain hidden near the shore in the area of their metamorphosis; one can find them there in great numbers by sweeping through the bushes and the undersides of large leaves of shore plants with a net. Here the two sexes mate at all times of day. The males attempt to mate with females of other species as well, but they succeed only with those of their own. This is because the copulatory organs are differently formed from one species to another and only those of conspecific partners are compatible, like lock and key. Therefore, given the uniformity in general appearance of the different species, the external reproductive organs offer the entomologist the most reliable way of distinguishing them.

Filipalps and setipalps

The stoneflies may be divided into two suborders, according to structure and way of life. (1) The FILIPALPS (Filipalpia, from the Latin *filum*, "thread," and *palpus*, "feeler") possess threadlike palps of the same diameter from base to tip. (2) In the SETIPALPS (Setipalpia, from the Latin *seta*, "bristle"), on the other hand, the palps narrow toward the end like

bristles. In both groups the mouthparts of the imago are simplified, but the filipalps can still handle solid particles of food with their mandibles; one American species is even destructive because it eats the buds of fruit trees. The setipalps, however, can only drink during their brief existence as imagos. As naiads, the small to medium-sized filipalps are vegetarians; they usually require about a year for their development. The setipalps, which are of moderate to large size, are proficient hunters during the three years or so they spend as naiads. They feed primarily upon the aquatic naiads of other insects. The naiads of the setipalp genera (e.g., *Paraperla*, *Isoperla*, and *Neoperla* in particular), which can be up to 3 cm long, are among the most impressive insect naiads in North American waters. Of course, because of their mode of feeding, they can never occur there in such multitudes as the filipalp naiads, which feed upon algae.

The female stonefly lays her eggs in flight or while sitting near the water so that she can immerse the tip of the abdomen along with the balls of eggs which are stuck to it. The eggs of the NEMOURIDS (the filipalp family Nemouridae) are held together by a mass of sticky substance which spreads out instantly upon touching the water surface, taking the eggs with it so that they sink to the bottom over a wide area. The eggs of other filipalps are provided with a gelatinous case which attaches them to the substrate. On the other hand, the warty or scaly case of the setipalp eggs is hard, and at one side of it there is a mushroom-shaped anchor plate.

As with other insect naiads, the duration of the development of stonefly naiads is dependent upon ambient temperature: the higher the temperature, the more rapidly development proceeds. In contrast to all other insect naiads, though, those of the stoneflies living in mountain brooks begin development when the water temperature is only slightly above the freezing point. Therefore these naiads can grow even in winter, when all about them other life is dormant. Many of them are actually dependent on cold water. During the ice ages they colonized all of central North America, and with the onset of warmer periods they withdrew, some of them to both Canada and the Rocky Mountains and some to only one of these two colder regions; others remained isolated in the central U.S.A. but took refuge in cold springs. Here they live today, ice-age relicts which bear witness to past glacial periods.

Stoneflies are known to have lived as early as the late Permian. Since then they have survived almost unchanged for a quarter billion years; the fact that they are to be found even today in cold running water is due not least to their low null temperature for development. The vegetarian filipalp naiads play the same role in the aquatic economy as the Mayfly naiads, that of primary consumers, while the predatory naiads of the setipalps are secondary consumers. Both groups of stonefly naiads share a common fate with the naiads of the Mayflies; their numbers are visibly diminishing as the waters become increasingly polluted with dirt and poisons. This in turn affects the higher consumer levels, particularly the fish population.

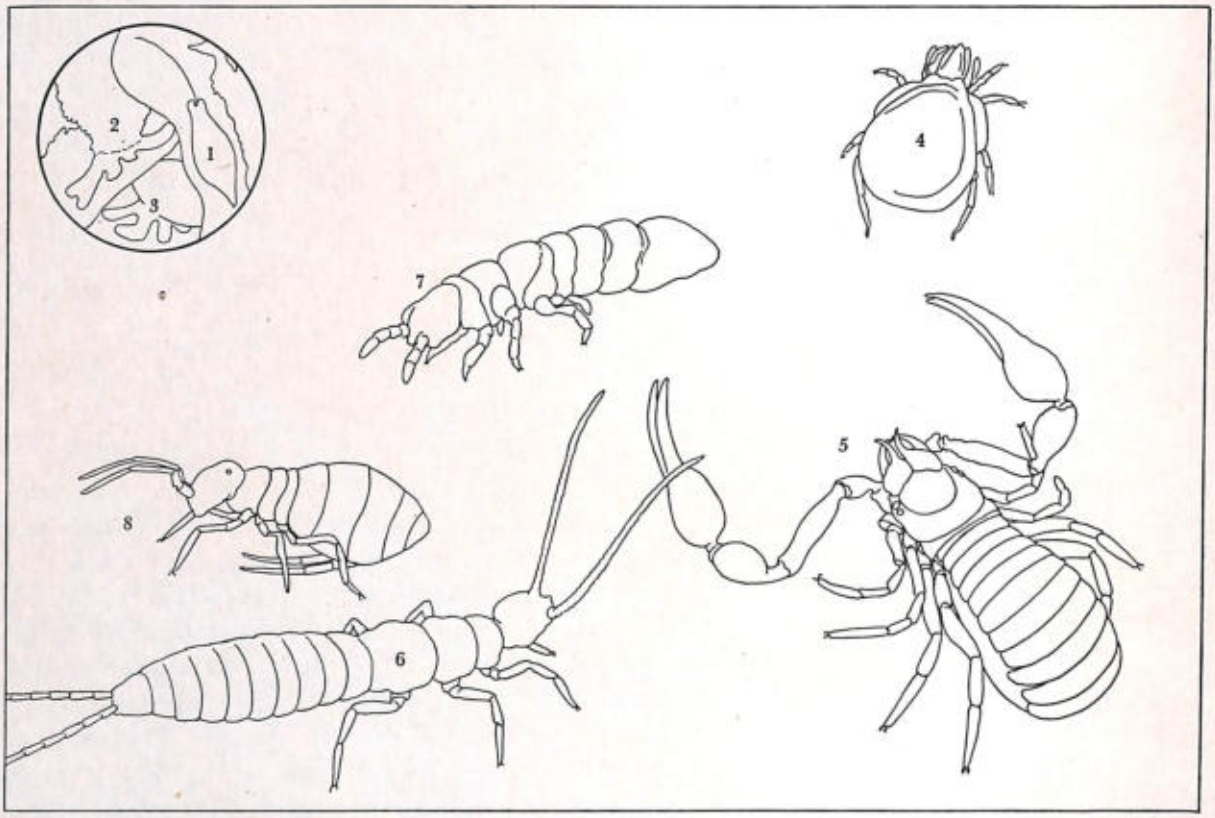
5 Grylloblattids, Grasshoppers, and Allies

Orders: Grylloblattodea, Orthoptera, and Phasmida, by P. Rietschel

Until the first quarter of this century, the grasshoppers, crickets, stick insects, and earwigs were placed together with the cockroaches and mantids in the order Orthoptera (straight-winged insects). But as knowledge of fossil insects increased it became evident that even in the Carboniferous these groups had separate origins. Therefore the insects which are derived from the primitive orthopterans (Protorthoptera) are placed in five separate orders. Those which are descended from the primitive cockroaches (Protelytroptera) are classified separately (order Dictyoptera, see Chapter 6). Of course, it must be admitted that these relationships are by no means completely understood for all the groups. Three closely related groups include the orders Grylloblattodea (three genera), Orthoptera (grasshoppers and the like), and Phasmida (stick insects, etc.) Dermaptera (earwigs, including the Diploglossata, a group of parasites with only one genus) form the fifth order. Altogether about 17,000 species have been described, of which the great majority belong to the Orthoptera.

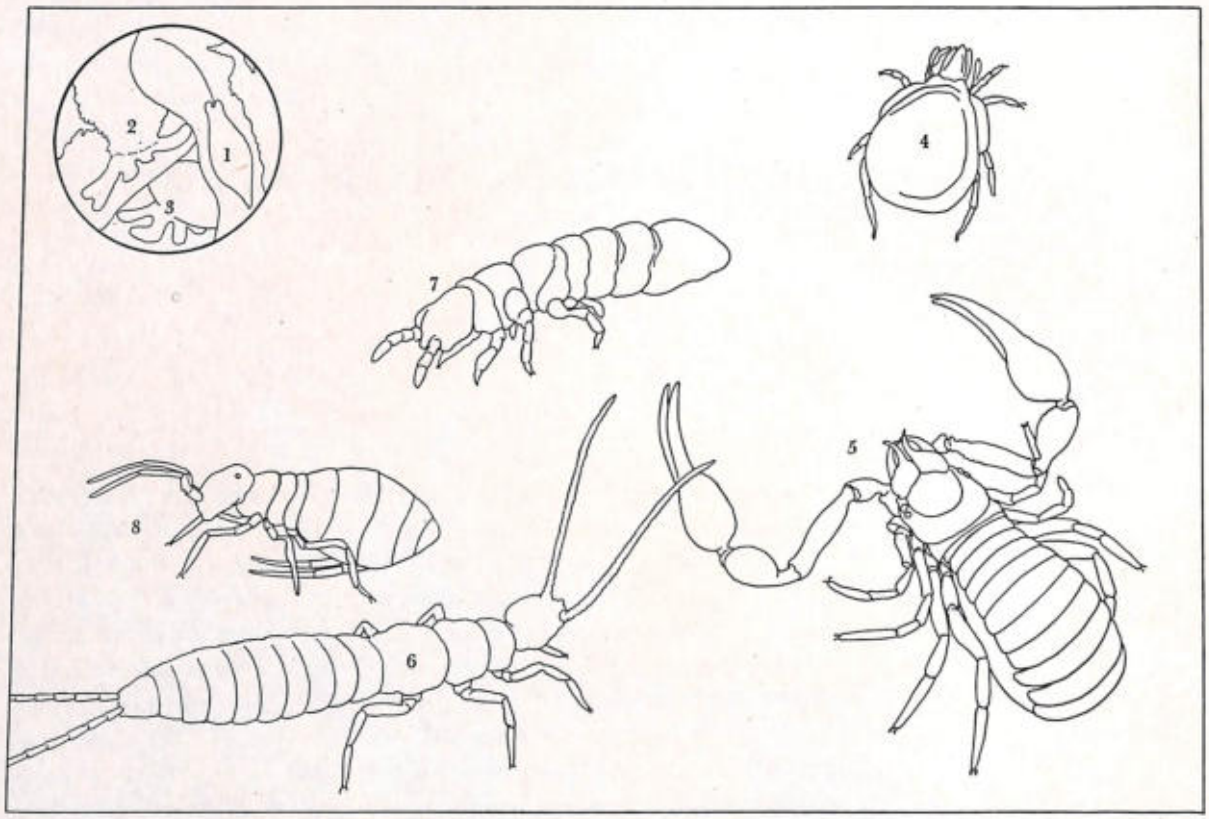
Order: Grylloblattodea

In 1914 the Canadian entomologist E. M. Walker described a remarkable wingless insect which lives in the Canadian Rocky Mountains, hidden under stones at altitudes between 450 and 2000 m. He called it *Grylloblatta campodeiformis*, implying a comparison with three other insects. (1) With the dipluran genus *Campodea* (see Chapter 2), it shares the attributes of blindness, lack of wings, and fragile skin; these are adaptations to life under stones, and give no indication of the evolutionary position of the genus *Grylloblatta*. (2) Like a cockroach genus *Blatta*, this insect has five-segmented legs and segmented caudal cerci; however, these properties are not characteristic of cockroaches alone, but rather are ancient elements of the basic insect structure. (3) The comparison with a cricket genus *Gryllus* was made on the basis of the six-part ovipositor, the construction of which resembles that of the Orthoptera. A separate order, Grylloblattodea, was recognized for these species. The paleontologist F. E. Zeuner considered the Grylloblattodea as surviving representatives of the Protorthoptera. The Canadian species of *Grylloblatta* is nocturnal, and



ANIMALS OF THE FOREST FLOOR IN CENTRAL EUROPE (II)

This double-page picture shows, much enlarged, a section of the Color plate on pp. 51/52. At the upper left a small section —the field of view of the binocular microscope— is still further enlarged. Single-celled organisms (see Vol. I): Flagellata (see Vol. I): 1, *Euglena viridis*, a flagellate which contains chlorophyll and therefore counts as a plant. Rhizopoda: two shelled amoebas, 2. *Difflugia pyriformis* and 3. *Arcella vulgaris*. Arachnids (see Vol. I): 4. the mite *Nothrus silvestris*, 5. the pseudo-scorpion *Neobisium simoni*. Insects: Diplura (see Chapter 2): 6. *Campodea staphylirus*, Springtails: 7. *Onychiurus* sp., 8. *Orchesella cincta*. The crumbly state of the ground is apparent. This is a prerequisite for fertility of the soil and is brought about primarily by the activity of soil-dwelling arthropods, which comminute the coarse elements of rotting plant remnants and pass them out in bits.



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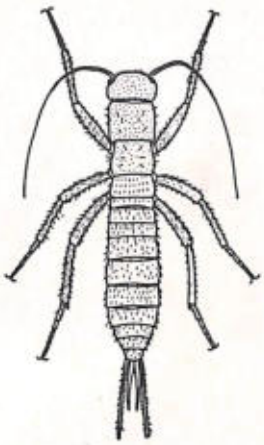


Fig. 5-1. *Grylloblatta campodeiformis*, L 30 mm.

feeds on both animals and plants. Its preferred temperature, about 4°C, is unusually low, and its embryological development proceeds at a correspondingly low rate. The nymph does not emerge from the egg for a year, and larval development, comprising eight molts, takes more than five years. As an imago, *Grylloblatta campodeiformis* lives for another two years, so that the animal enjoys altogether six to eight years of life, an exceptionally long time for an insect. Other members of the Grylloblattodea have been found in Japan and in the U.S.S.R.; three genera, comprising six species, are now known.

Order: Orthoptera

The order ORTHOPTERA includes the grasshoppers, crickets, and locusts. (The "seventeen-year locust" familiar to residents of the U.S.A. is actually a cicada; see Chapter 11.) Most Orthoptera are good jumpers. They perform this feat with the third pair of limbs, which have been modified into jumping legs; they extend the tibia away from the femur with a sudden movement. The extensor muscles involved are in the femur, which is therefore greatly thickened. Rotation occurs about the "knee" joint, which has a special protective device to prevent the tibia from being stretched too far. There are strong spurs on the free ends of the hind tibiae, which ensure that the legs do not slip on the substrate at the beginning of the leap. The hindlegs of those Orthoptera which burrow in the ground are also used to push the body forward, and those of the crickets are jumping legs as well. The two other pairs of limbs are usually walking legs, though the forelegs can also perform special tasks; in some predatory bush crickets the tibiae are covered with strong spurs which facilitate grasping and holding of prey. The forelegs of certain highly specialized burrowers such as the mole cricket have been transformed into powerful shovels. The forewings of the Orthoptera are usually sturdier than the hindwings; they are called tegmina (singular, tegmen) to distinguish them from the hindwings and the even more strongly modified elytra of beetles and dermapterans. In flight, the two wing pairs beat with a difference in phase. The greater part of the work is done by the hindwings, the surface of which is much enlarged by the posterior lobe or vannus. In many cases the wings are more or less—or even completely—regressed; even within one species some individuals may have short wings and others, long ones. Short-winged imagos look like nymphs (the larval forms) but may be distinguished by the fact that the forewings cover the hindwings in the adult, whereas in the nymph the hindwings lie over the forewings. The abdomen of female Orthoptera bears an ovipositor composed of six processes; this is the fundamental orthopteroid condition, found in the ancient Grylloblattodea. On the basis of both the form of this organ in the female and the length of the antennae—in the two sexes and in the nymphs—the Orthoptera are divided into two suborders: (1) the cave crickets, long-horned grasshoppers, and their relatives (Ensifera), with ovipositor shaped like a sword, and long antennae, often much longer than the body, with more than thirty segments; (2) the

short-horned grasshoppers, grouse locusts, and their relatives (Caelifera), with a strongly modified, compressed ovipositor which is used as a digging organ, and with short antennae having fewer than thirty segments. The Latin-derived name Ensifera means sword-bearer, and Caelifera means chisel-bearer. (See pp. 104ff.)

Suborder: Ensifera

The suborder Ensifera includes the primitive CAVE CRICKETS and CAMEL CRICKETS (subfamily Rhaphidophorinae). They have frail tegmina or lack wings entirely. Their roughly 1000 species occur throughout the world. In these, the chirping and auditory organs so characteristic of the other Ensifera are entirely absent. Since the Jurassic, to which the earliest traces of them have been attributed, they have become adapted to the most varied habitats. Wingless gryllacridoids hunt insects at night, and during the day they hide in rolls of leaves which they have shaped and spun together with silk from their labial glands. Species of the Indian *Schizodactylus* looks like a cricket, but the tips of its forewings spiral inward. It spends the day in the sand and hunts by night. The common cave cricket *Hadenoecus subterraneus* is also a hunter, although it is wingless and blind and spends its life in holes within limestone. Its relative, the camel cricket genus *Centhophilus*, may be encountered in greenhouses; their legs, antennae, and caudal cerci are longer than those of the cave cricket.

The subfamily PROPHALANGOPSINAE also can be traced back to the Jurassic. Of the ten families in existence at that time only one, with two genera and few species, has survived to the present. These Orthoptera possessed, and still possess, chirping organs on the tegmina, but (in contrast to the more highly evolved forms) they are the same on the two sides; moreover, the tympanate areas on the tegmina are not framed by veins.

Family: Gryllidae

Another group of Ensifera known to have existed since the end of the Jurassic is the CRICKETS (family Gryllidae). Here the chirping organs have reached the peak of perfection. They have moved closer to the wing joint —that is, to a position where a greater force is generated. Furthermore, the left tegmen develops somewhat differently than the right. This asymmetry is associated with the fact that in these insects the left tegmen always rests on top of the right tegmen. The first anal vein of the left (upper) tegmen bears on the underside a row of pegs, so that it serves as a stridulatory file, while the axillary vein, near the posterior margin of the right (lower) tegmen is bent upward to form a stridulatory ridge or scraper. The chirping noise is produced when the file is stroked over the scraper. It is amplified by an approximately circular wing membrane stretched like a drumhead between the second cubital vein and a branch of the first. This tympanate area is particularly well developed on the right (lower) tegmen. A resonating cavity between the wings and the back can be enlarged during chirping by depression of the abdomen. Usually only the males chirp, but in some species the females also do so occasionally.



Fig. 5-2. Stridulatory organ of a cricket (*Tettigonia viridissima*). Forewing drawn as though transparent, so that the stridulatory veins on the underside (1, 1′) are visible. 2, Left tegmen; 2′, Tympanate area on the right tegmen.

Chirping primarily helps the sexes to find one another; therefore the female must be able to hear it. The auditory organs of the crickets are located on the anterior tibiae, near the knee. Here the cuticle is thin, forming a tympanic membrane beneath which are air-filled enlargements of the tracheae; thus the membrane can be set into oscillation by sound waves. In primitive forms the tympanic membranes are entirely free, but usually the edges have folded over to cover the surface, leaving only a slit open. The oscillations of the tympanum stimulate an array of receptor cells, and this excitation is carried by the two auditory nerves. H. Autrum has shown that the crickets can perceive tones of over 90,000 cycles per second with these organs, exceeding our upper auditory threshold by more than two octaves. In fact, these receptors are most sensitive in the ultrasonic region. In correspondence with this auditory range, the stridulatory song includes frequencies of from 6000 to 100,000 cycles per second. But more than the simple ability to hear is required in order that the female locate the male; the female must also be able to determine the direction of the male's chirps. We have two ears to facilitate directional hearing; a sound coming from the side arrives at one ear sooner than at the other, and this time difference helps us to determine the direction of the sound source. The cricket cannot use this method, since its auditory organs, on two movable forelegs, are not only very close together but also continually changing in their separation. In fact, H. Autrum demonstrated that the crickets need only the organ on one leg to tell direction, since each organ has a directional characteristic, as does a directional microphone. The activity in the auditory neurons in response to sound is least when the sound impinges upon the side of the tibia which is forward during walking. Thus if the female simply orients herself so that the response to sound is minimized, she must be aimed toward the source of the sound. The males, too, have auditory organs, with which they perceive the songs of their rivals; in some species the males perform a regular antiphonal chorus.

Just as the male crickets are characterized by the tympanate areas on the tegmina, so can the females be identified by the large, laterally compressed ovipositor stylets with which they bury their eggs in plant tissue or (more rarely) in the ground. This organ may be so small that it barely extends beyond the end of the abdomen, but in other species it may be twice as long as the body. It is either straight or bent in a variety of ways. On casual observation it appears to be a single structure, but in fact it is composed of three pairs of body processes—the ventral, dorsal, and inner valves. These are joined to form a unit by the interlocking of single ridges on the dorsal and inner valves of each side with two grooves in the ventral valve on the same side. But there is no such connection between the two sides. The external copulatory organs of the males are small and complicated in structure. During copulation the sperm, enclosed in a case (the spermatophore), is attached to the outside of the female genital aperture. There is no penis as such.

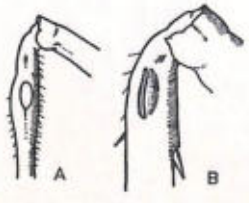


Fig. 5-3. Auditory organs of the Ensifera: A, open type (oak cricket, *Meconema* sp.); B, enclosed (wart biter, *Decticus* sp.).

The crickets have a mixed diet, some preferring vegetable food, and others, animal food. Although one may find them wandering about during the day, they are primarily nocturnal animals, and their song is associated in most people's minds with warm summer nights. Most of the 4000 or so species are tropical, but in late summer and early autumn one can find over forty species and species complexes, distributed among seven subfamilies, in North America. (See pp. 104 ff.)

Family: Tettigoniidae

The family of the KATYDIDS and LONG-HORNED GRASSHOPPERS (Tettigoniidae) is a large group of several subfamilies. One, Ephippigerinae, *Ephippiger vitium* (see Color plate, p. 115), however, is still to be found in isolated groups in the vineyard regions of southwestern Germany, a survivor from the warm period which followed the Ice Age. Here, on the southern slopes of the vineyards and the grasslands, the sharp metallic two-beat call of the males may be heard morning and evening. Another species, *Ephippiger ephippiger*, is distributed in eastern Europe and as far west as southeastern Austria. No species of this group occur in North America. These katydids are sometimes called saddle crickets because of the appearance of the pronotum, with its upward-curving posterior edge; the wings are regressed except for the song apparatus, which is present in and used by both sexes. Their food consists of the leaves of oak trees, grapevines, and other plants, as well as insects. The animals jump only short distances and thus can easily be caught in the hand. Then a curious behavior may sometimes be seen; as a means of defense, the katydids cause blood to flow out through the joint membranes of the thorax. A related species from northern Africa, *Eugaster guyoni*, is the real master of this tactic of reflex bleeding. This striking animal, black with brilliant red spots, squirts well-aimed streams of blood from the coxal joints at an attacker.

Other subfamilies

The PHANEROPTERINS (subfamily Phaneropterinae) include vegetarian, tree-dwelling crickets which are sometimes wingless and have very long antennae. They are green, brownish, or sometimes pinkish. Thirty-five or more representatives of this subfamily occur in the U.S.A., all with well-developed wings. They are among the most adept flyers of all the bush crickets. As in the other members of this family, the tympanic membranes on the anterior tibiae are entirely uncovered. Some common species include the green or sometimes pink ROUND-WINGED KATYDID (*Amblycorypha rotundifolia*), the destructive BROAD-WINGED KATYDID (*Microcentrum rhombifolium*), and the FORK-TAILED BUSH KATYDID (*Scudderia furcata*). The genus *Insara* has several uncommon, but striking, spotted species in the southwestern North American desert region. The southeastern region of the U.S.A. has a related genus, *Inscudderia*, with three interesting narrow-winged species associated with cypress and other vegetation. Occasional outbreaks of these strict vegetarians cause considerable damage to peas and beans, and potatoes and other root crops.

The tympanic membranes of the MECONEMATINS (subfamily Mecone-

matinae) are also uncovered. These crickets, which hunt insects in trees at night, are represented only in the Old World. None occur in North America. The OAK BUSH CRICKET (*Meconema thalassinum*) has wings which are as long as its body, but they bear no stridulatory organs. Nevertheless, the cricket is not mute; it beats on the substrate with one hind leg, oscillating the abdomen at the same time. The female lays her eggs in fissures of the tree bark or in the dried-up galls of the oak-gall wasp *Biorhiza pallida*. During egg-laying the females, which ordinarily live high in the crowns of the trees, are frequently found lower down on the trunk.

The CONE-HEADS (subfamily Copiphorinae) are characterized by the peculiar shape of the head, which is prolonged at the front into a cone or knob. The species in this family have a tympanic membrane which is covered except for a narrow slit. They inhabit moist regions. The RAPIER MEADOW KATYDID (*Conocephalus strictus*) is found throughout eastern North America, along with the SLENDER MEADOW KATYDID (*Conocephalus fasciatus*).

Subfamily: Tettigoninae

The PINE-TREE KATYDIDS (subfamily Tettigoninae) include the BIG GREEN PINE-TREE KATYDID (*Hubbellia marginifera*), which occurs in the southeastern U.S.A. The GREAT GREEN BUSH-CRICKET (*Tettigonia viridissima*; see Color plate, p. 115) is a similar European species. The WART BITER (*Decticus verrucivorus*; see Color plate, p. 115) is also a European species. The beautiful green color of these animals like that of many other grasshoppers, stick insects, the praying mantis, lepidopteran caterpillars, and other insects, does not come from the chlorophyll of ingested plants, but is a pigment formed by the insect itself. It is produced by the animals even when one eliminates chlorophyll from the diet. The tegmina of the great green bush-cricket are so long that they extend far beyond the abdomen. In North America, the GREEN CHAPARRAL DECTICID (*Cyrtophyllicus chlorum*) is similar to the genus *Tettigonia*, and is often found in the mountains of California. It is a large, predaceous species, with wings shorter than its abdomen. The green tegmina of the wart biter, covered with dark square spots, only just reach the tip of the abdomen. Unlike their relatives, these insects lay their eggs in the loose earth. The wart biter usually sings on the ground, while the other tettigonids produce their nightly song from the tops of bushes and trees. When taken in the hand, these large crickets can bite quite sharply, at the same time vomiting out brown stomach juices. A popular superstition has it that the bite and juice of the wart biter can remove warts from the skin. The insect was used for this purpose more than 200 years ago, when the Swedish natural scientist Linnaeus gave the animal its name. According to K. Harz, an expert in the Orthoptera, this natural therapy was being used with success in Silesia as recently as the end of the 1940's.



Fig. 5-4. Ovipositor of a cricket, cross section: 1. Dorsal valve, 2. Inner valve, 3. Ventral valve. 1 and 2 are joined to 3 by a tongue-and-groove arrangement.

In the subfamily Decticinae, which includes the wart biter, regression of the wings is common. The tegmina of female of *Dichopetala brevihastata* are merely scales, nearly covered by the pronotum, while in the

males they have disappeared except for the stridulatory organ. In Europe the inconspicuously colored *Pholidoptera griseoaptera* sings in late autumn, even after the first night frosts. The males occasionally sing antiphonally, particularly those of the wingless species *Pholidoptera aptera*—large, dark animals with black lobes at the sides of the pronotum bordered at the posterior edge by yellow. The contrasting coloration and the impressive size of this species make it one of the most striking insects of the Alps; it is quite common there in late summer, in bushes along the edges of woods. Among the biting crickets of the genus *Platycleis*, the TESSELLATED DECTICID (*P. tessellata*) has become established (about 1951) in California, where it is now common on Bermuda grass of roadside ditches in certain areas. It is an attractive-looking insect, but a feeble singer.

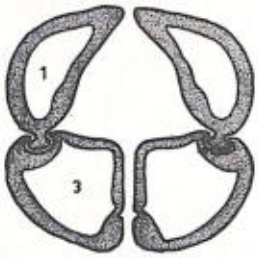


Fig. 5-5. Ovipositor of a gryllid, cross section: 1 and 3 as in the crickets (Fig. 5-4); the inner valve is regressed.

Finally, the subfamily Saginae should be mentioned; it is not represented in the New World, but *Saga serrata* is found in Austria, and *Saga pedo* in France. These slender grasshoppers, which may or may not be winged, have a row of spurs on the inner side of each of the forelegs and middle legs. They feed exclusively on other insects, rejecting any plant food; they use the spurs to grasp and hold their prey. The two species mentioned above lack wings. *Saga pedo* is represented in France by an entirely female subspecies, which reproduces parthenogenetically. Outside the Mediterranean region, Saginae occur in South Africa and Australia. This distribution, over a few widely separated (unconnected or disjunct) areas, can be taken as an indication of the great evolutionary age of the group.

Within the suborder Ensifera, the CRICKETS (family Gryllidae) diverged at an early stage in evolution. Examples have been dated as early as the end of the Triassic (about 200 million years ago), and crickets were common in the subsequent Liassic period. Like the Prophalangopsinae and in contrast to other tettigoniids, they have retained symmetry of the wings; the stridulatory apparatus extends over the whole length of each wing. Therefore the right tegmen may be laid over the left during chirping, or vice versa, but usually—again in contrast to the tettigoniids—the right is uppermost; in the mole crickets, though, the two arrangements are equally common. The displacement of the veins to form a tympanate area is not carried so far in these crickets as in the tettigoniids; still another difference is that the gryllids raise their tegmina vertically during chirping. The auditory organs of the gryllids are at the usual location on the tibiae of the forelegs; they are lacking in wingless (and hence mute) species. Although the stridulatory apparatus of gryllids represents a relatively low level of evolutionary development, the ovipositor has been secondarily simplified. It consists of only two pairs of valves, the inner pair having regressed. In the mole crickets, in fact, all three pairs of valves are almost completely regressed; for egg deposition in a subterranean nest, an ovipositor is not required.

The MOLE CRICKETS (subfamily Gryllotalpinae; see Color plate, p.

Subfamily: Gryllotalpinae

125) are large insects; all aspects of the unique body structure reflect their life as subterranean burrowers. The small conical head bears only moderately developed compound eyes and one pair of ocelli. The large pronotum almost completely surrounds the prothorax; the legs are modified into powerful digging tools. The broad, toothed tibiae can rotate on the femora in the horizontal plane but not in the vertical. The tympanic membranes of the auditory organs are almost entirely enclosed and thus do not become clogged with earth when the animal digs. The tibiae of the two other pairs of legs also are provided with strong spurs; the third pair, saltatorial in other crickets, here serves to lever the body forward. But a trace of the jumping behavior used for escape by its forebears remains: the mole cricket responds to attack by flinging the tibiae back —that is, by a correlate of the jumping movement which in the course of millions of years has become quite pointless! The European mole cricket *Gryllotalpa gryllotalpa* (see Color plate, p. 125), introduced into the eastern U.S.A., lives in soils which range from light sand to heavy clay; it usually comes to the surface only during the mating season, in May and June, when one can hear its call—similar to that of the bird called the goatsucker. Its tunnels run in all directions through the earth; near the nest, however, a helical tunnel opens at one end into the nest and at the other, some distance away at the surface of the ground. Where the ground is damp, secondary tunnels run down from the main passage to drain off the rain water. The nest itself is a cavity about as large as a hen's egg, with firmly compacted walls. Over it is a bare spot of earth; any plants which may grow there are killed when the roots are bitten through. Thus the ground above the nest is well warmed by the sun. The cavity usually lies 5 to 10 cm below the surface, but it can sometimes be as much as 1 m deep. In this nest, from May to November, the female lays 200–300 eggs in separate batches. One may therefore find eggs and young of different ages together. The eggs are cared for by licking, as are the young up to the second molt; this is a genuinely effective form of nursing, for without this care by the mother the eggs would become moldy or rot. Depending upon the temperature, the nymphs hatch from the eggs one and one half to four weeks after laying; in autumn it may take as much as five or six weeks. At first the young feed on humus and on the rootlets which hang into the nest hole and which are continually exposed by the mother as she rubs against the walls. The final (eighth) molt, which produces the imago, never occurs before the second year and may be delayed until the beginning of the third. Mole crickets can cause considerable damage by biting off roots, though they do this less by way of feeding than in clearing out their tunnels. As adults they live primarily on animal food, in particular grubs, wireworms, lepidopteran pupae, June beetles, and caterpillars which live in the earth—that is, primarily on pests; but they also eat earthworms, which are beneficial in that they make the soil friable. The crickets themselves are preyed upon by a number of birds, as well as by moles and

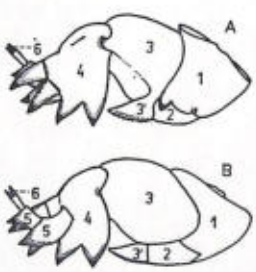


Fig. 5-6. Digging leg of a mole cricket (nymph, L 25 mm). A, right foreleg, inner side; B, left foreleg, outer side. 1. Coxa, 2. Trochanter, 3. Femur with hook 3′, 4. Tibia, 5. Tarsus, 6. Claws. Compare these components with the corresponding ones of the cylindrachetids (Fig. 5-9).

shrews. Frost and especially excessive dampness present a danger to mole crickets. In spite of their ungainliness they are quite nimble on the ground, and in the water are agile swimmers and divers. Mole crickets are known to have existed since the early Tertiary (lower Oligocene, about 35 million years ago); there are about forty species on the earth today.

Subfamilies: Gryllinae and Nemobiinae

Other crickets are familiar insects, with large, round heads, cylindrical bodies, and well-developed jumping legs with powerful femora and tibiae bearing two rows of strong spurs. They are either burrowers (subfamily Gryllinae) or ground-dwellers which do not dig (subfamily Nemobiinae). All of them feed on both animals and plants, and the mouthparts are as little specialized as those of the other Orthoptera; the mouthparts are of the "orthopteroid" type. But the Gryllinae have in addition a sponging proboscis, remarkably similar to that of the fly, for taking up fluids. Whereas the proboscis of the fly is formed from the labium, the cricket proboscis has arisen from the hypopharynx. When not in use it is drawn into the underside of the hypopharynx, an inconspicuous little sac. For use, it is everted by blood pressure, disclosing a delicately branched system of little channels which cover its surface and join to form a pair of larger channels; these lead to the oral cavity. These channels correspond, in both structure and function, to the "pseudotracheae" of the fly proboscis (see Chapter 19). The surprising parallelism between the two sponging proboscises is not due to inheritance from a common ancestor, for crickets and flies are quite far apart phylogenetically. The two organs have developed independently in evolution. This is a prime example of convergence, that is, the similarity between two originally different structures has evolved as a consequence of adaptation to similar requirements. The FIELD CRICKET *Gryllus assimilis* (a complex of species) has long been part of the fauna of the U.S.A., where it spends the winter as a nymph in a burrow it has dug about 30 cm underground. The HOUSE CRICKET (*Acheta domestica*; see Color plate, p. 126), on the other hand, is associated with human culture; its preferred temperature is 31–32°C, so that it is dependent on finding warm rooms such as furnace rooms, kitchens, and bakeries. In the open, the house cricket inhabits decaying vegetation in compost piles, which are warm from fermentation, sometimes finding adequate warmth there even in winter. Some householders may be annoyed by their monotonous nocturnal chirping, though the romantically inclined find it charming. The STRIPED GROUND CRICKET (*Allonemobius fasciatus* (subfamily Nemobiinae), has no sponging proboscis and its forewings are much shortened; the hindwings are entirely regressed. It lives primarily in the leaf litter of woods in eastern North America; there one can find the small nymphs in the spring, though the adults do not appear until August. In the autumn both adults and nymphs of all stages are to be found, but the adults and older nymphs seem to perish during the winter, since in spring only young nymphs are present. In England their development is said to take two years.

Other cricket subfamilies

The ANT-LOVING CRICKETS (subfamily Myrmecophilinae) are entirely wingless and have powerful jumping legs; they live as parasites in ant colonies, where they occasionally, as F. Silvestri observed, even eat the young of the ants. Only 2–3 mm long, they are the smallest orthopterans. There are four American species of *Myrmecophila*, associated with various species of ants, while the European species, *Myrmecophila acervorum*, is the tenant of species of small ants as a nymph and then, after the final molt, moves into the colony of a larger species. The behavior of these crickets is so perfectly adapted to that of the hosts that the latter apparently do not recognize them as strangers and even feed them, mouth to mouth. The American species are distributed along the coast from California to British Columbia, and in arid regions from Washington to Arizona and Mexico, Nebraska to Texas and New Mexico, and east to Maryland. Within their range of distribution, they are more common in the southern areas.

The tropical PHALANGOPSINS (subfamily Phalangopsinae) includes very large crickets with small heads and well-developed stridulatory organs. Most of the numerous species live in the forests, but there are also more than twenty species which have become cave dwellers.

The TREE CRICKETS (subfamily Oecanthinae) are widespread in all the warmer countries of the earth, although they comprise few species. In America there are several species, the SNOWY TREE CRICKET (*Oecanthus niveus* complex), found throughout most of the region from the U.S.A to Central America, occurs in trees and shrubs and feeds on aphids. The tegmina are entirely devoted to the production of song; during chirping they are held vertically, but they cannot be spread out and the animal cannot fly. In contrast to all the other tree crickets, the European FLOWER TREE CRICKET (*Oecanthus pellucens*) lives in flower beds; the calls which the males produce there can be heard over a great distance. The sound of these species forms an inseparable part of the warm summer nights in the country and is often used as a background for such scenes in films, to intensify the mood. After mating, the females lay their eggs in the stems of trees, shrubs, or flowers, and the young feed on aphids, or rarely on blossoms. A glandular pit on the dorsal thorax of the male plays an important role in mating. At the edge of this pit there are two paired tufts of hair, which produce a scent substance, and the glands themselves produce a proteinaceous secretion. The female, attracted by the song of the male, pushes herself up onto his back from behind and crouches over this organ; at the same time, the male depresses his abdomen and pushes himself back under the female. When they are properly aligned for copulation, with the male below the female, the male attaches the full spermatophore to the femal genital aperture; at this point the female begins to lick out the contents of the pit in her mate's back. After about a quarter hour she has finished, and the partners separate. Meanwhile, the sperm have left the spermatophore and entered the female's reproductive

tract. The female then eats the empty spermatophore, and is once again ready for impregnation. The dorsal pit, filled with a substance appetizing to the female, diverts her from eating the spermatophore too soon, before it has emptied.

Suborder: Caelifera

The SHORT-HORNED GRASSHOPPERS and their relatives (suborder Caelifera) are distinguished from the Ensifera not only by the different shape of the ovipositor and the shorter antennae, but also by many other characteristics which have developed differently in the course of evolution. The Caelifera do have stridulatory and auditory organs, but they are located elsewhere on the body. One can therefore infer that Caelifera and Ensifera had already diverged at a time in evolution when the stridulatory and auditory organs had not yet been developed. Unfortunately, there is no fossil evidence on this point; though the formations of the intermediate geological ages contain numerous examples of Ensifera, no Caelifera have been preserved. It is only in the recent geological ages, in the Eocene (about 50 million years ago), that they appeared, and then they were quite common. Today they inhabit every meadow in countless hordes; the plagues of locusts mentioned in the Bible, like those which still occur, are composed entirely of Caelifera.

The instruments which produce the songs of these grasshoppers differ; usually the file is a toothed ridge on the inner side of the jumping-leg femur, and the scraper is an angular radial vein on the tegmen. Chirps are produced when the file is rubbed across the scraper. In the band-winged grasshoppers, however, the scraper is on the femur and the file is on the tegmen, where it is formed by knobby thickenings of a longitudinal vein. An Italian species actually chirps by rubbing the tips of the mandibles together, and some other grasshoppers of various families rub the femur of the hindleg over ribbed surfaces on the abdomen. The auditory organs, to be found in the animals possessing stridulatory organs, are more uniformly constructed throughout this suborder. The tympanic membranes are on either side of the first abdominal segment, so that their orientation to one another is fixed. This makes possible directional hearing on the basis of the time difference between the arrival of the sound at the two organs. The Caelifera perceive sound waves at frequencies between 500 and 20,000 cycles per second; in contrast to the Ensifera, their hearing does not extend into the range of ultrasound. The receptor cells are arranged in several groups, and each group is most responsive to a different frequency of sound, so that these grasshoppers can even distinguish pitch. Accordingly, their songs are much more elaborate than the chirps of the Ensifera. There is a calling song, a courtship song performed before the female, a jumping sound which is made before the insect leaps, and a rivalry song produced in the presence of another male. But the many variations arise not so much from differences in pitch as from alterations in rhythm. These calls have been studied most intensively by Richard Alexander, Donald J. Borer, and Thomas Walker; a knowledge of them

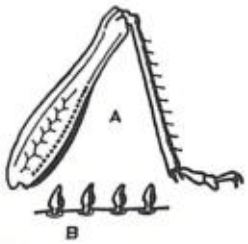


Fig. 5-7. Stridulatory organ of a grasshopper. The row of dots on the inner side of the femur is the toothed ridge. In B, part of it is shown much enlarged.



Fig. 5-8. Grasshopper laying eggs.

can be as helpful to one wishing to identify grasshoppers as the songs and calls of birds are to the bird watcher.

The diet of the Caelifera also differs from that of the Ensifera; they are all strict vegetarians, and many live primarily on grasses. Certain species prefer the foliage of vegetables, and during local outbreaks they can cause damage to potatoes, carrots, and turnips. Nor do the migratory locusts (the plague locusts of Biblical fame) limit their depredations to grain.

The different structure of the ovipositor in the two suborders necessitates different egg-laying procedures. The female Caelifera drill a deep hole in loose earth with the abdomen and in it they lay their eggs, enclosed in a packet (the oötheca) which holds the individual eggs together in a foamy mass. To make such a deep hole, the abdomen of the grasshopper must be markedly extended. This is done by pumping air into the capacious tracheal sacs. The joint membranes of the posterior abdominal segments, previously folded in, are stretched out. In this way the length of the section extending from the fifth segment to the last one, only 1 cm long in some species, can be quadrupled, simply by stretching the membranes joining these few segments!

The migratory locusts, by B. Grzimek

"Then the Lord said to Moses, 'Stretch out your hand over the land of Egypt for the locusts, that they may come upon the land of Egypt, and eat every plant in the land, all that the hail has left.' So Moses stretched forth his rod over the land of Egypt, and the Lord brought an east wind upon the land all the day and all that night; and when it was morning the east wind had brought the locusts. And the locusts came up over all the land of Egypt, and settled on the whole country of Egypt. . . . They ate all the plants in the land and all the fruit of the trees which the hail had left; not a green thing remained, neither tree nor plant of the field, through all the land of Egypt."

Locust swarms

Nowadays this Old Testament plague sounds like a legend, but it should not; plagues of this sort ravage wide expanses of the earth now as they did then. Several species of spur-throated grasshoppers cause locust plagues even today in Africa and other parts of the world. Their occasional increase to tremendous numbers and widespread migrations caused great damage to food crops in recent times. In 1873–1875 in Europe and 1874–1877 in the U.S.A. the outbreaks were extremely severe. In the U.S.A. they originated in Utah and migrated east to the Mississippi River and south to Texas, destroying crops as they progressed. It was estimated that 124 billion insects occurred in a single swarm. Even today their frozen bodies are found in glaciers in Montana. In Cyprus a single locust migration produced over 40,000 bushels of eggs. In Breslau and Gotha commemorative coins were struck to mark a locust migration. The houses in southern Russia had to be closed in 1879/80, in order to keep the masses of insects outside; the streets were impassable. Elsewhere it was necessary to filter the water, because canals and streams were full of dead locusts. Even the ovens were stuffed with masses of locusts, so that

no one could bake bread. The railroad trains in the Don steppes ceased to travel; the rails were so well lubricated by the bodies of insects that the wheels had no traction.

In 1955, a swarm of migratory locusts 250 km long and 20 km wide attacked southern Morocco. Again, in 1961/62, there was a plague there which could not be effectively combated because vehicles were immobilized—the roads were muddy after a long period of rain. As a result, within five days the locusts had caused damage amounting to more than a billion francs in an area of over 5000 square kilometers. In the entire valley of the Sous River more than one-fifth of the agricultural land was destroyed, and the remaining fourth-fifths received half as much damage. In the five days, the migratory locusts consumed 7000 t of oranges, the equivalent of 60,000 kg per hour. This is more than the yearly consumption of the entire country of France. To compensate for the damage, about five undisturbed harvest years would have been necessary, but before such recovery could occur new swarms had invaded Morocco. Various groups of locusts destroyed about 150 square kilometers of cultivated land. More than twenty-five airplanes were used in an attempt to control the invasion with insecticides; these modern control methods of course encountered disapproval from environmentalists, since they can harm useful insects, fish, amphibians, reptiles, and birds. But without them, and if the weather had not been favorable for their distribution, the great citrus plantations between the two ranges of the Atlas Mountains would have been demolished. In 1966 the trains in South Africa were delayed because the tracks were covered with locusts. Hundreds of automobiles delivered insecticides which were used to protect the farming regions of the Orange Free State, an effort which cost well over a million dollars.

Only nine out of 5000

There are over 5000 species of Caelifera on earth, but only nine of them undertake such mass migrations. In the Old World these are primarily *Schistocerca peregrina* (see Color plate, p. 116) and *Nomadacris septemfasciata*, both of which belong to the family Catantopidae, as well as *Locusta migratoria* and *Locustana pardalina*, of the family Acrididae. In South America the best-known migratory locust is the cantantopid *Schistocerca paranensis*. In the U.S.A. the principal species is *Melanoplus sanguinipes*. Most of the other hopping and chirping Caelifera live alone and avoid approaching one another too closely, except in the mating season. The migratory locusts, too, usually behave in this way. But different generations can be in either a solitary phase, in which they live alone like their relatives, or a migratory phase in which they congregate and start off together on long trips. Animals in the two phases differ not only in shape and coloration, but also differ extensively in behavior and in the metabolism of the body. This urge to travel overcomes the migratory locusts only occasionally, in quite specific generations, and only in certain districts which evidently are particularly favorable to its development. As a rule, the ravenous hordes come only from these regions. Once

this fact had been discovered, a great deal had been gained in the war against these insects.

Not until several weeks or months after the locusts have passed the last molt and acquired wings do they become sexually mature. Most species also change color at that time; for example, in some the females become straw-yellow and the males, lemon-yellow. During the solitary phase the migratory locusts, like other grasshoppers and crickets, find one another only by their chirping; the pitch and the pattern of chirping ensures that only locusts of the same species mate. As long as the male plays his song, the female strives to reach him, but as soon as he stops she wanders aimlessly about. In the migratory phase, however, the animals gather in such masses that the sexes have little need to search for each other.

After copulation the females lay their eggs in the ground. For this purpose they have four chitinous plates at the extreme end of the abdomen, like all Caelifera, and the abdomen can in addition be appreciably lengthened by stretching the intersegmental membranes. With the abdomen, they dig a hole in the sand and deposit in it 30–100 eggs; the hole is then closed up by a plug of foam, which is permeable to air. In the year 1890, during an outbreak of locusts in Algeria, 560 billion eggs and 1450 billion freshly hatched nymphs were destroyed—if one includes the eggs in the females that were killed, this amounts to no less than 2720 billion locusts. After one insemination a female buries ten such clutches of eggs. Areas of ground which harbor such enormous numbers of locusts-to-be are easily recognized by the white dots of foam.

Fifty to sixty days later, depending upon temperature and humidity, the ground is covered with thousands upon thousands of small insects, creeping forward like worms. They are about 8 mm long; the nymphs must free themselves from an enclosing membrane before they can move their legs properly. But soon they are marching away in gigantic masses, all in one direction, crossing hills, ditches, and—with enormous losses—even rivers. During this march on foot the nymphs eat everything they can find; they continue to grow and molt five times. By that time they have become more than 3 cm long; though they have stumps of wings, they cannot yet fly.

When they are ready to molt for the last time the nymphs, still eating continually, seek out a stable position on a twig and cease moving. The new "skin," the future chitinous armor, is wrinkled and folded beneath the old cuticle, which has become too tight. Blood and air gradually collect in the animal's back, and these cause the old covering to burst open longitudinally. Slowly, very slowly, the locust creeps out in its final form. But the wings are still rolled together, forming an arch on the back. Little by little they unfold and are extended by the pressure of the blood, which flows into the many vessels of the wing. At last the locust is ready, and it beats its wings. But three weeks or even several months must pass before it can reproduce.

Locusts as food

The first great Greek historian, Herodotus, who died about 424 B.C., related that the inhabitants of the desert gathered, dried, and ground locusts; then, according to Herodotus, they mixed the flour with milk and ate it. Alfred Edmund Brehm claimed that migratory locusts have a disgusting taste and are of little nutritive value. But even today, in the oases of the Sahara, one is offered dried dates along with crisp fried locusts. To eat them, one first breaks off the head, the wings, and the lower part of the femur. These are not at all unpalatable; they are fatty and nutritious, and the gut, stuffed with plant materials, doubtless contains many vitamins. John the Baptist, who wandered for forty days in the wilderness living on locusts and honey, was therefore by no means on an ascetic diet. The flour made from locusts is often the only food of the present desert tribe of the Tuaregs in their caravans. Its unpleasant smell disappears when one mixes it with milk. Recently, tinned roasted locusts from Japan have been available even in western shops. They are said to taste good, something like the roasted larvae of bees, and furthermore are of interest to the zoologist because a large proportion of them have been infected by parasites of the beetle family Stylopidae (the twisted-winged insects; see Chapter 12)—as entomologists say, they are stylopized.

According to the investigations of Franz Kollmannsperger, the migratory locusts in the southern plains of the Sahara need no drinking water. However, they must eat incessantly, for their digestive process is adapted to extract water chemically from dry vegetable materials. They consume all sorts of plant substances, however dry they may be. Their chitinous covering, in contrast to that of many beetles, is permeable to water and does not prevent evaporation. Hence these locusts cool themselves by sweating and can survive in considerable heat; they even land on ground with a surface temperature of 58°C. According to R. Chapman, when *Schistocerca peregrina* nymphs in the second stage of development are tested in an experimental temperature gradient in the laboratory, they tend to avoid temperatures below 32°C and above 43°C. All the migratory locust species he investigated preferred temperatures around 40°C.

Some regions—especially warm, humid areas with abundant plant growth—are regular incubators for locust swarms. This is true, for example, of the Rukwa Valley in southwestern Tanzania, which forms part of the Great Rift Valley. Migrations flying to South Africa have frequently originated here. For this reason, as early as 1950 a dozen European officials settled in this remote valley to find ways of controlling the locusts; houses, streets, bridges, and airstrips were built. It is of course most effective to combat the locusts with insecticides soon after they have emerged from the egg. The red migratory locust *Nomadacris septemfasciata*, according to Chapman's observations in Tanzania, never flies at air temperatures below 18°C and flies only sporadically below 22°C; the preferred flight temperature is 29°–35°C. A wind of over 3 m per second inhibits flying. In the flights observed, the animals rose no higher than

7 m; they flew against weak winds but with strong ones. Thus it can happen that within a single swarm locusts at the bottom of the group fly in one direction and those above, in another.

After the last molt, when they have acquired full wings, the animals first fly about in circles, returning to the place where they took off. Only when nearly the entire swarm has assembled do they fly away. They depart even if there is adequate food in the place they were born; hence lack of food can certainly not be the reason for the transition from the solitary phase to the migratory phase and the massive migration. Researchers have attempted for some time to discover what actually brings these normally uncompanionable locusts together and drives them to distant lands. The experiments of Faure, Husain, and Mathur indicate that the appearance of the migratory phase can be ascribed to the population density of the species concerned. The more frequently the locusts encounter one another, the more likely they are to be transformed from independent individuals to soldiers in an enormous army. These three investigators kept young nymphs of solitary locust species in containers under very crowded conditions, and here too they acquired the characteristics of the migratory phase. When the locusts are forced to live at such close quarters, a stress effect apparently results. Stress, as the term is used in modern medicine and biology, is the alarm reaction of a living being which appears when the body is damaged—whether by cold, heat, infection, poisoning, emotional excitement, or the too-frequent interaction with conspecifics. In vertebrates, it may be accompanied by increased production of substances by the adrenal cortex and of certain other hormones, and a decrease in activity of the lymph glands. Thus the body defends itself against the stimulus which brings about the stress; with the locust, the corresponding reaction is the transition from the solitary phase to the migratory phase.

But this transformation requires some time; solitary locusts cannot begin migration immediately. The solitary phase is first followed by a generation in which the number of molts is smaller (six rather than the usual seven); the difference between male and female is less conspicuous. The nymphs become darker, and finally these animals lay eggs from which the migratory insects hatch. Moreover, when the travelers of the migratory phase are reconverted into solitary locusts, a further transitional generation is interposed. Even the nymphs of the migratory phase congregate, whereas those of the solitary phase tend to move apart.

These migrations are evidently not without a goal. To be sure, the armies of locusts which have settled in Germany and England probably had lost their way. The locusts which fly over the Sahara, though, reproduce in Morocco from March until July; they then proceed southward and in the plains regions of the southern Sahara and in the vicinity of the Niger, from July to October, again lay eggs. In discovering that the migrations of these locust species are due to stress imposed by crowding,

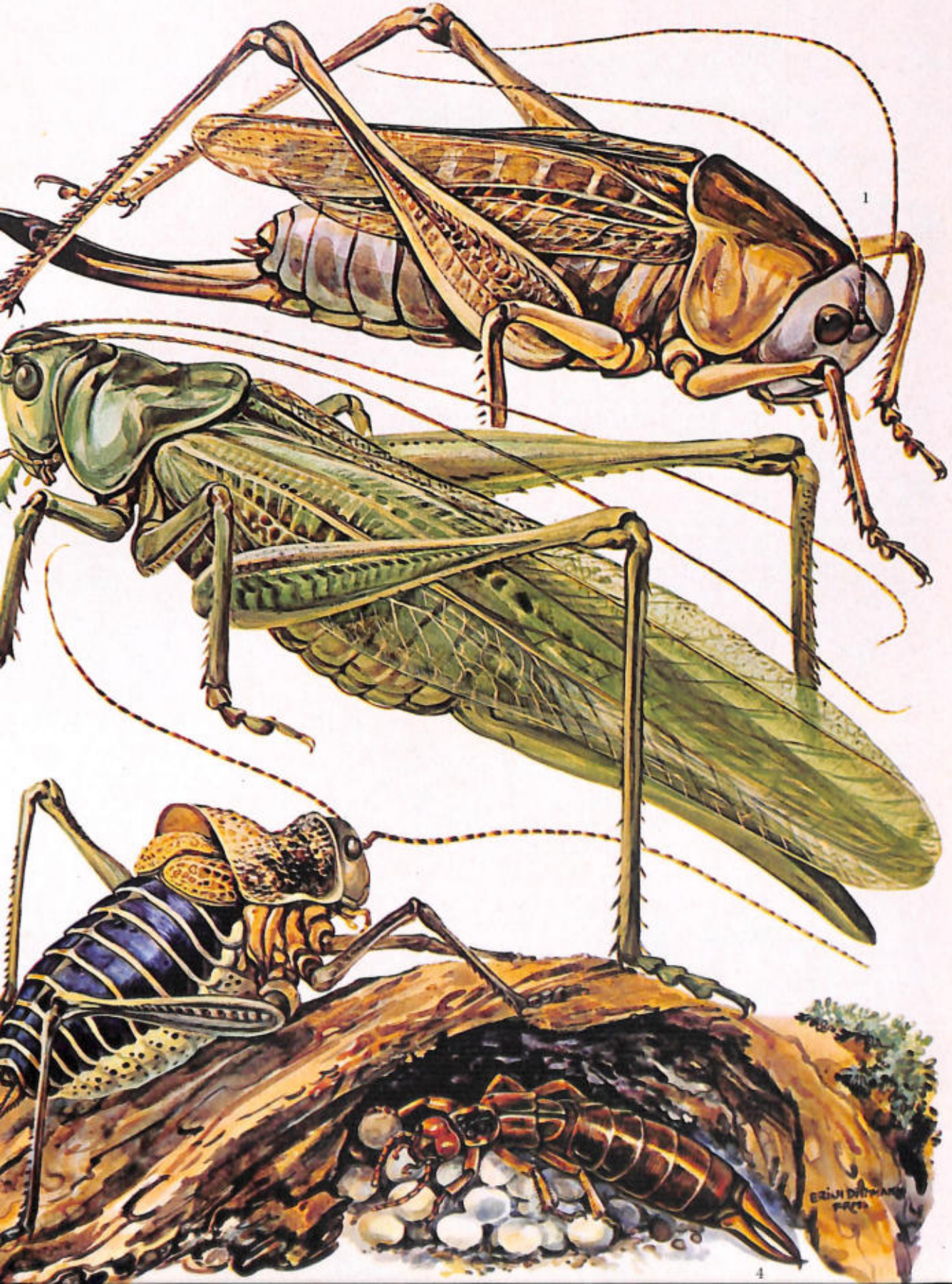
biologists have raised a question of great import for humanity. In view of the human population explosion, as a result of which we too can no longer escape continual encounters with our conspecifics, the lesson of the locusts transcends entomology and offers each of us something to think about.

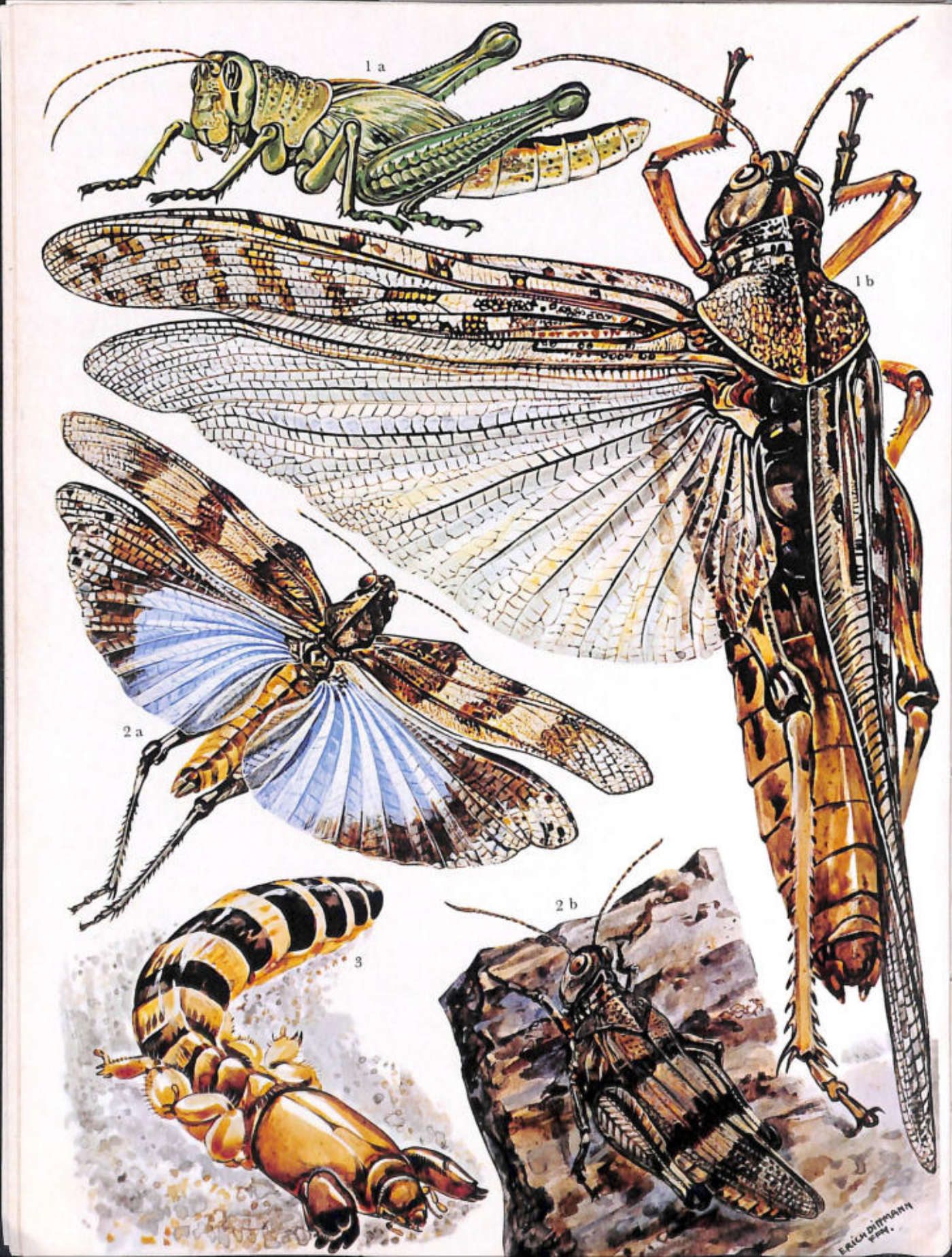
Family: Acrididae, by P. Rietschel

All of the migratory locust species are Caelifera, and some of them belong to the SHORT-HORNED GRASSHOPPERS (Acrididae). Apart from these —fortunately only few—migratory species, the family includes several thousand non-migratory species, more than any other family in the Orthoptera. Many species, divided into three subfamilies, are native to the U.S.A: the subfamily Oedipodinae (the band-winged grasshoppers), the Acridinae (slant-faced grasshoppers), and the Cyrtacanthacrinae (the spur-throated grasshoppers). The three subfamilies differ in the structure of their stridulatory organs, and the song of the band-winged grasshoppers is less varied; their repertoire includes neither the calling song nor the courtship song performed before the female.

Among the BAND-WINGED GRASSHOPPERS (Oedipodinae), there are many species with hindwings which display a lively coloration as they fly; these are blue in the American canyon-dwelling *Trimerotropis cyaneipennis* and the European desert-dwelling *Oedipoda caerulescens* (see Color plate, p. 116), and red in *Psophus stridulus*, *Bryodema tuberculata*, and *Oedipoda germanica*. One desert grasshopper from the Great Basin of the U.S.A., *Trimerotropis agrestis*, has yellow hindwings. All these colors are due to compounds of a single carotenoid with various proteins. The commonest of the American banded-winged grasshoppers, *Dissosteira carolina*, when startled flies for only a short distance and then suddenly seems to disappear. This phenomenon derives from three special characteristics: (1) The basic color of the animal is that of the ground in its habitat—whether gray, yellowish, brownish, or even black in burned-over areas. (2) Two or three dark stripes run across the body, over the tegmina, and, with no apparent discontinuity over the femora of the hindlegs; the effect of these is to divide the overall shape of the grasshopper into apparently unconnected parts. (3) In landing, the animal turns in a sharp arc so that it ends up sitting off to the side, away from the landing spot expected by an observer. The hindwings, so striking in flight, are completely covered when the grasshopper is at rest. The significance of the rattling or rasping noise produced by these grasshoppers is still unclear. The red-winged forms make the sound with the hindwings; they can rattle while sitting still and yet fly silently. Among the Oedipodinae are some of the most dangerous migratory locusts, *Locustana pardalina* and *Locusta migratoria*. The latter came in swarms to Germany, from the regions of the Danube where they reproduce, as late as the last century. But these regions were brought under cultivation and made unsuitable for locust reproduction; as a result, only rare finds of individuals of the species have been made in Germany in this century.

▷
Ensifera: 1. Wart biter (*Decticus verrucivorus*), 2. Great green bush cricket (*Tettigonia viridissima*), 3. Steppe katydid (*Ephippiger vitium*). Dermaptera: 4. Common earwig (*Forficula auricularia*) with eggs.


1
4


1 a
1 b
2 a
2 b
3
ERICH DITTMANN

The subfamily Acridinae is represented in North America by many grasshoppers of the genera *Achurum*, *Chorthippus*, *Leptysma*, *Stenacris*, and others; in summer these insects, which may be distinguished only after careful study with a hand lens, can be found in the meadows in great numbers. In some genera the antennae are thickened like clubs; the commonest of these is the short-horned grasshopper *Metaleptea brevicornis*. In arid regions one may encounter the gray creosote bush grasshopper *Clematodes larreae*, an uncommon species with excellent camouflage. Another species, *Mermirea maculipennis*, from central North America, is conspicuous by its coloration—a delicate green with contrasting stripes, yellowish-brownish beneath, with reddish hind legs. Another member of this group that is easy to recognize is the Mediterranean "long-nosed" grasshopper *Truxalis nasuta* (see Color plate, p. 92). It is found as far north as Lake Neusiedler, in the southern alpine valleys, and in the middle of the valley of the Rhone. This grasshopper is brown or green, with very long jumping legs and a sharply conical head bearing antennae which are sharply pointed at the tip. Finally this subfamily also includes a major pest, the Moroccan migratory locust, *Stauronotus maroccanus*, which is by no means restricted to Morocco. It is distributed throughout the Mediterranean countries; in the lowlands of the Danube it was the successor of the migratory locust *Locusta migratoria* around 1888, when the breeding grounds of that species disappeared under cultivation.

The other Orthoptera, by P. Rietschel

The distinguishing characteristic of the SPUR-THROATED GRASSHOPPERS (subfamily Cyrtacanthacridinae) is a conical or cylindrical hump on the underside of the prothorax; in other respects there is great variation among the species. We shall leave aside the question of whether this single conspicuous characteristic is an indication of a close relationship. One species found in Europe is *Calliptamus italicus*, whose hindwings are pink near the root and transparent near the tip. This species greatly prefers warmth and dryness; when there are several hot, dry years in succession its numbers multiply enormously and it enters a migratory phase in which the insects are larger, have longer wings, and can do appreciable damage. The sounds of this species are produced by rubbing the mandibles together. The species *Podisma pedestris* and the pretty *Miramella alpina*, covered all over with fine upright hairs, commonly occur in the mountains but are rare elsewhere. The gigantic (L. 6.5 cm) reddish-brown to gray-brown *Anacridium aegyptium*, which lives in Mediterranean regions, is often carried to other countries along with shipments of fruit and vegetables. It is not a migratory locust. But most of the migratory locusts do belong to the Cyrtacanthacridinae: the DESERT LOCUST (*Schistocerca peregrina* = *Schistocerca gregaria*; see Color plate, p. 116) the Central American *Schistocerca urichi*, the South American *Schistocerca paranensis*, the North American ROCKY MOUNTAIN LOCUST (*Melanoplus spretus*), and the African RED MIGRATORY LOCUST (*Nomadacris septemfasciata*).

This subfamily contains the most injurious American grasshoppers.

◁ Caelifera: 1. Desert locust (*Schistocerca peregrina*); a, nymph of the solitary phase; b, imago of of the migratory phase; 2. Blue-winged wasteland grasshopper (*Oedipoda caerulescens*); a, flying; b, sitting with the outline of the body disrupted by the dark cross stripes on wings and femora; 3. *Cylindracheta* sp.

The LUBBER GRASSHOPPER (*Romalea microptera*) is a very large, black species with brilliant red markings. This species is used extensively in the classroom for dissections. Species of the genus *Schistocerca* are widespread in North America. The largest genus, *Melanoplus*, with over 100 species, occurs throughout North America. Many species have showy hind wings, and several are of considerable importance because of the damage they do to crops.

Family: Tetrigidae

The PYGMY GRASSHOPPERS or GROUSE LOCUSTS (family Tetrigidae) are small grasshoppers lacking stridulatory and auditory organs. The tegmina are regressed, but the hindwings are normal. The adhesive pad found between the tarsal claws in all other Caelifera is absent in the grouse locusts. The most striking characteristic is the pronotum, drawn out into a long sharp point. This horn can extend far beyond the hind end of animal, and in many tropical species displays extravagant modifications of shape. There are more than 700 species of grouse locusts; most of them inhabit the tropics, although about twenty-five species live in the near-arctic region (see Vol. VII, Chapter 1). Most species are active throughout the year. In the north they may emerge on warm winter days for a brief period of activity. One species, *Tetrix subulata* is widely distributed in Europe and northern North America, where it inhabits moist meadows and lake shores.

Other families

The PROSCOPIDS (family Proscopiidae) are restricted to South America; these are extremely slender animals with sticklike bodies which can easily be mistaken for stick insects. They are nearly or entirely wingless, mute, and deaf. Their hindlegs have long, thin femora, and are only rarely used for jumping.

The PYGMY MOLE CRICKETS (family *Tridactylidae*) display in many respects a relationship to the pygmy grasshoppers, but all of the approximately fifty species are soil burrowers (hence the English name). The scientific family name (meaning three-fingered) comes from the peculiar structure of the hindlegs: the unsegmented, extensively regressed tarsus is joined to the end of the tibia between two enlarged spurs, so that the tibia appears to end in three fingers. Four species inhabit the Mediterranean countries, and two species occur in North America.

Closely related to these, but even better adapted to the burrowing way of life, are the CYLINDRACHETIDS (family Cylindrachetidae; see Color plate, p. 116). The head bears short antennae, and the lateral eyes are no longer compound but have regressed to form simple eyes. The large pronotum is cylindrical, as are the remainder of the thorax and the long abdomen which is continuous with it. The forelegs and, to a lesser extent, the middle and hindlegs, have been modified into digging tools. Because of these characteristics, the cylindrachetids were once considered to be mole crickets. But the Ensifera and Caelifera have acquired this adaptation for burrowing independently; the similarity is due not to relationship but to convergent adaptation. In the terminology of A. Remane,

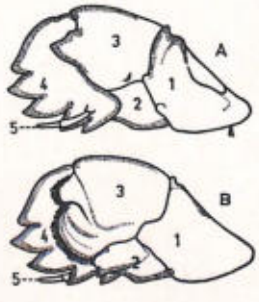


Fig. 5-9. Digging leg of a cylindrachetid (nymph, L 42 mm): A, right foreleg, inner side; B, left foreleg, outer side. 1. Coxa, 2. Trochanter, 3. Femur, 4. Tibia, 5. Tarsus. Compare these elements with the corresponding ones of the mole cricket (Fig. 5-6).

animals which under similar living conditions acquire a similar shape constitute a life-form type. Thus the mole crickets, the pygmy mole crickets, and the cylindrachetids, as well as the marsupial moles and the two eutherian mole families (see Vol. X), belong to the same life-form type. The few species of cylindrachetids inhabit Australia, New Guinea, and Patagonia.

6 The Walkingsticks, Mantids, and Cockroaches

The crickets, grasshoppers, and locusts discussed in Chapter 5 now form a separate order, the Orthoptera. Older classifications also placed the walkingsticks, mantids, and cockroaches in that order. Recent paleontological studies reveal, however, that five distinct groups arose in the Carboniferous. The interrelationships of these groups were briefly discussed in Chapter 5. Of the subjects of this chapter, the STICK INSECTS and LEAF INSECTS are included in the order Phasmida. The remainder of the chapter concerns the MANTIDS and COCKROACHES (order Dictyoptera).

Order: Phasmida

The scientific name Phasmida refers to their weird appearance (the Greek φάσμα means apparition). One can appreciate the significance of this appearance if one observes the animals in their natural surroundings, for it is obviously an excellent form of camouflage, imitating the twigs and leaves. This sort of imitation of parts of plants is called phytomimesis. The significance of the English names for these insects is obvious; the Germans call them by similar names: stick insects, wandering leaves, or wandering branches (see Color plate, p. 125). Phasmids should not be called "grasshoppers," since they cannot jump; rather, they stroll slowly along, and even these movements are largely restricted to the nighttime. During the day they remain motionless in one spot. One can even handle them without their making any attempt at flight or defense, and a light pressure on the underside of the thorax induces a condition of rigidity. If they were to move during the day, these gigantic insects (some reaching 35 cm in length!) would forfeit the protection phytomimesis affords. Another protective adaptation of some stick insects is the capacity for physiological color change. The color is light by day and dark by night; this diurnal alternation continues for weeks even when the animals are kept in constant darkness. Apparently control of the rhythm of light and darkness is located in the central nervous system and affects the entire organism through the production of hormones. These induce appropriate changes in the pigment cells of the skin, causing the brown pigment granules to migrate up and down and the orange-red ones to spread out

and gather together, producing the rhythmic color changes. In addition, stick insects, like many grasshoppers and mantids, display a so-called morphological color change: at a certain stage of larval development the animal assumes a color like that of its substrate; once set, the color is maintained even on backgrounds of other colors. Many stick insects can reproduce parthogenetically. In *Carausius morosus*, for example, there is only one male for every thousand females. Another widespread peculiarity is the ability to cast off legs—by breaking them at a specific spot between the trochanter and femur—and then replacing them at the next nymphal molt (autotomy followed by regeneration).

The Phasmida, with approximately 2000 species, inhabit primarily the tropical countries, Asia in particular. One species, the MEDITERRANEAN STICK INSECT (*Bacillus rossii*; see Color plate, p. 125), has penetrated as far north as southern Europe. Two southern species from New Zealand have also settled in Europe, on the southwestern tip of the Scilly Isles off the coast of England. Being undemanding vegetarians, several kinds of stick and leaf insects have become favorite terrarium pets and laboratory animals; in addition to the Mediterranean stick insect, these include the Indian *Carausius* (*Dixippus*) *morosus*, *Prisomera amaurops*, and the LEAF INSECT (*Phyllium pulchrifolium*; cf. Color plate, p. 125), as well as the American walkingstick, *Diapheromera femorata*.

Order: Dictyoptera

The order Dictyoptera contains two groups of animals descended from the cockroachlike insects which lived in the early ages of the earth's history. These two groups—the cockroaches and mantids—have since followed widely divergent lines of evolution. They now have little in common, apart from a few primitive traits such as the biting mouthparts, the five-segment tarsi, and the structure of their coxae and wing venation. The cockroaches have retained the primitive characteristics of their nocturnal ancestors, while the mantids became highly specialized daylight hunters. The termites (order Isoptera, see Chapter 7), while retaining primitive physical characteristics similar to certain cockroaches, have elaborated the undeveloped gregarious tendency of the cockroaches into a complex social structure.

Suborder: Mantida, by P. Rietschel

The MANTIDS (suborder Mantida) are cockroach-related insects of a wide range of size (L 1–16 cm) which hunt by day and are thus very different from the largely vegetarian, nocturnal cockroaches. Their lively coloration may serve as camouflage or as a lure. They are predominantly visual animals with a movable head, slim necklike prothorax, and highly specialized prehensile legs. Geologically speaking they are modern animals, the earliest known examples being from Lower Tertiary amber; today there are about 1500 species, primarily in warm countries.

The praying mantis

In North America one may best become acquainted with these strange animals in their natural situation by carefully searching the tall vegetation in the garden in late summer. Along with a few smaller species, the large PRAYING MANTIS (*Mantis religiosa*; L up to 7.5 cm; see Color plate, p. 125)

is so common in northeastern North America that it may be observed in all stages of its life. It was introduced about 1899, near Rochester, New York, on nursery stock, and has since been cultivated for release as a pest-control measure. It also occurs in northern Africa, Europe, and temperate parts of Asia. Even so, the population is endangered, and great care should be taken that it continues to be propagated. The English name has arisen from the position of the prehensile legs when the animal waits to make a kill; this imaginative misinterpretation of the animal's predilection has also found expression in the Latin specific name and in the common names of other languages: "Gottesanbeterin" in Germany, "prégadiou" in southern France, and "louva dios" in Spain. The generic name, *Mantis*, was given by Linnaeus; it is Greek for "soothsayer" or "prophet," and in the center of their range in Africa *Mantis* species play a considerable role in native representations of gods and spirits. The praying posture of the prehensile legs comes about because the femora are folded closely against the long, free-hanging coxae, and the tibiae, in turn, are folded tightly back against the femora; the two legs are held close together in front of the prothorax. Both femur and tibia are equipped with two rows of spines which stand opposite one another when the leg is bent. In addition, the tibiae end in a long, sharp, curved hook like a grappling iron. The thin, five-segment tarsus of the prehensile leg plays no role in prey capture, though it is used in walking. To strike, the coxae are jerked forward, femora and tibiae extend, and the prey is caught by the hooks and held between tibia and femur, where the rows of spines prevent its pulling free. Then the femora are folded back against the coxae and the coxae are retracted. All this happens within about one-twentieth of a second, so that the surprised prey animal has no time to flee. Now the legs return to the "praying" posture and the prey is held directly before the mantid's mouth to be consumed at leisure. It is not only insects that meet this fate; the larger mantids can overcome small vertebrates such as lizards, frogs, and young birds. Their appetite is so indiscriminate that they readily devour other mantids. Therefore anyone wishing to keep mantids captive is well advised to keep them separate; even the larvae which emerge from the egg capsules must be separated as soon as possible.

One consequence of this cannibalism is that many a male suitor finds himself in the arms and then in the stomach of his intended mate. Even during mating the mantis female often begins to eat the male, starting with the head, while his hind end staunchly continues with copulation. This custom of conjugal murder, which seems so irrational to us, is not at all irrelevant for preservation of the species. Wolfgang von Buddenbrock wrote, "The bloodthirstiness of the females is associated with the fact that they have a very high protein requirement, because of their rapid production of eggs ... as far as the male is concerned, this is simply a confirmation of the old law that nature is concerned only with the species and not with the individual. Once the male has unloaded his supply of

sperm at the right place, he has finished his duty to the species." So the female praying mantids, like many spider and ant-lion females, are acting entirely to the advantage of the species.

The eggs of the mantids, like those of cockroaches, are protected by an egg capsule formed by the mother. Its structure is foamy and papery, and the shape is variable, that of the German praying mantis being flat on the underside and arched like a shield above. Each capsule contains 100 to 200 eggs, and the capsules produced by one female mantid generate altogether 1000 to 1200 offspring. The eggs survive the winter even at low temperatures and hatch in the spring. As with other lower insects, the larvae are at first enclosed in an embryonic cuticle. When they burst through this they make the first molt; they now have free prehensile legs which they soon use in hunting the smallest insects, particularly aphids. In so doing, they disperse themselves over a broad area, so that encounters between siblings, which would be followed by fratricide, are largely avoided. The implications for the insect breeder are clear: eggs collected in the south during late summer or autumn should be kept cool over the winter and into the spring until enough aphids are available. Then, after hatching, use separate cages!

Fantastic structural modifications are often found in mantids native to the warmer countries. Protuberances on the head and leaflike expansions of the middle and hind femora and abdomen occur even in the southern European species *Empusa egena*. The Malaysian species of the genus *Hymenopus* add to this shape a bright coloration. It has been reported that when sitting among flowers the animals can scarcely be distinguished from their surroundings. The African species *Idolum diabolicum* (see Color plate, p. 139) is renowned for its similarity to a blossom; the prothorax and anterior femora of this mantid are much widened and magnificently colored. In the illustration it is shown with prehensile arms spread out. It is claimed that this posture, making the animal look like a flower, attracts flower-visiting insects. But in other mantids this is the typical defense posture, adopted in response to a threatened attack. Has the behavior of this particular mantid become modified? Or does it in fact capture prey in the traditional manner? A documentary film of prey capture by this mantid could answer the question.

Suborder: Blattaria, by P. Rietschel

The COCKROACHES (suborder Blattaria) have kept closest to the structure and way of life of their ancestors. The name cockroach is derived from the Spanish word *cucaracha*. Nocturnal animals, they depend primarily on the sense organs of the antennae and the subgenual organs of the tibiae, which respond to vibration; the eyes are relegated to a subordinate role. The pronotum, as in the oldest insects (the Palaeodictyoptera of the Carboniferous), has broad folds at the sides and covers most of the head. The flattened body is adapted to life in narrow hiding places. The walking legs are long and thin but have strong muscles, permitting the animal to run quite briskly and—though it is not built for it—even to make small

jumps. Of the two pairs of wings, the anterior pair forms sturdy wing covers in which the characteristic venation still appears distinctly. This includes the short subcostal vein on the anterior margin, which ends near the base of the wing; from there on, out to the wingtip, numerous branches of the radial vein end on the anterior wing margin. This pattern of venation, together with the large pronotum, shows unmistakably that the impressions in stones from the Carboniferous (about 350 to 280 million years ago) were made by cockroaches. The delicate hindwings have a broad anal lobe which is folded like a fan under the forewings. The abdomen in both sexes bears a pair of segmented caudal cerci, and the males have in addition a pair of unsegmented styli on the ninth sternite (the "subgenital plate"). As early as the Carboniferous the cockroaches were widespread, with many species and individuals. Between 3000 and 4000 species are known to exist today.

The cockroaches are surely among the least popular insects. None of them is parasitic, nor are they poisonous, but about half a dozen species have become cohabitants within human communities, and there are both hygenic and economic reasons for not tolerating them. The small WOOD COCKROACHES (genera *Ischnoptera* and *Parcoblatta*) live inconspicuously in the forests of eastern North America, but by far the greatest proportion of the species in existence inhabit warm, humid localities in the tropics and subtropics. Here they have remained true to the way of life of their ancestors, which dwelt in great numbers in the moist, warm earth beneath the scaly-leaved trees of primeval forests, a quarter of a billion years ago. The profound transformation of both the plant and animal worlds which has taken place since then has not affected these nocturnal animals, since they are so flexible in their feeding habits. The crannies and crevices into which they can escape within seconds offer them protection even from modern animals; their eggs are not abandoned, defenseless, to the enemy—they lie in orderly rows within a hard capsule, the oötheca, formed by the mother. This looks like a dainty ladies' handbag, and it opens similarly at the upper edge when the nymphs hatch out. In many species, the females carry this oötheca about with them, sticking out of their genital apertures, for some time so as to prevent its being attacked; others deposit it earlier but camouflage it.

Not a great deal is known about the way of life of those cockroaches which live in the open, but those living as vermin in human settlements are very well known indeed. With their present worldwide distribution, it is practically impossible to determine their original homeland. Perhaps it is in the nature of mankind to attribute it to one's neighbors. Karl von Frisch has written of the cockroach, "In some parts of southern Germany they are known as Prussians, in the north as Swabians, in West Germany they are called Frenchmen and in eastern Europe, Russians. In Russia, again, they are the Prussians." Even the scholarly Swede Carl Linnaeus succumbed to this tendency when he gave one household cockroach the

▻
Orthoptera: 1. Mole cricket (*Gryllotalpa gryllotalpa*; L 45 mm; see Chapter 5), 2. Mediterranean stick insect (*Bacillus rossii*; L 80–105 mm; see Chapter 5), 3. *Anchiole maculata* (L 180 mm), 4. The leaf insect *Phyllium bioculatum* (L 90 mm; see Chapter 6). Mantida: 5. Praying mantis (*Mantis religiosa*).

▻▻
Orthoptera: 1. House cricket (*Acheta domestica*; L 16–20 mm; see Chapter 5); a, head with sponging proboscis everted, seen from the side; b, seen diagonally from below; c, sponging proboscis, distended with blood and showing the branched "pseudotracheae." Blattaria: 2. German cockroach (*Blatella germanica*), the female carrying an egg capsule at the hind end; a, egg capsule from the side; b, from the front. 3. Oriental cockroach (*Blatta orientalis*); a, egg capsule from the side; b, from the front. 4. American cockroach (*Periplaneta americana*); a, imago; b, larva; c, egg capsule from the side; d, from the front.


2
5


1


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1 c
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species epithet *germanica*. We do know that the common cockroach made its home in Germany as early as one of the warm periods between the Ice Ages; discoveries in a peat bog near Hohenwestedt, in Holstein, bear witness to this. But the question remains open whether northern Germany at that time was part of their natural area of distribution or whether they had already become associated with humans who brought them there.

The German cockroach

The most common cockroach found in human dwellings throughout the world is the GERMAN COCKROACH (*Blatella germanica*; L 8–13 mm; see Color plate, p. 126). Both sexes have wings, but hardly ever use them. When pursued, these cockroaches save themselves by their nimble running (up to 29 cm/sec!) and often, when they are on walls, by jumping down. It is true that they lack endurance, but this is not needed; due to its small size, the cockroach can quickly find a suitable refuge. During her lifetime the female lays three or four egg capsules, each of which contains about thirty eggs; she carries them about with her for twenty-four to forty days until they hatch. The nymphs develop into imagos in another two to three months. Thus there are several generations per year. Because the German cockroach is the least demanding of the domestic cockroaches with respect to warmth and humidity, and since it is small enough to find hiding places everywhere, it is now the most common cockroach in rooms where humans live. Recently a second small species has joined it—the BROWN-BANDED COCKROACH (*Supella supellectilium*; L 10–14 mm). This species probably originated in tropical Africa; it first appeared in Florida in 1903, and in Europe in 1910, in southern France. In the meantime it has also become established in southern Germany, and in many households both it and the German cockroach are found together.

The Oriental cockroach

The second most common species found in houses is the ORIENTAL COCKROACH (*Blatta orientalis*; L 18–30 mm; see Color plate, p. 126). Only the males of this species have fully developed wings; in the females the forewings are shortened and the hindwings regressed. The female of the Oriental cockroach lays five to eight egg capsules, each containing an average of sixteen eggs, before she dies. The capsules are carried about with the mother for only a short time, and are then dropped at random. After two to three months the nymphs hatch; the rate of growth is extremely variable, so that they may reach the imago stage in as little as four months or not until four years have passed. The Oriental cockroach used to be very widespread, in kitchens, bakehouses, and other warm rooms; but with advances in building construction and methods of control it has become more rare in human habitations. *Blatta orientalis* still lives in the open in the region of the Caucasus Mountains, Crimea, and central Asia.

The large cockroaches

Even more warmth is required by the large cockroaches of the genus *Periplaneta*. The AMERICAN COCKROACH (*Periplaneta americana*; L 28–45 mm; see Color plate, p. 126) and the AUSTRALIAN COCKROACH (*Periplaneta australasiae*), which is often transported with shipments of imported

goods, are therefore most often encountered in the tropics and in the warm environment of greenhouses. It occurs in the wild in Florida. The female produces a large number of egg capsules, one after another, which she carries with her only briefly. Ultimately, however, she does not simply drop them, as does the Oriental cockroach, but rather digs a pit, deposits a capsule in it, collects various materials to camouflage the site, and glues the whole thing together with a sticky substance produced from her mouth. This is a genuine "brood care" behavior. Furthermore, these cockroaches show the beginnings of social behavior. When disturbed, a cockroach warns its conspecifics by producing odorous substances from special glands, and by making warning noises, in part with the forewings and in part by dragging the spurs at the ends of the tibiae over the ground. These large cockroaches are also quite capable of running silently. The warning noises are detected by the other cockroaches when the subgenual organs on the tibiae respond to the vibration of the ground. The Australian cockroach is also a skilful flyer. A third cockroach occasionally found in greenhouses in Europe is the SURINAM COCKROACH (*Pycnoscelis surinamensis*), from southern Asia. It is circumtropical, and is established from Florida to Texas.

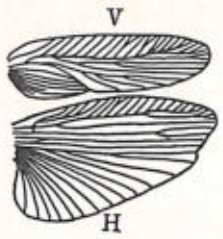


Fig. 6–1. Forewing (V) and hindwing (H) of the German cockroach (L9.7–11.5 mm).

The food of cockroaches

Cockroaches break up their predominantly vegetable food into small bits with the biting and chewing mouthparts and with the teeth of the gizzard. The German cockroach and the common cockroach prefer food containing sugar and carbohydrates, but will also try out all sorts of other possible (and impossible) substances (see Chapter 1). Nor do they disdain meat; not only their own egg capsules, but even wounded members of the same species often fall victim to the hunger of their healthy confreres. Some cockroaches feed on dead wood; *Panesthia javanica* digests it by means of bacteria in the crop which can break down cellulose, and *Cryptocercus punctulatus* harbors in its hindgut flagellates of the same genera as those in the gut of termites. The other cockroaches also house symbiotic guests. Single cells within their fat-bodies are crammed with bacteria, without which the cockroaches can develop only slowly and never form mature ovaries. Here, too, the close relationship between termites and cockroaches is apparent: *Mastotermes darwiniensis*, the most primitive of the present-day termites, also has symbiotic bacteria in its fat-body.

Their search for food leads the cockroaches of human settlements to garbage cans, contaminated, disease-infected, or decaying animals, and feces, as well as to human food. Organisms causing decay and disease then adhere externally to the cockroach in great numbers, and are also taken in with food and deposited elsewhere with the excrement. This passage through the cockroach gut has been demonstrated for pus-generating staphylococci and the bacilli causing tuberculosis, typhus, paratyphus, dysentery, and anthrax, as well as *Escherichia coli*, and *Vibrio comma* which causes cholera. E. Martini notes: "The sense of revulsion one feels toward

cockroaches is thus entirely justified, though the weight of evidence is not yet sufficient for the public health services to take steps against them." It is enough, though, if the individuals responsible for private houses, public kitchens, and above all hospitals refuse to tolerate cockroaches there. The poisons previously used against them had to be ingested (sodium fluosilicate or borax, mixed with sugar as bait); nowadays organic phosphate poisons, which need only touch the animal, serve better. These are usually applied as a dust. An additional means of combatting cockroaches is to catch them in traps. The expensive fumigation of entire buildings is frequently necessary because of the resistance of most species to modern insecticides.

7 The Termites, Earwigs, Webspinners, and Zorapterans

Order: Isoptera, by E. Ernst

The TERMITES (order Isoptera), which seek warmth and humidity, are similar to the cockroaches in many ways. Despite their inclusion in a "lower" insect group, they have developed a remarkable social behavior which sets them apart from the great majority of other insects (with the exception of some Hymenoptera; see Chapters 17 and 18). Their permanent and well-ordered family communities, highly developed in some species, show a distinct division of labor which is reflected in the different forms of these insects (polymorphism of castes).

Termites are slender insects of moderate size. The abdomen is joined to the thorax without any constriction. The length of the reproductive individuals is 5–22 mm, of the workers, 2–12 mm, and of the soldiers, 3–20 mm. Reproductives are winged (wingspread 10–90 mm), light brown to black, with a round, freely movable head; they have biting mouthparts, segmented antennae rather like strings of pearls, and dark compound eyes at the sides of the head. On the thorax there are two pairs of membranous, identically shaped wings, which at rest lie over the back and extend beyond the body. After swarming has taken place, the wings break off near the base along a pre-existing suture, so that only small wing scales remain. The legs are all identical, and each ends in two claws; the tarsi consist of four (or, rarely, five) segments. External genital organs are lacking. Males and females may be distinguished by the posterior sterna: in males they are all the same, whereas in females the sternum of the seventh abdominal segment is enlarged and covers the genital aperture. The workers and soldiers are described below.

Termite castes

A termite colony generally consists of one pair of continually active (functional) reproductive individuals—the king and the queen—and their offspring—termed larvae, nymphs, workers, or soldiers, according to their age and body structure (see Color plate, p. 145). The development of the termites, like that of their relatives, involves a direct or incomplete (hemimetabolous) metamorphosis (see Chapter 1). The nymphs have the general appearance of termites as soon as they hatch from the eggs;

they then either become soldiers and workers by passing through several nymphal stages, separated by molts, or they grow through nymphal stages into reproductive individuals. Only the latter correspond to the adult, sexually mature imago form; the infertile castes of wingless and usually blind workers and soldiers are the result of a specialized, incomplete development (cf. Color plate, p. 145).

The workers are smaller than the reproductive termites. The head is rounded and pale; eyes are always lacking, and the wingless thorax is narrow. In the soldier, the head is modified into a defensive weapon; the biting type of soldier has powerful mandibles, which may be of various shapes, and the so-called nasuti (the Latin *nasutus* means large-nosed) have a spherical head with the forehead drawn out into a conical process. The cuticle of the abdomen is so soft and thin in the workers and soldiers that the gut contents show through. Their reproductive organs are only slightly developed—a sign that physical development has stopped at a juvenile stage. But the primordia of these organs show that in all castes of termites, in contrast to the bees, ants, and other hymenopterans, both sexes are usually represented.

The name termite is derived from the Greek word τέρμα, meaning end. The Romans used the word *termes* for wood-destroying animals in general, the gnawing of which "put an end" to the wood. When Linnaeus set up his system of binomial nomenclature in 1758, he used this name. But at that time essentially nothing was known about the termites. An insect collector from Livonia, J. G. König, who lived for a long time in India and in 1779 wrote about the "white ants" of the Madras district, may be considered the first serious termite researcher. Two years later Henry Smeathman, as a result of his travels in Africa, wrote a famous letter to the Royal Society in London, in which he referred with obvious respect to the astonishing social life of the termites. At the time, these publications were met with both admiration and doubt. Since then, termitologists have penetrated a great deal further into the secrets of the hidden world of termites, but much remains unexplained even today.

They are not "white ants"

Superficially, the social structure of termite colonies resembles that of the more familiar ants. That is why they acquired in antiquity the unsuitable—in fact, completely false—name "white ants," which even later researchers have often used. The expression has become so well established that it probably cannot now be stamped out, in spite of the rational arguments against it. Nevertheless, ants and termites differ—even apart from their morphology—in essential aspects of development, behavior, and social structure.

The ants, together with the (also in part social) wasps and bees, belong to the distantly related order Hymenoptera (see Chapters 17 and 18). In contrast to the Hymenoptera, the termites undergo incomplete metamorphosis. The winged reproductive individuals embark upon a swarming flight and then divide up into pairs; each pair digs a nuptial chamber,

where copulation occurs. All the eggs are fertilized and develop into either male or female offspring. Each termite colony includes both a king and a queen and thus represents a biparental family, whereas an ant colony is founded by only a queen and thus is a matriarchy.



Fig. 7-1. Distribution of the termites.

All species of termites live in communities. In their behavior, we know of no traces of the origin of social life such as are shown by the bees, for example, in their varying kinds of brood care. But a clue to the way termite social structure may have arisen is provided by the wingless North American BROWN HOODED COCKROACH (*Cryptocercus punctulatus*), which leads a subsocial life. These cockroaches live in loose associations under the bark of trees, feeding on the wood. They digest the cellulose by means of certain flagellates (see Vol. I) which live in the gut. Freshly hatched roaches, however, do not have such flagellates, and in order to acquire them they must eat the excrement of an older nymph. But these older nymphs release transmittable forms of the flagellates only when they molt, and the adult animals of course no longer molt. Thus when sexually mature roaches found new colonies, they must take along nymphs which are still capable of molting. For this reason, they are forced into a subsocial mode of life. Since *Cryptocercus punctulatus* has remained at a very primitive level, and the flagellates in its gut are similar to those found in the guts of primitive termites, it is tempting to seek in this correspondence the origin of termite social life.

Relationship to cockroaches

The structure of the termite body also indicates a close relationship to the cockroaches. Their evolutionary development took place comparatively recently. Whereas the present-day human species is at most a few hundred thousand years old, and the bees and ants appeared over 150 million years ago, the termites can be traced to an origin only about 40 million years ago. However, it was much earlier, geologically speaking, that they and the cockroaches separated from their common ancestors, a primitive pterygote. The present-day termite families evolved and dispersed during the Eocene. Some genera found today are also known as fossils.

The termites are definitely tropical and subtropical animals. They have become particularly abundant in the warm, humid climate of the evergreen rainforests, but even in the savannas their mounds of earth are occasionally so numerous that they are a distinguishing feature of the landscape. Some genera have also ventured into the warmer regions of the temperate zone, and only one, *Reticulitermes*, the subterreanean termites, reaches the northern U.S.A.

Classification of the 1800 species

Before proceeding to the details of termite life and behavior, we shall summarize the systematic relationships of the present-day termites, with brief references to their distribution and habits. At present about 1800 species of termites are known, distributed among about 200 genera grouped into seven families: (1) Mastotermitidae, (2) Kalotermitidae, (3) Termopsidae, (4) Hodotermitidae, (5) Rhinotermitidae—these first

five are often lumped together as lower termites—(6) Serritermitidae, and (7) Termitidae, or higher termites.

The terms lower and higher refer to the evolutionary sequence which has led from the primitive, less specialized groups to those forms which have developed further in a given direction. Such development is recognizable not only in the structure of the body but especially in the social organization and general way of life. For example, the five families of lower termites have in common the possession of intestinal flagellates which can decompose cellulose.

Family: Mastotermitidae

The most primitive are the MASTOTERMITIDS (family Mastotermitidae). In the Eocene, 40 to 60 million years ago, they were distributed worldwide. Today there is only one species, the DARWIN TERMITE (*Mastotermes darwiniensis*); a native of tropical northern Australia, it can be distinguished from the remaining termites by the lobed hindwings, five-segment tarsi, and other primitive characteristics. Their relationship to the cockroaches is also evident in that *M. darwiniensis* has both flagellates and symbiotic intestinal bacteria, and the eggs are deposited in packets of twenty to twenty-four.



Fig. 7-2. Winged reproductive individual of the Darwin termite (*Mastotermes darwiniensis*), with lobed hindwings.

The nests of *M. darwiniensis* lie in hollows underground or in rotting trees. The space in which they live is divided by walls into many chambers. Large nests house several million termites. The social structure of this species is not well known; usually there is no true "royal pair," but rather several nymphs become prematurely functional sexually, serve as "supplementary queens," and lay eggs. Parts of a large community can break away and form new colonies. This species attacks plants, trees, and building timber through underground passages; their menu is extraordinarily varied.

Family: Kalotermitidae

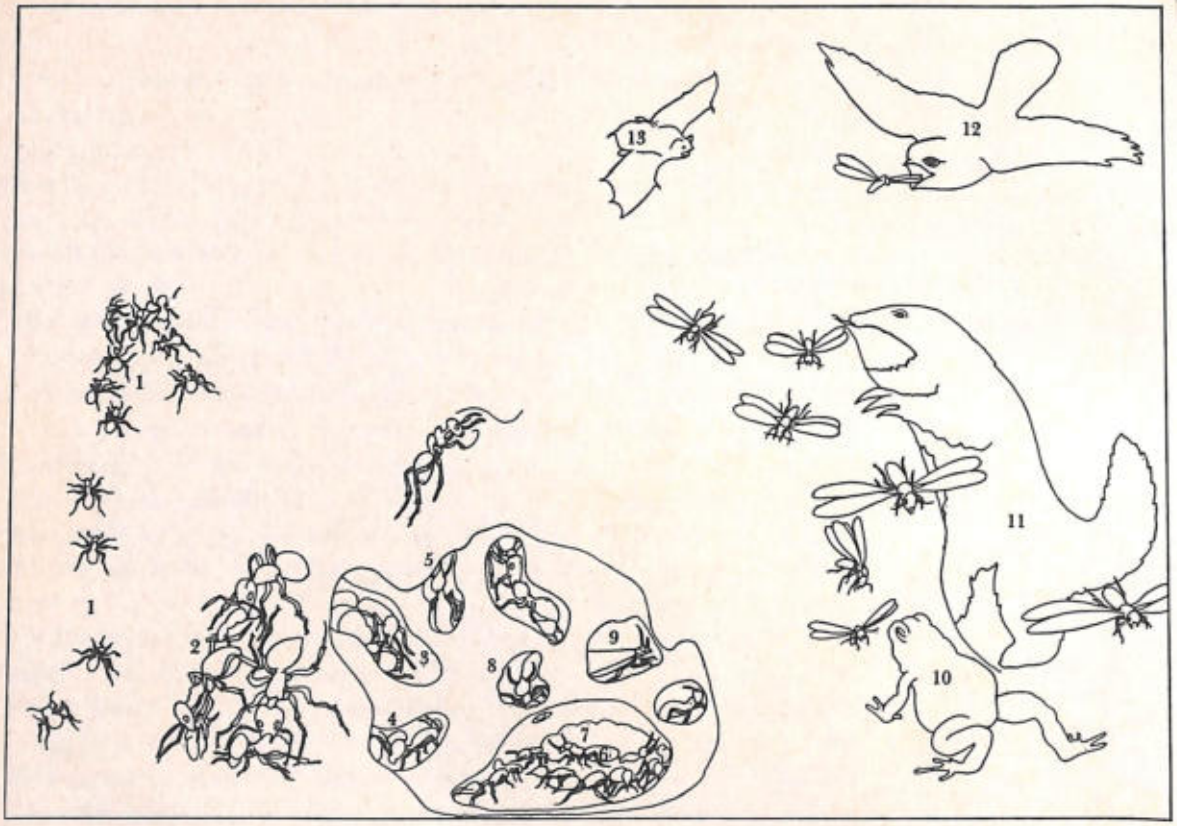
The KALOTERMITIDS (family Kalotermitidae) have also remained at a relatively simple level of social organization. The reproductive individuals have oval heads, with small eyes; the pronotum is flat and wider than the head. The anterior wing scales are large, with distinct veins in the anterior parts. The soldiers usually have large, somewhat elongated heads and powerful jaws well supplied with teeth. There are twenty-one genera, the 300 species of which are distributed in all parts of the earth.



Fig. 7-3. Head and prothorax of *Incisitermes minor*; the soldiers of the kalotermitids have large, elongated heads with strong toothed mandibles.

These dry-wood termites live in small colonies (up to 3000 members) within the wood, which thus serves simultaneously for food and shelter. The wood is hollowed out to form a nest with irregular chambers connected by narrow passages. As the colony grows, the nest is gradually enlarged. There is no true worker caste, but a hint of it is found in the so-called pseudergates, the older nymphs which are capable of working.

Most species of the kalotermitids are found in coastal regions and on islands, and many of them are harmful. On the island of Ceylon, *Postelectrotermes militaris* and *Neotermes greeni* live in tea plantations and commercially valuable trees. In Java, *Neotermes tectonae* makes its home in teak trees. Other species of *Neotermes* prefer cocoa trees. The species of



DANGER TO THE TERMITE COLONY

Driver ants (Dorylinae; see Chapter 18) overrun a termite fortress under an acacia tree in the African steppe. Their advance guard has climbed the first tower (1). The masonry is still soft here, and the attackers tear it apart and force their way into the castle. At the front left (2) victorious intruders are dragging the corpses of their opponents out of the building.

In the middle of the picture, where the wall is cut away, a nasutus squirts the glue produced in its frontal gland onto an ant (3). Below this, construction workers are in the process of walling up the entrance to the queen chamber (4). A blind nasutus waits for the attackers in a passage (5). At the very bottom lies the chamber of the king (6) and queen (7). Despite the battles taking place in the hill, the *ca.* 5-cm-long queen steadfastly continues to lay eggs, which are immediately carried away into the brood chambers; meanwhile other workers provide the front part of the royal egg-laying machine with food. This is done through a single tiny opening (8) above the head of the queen. In the round hole at the right there appears an alate of the termite colony (9). The right half of the picture shows a swarm of termites in the twilight. For countless animals this is a death flight, but for the few survivors it marks the beginning of a new colony. The enemies of the termites rush to the scene: the leopard toad (*Bufo regularis*, 10; see Vol. V) and the scaly anteater (*Manis temmincki*, 11; see Vol. XI); from the air, a goatsucker (*Caprimulgus fossii* 12, see Vol. VIII) and a bat (Vespertilio spec., 13; see Vol. XI) dive down to exact their toll.





the genus *Kalotermes* are found primarily in warm, temperate areas. The YELLOW-NECKED TERMITE (*Kalotermes flavicollis*) lives in grapevines and old trees on the Mediterranean coast and seldom enters houses. The species of the genus *Incisitermes* destroy the wood of buildings in Central America and the western U.S.A. The depredations of the WOOD TERMITE or POWDER POST TERMITE *Cryptotermes* spp. are of particular economic importance. The soldiers in this genus have a short head, the front surface of which is vertical; they use it like a plug to close off the narrow passages through the wood. These termites can even live in isolated bits of wood, such as beams or pieces of furniture, and are very easily transported. In this way the species *Cryptotermes brevis* (from New Orleans to Miami), *C. dudleyi*, *C. domesticus*, and *C. havilandi* have become established in most of the tropical port cities.

Family: Termopsidae

The TERMOPSIDS (family Termopsidae) used to be widespread; fossils have been found in Europe and North America. The pronotum of the reproductive individuals is flat and somewhat narrower than the rounded head; the antennae may be very long. The anterior wing scales (the remnants of the wings) are distinctly larger than the posterior wing scales; they are covered with dense networks of veins, the anterior veins being particularly pronounced. The soldiers have very large heads and powerful toothed mandibles. They can now be found only in isolated areas, predominantly outside the tropics.



Fig. 7-4. Head of a soldier of *Neotermes sanctaecrucis*.

The colonies of these damp-wood termites usually dig their tunnels in the decaying wood of old trees. Each colony is composed of at the most 10,000 animals. The social organization, like that of the kalotermitids, is quite simple; there is no worker caste. Three subfamilies, with a total of fifteen species, may be distinguished:

A. The TERMOPSINES (subfamily Termopsinae): A primitive species, in the western Himalaya and in Kashmir, is *Archotermopsis wroughtoni*; it lives at altitudes of up to 3000 m, in dead conifers. The genus *Zootermopsis* includes the three American species *Z. nevadensis*, *Z. angusticollis*, and *Z. laticeps*; these are found on the west coast of North America, where they sometimes form extensive colonies in the large sequoia trees, and in cottonwood from southwestern Arizona to Texas.



Fig. 7-5. The mandibulate soldiers of the dry-wood termites can block up their narrow tunnels in wood, using the head as a plug, as *Cryptotermes cavifrons* does here.

B. The STOLOTERMITINES (subfamily Stolotermitinae): The bodies of both the reproductive individuals and the soldiers are flattened. There is a single genus with six species, including the South African *Stolotermes africanus*; the other five species are in eastern Australia, Tasmania, and New Zealand. All of them live in rotting wood.

C. The POROTERMITINES (subfamily Porotermitinae): The head is flattened and the rest of the body cylindrical. There is just one genus, with three species, found on the edges of the southern continents: *Porotermes quadricollis* in southern Chile, *P. planiceps* in South Africa, and *P. adamsoni* in southeastern Australia and Tasmania. This peculiar distribution suggests that the three areas were at one time joined in the Antarctic.

Family: Hodotermitidae

The HODOTERMITIDS (family Hodotermitidae) are closely related to the family just mentioned. They have strikingly long antennae with twenty- three to thirty-one segments. The pronotum in reproductive individuals is narrower than the head and bulges outward in front. The heads of the soldiers are round to oval and bear dark compound eyes and mandibles with long teeth. In this family there are true workers, which also have eyes. The family includes three genera comprising sixteen species.

The colonies of the hodotermitids, housed in subterranean hollows, may be very populous. The workers come to the surface through broad tunnels to gather plant materials, even by day. For this reason they are often called harvester termites, although this name could equally well apply to some genera of the higher termites. The workers first take the leaves off the plants and then bite the stems into short pieces which they carry to the nest and store there. The soldiers seldom come into the open; they sit in the tunnels guarding their entrances.

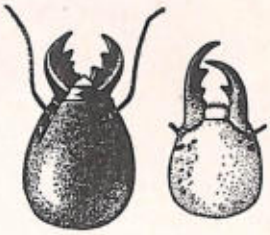


Fig. 7-6. The soldiers of the hodotermitids have round or oval heads with long toothed mandibles (left, *Hodotermes mossambicus*; right, *Hodotermes erithreensis*).

The genus *Hodotermes* is restricted to the eastern half of Africa; *Hodotermes mossambicus* may be encountered from Ethiopia to South Africa. Two species of the genus *Microhodotermes* live in northern Africa and one, *M. viator*, in South Africa. The genus *Anacanthotermes*, with twelve species, occurs in deserts and other dry areas from Algeria as far east as central India and even in some parts of southern India.

Family: Rhinotermitidae

The RHINOTERMITIDS (family Rhinotermitidae) are small, inconspicuous wood-eaters with subterranean nests. Both the reproductive individuals and the soldiers have well-developed frontal glands (a defensive device which will be discussed in detail for the Nasutitermitinae) with their openings visible on the head; the pronotum is flat, with anterior and posterior indentations. In the soldiers, the frontal gland may extend back into the abdomen. Occasionally there are two forms of soldiers. The workers have a saddle-shaped pronotum. The destructive activity of many species of the rhinotermitids is much feared. There are six subfamilies with fourteen genera and about 170 species:

A. The PSAMMOTERMITINES (subfamily Psammotermitinae): The soldiers have flattened bodies. Species of the genus *Psammotermes* prefer the dry regions of Africa, Madagascar, Arabia, and India, where they feed on grasses and wood.

B. The HETEROTERMITINES (subfamily Heterotermitinae): The soldiers are small, with narrow heads and saberlike mandibles. The genus *Heterotermes* is found in the tropics and subtropics. The genus *Reticulitermes* lives only in the northern temperate zone; the most important species are *Reticulitermes speratus* and *R. chinensis* in eastern Asia, and *R. hesperus* and the EASTERN SUBTERRANEAN TERMITE (*R. flavipes*) in the U.S.A. In southern Europe, *R. lucifugus* lives underground or in old rhizomes, but occasionally invades buildings.

C. The STYLOTERMITINES (subfamily Stylotermitinae): This comprises

▷ The mantid *Idolum diabolicum* in defense posture. Whether this African species also adopts this posture when lying in wait for prey, hiding itself among flowers of similar appearance, is not yet clear.





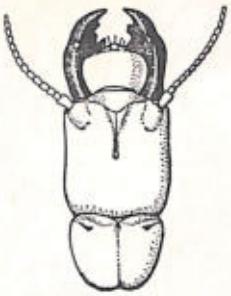


Fig. 7-7. Head and prothorax of a soldier of *Psammotermes allocerus*, with pincerlike mandibles.

three little-known Indian species of the genera *Stylotermes* and *Sarvaritermes*.

D. The COPTOTERMITINES (subfamily Coptotermitinae): The frontal gland is tiny in reproductive individuals, but in soldiers it is large and directed forward. The only genus, *Coptotermes*, is found everywhere in the tropics. The nests, located underground or in old trees, are subdivided by lamellae made of wood which resemble cardboard. In Africa, *C. sjöstedti*, *C. intermedius*, and *C. amanii* are very common. Of the many Indo-Malaysian species, only *C. gestroi*, *C. havilandi*, and the rubber-tree dweller *C. curvignathus* will be mentioned. The species *C. formosanus* was transported from eastern Asia to Africa and the U.S.A. In Australia, *C. acinaciformis*, *C. frenchi*, and *C. lacteus* build mounds of earth with cardboardlike centers.

E. The TERMITOGETONINES (subfamily Termitogetoninae): Little is known about the genus *Termitogeton*; it lives in Borneo and Ceylon, in rotting wood.

F. The RHINOTERMITINES (subfamily Rhinotermitinae): The labrum of the reproductive individuals and soldiers is long, with a groove for the secretions of the frontal glands. The genus *Prorhinotermes* lives in damp wood, primarily in the Indo-Malayan region and on the islands of the South Seas. The genus *Schedorhinotermes* is widespread in the tropics but absent from South America; there, *Rhinotermes* is found in the same ecological niche.

The SERRITERMITIDS (family Serritermitidae, or sawtooth termites) all belong to a single species, *Serritermes serrifer*. This rare Brazilian termite was long regarded as a rhinotermitid, and then later was counted among the higher termites (Termitidae). But in order to emphasize the special peculiarities of its structure, it has recently been classified as a separate family. Nothing is known of its behavior. It was found in humus, and the shape of the teeth on the mandibles of the workers suggests that these termites also feed on humus.

Family: Termitidae

The HIGHER TERMITES (family Termitidae) are distinguished by the great variety in their nest construction and way of life. The opening of the frontal gland in the reproductive individual is often indicated by a light-colored fontanelle area; the pronotum is usually flat and narrowed toward the back, and the anterior wing scales are always short. The soldiers have a frontal gland; head and mandibles are quite variable in form, and the pronotum is saddle-shaped. There are workers in all species. They lack intestinal flagellates. The higher termites no longer depend on protozoans. Instead, they gather leaves, lichen and seeds which are digested by bacteria. Some cultivate fungi and have fungus gardens similar to atta ants (see Chapter 19). Three-quarters of all termites belong to this group; it contains 150 genera and about 1350 species.

◁ The praying mantis holds a captured insect in its prehensile legs and eats it. A characteristic of the praying mantis is the highly mobile three-cornered head.

The majority of the higher termites dwell below ground. Many species form giant communities with huge nest hills above ground. Because the

number of species is so large, this family seems quite heterogeneous. Phylogenetic research also reflects the complexity of the group; the teeth on the mandibles of reproductive individuals and workers show that the genera cannot be arranged in a single continuous series. Rather, the tree of evolution of the higher termites is extensively branched. Within each of the four subfamilies the genera can be subdivided into several large groups. Each of these might be grouped as a separate subfamily, with the present subfamilies elevated to the rank of families. There are so many species that only a few typical, biologically interesting examples from the four subfamilies can be mentioned here.

A. The AMITERMITINES (subfamily Amitermitinae): In the reproductive individuals the most anterior tooth of the mandible is either shorter than the second or of equal length. The soldiers have either oval heads and sickle-shaped mandibles with one or two teeth in the middle, or elongated heads and strong saberlike mandibles with sawteeth on the inner edges. Many species feed on rotting wood or humus. There are twenty-five genera, some with many species, in all warm regions of the earth.

The species of the genus *Anoplotermes* have no soldiers. The South American species build hollow earthen nests in the shape of pillars. The African species, on the other hand, live below ground; they hang pockets of earth the size of one's hand on twigs and bushes, where the winged reproductive individuals (alates) stay prior to swarming. Species of the genus *Microcerotermes* occur in all tropical regions, where they predominantly build round nests of a cardboard-like material, which are either hidden in the ground or hung up on trees. Black nests of the same substance stand on the ground in the jungles of western Africa; these are produced by the closely related *Cephalotermes rectangularis*. The Indo-Malayan *Globitermes sulphureus* builds hills of soil with an inner core of cardboard, shaped into lamellae and perhaps serving as a reserve store of food. The genus *Amitermes* is particularly widespread and rich in species; some species build hill-type nests of a mixture of soil and wood, while the compass nests of the well-known Australian MERIDIAN TERMITE (*Amitermes meriodionalis*) are 3–4 m high and wedge-shaped, with the long axis always aligned north-south. Close relatives are the western Australian species of *Drepanotermes*; their nimble workers come into the open even during the day, as long as the sky is overcast, to forage for plant material.

B. TRUE TERMITES (subfamily Termitinae): In the reproductive individuals, the most anterior tooth of the mandible is distinctly larger than the second. The head of the soldier may be rounded, rectangular, or elongate; the labrum is tongue-shaped or deeply depressed; the opening of the frontal gland lies far anterior, often under a frontal ridge, and is surrounded by hairs; and the mandibles, shaped like sabers or stilettos, are usually slender and lack teeth. Occasionally the right mandible is shaped differently than the left. There are sixty genera with about 350 species, most of them in Africa.

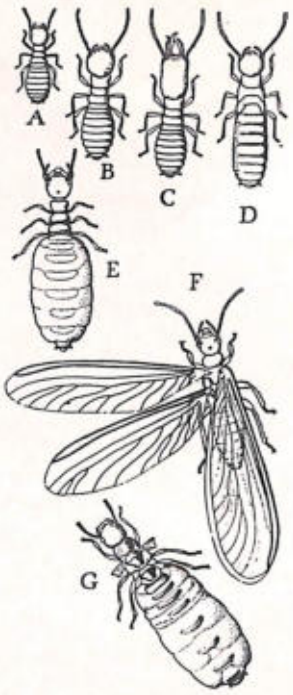


Fig. 7-8. The castes of *Reticulitermes flavipes*: A, nymph; B, worker; C, soldier; D, supplementary reproductive individual with wing buds; E, wingless supplementary reproductive; F, winged reproductive; G, reproductive after the discarding of the wings and swelling of the abdomen.

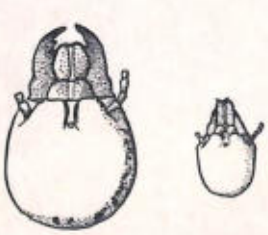


Fig. 7-9. Head of a large soldier (left) and a small soldier (right); *Schedorhinotermes marjoriae*.

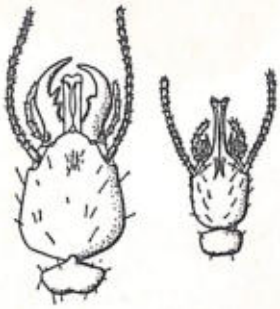


Fig. 7-10. Head and prothorax of the two types of soldiers *Rhinotermes latilabrum*: large soldier (left) with well-developed mandibles, small soldier (right) with mandibles largely regressed.

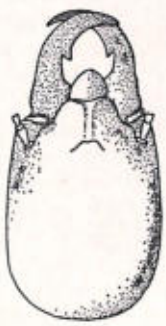


Fig. 7-11. Head of a soldier of *Amitermes messinae*, with sickle-shaped mandibles.

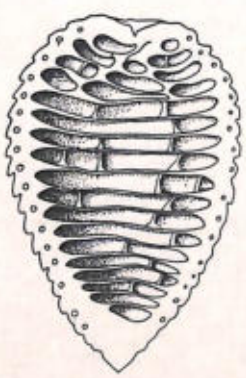


Fig. 7-12. Longitudinal section through a subterranean nest of *Apicotermes*, with many interconnected stories and ring channels in the wall.

Despite the variability among the soldiers, the different species in this subfamily have a uniform way of life. Almost all of them feed on humus, and most live in small colonies hidden underground in jungles and savannas. Only a few species use their abundant excrement to build nests of earth.

Thirteen species of the genus *Apicotermes* embed their artfully designed clay nests in sandy soil. The interior of the nest is divided by thin horizontal structures into several stories, connected by ramps or spiral staircases. From outside, a regular arrangement of very fine openings can be seen; these pores and slits, too small for the termites to pass through, serve to ventilate the nest. Often the wall also encloses inaccessible ring-shaped galleries which are connected with both the outside and the interior. The nests of each species are erected according to a fixed plan; the more complicated methods of construction can be derived from the simpler, so that the evolutionary development of this behavior within the genus can be followed from species to species.

The small earthen nests, masses of which are sometimes found in the African savannas and forests, are usually those of species of the genus *Cubitermes*. In western and central Africa these nests often look like large mushrooms or small pagodas; the broad overhanging roofs, often one above another, protect the honeycombed tower from rain. Above the nests built against large jungle trees by *Cubitermes fungifaber* and *C. intercalatus* there are lean-to roofs which likewise deflect the water running down the treetrunks. The building behavior of the closely related genus *Procubitermes* includes only a suggestion of this mode of construction: *P. arboricola* glues its cylindrical nest of earth onto trees at a height of 1 to 2 m and, above it, affixes finger-thick ridges of earth in a herringbone pattern with the free ends sloping down.

The genus *Termes*, with its many species and worldwide distribution, belongs to a third group within the subfamily Termitinae. Its small soldiers have an elongated head with rectangular labrum. The mandibles are as long as the head capsule itself and have been transformed into snapping stylets. Some *Termes* species, among them *T. hospes*, are exceptional within the subfamily in that they feed on rotten wood and build fragile nests of a mixture of cardboard and earth. Most species live in narrow subterranean systems of passages or move into the nests of other species: the South American *Termes fur* and *T. inquilinus* are found exclusively in the nests of *Constrictotermes*, and the only known dwellings of *T. winifredae*, in South Africa, are the nests of species of *Amitermes*.

The last group of true termites is typified by the Indo-Malayan genus *Capritermes*. The soldiers are somewhat stronger than those of the previous group, and are conspicuous by the size and dissimilarity of the two mandibles; the right mandible is shorter and straight, while the left is bent in the middle several times and twisted about the long axis in such a way that the tip again lies flat. In the narrow, subterranean tunnels of the nest

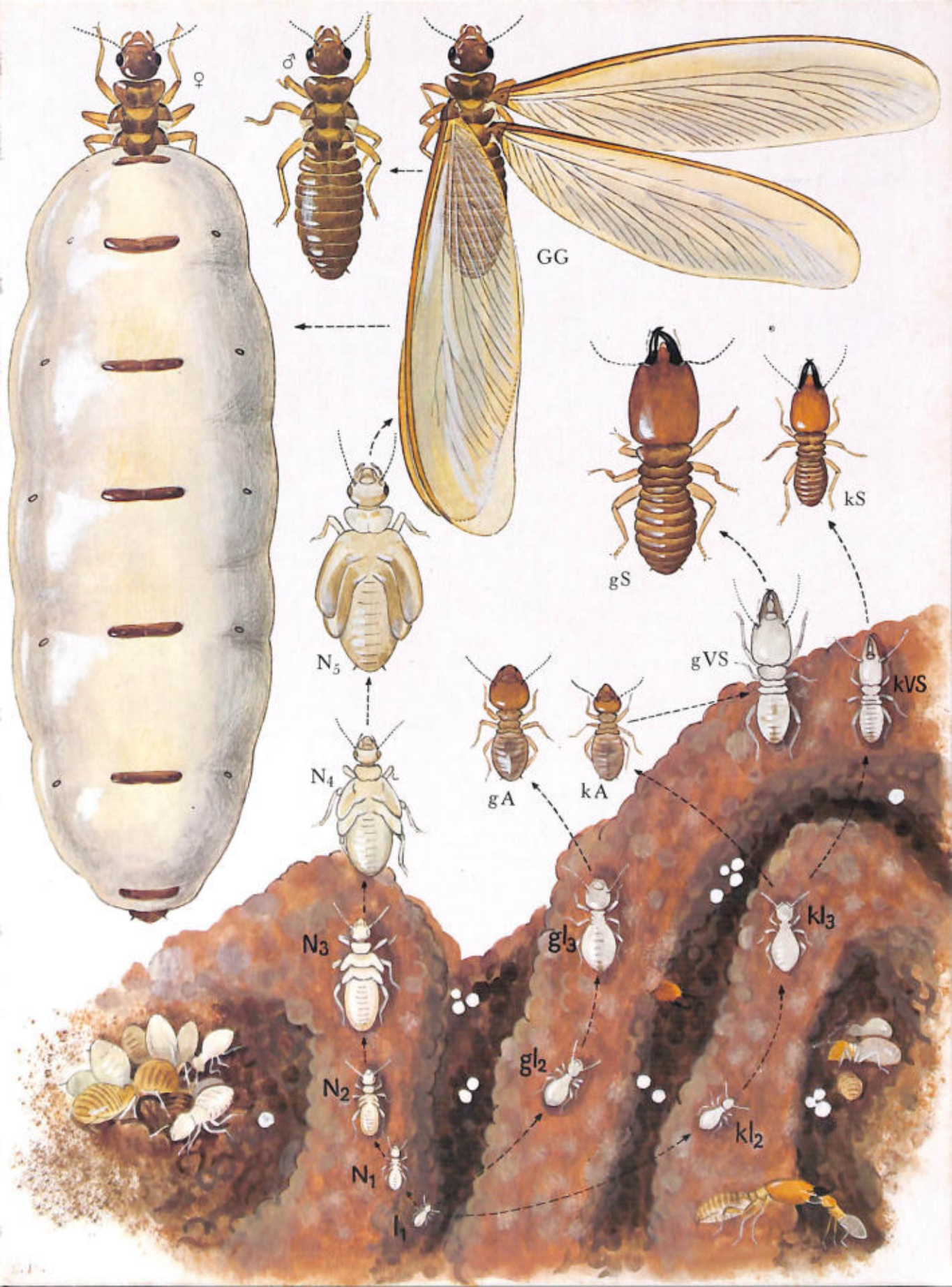
these snapping mandibles are a very effective weapon. In tropical South America the group is represented by the genus *Neocapritermes* and in Africa, by *Promirotermes* and *Pericapritermes*.

C. The MACROTERMITINES (subfamily Macrotermitinae): In the reproductive individual the first tooth of the mandible is somewhat smaller than the second; the labrum displays a cross-band of chitin. The soldiers' heads are usually oval. The mandibles are saber-shaped. In several genera there are two different soldier forms, and the workers also can be of two sizes.

The macrotermitines are distinguished from all other groups of termites by their practice of cultivating fungi. From the wood and plant materials brought into the nest, they prepare a spongy, cellulose-rich culture medium which may entirely fill up the nest chambers. On these combs, certain species of fungus (those of the genus *Termitomyces*) thrive, altering the woody materials so that they become digestible by the termites; later the termite workers eat the oldest parts of the fungus comb (the American leaf-cutting ants, on the other hand, eat just the cultured fungi; see Chapter 18). Some species of macrotermitines form gigantic colonies and erect correspondingly large nest hills, which are a characteristic feature of the landscape. Most species, though, dwell in scattered chambers or in large, greatly subdivided underground caves. Very frequently they appear in human settlements and cause considerable damage to structural wood as well as to agriculture and forestry. The subfamily consists of thirteen genera with about 300 species, all of which inhabit either Africa or southeastern Asia.

Ancanthotermes acanthothorax, of western and central Africa, has three soldier forms, with spinelike projections on the pronotum and notum. The agile movements and dark brown color of these termites lend them an antlike appearance; when columns march across the floor of the jungle one can hear a light rustling sound. The soldiers of the species of the genus *Pseudacanthotermes* have only two spines, located on the anterior edge of the pronotum; the small soldiers are extraordinarily nimble. The genus *Protermes* is restricted to the African rainforests; the nests of their species are built of mud and sand, shaped like flattened domes, and traversed by broad channels which open to the outside in low chimneys. The nests of *Sphaerotermes sphaerothorax* lie among the roots of jungle trees; though they make fungus combs, there are said to be no fungi on them. The reproductive individuals and soldiers of the GIANT TERMITES (genus *Macrotermes*) are very large; the heads of the larger soldiers narrow anteriorly. In Indochina and Indonesia the most widespread species are *Macrotermes carbonarius* and *M. gilvus*; the latter builds extensive, grass-covered cupolas of earth. The African species, among them *M. imperator*, *M. lilljeborgi*, and *M. mülleri*, occur only in the rainforest; there, even by daylight, one may observe their columns of harvesters collecting leaves, which they cut into round pieces. When danger approaches, the soldiers

The castes of *Bellicositermes natalensis* and their development. From eggs laid by the queen (♀), the tiny nymphs of the first stage (1_1) hatch. Development to alates occurs by way of five nymphal stages (N_1–N_5), in each of which the wing primordia become more evident. After swarming, the reproductives (GG) discard the wings and, in pairs, form new colonies. While the king (♂) retains his original size, the abdomen of the queen (♀) is distended by the enlarged ovaries. Development of the infertile worker and soldier castes also begins with the small first-stage nymph (1_1). The male nymphs of stages 2 and 3 (gl_2, gl_3) are somewhat larger than the corresponding female nymphs (kl_2, kl_3); they molt to become male large workers (gA) or female small workers (kA), respectively. The large and small soldiers (gS, kS) arise from the small workers or the small nymphs of stage 3, respectively, by way of white preliminary (presoldier) stages (gVS, kVS). The soldiers of this species are thus always female.


♀
♂
GG
gS
kS
gVS
kVS
gA
kA
N5
N4
N3
N2
N1
I1
gl3
gl2
kl3
kl2



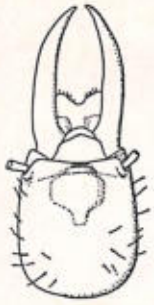


Fig. 7-13. Head of a soldier of *Procubitermes sjöstedti*, with saberlike mandibles.



Fig. 7-14. Mushroom-shaped earthen nest of *Cubitermes fungifaber* in a jungle on the Ivory Coast.

◁ A nest made by *Bellicositermes bellicosus* in the eastern African savanna.

produce a rustling noise, which leads to the immediate retreat of the workers into the subterranean nest.

Termites of the genus *Bellicositermes* are closely related to those of the genus *Macrotermes*, but they are distinguished by both morphological and behavioral features. The oval head of the large soldier barely narrows anteriorly, while the small soldier has legs which are not so long and antennae shorter than the width of the head. They inhabit primarily savannas, and the workers do not come into the open in search of food; they provide themselves with covered passages along the ground and protect feeding areas on the surface with a roof of clay. Three species of this genus, widespread in Africa, build striking nests; sometimes they contrast with the surrounding soil because the termites have carried the necessary structural materials—sand and clay—up from deeper layers of the earth.

The largest of these animals, *Bellicositermes goliath*, piles up massive domes of earth which may reach a height of 2 to 5 m and a diameter of 10 to 20 m; the dwelling area itself, however, occupies only a small part of the total volume. The termite fortresses shaped like haystacks, pyramids, or towers, which have been admired and described so often by travelers and termitologists are the nests of *Bellicositermes bellicosus* (see Color plate, p. 146), and *B. natalensis* (see Color plate, p. 145). A surprisingly orderly living space is hidden beneath the hard, thick outer wall. The outer cells contain the fungus gardens and the inner stories and chambers contain the eggs, juvenile stages, workers, and soldiers; in the center there is a particularly thickwalled chamber with only a few entrances. This "queen cell" contains the founding pair, the small king and his enormously swollen queen. Both of them are continually provided with food, in the form of saliva, by the workers. The queen lays tens of thousands of eggs every day.

The pyramidal nests of *B. natalensis* in western Africa are characterized by a peculiar structural element. Vertical ribs stand out like buttresses on all sides; unlike the massive nest wall, the ribs are penetrated by numerous canals. Fine passages leading almost to the surface make the walls of the ribs porous. At both top and bottom the ribs communicate with the living area. The suspicion that the ribs function as "external lungs" for the nest has been confirmed by detailed investigations. With these colonies of millions of individuals, a supply of fresh air is of course vital; if the nest were hermetically sealed the enclosed oxygen would last for at most twelve hours. Adequate air circulation is generated by the system of ribs: the air in the ribs is warmed by the rays of the sun and rises, entering the living space by way of the upper channels. At the same time the used air is sucked out through the cellar and into the ribs. While moving through the ribs, the air slowly exchanges with fresh air through the porous surface. The ribs, of course, are subject to the daily temperature fluctuations in the environment; at night and early in the morning the air in them is cooler

than in the living area, which these termites always keep at around 30°C. Then the airstream flows in the reverse direction. By using smoke, one can make these very slow ventilating currents visible.

In other regions the nests of *B. natalensis* have no ribs. Instead, the entire air mass in the nest is replaced; the air rising from the living space passes out through thin-walled places at the peak of the nest, while fresh air is drawn in through openings at the base of the nest or through subterranean channels. This nest-conditioning is a factor in the wide distribution of the *Bellicositermes* species in Africa.

The genus *Odontotermes* includes many species. The soldiers vary greatly in size and shape of head. Most species live in dense nests underground. Some, for example, *Odontotermes redemanni* from Ceylon and India, or *O. badius* in Africa, build high hills of earth penetrated by ventilation channels. The queens can be as large and fertile as those of the species of the genus *Bellicositermes*. The tightly stretched cuticle on the flanks of the abdomen appears to be covered with warts. The genus *Ancistrotermes*, with but a few species, occurs only in Africa. Its species have habits resembling those of the species of the genus *Microtermes* of Africa and Asia, with its tiny workers and soldiers. The subterranean nests consist of small, scattered chambers filled with spherical fungus gardens. Occasionally *Microtermes* species move into the nests of other termites.

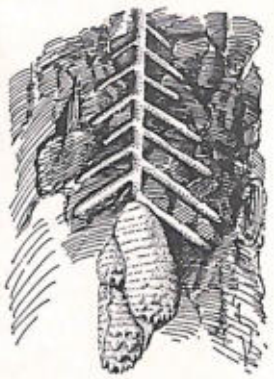


Fig. 7-15. Earthen nest of *Procubitermes arboricola* on a tree trunk in the Congolese jungle. Ridges of earth arranged in a herringbone pattern divert rainwater running down the trunk.

D. The NASUTITERMITINES (subfamily Nasutitermitinae): These are characterized by the unique armament of the soldiers. The labium of reproductive individuals is broad and lacks chitinous cross-banding, and the foremost tooth of the mandible may be either small or pronounced. The soldiers of some South American genera have large rectangular heads with powerful daggerlike mandibles; in all the other species, though, the soldiers are typical nasuti, with the head shaped like a retort, forehead drawn out into a conical nozzle, and mandibles much regressed. There are two groups of genera, forming a total of more than fifty genera and almost 500 species, distributed throughout the tropical regions.

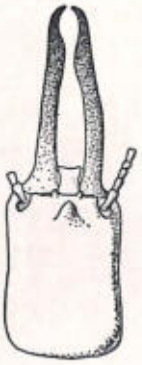


Fig. 7-16. The soldiers of *Termes* have an elongated head and stilettolike mandibles (here, *Termes ondontomachus*).

Within this subfamily one can readily follow the course of evolution from the mandibulate to the nasute soldier. Even among the primitive genera, with mandibulate soldiers, the group split into two main parallel branches, one of which became adapted to feeding on humus. The true nasuti arose only later, independently in each branch. The development of the frontal gland continued to progress, while the mandibles regressed to form toothless, nonfunctional mouthparts. The frontal gland of the nasuti takes up the whole back of the head and opens at the tip of the head projection. It secretes a sticky substance which the soldiers squirt in a fine stream at enemies (ants) trying to force their way into the nest; this renders the intruders incapable of movement. The nasuti are small, but when danger threatens they turn out in great numbers and quickly discover and surround the enemy. When columns of workers go out in search of food,

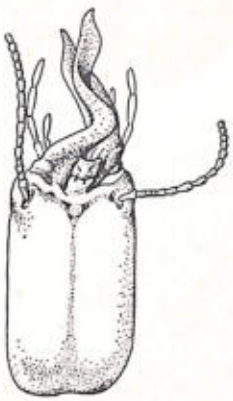


Fig. 7-17. In *Pericapritermes appellans* and its relatives, the left mandible is lengthened and multiply bent.

the soldiers form a cordon at either side, with their noses pointing outward. The effectiveness of this chemical defense has made it possible for the nasuti to do without the mandibular weaponry; it has certainly also contributed to the success of this subfamily, which started in South America, in its colonization of the warm, humid regions of southeastern Asia, Australia, and Africa.

The first group of nasutitermitine genera, the PROCORNITERMITINES (Procornitermitini), includes termites which feed on plants or dry and rotted wood. They build their nests with soil or cardboardlike material. The most primitive genus in the subfamily is considered to be *Syntermes*, the twenty-three species of which are distributed in the northeastern part of South America. These animals live underground or in hills of earth, and gather dead leaves and blades of grass. The species of the genus *Procornitermes* construct subterranean nests the size of a human head, made of clay and divided into stories. In South America one often sees the hard earthen hills of *Cornitermes* species.

In this group most species which have nasuti live outside South America. The only new World genus is *Constrictotermes*. The nests of its species are stuck to trees and provided with water-repellent roofs. In the Indo-Malaysian tropics, the genera *Hospitalitermes*, *Bulbitermes*, and *Longipeditermes* are represented by numerous species, many with large populations. Usually they hang their carboardlike nests in trees. The genus with the most species, *Nasutitermes*, is found in all tropical regions and lives primarily in arboreal cardboardlike nests; some Australian species (for example, *Nasutitermes exitiosus* and above all *N. triodiae*) erect large structures of earth, shaped like slender pillars 6 to 8 m high, which are among the tallest termite nests. It is striking, moreover, that in those regions without fungus-growing termites, other genera which elsewhere live underground have taken up the construction of hills. The numerous species of the genus *Trinervitermes* from the African and Indian savannas, should be mentioned; they gather grass and store it, usually in small dome-like nests. The same behavior is displayed by the Australian genus *Tumulitermes*. Both genera are often referred to as harvester termites.

The second group of genera in the subfamily Nasutitermitinae is the PARACORNITERMITINES (Paracornitermitini). They have become completely adapted to feeding on humus. The more primitive genera *Paracornitermes* and *Labiotermes* are restricted to South America; the twenty species of *Armitermes* are found from southern Brazil to Honduras. The more highly evolved genera, with very small nasuti, have become distributed throughout the tropical latitudes. The species of the South American genus *Subulitermes* and the African genera *Eutermellus* and *Mimeutermes* live hidden in the ground in small colonies.

The termite way of life

This brief but systematic tour makes it evident that the abundance of termite types necessitates our selecting only a few for discussion of their habits. Moreover, one can expect that these will be quite varied as well.

It is a long way from the simple colony of the primitive wood termite to the highly evolved communal life of, for example, a fungus-growing species of the genus *Bellicositermes*. There is such a wide range of behavior that here, too, we must be content with a sample.

Division of labor in termite society

The social organization of the termites is based on the existence of different castes of animals, and is characterized by strict division of labor. The reproductive caste provides for the continuation of the species, and when a new colony is founded the two reproductives initially perform all the vital activities themselves. Later they confine themselves to reproduction, turning over all the other tasks to their progeny. The soldiers serve exclusively to protect the colony. The workers are responsible for the acquisition and distribution of food, as well as for nest building and care of the young.

A peculiarity of termites is the reluctance of the colonies, once founded, to move; this means that they, like plants, must overcome special problems in the maintenance of the species. As a rule new colonies are founded by winged male and female reproductives (alates) which leave the parental nest at certain seasons of the year—in the tropics, usually at the beginning of the rainy season. The alates of the lower termites usually continue to swarm in small groups for weeks, whereas in the higher termites tens of thousands of them rise into the air at once, like a column of smoke. The other castes also participate in this important social event. The workers often prepare special flight ramps. When ready, they open the exit doors, which are then guarded by the soldiers. In general, the alates do not go far from the nest. Those of some termite species fly toward conspicuous structures in the landscape. Species of *Allognathotermes*, *Pseudacanthotermes*, and *Microtermes* form partnerships between males and females during the flight. But usually the male and female alates come to earth singly. There they discard their now superfluous wings, and search for a partner. In this process both sexes may run about at random, as in species of *Cryptotermes* and *Kalotermes*. Sometimes, however, the female, as in species of *Odontotermes*, stands still and attracts the male by her posture or by releasing an odorous substance (sex pheromone). Once pairs have been formed the two termites run in tandem, the female ahead of the male. This tandem running might be regarded as a sort of "engagement ceremony," for it is not accompanied by copulation; the couple in fact are looking for a place to live.

The choice of a nesting place is of course determined in large part by the way of life of the species. Whereas the wood termites (Kalotermitidae and Termopsidae) hide themselves directly in wood, the soil termites construct the nuptial chamber underground. The young pair of termites cooperates in digging and finally in closing the chamber off from the inimical outside world. Only a few pairs survive to complete this task. Even when they are swarming out of the nest the majority fall prey to birds or bats, and on the ground amphibians, lizards, snakes, and above

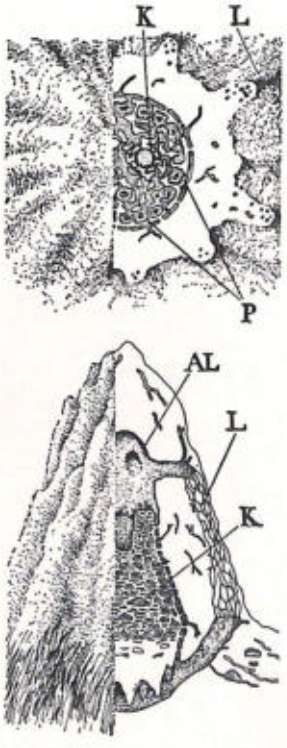


Fig. 7-18. Nest of *Bellicositermes natalensis*, cut out to show a longitudinal section (below) and cross section (above). K, queen cell; P, fungus garden; L, ventilation channels in the ribs; AL, opening of one such air shaft.

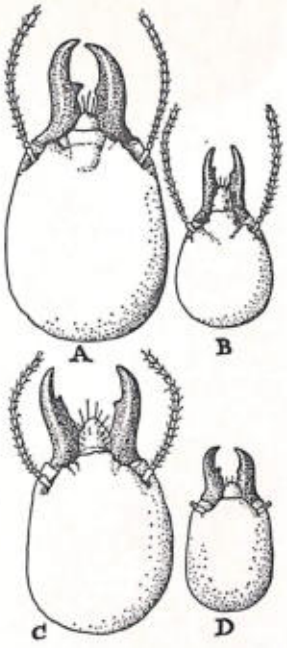


Fig. 7-19. Head form in *Odontotermes badius* (A), *O. latericius* (B), *O. transvaalensis* (C), and *O. montanus* (D).

all ants lie in wait for them; in fact, they are even regarded as delicacies by the native humans. But the withdrawal of a pair into a protected world of their own marks the beginning of a new termite colony.

Copulation takes place in the nuptial chamber. The eggs which are then laid, and the emerging larvae, are cared for and fed by the young couple. Founder termites which make their nests in wood take in food in the process, whereas those living in the soil must draw upon the reserves stored in the fat body. Additional nutrients are supplied by the decomposition of the now redundant flight muscles and the eyes. The parents feed their nymphs with saliva; in the lower termites the nymphs also suck up the hindgut fluid of the parents, thus acquiring the vital flagellates. As a result of this bottleneck in the food situation, the conditions of life in the young colony are rather unfavorable during the first four to six months. Matters improve only when the first workers have grown up and can gather food. Then the queen is relieved of the task of brood care; she returns to the interrupted process of egg laying and from then on, with the king in constant attendance, devotes herself solely to reproduction. Caste formation in the young colony thus permits the division of labor.

Egg laying

Termite colonies grow very slowly. It takes years until the small communities of wood termites, with queens which lay 200 to 300 eggs a year, have accumulated a few thousand members. In contrast, the queens of some fungus-growing types, for example, species of *Protermes*, *Bellicositermes*, and *Odontotermes*, become extraordinarily large and fertile. The abdomen is stretched by the swelling of the ovaries, which also involves—and this is most unusual for an insect—an increase in the number of the ovarioles. The abdomen of a 12-cm-long queen of *Odontotermes* species contains more than 5000 ovarioles. The queen grows to look more and more like a sausage and finally can hardly move. She has become an "egg-laying machine," producing 30 to 40 thousand eggs a day. Her community requires decades to mature, comprises several million descendants, and probably continues to exist for as many decades again.

Some termites colonize not by sending out swarms of alates, but by the breaking away of part of an existing colony, rather as the bees do when they swarm. In this daughter community, a supplementary reproductive caste is formed. This type of multiplication of colonies is found primarily in the lower termites; it seems to be the rule with *Mastotermes darwiniensis* and *Reticulotermes flavipes*. Even under unfavorable climatic conditions, when the termites must live predominantly underground, they colonize in this way; an example is the eastern subterranean termite *Reticulotermes flavipes*, which was carried from North America to Europe. The generation of daughter colonies has also been observed in species of of the eastern African genera *Schedorhinotermes* and *Coptotermes*. Such offshoots have good prospects in the struggle for existence, since the reproductive individuals are accompanied by functional soldiers and workers at the outset.



Fig. 7-20. Nasutus of a nasutitermitine.

All the eggs laid by the queen are carried into the brood chambers by the workers and cared for there during the development of the embryo, which requires twenty to sixty days. After hatching, the nymphs grow in a stepwise manner, molting from time to time as they pass through the various stages of juvenile development. This incomplete (hemimetabolous) development leads from the nymph, by way of nymphs with wing primordia, to sexually mature, winged adults; divergences at certain stages from this sequence produce the infertile workers and soldiers, which are in all respects immature forms, with arrested physical development. But termites are also exceptional in that they can develop sexual organs in certain juvenile stages. These become the supplementary reproductives mentioned above; they are neotenic animals, capable of reproduction while otherwise retaining juvenile characteristics.

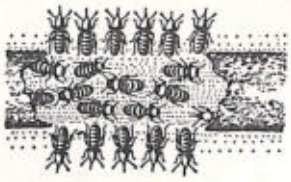


Fig. 7-21. If part of the trail is in the open, or a covered gallery is partly destroyed, the workers are protected by cordons of nasuti; the path is usually marked by drops of excrement.

Workers and pseudergates

The development of castes in the various families of termites does not follow a single pattern. For example, the kalotermitids and termopsids lack true workers; their tasks are performed by older larvae, called pseudergates. The pseudergates of the yellow-necked termite (*Kalotermes flavicollis*) may undergo any number of molts, while their body form does not change (i.e., they undergo "stationary" molts). But while in this suspended state, they are also capable of developing further at any time, either by way of nymphal stages into alates, by way of presoldier stages into soldiers, or even into neotenic supplementary reproductives Similarly, nymphs can be transformed into soldiers or supplementary reproductives, or even undergo regressive molts, becoming pseudergates.

The rhinotermitids possess a true worker caste. The workers of *Reticulotermes flavipes* arise from third-stage nymphs. In addition there are pseudergates, produced from the younger nymphal stages by molts in which the wing primordia regress. Both workers and pseudergates continue to molt at regular intervals, and most stages are capable of deviating from this pattern of development to become soldiers or supplementary reproductives.

In the higher termites, two nymphal stages precede the worker form. The transition from the whitish, inactive nymph to the independent worker occurs without any special changes in body structure. But the alteration of behavior is clear, and the transition to the worker is further denoted by the fact that the gut content of the worker is visible through the body wall. In most genera the workers continue to molt, evidently never reaching a final stage. Soldiers, as a rule, arise from the first worker stage and may be either male or female, varying from genus to genus, though they never reach sexual maturity.

A special position is occupied by the fungus-growing Macrotermitinae. Their nymphs pass through three stages. Those of the first stage are all alike, but in the two subsequent stages the male nymphs become somewhat larger and finally develop into large workers. The female nymphs,



Fig. 7-22. Pillar nest of *Nasutitermes triodiae* in Australia.

smaller than the male, become either small workers or soldiers. As already mentioned, there are genera in this group with two soldier forms; here the small soldiers have come from the small nymphs and the large soldiers, from the small workers (see Color plate, p. 145). Except for the species of the genus *Sphaerotermes*, the soldiers of all fungus-growing species are female.

The greatest potential for alternative development of the juvenile stages is found in the lower termites; the reproductive and infertile castes do not separate until quite late. In the higher termites this separation occurs as early as the first nymphal molt; there the possible alternatives for development are so restricted that eventually the infertile castes arise only from a certain stage and sex.

Social regulation

In termite colonies there is a well-adjusted balance in the numbers of individuals in the different castes; should the proportions be disturbed, they are brought back into equilibrium. This social regulation is particularly pronounced in the lower termites. Thus, if a group of yellow-necked termites is for some reason composed exclusively of nymphs, it very quickly develops a number of supplementary reproductives; a few nymphs become soldiers, some go on molting to become alates, and all the rest develop regressively into pseudergates. The initially uniform group quickly transforms itself into an optimally balanced community composed of all castes.

We now know that the castes of the lower termites are not, as was previously claimed, fixed in the egg, but rather are determined by the social environment during juvenile development. Termitologists once assumed that the fate of juveniles was influenced by the kind or quantity of food. Thorough investigations in the last two decades have shown, however, that the various castes, by their very presence in the colony, exert a specific inhibitory effect upon the juvenile stages which are still uncommitted or equipotent. If one removes the reproductives from a colony of yellow-necked termites, all the newly molted pseudergates and nymphs transform themselves into neotenic supplementary reproductives, though only one pair of these is left alive; the inhibitory effect of this couple then prevents the further formation of neotenics.

Hormonal determination of caste

Caste determination is brought about mainly through the release of hormones, the effectiveness of which lasts only a short time. Therefore, they must be distributed quickly throughout the colony, by the intensive exchange of food. To distinguish them from ordinary hormones, which are control substances within the body of the animal producing them, these inhibitory substances were first called ectohormones, then social hormones, and finally, pheromones. By definition, they are produced by one animal and have a certain effect on another animal of the same species. Presumably, the inhibitory pheromones of the termites affect the endocrine system and thus the balance of hormones in the juvenile stages. Maintenance of caste equilibrium depends upon several pheromones.

These, singly or in combination and in accordance with the quantities in circulation, either inhibit or facilitate the formation of a caste. Other factors also play a role; for example, the development of nymphs depends on the season of the year.

In the higher termites, the process of caste determination is not so well understood. It has not yet been discovered, for example, whether the castes are predetermined in the egg, perhaps by the action of particular genes; the obvious early separation of the nymphal stages at least suggest a genetic basis. On the other hand, the developmental potential of the juvenile stages is not entirely restricted even in the higher termites; here, too, nymphal development is under the influence of the seasons.

Defense of the community

The task of the soldiers is to defend the termite colony against intruders, in particular predatory ants. To alarm the colony, the soldiers beat their heads against the ground. The mandibulate soldiers of the basic type, for example, those of *Cryptotermes* species, are also physically well suited for shutting off the narrow connecting passages (see Fig. 7–5). Usually the biting mandibles are equipped with strong teeth and sometimes even with hooks (as in *Amitermes* spp., Fig. 7–11). Some soldiers wield toothless daggers; examples include species of *Procubitermes* (Fig. 7–13) and *Bellicositermes*. The mandibles may also be transformed into slender stilettos (*Termes* spp. Fig. 7–16) or snapping weapons shaped differently on the two sides (*Pericapritermes* spp. Fig. 7–17); the tips of such weapons are first pressed together and then slid apart, wounding the enemy with a rapid blow. Other soldiers (e.g., *Rhinotermes* spp.) use the fluid produced by the frontal gland as an aid in battle. The development of a squirting apparatus in the true nasuti (in the Nasutitermitinae) made this mode of defense so effective that these animals dispense with mandibles altogether. In no case, though, are the termite soldiers capable of feeding themselves.

Gathering and distributing food

The most important task of the workers is the acquisition and distribution of food. The wood termites, of course, live directly within their food, but other workers leave the nest, by subterranean tunnels or along covered paths, in order to get to the food sources; only in a few species do they forage for grass and leaves in the open. The workers bring in food and pass it on to their nestmates either by vomiting from mouth to mouth, or after it has passed through their alimentary canals. Certain stages: nymphs, reproductives, and in some genera even the soldiers, are fed exclusively with saliva. This incessant exchanging of food (trophallaxis) also serves to distribute the caste-determining pheromones just described.

Digestion by means of symbionts

Termites cannot digest their main food, cellulose. Lower termites depend upon the assistance of protozoans (flagellates; see Vol. I) which settle in the hindgut. In contrast to the cockroach *Cryptocercus punctulatus*, the termites lose their symbionts at each molt, but regain them from a sibling. The higher termites, too, usually have special aids to utilize cellulose. Many species have become adapted to the consumption of plant

remains decomposed into humus by fungi and bacteria; these include the true termites and some amitermitines and nasutitermitines. The harvester termites (species of *Trinervitermes* and *Tumulitermes*, as well as species of the amitermitine *Drepanotermes*) first let the food ferment in the nest. The fungus-growers (Macrotermitinae) process the wood brought into the nest to make fungus gardens where the wood is transformed by the fungi into digestible food.

Nest construction

The workers are also responsible for nest construction. Among the wood termites, they gnaw out the chambers of the nest. In the great majority of termite species the workers dig subterranean systems of passages and hollows. In a never-ending sequence of tiny efforts they create complex structures of earth or wood, the size of which—in proportion to the human scale—can exceed by far that of the largest skyscrapers. The termite nest offers its soft-skinned inhabitants protection from their many enemies. Moreover, these amazingly elaborate structures erected by blind workers have effective air-conditioning systems which provide the colony as a whole with a carefully regulated environment.

Termite society as a superorganism

If we compare the individual termites of a colony with the cells of an organism, and the castes with its organs, the view is inescapable that the society as a whole represents a higher unit of life, a superorganism as it were, the components of which are interdependent in every respect. This concept has been put forth in particular by the American termitologist A. E. Emerson. This is of course not an explanation of the behavior and achievements of the termites, but the mechanisms responsible may be more readily understandable in the framework of the community they serve.

The termites have become totally adapted, in both body and behavior, to this communal way of life. Each caste, like the tissues of an organism, can carry out only certain tasks. The individual termite is incapable of preserving itself or the species; without the shelter of community cooperation it must perish. Dependence upon food holds each termite in its place, and the exchange of food plays a critical role in the maintenance of a unified, closed community. In raising the young within the bonds of the family, in apportioning work appropriately, and in controlling optimally the physical environment within the nest, the termites have developed effective and admirable procedures and social organization. But we should not forget that, although they are the oldest social insects, they have not succeeded in the course of hundreds of millions of years in gaining true ascendancy upon the earth.

The individual: gear in a machine

"Insect social systems are based upon complete dedication of the individual to the interest of the State," said Adolf Remane; he continued, "The individual is a small gear in the machinery of the State and operates exactly as the preservation of the State demands. Insect States are nearly perfect functional organizations." In contrast, all the higher social structures among the vertebrates—including humans—are based upon groups

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The individual: gear in a machine

"Insect social systems are based upon complete dedication of the individual to the interest of the State," said Adolf Remane; he continued, "The individual is a small gear in the machinery of the State and operates exactly as the preservation of the State demands. Insect States are nearly perfect functional organizations." In contrast, all the higher social structures among the vertebrates—including humans—are based upon groups

in which the members know one another personally (individualized associations; cf. Vol. XI) and within which there exist rank orderings. Disputes among the members of the community control the origin, the maintenance, and all changes of the rank order; therefore these struggles between the elements of higher vertebrate communities are fundamental to their organization. This kind of organization, much more flexible and adaptable than insect society, enabled humans to develop the most varied types of community structures and, with them, to rise to the position of "masters of creation." A human state in which each individual is only a cog in the works, as in the "states" of termites, is irreconcilable with the essential nature of man and with his personal consciousness; an organization of that sort could be realized only by the total suppression of everyone and could therefore not endure. It is thus not without reason that termite society has become a symbol of an inhuman form of government. Time and again dreadful visions of the future are suggested in which either the termites manage to become lords of the earth—which, as we know, is impossible—or humanity, as a consequence of overpopulation, is eventually forced to go the way of the termites. In 1933 the zoologist K. Escherich, specialist in termite research and forestry, gave a speech on the occasion of his inauguration as Rector of the University of Munich, in which he warned against this erroneous line of thought; the title of the speech was "The Termite Delusion."

Paragons or monsters ?

The next order in the superorder Orthopteroidea is the EARWIGS (Dermaptera). The scientific name means skin-winged, and refers to the large, fragile hindwings. But this is too close in meaning to the scientific name for the bees, ants, etc. (Hymenoptera) to be adopted in the common name for the order. Hence the persistence of the popular name, earwigs, although this name is misleading. These harmless animals do not creep into human ears, much less bite into the eardrum with their pincers, as superstition has it. The most striking characteristic of the earwigs is the strong pincers on the abdomen. An indication of the origin of these is found in the primitive DIPLATYIDS (Diplatyidae), the nymphs of which bear segmented caudal cerci instead of the pincers, until the last molt. Then the basal segments of the two cerci become a pincer, all the remaining segments being discarded. The earwigs are nocturnal hunters, using the pincers to grasp flies and small caterpillars which they then push over the back and up to the mouth. Besides their role in prey capture, the pincers are used in defense and, in the flying species, for unfolding the wings. The forewings of the earwigs are much shortened elytra; surprisingly, the hindwings, large in area but cleverly folded like a fan, fit beneath them. Regression of the wings is common.

Order: Dermaptera

There are about twenty earwigs native or introduced into North America, distributed among five families. Four species belong to the TRUE EARWIGS (family Forficulidae), the most frequently encountered

▷
Book lice: 1. *Liposcelis divinatorius*, 2. *Trogium pulsatorium*.
Biting lice: 3. Dog louse (*Trichodectes canis*), 4. *Philopterus ocellatus*, a crow louse, 5. *Columbicola columbae*, the slender pigeon louse.
True lice: 6. Clothes louse (*Pediculus humanus humanus*), 7. Crab louse (*Phthirus pubis*), 8. Hog louse (*Haematopinus suis*; L 3–6 mm).


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Fig. 7-23. Earwig (*Forficula auricularia*), brooding female with eggs.

being the COMMON EARWIG (*Forficula auricularia*; see Color plate, p. 115). They can be found during the day, often in large sleeping communities, underneath bark, boards, or stones, in fact, anywhere that affords close contact on all sides. In autumn the adults move into winter quarters, singly or in pairs, not uncommonly digging their own holes in the earth for the purpose. Though in summer they mate indiscriminately with one another, they live monogamously in winter. When egg-laying begins in early spring the female changes her behavior; she lives entirely for the care of the young and vigorously repels any intruder, including her mate. The forty to fifty eggs in the clutch are licked continually, for if they were not they would soon become infected with fungi. The eggs are gathered into a pile, and even young larvae which stray too far away are fetched back by the watchful mother. But soon the young become independent; they join the sleeping communities of the adults and by autumn they are adult themselves. A few days or weeks after the last molt they become sexually mature, and thereafter live for another eight to ten months. Although the common earwig has fully developed hindwings, it has seldom been seen to fly. In contrast, the SMALL EARWIG (*Labia minor*, family Labiidae) flies readily and occasionally comes to lights at night. *Labidura riparia*, from Europe, lives singly in the sand of coasts or riverbanks, in the tunnels it digs, but may also be found far from water. This species belongs to the family Labiduridae, as does the black-brown, wingless SEASIDE EARWIG (*Anisolabis maritima*, family Carcinophoridae,) which one may find under stones throughout the Mediterranean countries, and which reportedly occurs in North America. Most of the roughly 1100 earwig species lives in the tropics and subtropics; the earliest fossilized remains come from the Tertiary (lower Miocene, about 25 million years ago).

The genus *Arixenia*, the only genus in the suborder Arixenina, has two species, which differ widely from the other earwigs, presumably as a result of their parasitic way of life. Both species are wingless, have regressed eyes, and are viviparous. Their caudal cerci are unsegmented, like the pincers of the other earwigs, but they are much more delicate and covered with hairs. *Arixenia esau* was found in Borneo in the fur of a bat, whereas *Arixenia jacobsoni* was discovered in great numbers in the guano inside a Javanese bat cave.

The suborder Diploglossata, with one family, Hemimeridae, has diverged even further from the ancestral form—which it perhaps shares with true earwigs—through its parasitic existence. The eight species which have been described are so similar to one another that they have been ascribed to a single genus, *Hemimerus*. They are about 1.5 cm long, blind, and completely without wings; the caudal cerci are soft, unsegmented, and hairy. All eight species are parasitic on the various subspecies of the African giant hamster rat (*Cricetomys gambianus*; see Vol. XI), feeding on the scales shed from the host's skin. The entire development into an independent larva occurs within the mother's body. The eggs are

◁
Above, aphid colony (family Aphidae; see Chapter 11); the female in the middle of the picture is giving birth to a young nymph.
Below left: Kissing bug nymph (*Reduvius personatus*; see Chapter 10), camouflaged with dust but with the antennae (lower left in picture) free of dust.
Below right: a thrips of the family Thripidae (see Chapter 9) as seen under the microscope.

poor in yolk and thus lack the necessary reserve of nutrients, so the mother and offspring together generate a placenta, by way of which the mother transmits nourishment to the developing embryo—an astonishing parallel to the embryonic development of mammals (see Vol. X).

Webspinners and zoropterans, by P. Rietschel

While the termites are clearly and unambiguously related to the cockroaches, there are orders of insects whose evolutionary origin is shrouded in darkness, for example two curious orders, the Embioptera and Zoroptera. Both orders display primitive traits which would put them near the origins of insect evolution, but they do not appear to be particularly closely related to any of the known primitive groups.

Order: Embioptera

The WEBSPINNERS or EMBIIDS (order Embioptera) are also small insects (L 15–20 mm), of a dusky color, with biting mouthparts; the males are winged while the females, similar in appearance to the larvae, lack wings. Both imago and nymph of both sexes have silk glands in the enlarged "heel" of the anterior tarsi. Groups of webspinners cooperate in spinning threads of silk into tunnels under stones and bark, in which they live as a community. They have existed since the Lower Permian and even then resembled the present-day species of the genus *Clothoda*. Now there are about 150 species in the tropics of the Old World and the New, extending as far north as the southern regions of Europe, Russia, and in North America to Florida, Texas, and southern California.

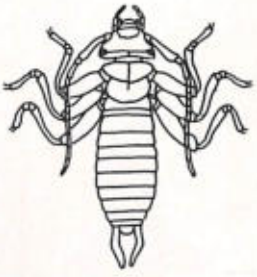


Fig. 7-24. *Arixenia jacobsoni* (L 20 mm).

The webspinners are one of the few insect orders which the insect hobbyist will seek in vain in central Europe; the northernmost species are found at the level of the Mediterranean coast. The winged males sometimes fly to lights at night, but one can find both sexes, and the larvae, only by turning over stones. Their presence is revealed by bluish-white tubes of spun threads running horizontally and down into the soil. The nymphs grow in the tubes; like the adults, they have silk glands in the tarsi and participate in building the nest. Here one can recognize the beginnings of an organized society. Of course, simply turning over the stones does not reveal a great deal about the inhabitants of the silken tunnels. When exposed to daylight, the webspinners flee to the depths, running backward just as dextrously as forward. But usually by digging after them one can catch a few of the twenty or so inhabitants. One plea, though, to all amature entomologists interested in the rich animal life to be found under stones: After your search, always put the stones back in their original positions! Otherwise your urge to investigate will have destroyed the homes of countless animals. One well-established webspinner area, near Rovinj in Istria, Yugoslavia, was entirely laid waste in 1968 by the negligence of unknown "zoologists."

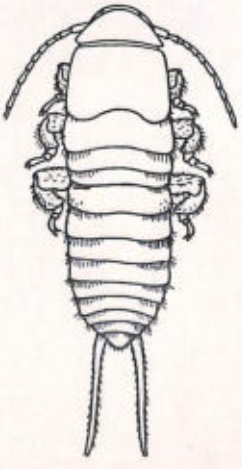


Fig. 7-25. *Hemimerus bouvieri* (Diploglossata; L 12 mm).

The brownish or yellowish-brownish webspinners have a large head with mouthparts directed forward, protruding compound eyes but no ocelli, and antennae consisting of many segments and shaped like threads or strings of beads. The mandibles of the males are more slender and have fewer teeth than those of the females and larvae. One may therefore infer

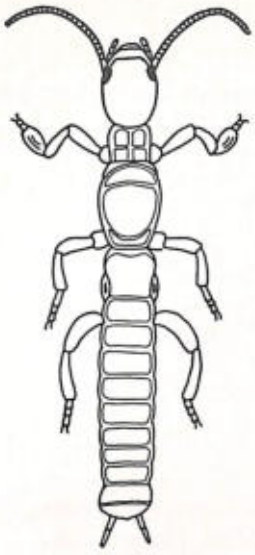


Fig. 7-26. The webspinner *Embia sabulosa* (L 8 mm).

that the two sexes subsist on different food, though it has proved possible to raise them on the same vegetarian diet. In both sexes the thorax and abdomen are more narrow than the head; the male usually has two pairs of wings, smoky gray in color and with few veins. The forewings and hindwings are identical and, like those of the damselflies and termites, lack lobes on the posterior margin; the anal lobe is barely developed. The most striking characteristic of the webspinners is the enlargement of the first tarsal segment of each foreleg. These contain the silk glands, which open at the tip of the hollow "spinning hairs" on the undersides of the first and second segments. The second pair of legs is more fragile, while the third has thickened femora with strong extensor muscles for the tibiae. The hindlegs push the body forward, in a form of locomotion also encountered in the burrowing mole crickets and *Cylindracheta* spp. (see Chapter 5). All of the tarsi are composed of three segments. The slender abdomen bears a pair of caudal cerci, symmetrical in the female but, with few exceptions, differing in size on the two sides in the male. Since the female genital opening at the posterior edge of the eighth abdominal sternite is not provided with an ovipositor, the wingless female is identical to a nymph; the last molt, which leads to sexual maturity, is not accompanied by any morphological change.

Order: Zoroptera

The ZOROPTERANS (order Zoroptera) are small insects (L 2 mm) with nine-segment antennae shaped like strings of pearls. Both winged and wingless individuals occur within a species, and these may be of either sex; the winged individuals have both compound eyes and ocelli and the thorax is covered by a hard shield, while the wingless forms are eyeless and the cuticle of the thorax is soft. The forewings and hindwings are dissimilar, with few veins, and they may be cast off as in the termites. The zoropterans form small colonies near the ground, but there is no division of work between the winged and wingless individuals. Their geological age is unknown; there are now twenty-two species, all belonging to one genus (*Zorotypus*), known from the East Indies, Ceylon, Hawaii, Florida, Oklahoma, the West Indies, South America, and western Africa. Two species occur in the U.S.A.

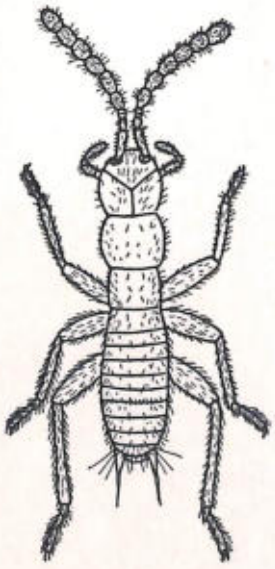


Fig. 7-27. The zoropteran *Zorotypus guineensis* (L 2 mm).

8 The Lice

Orders: Psocoptera, Mallophaga, and Anoplura, by P. Rietschel

The LICE are usually placed in three orders, Psocoptera (book lice), Mallophaga (biting lice), and Anoplura (sucking lice). Some authors place all three orders in a superorder (Psocia) and lump the ectoparasitic lice as a single order, the Phthiraptera. Apart from a few internal characteristics, these groups have little in common structurally, but the habits of the different species indicate that they are related; taken together, they exhibit a uniform pattern of evolutionary development. It is certain, however, that none of the present-day species has arisen from any species of the extant orders. The book lice live in damp places, feeding primarily on mold, and some species are still able to fly. Some of the flightless book louse species are, along with fleas, beetles, and mites, the most common symbionts in bird nests. Bird nests may also have been the habitats of the ancestors of one of the two subgroups of the animal lice, the biting lice. Presumably they moved into the feathers of the birds, where they found warmth and could feed on the scales and dust shed from the skin and feathers. Some species, though, are not restricted to this keratinous food, but use their biting mouthparts to draw the blood of their hosts. Thus they have become true parasites. At several stages in evolution, biting lice have switched from birds to mammals, and it may be from these fur-dwellers that the true lice (the Anoplura) arose. The latter depend entirely upon blood for food; both externally and internally, they are adapted to this parasitic way of life. If these modes of feeding are considered in sequence, they illustrate one of the many ways that parasitism may have evolved.

Order: Psocoptera

Distinguishing characteristics

The BOOK LICE (order Psocoptera; see Color plate, p. 157), also called bark lice, are mostly small insects (L 1–10 mm) with relatively large heads. The shield-shaped median plate (the postclypeus) on the front of the head is usually bulbous, the antennae are slender, the eyes protrude, and the mouthparts are of the biting type, modified through the elongate, chisel-like lacinia of the maxilla. The wings are often regressed; when present, they have few veins and are coupled in flight. The abdomen lacks cerci, but in the male there is a pair of styli like that of cockroaches. Examples

have been dated as early as the Jurassic (140–180 million years ago); now there are about 1100 species, about 143 of which are native to the U.S.A.

Occurrence and habits

Book lice, according to St. v. Kéler, are frequently encountered "in musty clothes cupboards, storerooms, old upholstered furniture, books which have long been untouched, old papers and files, dusty drawers, collections of insects and plants that have not been properly cared for, etc." But their presence is by no means a sign of neglect; they may also be found in the material of the floors and under the wallpaper of clean, pleasant new buildings which have not yet been thoroughly dried out. Under such circumstances, mold develops, and book lice (like the cryptophagid beetles, springtails, and mites) feed preferentially on mold. Their presence indicates dampness; rather than poison these harmless insects, one need only eliminate the dampness and they will disappear of their own accord. There are four species of book lice which live in the rubbish on the floors of beehives, where they eat fallen clumps of pollen that the bees discard, as well as the eggs of the greater wax moth, also found there. In eating the pollen they do no damage, and in destroying the moth eggs they perform a genuinely useful function. Many book lice are found under the bark of trees, where mold is probably their main food. Winged species are encountered on the leaves of the trees. They prefer wilted leaves and probably feed on the fungi which infect them. The free-living book lice species are not restricted to particular plant species, but it is not yet clear whether there is a close association with particular species of algae, fungi or lichens which grow in the plants.

In most book louse species the two sexes occur in roughly equal numbers, whereas in some the males are rare or have never been seen at all. In the latter species the females reproduce parthenogenetically. The eggs are simply stuck onto the substrate; except in cases where the eggs remain over the winter, the nymphs hatch in one to three weeks. The nymphs of the wingless species are very similar in appearance to the adults; those of the winged species soon show signs of the developing wing sheaths. After five to eight molts the book lice are mature. The entire course of development is so rapid that several generations can succeed one another in a year. The free-living species usually pass the winter as eggs, whereas the colder months are no hindrance to the uninterrupted reproduction of those which live in buildings.

The most common species in Germany

Of the approximately fifteen species of wingless book lice found in houses, the two most common species are *Liposcelis divinatorius* (L 1 mm; see Color plate, p. 157) and *Trogium pulsatorium* (L 1.5–2 mm, see Color plate, p. 157). Why the first of these was given the species name meaning soothsayer is unclear, but that of the second (*pulsator* means knocker) refers to the ability of the females to produce knocking or ticking noises. To do this, the louse strikes her abdomen against loose wallpaper or some other resonating substrate; there is a button-shaped thickening on the ventra surface, lacking in the males. It is not known how the males perceive the

ticking. *L. divinatorius* females also have such a ventral organ, but no one has yet heard them ticking. Because of this harmless activity, superstition has given *Trogium pulsatorium*, like the beetle *Xestobium rufovillosum*, the name death watch.

Research on book lice is made more difficult by their small size; with the unaided eye one cannot even identify the species. On the other hand, their minuteness makes it possible to raise them in tiny glass chambers, in which one may follow their entire development from egg to imago with a strong lens or low-power microscope. The poet and zoologist Hermann Löns earned his Doctor's degree by a dissertation upon the book lice, and ten years after his early death science honored him for his contribution to the study of these inconspicuous insects by naming a genus *Loensia*.

Orders: Mallophaga and Anoplura

The ECTOPARASITIC LICE (orders Mallophaga and Anoplura) correspond more closely than the book lice to the prevalent idea of a "louse." They live as external parasites in the feathers or fur of warm-blooded animals; away from this habitat, they can survive only for a short time. They never have wings. Their eyes are more or less regressed. The coloration is inconspicuous and the body generally flattened. These lice glue their eggs to the feathers or hairs of their hosts, and the nymphs live in the manner of the imago from the moment they hatch out. Most animal lice are strictly associated with one host genus or even with a single host species. The group is composed of two orders, the biting lice (Mallophaga) and the true or sucking lice (Anoplura). The characteristics shared by the two orders may have arisen from adaptation to the same circumstances; it is not yet clear to what extent there is a close evolutionary relationship.

Order: Mallophaga

The BITING LICE (order Mallophaga; see Color plate, p. 157) are small insects (L 1–4 mm) of louselike shape which sometimes run along the skin and sometimes climb and cling to hairs and feathers. The mouth parts are of the biting type, so that they do not suck blood (but occasionally they eat it). The great majority are parasitic on birds, but some groups have transferred to mammals. On the geological time scale they are recent arrivals; having arisen no earlier than the birds, they have probably been in existence since the Cretaceous or Lower Tertiary. Today there are about 2700 species.

Distinguishing characteristics

The order is divided into three parts (groups of families): 1. the Amblycera, with antennae shaped like clubs or knobs and carried recessed in grooves, like those of fleas, so that they are usually invisible; 2. the Ischnocera, with thin, free-standing antennae of three or five segments; and 3. the Rhynchophthira, with head elongated into a proboscis, the end of which is barbed and bears outward-turned biting mandibles. This third group includes only one family, with one genus and two species; the ELEPHANT LOUSE (*Haematomyzus elephantis*) is parasitic on the skin of both the Indian and the African elephant. All the biting lice, as the name implies, have strong, biting mandibles. Those parasitic on birds are also called

"bird lice," and the few which parasitize mammals have common names reflecting those of the hosts. The distinction between bird and mammal parasitism is not indicative of a special evolutionary relationship, for the transition from birds to mammals has been made several times in both the Amblycera and the Ischnocera. Most of the amblyceran bird parasites can run swiftly along the skin; the antennae, recessed in grooves, do not hamper them as they race through the thickets of feathers, and the legs are equipped with large adhesive pads so that they have adequate traction on the skin. On the other hand, a few of the Amblycera which live on mammals and all of the Ischnocera—both the bird and the mammal parasites—are adapted for clasping and climbing; they have short legs bent inward. The double claws at the end of the foot are well suited to clamping onto plumage, with its regular array of barbs and barbules, but they are not able to hold firmly to the single hairs of mammals. Therefore the lice of this type which live on mammals have only one claw at the end of the tarsus and this, in conjunction with a tarsal pad or tibial process, forms an effective pair of pincers (see Fig. 8–1). The tarsi of the elephant louse are each armed with one powerful claw, which digs into the rough elephant skin like a crampon. The tarsi of the middle and hind legs also have slender accessory claws.

The biting lice subsist, in birds, on scales which fall from the skin and debris and dust from the feathers; on mammals they eat skin oil (sebum) and cast-off bits of the horny layer of the skin. The midgut secretes a special enzyme which converts keratin into a digestible protein. This rare ability to digest keratin is shared by the biting lice and the larvae of both clothes moths and hide beetles. They also readily eat clotted blood on the skin, and some species have gone so far as to produce the bleeding themselves, with their biting mandibles. These have thus become true blood parasites. The PELICAN LOUSE (*Piagetiella* spp.) no longer lives on the skin but rather in the pouch at the host's throat, where it feeds on blood. But it still sticks its eggs to the feathers, following the custom of its ancestors. The CHICKEN BODY LOUSE (*Menacanthus stramineus*) and the SHAFT LOUSE (*Menopon gallinae*) also use the blood of their hosts as a secondary food. But the louse best adapted to regular feeding on blood is the elephant louse. In the process it has become so strongly modified that some entomologists put it in a special suborder, parallel to the Mallophaga; but its relationship to the Mallophaga is obvious.

Most animal lice are strictly associated with a single host species and cannot live on other species. Thus, the young cuckoo in the nest is constantly in contact with its foster parents and their lice, but none of these song-bird lice establishes itself on the cuckoo (cf. Vol. VIII, Chapter 11). Although there are CUCKOO LICE (three species, of the genera *Cuculoecus*, *Cuculiphilus*, and *Cuculicola*), the cuckoo can never acquire these from its foster parents, for they harbor only their own species. It is only when mating with a louse-infected cuckoo that such a transfer can take place.

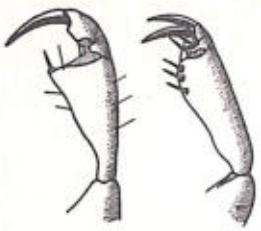


Fig. 8-1. Grasping tarsus of the cattle louse *Bovicola* sp. (left) and the pigeon louse *Columbicola* sp. (right).

If, in the course of time, a group of birds or mammals of one species evolves into a distinct subspecies and finally into a new species, its lice may change along with it, forming a new species of their own. Over longer periods of time, host and parasite can form new genera or even higher systematic groups. In the ideal case, then the systematic arrangements of host animals and their lice should be quite similar (Fahrenholz's rule). There may be various reasons for departures from this rule: 1. Not all groups of biting lice are obligatorily associated with particular host groups. For example, species of the bird-louse genus *Colpocephalum* live primarily on walking birds and diurnal birds of prey, but some live in the plumage of fowl, pelecaniform birds, and ravens; a few live in the feathers of gulls, flamingos, ducks, and parrots. 2. Even within the groups closely bound to certain hosts, there are species which have transfereed to and become adapted to a new host. Thus, there are seventeen species of the family Boopidae which live in the fur of Australian marsupials, most of them on kangaroos. In the boopid genus *Heterodoxus* three species live on kangaroos, but a fourth, *Heterodoxus spiniger*, has transferred to the dog—which is not native to Australia! 3. Even in the ideal case, the systematics of hosts and parasites will agree only if they reflect the true relationships within both groups. If either the bird systematist or the louse systematist has made a mistake, the two systems cannot correspond. Errors in one systematic arrangement may thus be suggested by comparison with the other. In Chapter 10 of Volume VII one learns that the flamingoes, because of their very long legs, used to be classed with the herons and storks, while some zoologists assumed a close relationship to ducks. What can the systematics of bird lice contribute to this question? Flamingoes house a total of five species of lice. Two of them are Amblycera: *Colpocephalum heterosoma*, as mentioned previously, is characterized by loose association with the host, so that its distribution offers no guidance. The other species, *Trinoton femoratum*, belongs to a genus the other sixteen species of which live only on ducks and their relatives. The remaining three flamingo lice are Ischnocera: *Anaticola candida*, *Anaticola phoenicopteri*, and *Anatoecus pygaspis*. The two generic names themselves betray the fact that these lice are duck parasites (*anas* is Latin for duck). In fact, these two genera together include forty-eight more species, all of which live on ducklike birds. The herons and storks also have specific lice, such as the approximately fifty species of the genera *Ciconiphilus*, *Ardeiphilus*, *Ardeiphagus*, and *Ardeicola*, but not one of these species is found on flamingoes. All these results speak in favor of the relationship of flamingoes to ducks, and against that to herons and storks. The converse may also occur: the systematics of birds may be of assistance in solving problems of louse relationships. For example, if among the hosts of the numerous species of *Colpocephalum* (referred to previously) about one-third are herons and storks and another third are hawks and their relatives, this may raise some doubt in the minds of systematists as to the homogeneity of this genus.

The biting lice have no effect on human health, since none of the species which live on domestic animals is capable of existence on humans. But to the domestic animals, they can be a severe threat. The chicken alone harbors seven species of bird lice, and a massive infestation can be lethal to young fowl. They also do appreciable damage to adult chickens; Edgar and King determined that the laying capacity of louse-free hens is eleven percent greater than that of infested hens. Four species of bird lice live in the plumage of homing pigeons; among them, *Columbicola columbae* (see Color plate, p. 157) can be found primarily on the underside of the wing feathers, but *Campanulotes compar* is normally on the contour feathers of the neck. The lice which cling and climb prefer certain regions on the host, while those which walk on the skin (particularly those of the family Menoponidae) do not adopt a fixed territory on the host. The lice on European domestic mammals are almost exclusively Ischnocera; only in South America have the amblycerans succeeded in transferring from their bird hosts to mammals. There, they live in the fur of marsupials, rodents, and one species of nocturnal monkey. One South American native, the guinea pig, was brought to Europe as a domestic and laboratory animal; it carried its lice with it and has retained them.

Those Ischnocera which have made the transfer from bird feathers to mammalian hair are classified together in the family Trichodectidae. Three species of *Cebidicola* live on South American howler and spider monkeys, and one species (genus *Lorisicola*) lives on a loris. The genus *Damalinia* includes the lice infesting European ungulates: *D. equi* on the horse and donkey, *D. bovis* on cattle, *D. ovis* on sheep, *D. caprae* on goats, *D. longicornis* on red deer, and *D. tibialis* on fallow deer. Many species of the genus *Felicola* live on civet cats; the genus also includes *F. vulpis*, which inhabits foxes, and the CAT LOUSE *F. subrostratus*. The many species of the genus *Trichodectes* dwell primarily on predatory animals of the marten family, but also on a few species of bears; one species has adopted the domestic dog. This DOG LOUSE (*Trichodectes canis*; see Color plate, p. 157) can endanger the dog's health, since it an intermediate host for the larval form of the dog tapeworm *Dipylidium caninum*. But the great majority of European mammals (insectivores, bats, rodents, hares, pigs, and seals) have been spared from infestation by the lice.

Order: Anoplura

The TRUE or SUCKING LICE (suborder Anoplura; see Color plate, p. 157) are small insects (L 0.35–6 mm) of the louse type. They are adapted to the climbing and clinging habit, and have completely transformed, piercing-sucking mouthparts; all of them are blood suckers, parasites upon higher mammals (never on marsupials). They are a young group, probably developing along with the higher mammals, that is, during the Tertiary. Now there are about 250 species.

The true lice are even more perfectly adapted to the parasitic life than are the biting lice. The piercing-sucking mouthparts have been so strongly modified that only recently has it been possible to interpet the parts from

which they are derived. The mandibles and maxillae are regressed. The piercing proboscis is composed of three stylets, of which the two upper ones surround the channel through which food passes. The lower stylet forms a groove, concave upward, with four toothed processes at the tip; this operates to stab and saw through the skin of the host. Between the lower stylet and the two upper ones runs the salivary channel. The two upper stylets are considered to be derivatives of the hypopharynx, while the lower is regarded as the modified labium. In accordance with their climbing and grasping habit, they have short, inwardly bent legs with a large terminal claw which can be folded in. This pushes against a thumb-like projection of the tibia, forming a forceps which can grasp a hair tightly. Their mechanical stability is further increased by the fact that the tarsus consists of only one segment, and this is frequently fused with the tibia. Feeding only on blood the true lice evidently fail to acquire all the necessary vitamins; these are provided by bacteria which live in symbiosis with the lice, sometimes between the intestinal cells but usually in special organs (mycetomes; see Chapter 1) which, during the larval period, are densely packed with bacteria. When the female lice reach sexual maturity, their bacteria migrate to the ovaries and finally into the eggs, being transmitted to the next generation. In the male lice, too, the mycetomes often degenerate with sexual maturation. In the larvae of the lice parasitic on humans the mycetome can even be seen from outside the body, as a whitish-yellow disc below the dark, blood-filled gut.

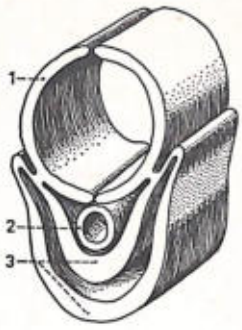


Fig. 8-2. Diagrammatic cross section through the proboscis of a true or sucking louse. 1. Upper stylet, enclosing the food meatus, 2. Salivary channel; 3. Lower stylet.

Family: Haematopinidae

The true lice are divided into six families, two of which are closely associated with particular orders of animals: the primate lice with the primates (see Vol. X) and the Echinophthiriidae with the aquatic seals (see Vol. XII). In contrast, the hosts of lice from the family Haematopinidae are more widespread; these are primarily the Artiodactyla (cloven-hoofed animals) and the rodents, but also include Perissodactyla (horse, rhinoceros, etc.), hares, aardvarks, and—the only predatory animal—the domestic dog. But even among the haematopinids, with their variety of hosts, a degree of preferential association is evident: lice of the genus *Microthoracius* live on the dromedary in Africa and on llamas in South America. Species of the genus *Haemodipsus* occur only on hares and rabbits, and species of the genus *Solenoptes*, only on Artiodactyla. Other species originally parasitic on the latter animals belong to the genus *Haematopinus*. Its most common species is the HOG LOUSE (*H. suis*; see Color plate, p. 157). But one species of this genus, the HORSE LOUSE (*H. asini*) infests Perissodactyla. Another genus associated with the Artiodactyla includes the SHEEP LOUSE (*Linognathus ovillus*), the GOAT SUCKING LOUSE (*L. stenopsis*), and the LONG-NOSED CATTLE LOUSE (*L. vituli*), as well as one species parasitizing a predatory animal: the DOG SUCKING LOUSE (*L. setosus*). Species of lice of the genus *Polyplax* are parasitic on rodents; the SPINED RAT LOUSE (*Polyplax spinulosa*) transmits the blood flagellate *Trypanosoma lewisi* from rat to rat.



Fig. 8-3. Grasping tarsus of the last-stage nymph of the hog louse (*Haematopinus suis*). The tibia (with thumblike projection and pad) forms a unit with the tarsus until the final molt.

Family: Echinophthiriidae

A second family of true or sucking lice is the ECHINOPHTHIRIIDS (*Echinophthiriidae*), which has been found exclusively on seals (true seals, sea lions, and elephant seals). We can be sure that these hosts have not acquired their lice since adopting the aquatic environment; their common ancestor, a terrestrial predatory animal, must already have housed them. Since then, the lice have undergone divergent adaptation along with the hosts. This holds particularly for the respiration of the louse, when its host is in the water. In the SEA-LION LOUSE (*Antarctophthirus microchir*), the spiny hairs on the rounded body (not flattened, as is usual for lice) are modified into scales. The skin of the elephant seal, which at intervals sheds the outer horny layers in tatters, and the peculiar hair of this large aquatic mammal, demand special adaptations of the SEA-ELEPHANT LOUSE (*Lepidophthirus macrorhini*). It burrows deep passages in the skin and lives in them. When the elephant seal stays underwater for long periods, the temperature of the skin becomes so low that the lice fall into a state of rigor in which they need not breathe.

Family: Pediculidae

A third family of true or sucking lice is parasitic only on members of the order Primates. These PRIMATE LICE (family Pediculidae) are divided into two subfamilies, the Pedicininae (on Old World monkeys) and the Pediculinae (on lemurs, anthropoid apes, and humans). The best-investigated lice, of course, are "ours," the slender BODY LOUSE (*Pediculus humanus*) and the more compact CRAB LOUSE (*Phthirus pubis*, L 0.8–1.5 mm); both of these are shown on the Color plate on page 157. As the host of two species of lice, man, like cattle, is an exception to the rule: ordinarily, among the true or sucking lice, only one species has become adapted to any given species of mammal. Like the biting lice, for which it is often the case that several species occupy a single host, human lice have divided their mutual host into territories: the crab louse lives in the pubic hair and the hair in the region of the anus, but can also colonize the armpit hair, beard, eyelashes, and eyebrows. The second human louse is divided into two subspecies according to habit of life: the BODY LOUSE (*Pediculus humanus humanus*; L 2–3.5 mm) and the HEAD LOUSE (*Pediculus humanus capitis*; L 1–2 mm). The body louse lives in clothing and only moves onto the skin in order to eat, but it is not dependent upon clothing: the French parasitologist E. Brumpt found it in the naked African population around Lake Rudolf in Kenya "in extravagant numbers in the glass-bead necklaces." In contrast, the head louse is restricted to the hair of the head. Despite this difference of habitat, these two lice differ only slightly in shape and are considered as subspecies of a single species, since they can interbreed to produce offspring (though such offspring include many sexually intermediate forms as well as fertile individuals). The chimpanzee has its own louse species (*Pediculus schaeffi*), while that of the gorilla is a relative of the crab louse. The head and crab lice glue their eggs (nits) to the hairs in the region where they live, whereas the clothes louse mainly uses the folds of the seams in clothing. The number of eggs laid by one

Human lice

female is not particularly large, for a parasite; a crab louse lays about forty during its life, a head louse, 80–100, and a clothes louse 200–300. But they develop so rapidly that the generations follow one another at intervals of about three weeks. Thus a single mother louse, under favorable conditions, can inundate her host with her progeny in a few months.

Infestation with lice has consequences for humans which in part are rather harmless, but which may be extremely dangerous. The bite of the crab louse leaves a large (1–2 cm) spot. Bites by the clothes louse make a dark stain on the skin, concentrated between the shoulder blades but also extending over a larger area. This syndrome has been called the tramp disease. But the clothes louse is much more dangerous as a transmitter of pathogens for relapsing fever, trench fever, and above all, typhus. The latter is without doubt among the pestilences which formerly killed large fractions of the human race. Not until the civilized peoples developed the habit of changing and washing their clothes at short intervals was the transmitter, the clothes louse, deprived of the opportunity to complete its roughly three-week-long development on the host. In fact, it has come to seem quite natural in civilized societies that no one has lice and there are no epidemics of typhus. But the situation quickly changes when life is disrupted by war and other disasters. These make the customary laundry procedures impossible and bring the louse-free majority into contact with the small minority of negligent louse carriers. Suddenly the lice and the epidemics reappear. The number of their victims throughout world history is difficult to estimate. In Russia alone, during the years of the Revolution (1918–1922), ten million people fell ill with typhus and three million died of it. On the other hand, it is amazing but true that there are in this world humans who actually regard an abundance of lice as the sign of vigorous health and, therefore, obstinately resist their removal.

Lice as disease transmitters

9 The Thrips

Order: Thysanoptera, by R. zur Strassen

Distinguishing characteristics

The THRIPS (order Thysanoptera) are primarily small, inconspicuous insects. Next to the variety of much more striking beetles, butterflies, or flies, they are only too easily overlooked. In English their name means fringe-winged insects, appropriate because the wings are bordered by hairs like eyelashes. Because of the formation at the end of the tarsal segments, which was mistakenly thought to be an eversible vesicle, the thrips were earlier called Physopoda (bladder-feet). There are two suborders, with six families and about 4000 species, over 600 of which occur in the U.S.A.

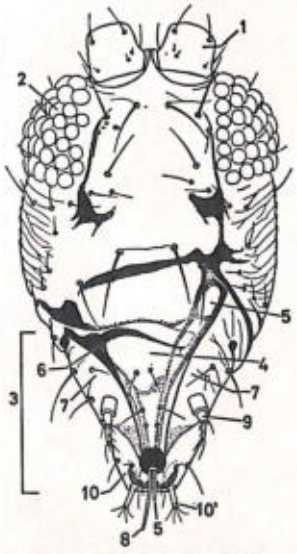


Fig. 9-1. Underside of the head of the cabbage thrips (*Thrips angusticeps*): 1. First antennal segment, 2. Compound eye, 3. Mouth cone, 4. Labrum, 5. Left mandible, 6. Withered right mandible, 7. Basal segment of maxilla, 8. Protruded hypopharnyx of the right maxilla, 9. Maxillary palp, 10. Labium, 10'. Labial palp.

The thrips are 0.5–13 mm long. The body is slender and cylindrical, flattened to a different extent in different species, and narrowed toward the end of the abdomen. Despite their minute size they are often strongly armored (sclerotized), so that an attempt to mount them on an insect pin even with an extremely sharp point usually fails as the pin slips off to the side. Most species are too small for this procedure, however, and are mounted instead on glass slides. The coloration is usually homogeneous, primarily brown or black but often yellow. The legs are simple in structure and of the walking-leg type; the forelegs of the males of many species are much thickened. The tarsi have one or two segments and are equipped with an adhesive lobe at the end; this lobe can be folded, but not everted and drawn in again (as Priesner has recently demonstrated). There are two pairs of very narrow wings, which cannot be folded; they are bordered by a delicate fringe, so dense that it prevents the air from flowing through. It is only because of this fringe that the wings have a surface area large enough for flight. At rest they lie one above the other over the abdomen. Many species lack wings in either one sex or both, or the wings may be reduced to stumps. The abdomen consists of eleven segments, of which the terminal one is much regressed, so that the tenth segment appears to be the last. There are always only four Malpighian tabules (see Chapter 1). The tracheal system communicates with the exterior through three or four pairs of spiracles.

Structure and habits

The mouthparts of the thrips are of the piercing-sucking type; they have moved far back onto the underside of the head. Here there is a mouth cone formed from the labrum and labium together with the basal segments of the maxilla. Inside this hollow cone lie the parts of the left mandible which have been transformed into a piercing apparatus, and the glossae of both maxillae. The right mandible is withered to a remarkable extent, so that the mouthparts are shaped differently on the right side than on the left, which affects the shape of the whole underside of the head. While the left mandible operates as a protrusible and retractable piercing stylet, the glossae of both maxillae have joined to form a suction tube. As this adaptation suggets, the thrips are usually plant-juice suckers; but some species are predators on mites, aphids, coccids, and even the nymphs of other thrips. Many thrips also subsist on the pollen of flowers or on fugus spores, which they shovel up to the mouth opening with the modified maxilla and then suck in.

The compound eyes of the thrips are quite variable in size. They range from small eyes lying only on the sides of the head, through many intermediate stages, to large ones which meet in the middle of the head. In the former there may be as few as four facets on each side, but in the latter they may exceed 300. In thrips which are capable of flight there are three ocelli lying between the compound eyes; these are usually lacking in flightless animals. The antennae consist of four to nine segments, many of which have sensory fields or cones.

A female lays, on the average, twenty to forty eggs during her lifetime; the highest number discovered so far was 120. The eggs are never round, but rather of an elongate and sometimes asymmetrical shape. Each individual animal undergoes a modified incomplete metamorphosis: the egg stage is followed by two stages which resemble the imago; these are followed by a pronymphal stage and that, in turn, by one or two semidormant nymphal stages (that is, they retain the ability to move) which finally give rise to the imago. There is no alternation of generations. The life span of an adult thrips in the reproductive period varies from eighteen to seventy days. Some animals survive over the winter, in which case they can reach an age of eight months. In the cool and moderate temperature zones there are, as a rule, one to three thrips generations per year, while in the warm regions there may be four to seven and in special cases even ten. In the laboratory, as many as twenty generations per year have been raised. In some species reproduction occurs mainly parthenogenetically, sometimes in an uninterrupted sequence extending over countless generations. Here it always takes the form of thelytoky, that is, only female offspring arise from the unfertilized eggs. The males of such species are extremely rare.

Although the thrips are almost ubiquitous, it is probably a rare layman who even suspects the existence of these small insects. They sit in nearly every blossom, every tree harbors a number of them, and they colonize

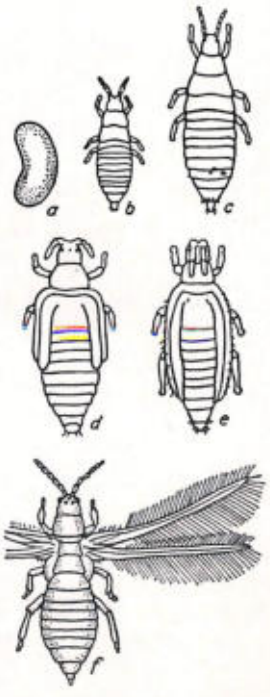


Fig. 9-2. Metamorphosis of the pear thrips (*Taeniothrips inconsequens*): a, egg; b, first and c, second nymphal stage; d, third nymphal stage (pronymph); e, fourth nymphal stage; f, imago.

every meadow. If one shakes a few flowers of dandelion, lupine, or rose out over one's opened hand, one can see the 1–2-mm-long thrips running away across it. They inhabit all parts of the earth, even the inhospitable regions beyond the polar circles and the semi-deserts of the dry regions of the continents. In the mountains they are to be found at altitudes above 3000 m. Certain species of thrips (as happens among the other insects as well) are distributed throughout the world. Most of the thrips, including the juvenile stages, live as juice suckers on plants—that is, on flowers and leaves, in buds and leaf galls, between petiole and stem, in the bulbs of Liliaceae, on the fields of algae growing on tree trunks, and in short grass. Other thrips find a home on and under bark, on dead wood, in rotting leaves, in dry bundles of grass, in ground litter, on fungi, and in the passages made by wood-boring insects, where they feed on the spores of the fungi which live there. Recently in South Africa, Hartwig discovered thrips even inside the nests of termites; there they must have adopted the habit of feeding on the moldy pastures of the fungus gardens. Many of the thrips which live under bark or scales of bark, like some of the grass dwellers, have adapted to these confined spaces by a marked flattening of the body.

There are surprisingly many thrips species which can do considerable damage to the plants on which they feed, when there is a population outbreak. In rapid succession, one cell after another is destroyed by being sucked out through a single puncture; once the plant tissue has lost its chlrophyll in this way, its metabolic processes are disrupted. Air enters the empty cells, giving the affected parts of the leaves a silvery shine. At the same time, the feeding thrips deposit their fluid exrement which remains on the silvery surfaces as tiny dark specks. Many millions of individuals simultaneously occupying a stand of plants can destroy it. Finally, some of the thrips have been recognized as transmitters of plant virus diseases.

Enemies

As minute as most thrips are, they are nevertheless hunted by an enormous number of enemies. To be sure these hunters are themselves hardly larger than their prey. Particularly worthy of mention are the jumping spiders and predatory mites. Among the insects, there are small damsel bugs, flower and plant bugs (see Chapter 10), some of the thrips themselves, small predatory flies of various families, small carabid beetles, rove beetles, and ladybugs (see Chapter 13), certain wasps parasitic on insect eggs (Trichogrammatidae, Mymaridae, and Eulophidae; see Chapter 17), some solitary wasps (see Chapter 18), and the green lacewing and dusty-wing neuropterans (see Chapter 12). Nematodes (see Vol. I) live as parasites in the bodies of the thrips; in fact, according to Uzel, one thrips may contain up to 200 worms at a time. Thrips are even subject to fungus diseases.

Fossil thrips

The numbers of thrips which have been found as fossils is small. Such minute beings have small prospects of being discovered by an expert eye millions of years after being embedded in rock. Nevertheless, such finds

have been made, in the lignite deposits at Rott in the Siebengebirge region of Germany. These roughly thirty-million-year-old deposits, from the Upper Oligocene, flake off into very thin plates (so-called paper coal) and now and then reveal delicate impressions of the tiniest insects, including thrips. Of course, it is difficult to interpret such impressions correctly. Even better preserved were the thrips which, also during the Tertiary period, were trapped in fresh, still-soft resin; these have come down to us as inclusions in Upper Eocene amber. Despite their great age, 40 to 50 million years, some of the amber thrips differ only at the species level from forms alive today.

The few fossil finds give little idea of the position the thrips occupy in the evolution of the insects. For decades entomologists could not agree. At first, because of the piercing proboscis, the thrips were counted as true bugs (Hemiptera; see Chapter 10) in which case their closest relatives would be the Homoptera (cicadas, aphids, etc.). Later they were classified as Corrodentia, a group which at that time included termites, book lice, and animal lice. Finally, about the middle of the 19th Century, many scholars regarded the thrips as a group derived from the orthopteroid insects, the cockroaches, mantids, and grasshoppers. The view now held is that the thrips constitute a separate order, Thysanoptera, of equal rank and similar position to the orders Psocoptera, Mallophaga, and Anoplura.

There are two suborders, distinguished by the shape of the last abdominal segment and by the presence or absence of an ovipositor apparatus: the Terebrantia and the Tubulifera.

Suborder: Terebrantia

Females of the BORING THRIPS (suborder Terebrantia) possess, as an appendage of the eighth and ninth abdominal segments, an ovipositor adapted for drilling; the eggs are buried in plant tissues. The forewings have a marginal vein. The males are often considerably smaller than the females, with the abdomen rounded at the end and frequently with pore fields on the sternites. There are five families: 1. Aeolothripidae, twenty-seven genera with about 210 species altogether; 2. Heterothripidae, eight genera with sixty-two species; 3. Thripidae, 195 genera with 1575 species; 4. Uzelothripidae, only one genus with one species; 5. Merothripidae, one genus with eighteen species.

The three smaller families, with only a few species, are of little significance and therefore will only be mentioned in passing. The Heterothripidae are almost entirely restricted to North and South America, although two species live in Australia and one lives in central and eastern Europe. LARGE-LEGGED THRIPS (Merothripidae) are slender, fragile-looking animals, of which there is only one common American species, in the eastern U.S.A.; it feeds on fungus and debris. The single species of Uzelothripidae has been found only in the delta region of the Amazon. The more important families of the suborder, however, the Aeolothripidae and the Thripidae, are distributed worldwide.

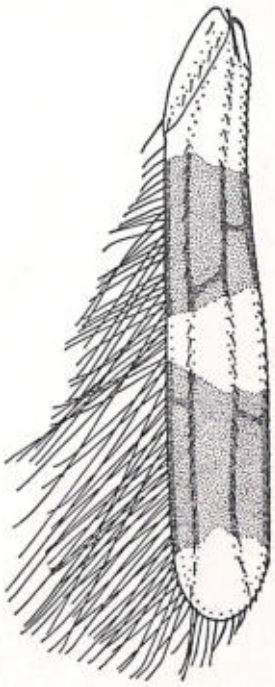


Fig. 9-3. Wing of *Aeolothrips intermedius*.

Thrips of the family Aeolothripidae are long-legged, agile runners. The tip of the ovipositor is bent upward. There are fields of sense organs on the third and fourth segments of the antennae. The most varied genus, with almost eighty species, is *Aeolothrips*; the most common thrips of all belong to some of these species. A few species live by hunting small arthropods. One of these is the North American *Aeolothrips fasciatus* (also found in the temperate zones of Asia and Europe); it was known to Linnaeus. The most common species in northern and central Europe is *Aeolothrips intermedius*, obtainable in the spring from almost every flower. Larvae of the predatory North and South American *Franklinothrips vespiformis* have been observed to pupate by spinning themselves into a loose cocoon in the earth.

The COMMON THRIPS (family Thripidae; see Color plate, p. 158) are usually less than 2 mm long. The tip of the ovipositor is bent down, and there are sensory cones on the third and fourth antennal segments. Most of the thrips which do serious damage are in this group. In greenhouses, these are primarily the BANDED GREENHOUSE THRIPS (*Hercinothrips femoralis*) and the GREENHOUSE THRIPS (*Heliothrips haemorrhoidalis*). Both of these occasionally become severe pests in the tropics and subtropics. The best-known thrips is the ONION THRIPS (*Thrips tabaci*). Other important pests are the CITRUS THRIPS (*Scirtothrips citri*), the GLADIOLUS THRIPS (*Taeniothrips simplex*), and the PEAR THRIPS (*Taeniothrips inconsequens*). The genus *Scolothrips* includes PREDATORY THRIPS species, almost all of which hunt spider mites; according to Fritzsche one thrips can devour up to nine mites a day. Species of the genus *Dendrothrips* are good jumpers; one example is the brightly colored PRIVET THRIPS (*D. ornatus*). Two widespread species of EUROPEAN GRAIN THRIPS, *Limothrips cerealium* and *Limothrips denticornis*, have a tendency to make impressive mass flights in the summer. The females then swarm in millions, and often land on human skin, where they are annoying in spite of the insignificance of their bites. These swarms usually occur in sultry weather, so that these thrips in past ages acquired the name storm flies; the electricity in the air is probably involved in synchronizing these flights.

Suborder: Tubulifera

In the other suborder, the Tubulifera, the females have no ovipositors. The eggs are attached to exposed surfaces (if on leaves, they are often placed close by a vein) or pushed into cracks or under the scales of plants. These thrips are 2–13 mm long. The forewings have no marginal vein. The two sexes are almost identical externally, with a tubular tenth abdominal segment. There is only one family, the BANDED THRIPS (Phlaeothripidae), with 380 genera comprising around 2200 species, subdivided into three subfamilies (Megathripinae, Phlaeothripinae, and Urothripinae).

The subfamily Megathripinae includes thrips which feed on fungus spores. To this subfamily belong the largest thrips, such as the 13-mm-long *Mecynothrips wallacei* of New Guinea. The largest species in central

Europe is *Megalothrips bonannii* (6 mm), which lives on dry branches. Bournier was able to demonstrate the presence of mycetomes (see Chapter 1) with symbiotic bacteria in the southern European *Caudothrips buffai*. *Diceratothrips armatus* and *Sporothrips amplus*, from the southern U.S.A., have been said by Hood to produce sounds, though it is not known whether this is an adaptive behavior; the anterior coxae of the males have a rippled stridulatory surface over which a projecting ridge at the base of the anterior femur rubs.

Most of the banded thrips belong to the subfamily Phlaeothripinae. Here, too, numerous species feed on fungus spores, but many others suck the juices of plants; some produce galls, and others live as predators. Those which live in the open move more rapidly than the sluggish forms which remain in hiding. But very few are capable of the speeds common among the boring thrips. When disturbed, many species defend themselves by arching the abdomen upward. The largest genus, with about 185 species, is *Haplothrips*, with *H. aculeatus* the most common in Asia and Europe, and the MULLEIN THRIPS *H. verbasci* in the U.S.A. A closely related species is *Karnyothrips melaleucus*; this subtropical animal has a two-toned pattern of coloration and hunts the mealy bugs which live in the grass. The CUBAN-LAUREL THRIPS, *Gynaikothrips ficorum*, is representative of all the gall producers, as is the European *Phlaeothrips coriaceus* of those thrips which live in bark.

Thrips of the subfamily Urothripinae have a narrow abdominal tube with extraordinarily long hairs; they are small and usually wingless, and they move very slowly. In southern Europe *Amphibolothrips grassii* lives in ground litter, and *Urothrips minor* has been found in South African termite nests.

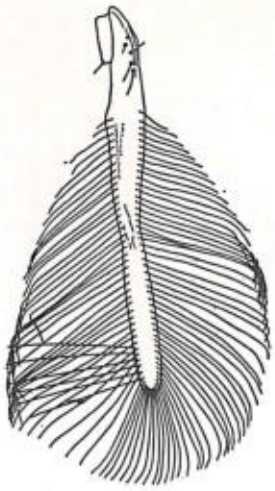


Fig. 9-4. Wing of the banded thrips *Haplothrips aculeatus*.

10 The True Bugs

Order: Hemiptera, by P. Rietschel

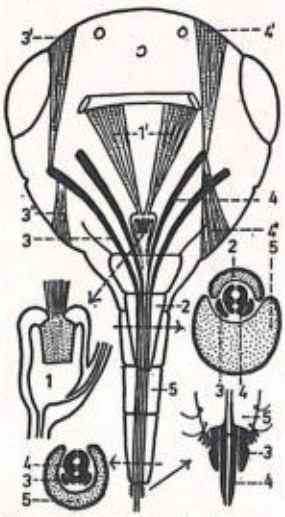


Fig. 10-1. Head of a bug (middle), drawn as though transparent so that stylets and saliva pump are visible. Left, saliva pump and cross section through the proboscis base and surface view of the tip. 1. Saliva pump, 1'. Its muscles, 2. Labrum, 3. Upper mandible, 3'. Its extensor muscles, 3", Its retractor muscles, 4. Lower mandible, 4'. Its extensor muscles, 4". Its retractor muscles, 5. Labium (proboscis sheath).

The order containing the TRUE BUGS (Hemiptera) includes insects of widely differing sizes (L 0.5 mm–5.5 cm) which, with respect both to shape and to habits, show great variation. Only the structure of the piercing-sucking mouthparts betrays the evolutionary relationship of the roughly 23,000 species—about 4500 species in the U.S.A. Bugs have existed since the Triassic (about 230–180 million years ago).

The order Hemiptera (which means half-wings) is closely related to the Homoptera (which means wings the same; see Chapter 11). To the latter group belong the cicadas, psyllids, whiteflies, aphids, mealy bugs, and scale insects. "Nothing but vermin!" some will say with disgust, and in fact a few species of bugs are troublesome parasites and even dangerous transmitters of disease, and some (but by no means all) plant-sucking types are considered undesirable by foresters, farmers, gardeners, and those who grow house plants. Thus the bugs deserve our sympathy, and not only because they have been so maligned; they are of interest for their own sake. Only one other group of insects (the Coleoptera; see Chapter 13) is their equal in degree of adaptation, in both structure and behavior, to the most varied environmental conditions. Only in the structure of the piercing-sucking beak, or rostrum, have they retained amazing similarity to the ancestral form.

The rostrum is really the long, segmented labium, the upper side of which is folded to form a groove in which lies the bundle of stylets. It is broadened at the base, where it is covered above by the sharply triangular labrum. During piercing, the rostrum does not enter the tissue along with the stylets, but rather serves to guide them; its tip, richly supplied with organs of smell and touch, seeks and finds the most favorable spot for the bite. Then the stylets, modified mandibles armed with external barbs at the tip, carry out stabbing movements in alternation with the glossae of the maxillae, also transformed into long, thin stylets which slide between the mandibular stylets. These movements produce the bite. The maxillary stylets are hollowed out so as to form two one-way channels, one to

bring the fluid food up to the gullet, and one through which the saliva emerging from the hypopharynx is driven, by a tiny piston pump, down into the piercing channel. The structure of the mouth parts permits only fluid food to be taken in. This is usually the juice from the sieve tubes in the vascular bundles of plants; in this case the saliva serves to facilitate the passage of the stylets between the cells to the vessels. But in some hemipterans and aphids the saliva kills the cells in the vicinity of the bite and liquefies them. The saliva of predatory bugs also contains digestive enzymes, liquefying the animal into which it is injected from inside so as to provide even these bugs with fluid food. Finally, the saliva of the blood-sucking bugs prevents coagulation of the blood, and thus keeps their extremely narrow food channel from being obstructed. Their saliva also causes an increased flow of blood toward the bite, and is the reason for the itchy swelling which appears there.

Order: Hemiptera

The order Hemiptera includes insects, usually flattened in shape, with dissimilar forewings and hindwings (hence the name). The hindwings are entirely membranous, whereas the forewings, called "hemelytra" (hemielytra), are divided into a membranous outer part and a thicker inner part, the corium. The anal field at the posterior edge of the corium is flexibly attached and is known as the clavus. The tip of the corium is also often separate, forming the triangular cuneus. There is a large pronotum (the dorsal plate of the prothorax) and a triangular scutellum formed by the dorsal plate of the mesothorax. Most of the rest of the body is covered by the wings, which at rest are laid flat across one another. The larva resembles the imago, but is wingless.

The Hemiptera are classified into suborders on the basis of habitat; the terrestrial bugs belong to the Geocorisa and the aquatic bugs, to the Hydrocorisa. Those living on the water surface are counted as terrestrial. This division probably does not correspond to the true relationships, but for lack of a better one it will be retained here to facilitate this summary. The terrestrial bugs differ from the aquatic ones by their longer antennae (longer than the head), the possession of adhesive organs on the tarsi, and the presence of odor glands. None of these characteristics would be of any use to water bugs, and so they disappeared whenever a branch of the terrestrial bugs took to the water.

An impressive characteristic of the terrestrial Hemiptera is their peculiar smell. It is familiar to anyone who, in picking raspberries, has come upon berries previously visited by a stinkbug. The odoriferous substance is produced in glands on the dorsal side of the abdomen in the larva; the glands of the imago are in the metathorax, since they would lose their effectiveness if hidden by the wings. One effect of the odor is to repel ants and other enemies; in addition, the substance produced by the glands contains a poison which is lethal even if only squirted onto the surface of an insect's exoskeleton. This property is due to a fat-dissolving component, tridecane, which opens a way for the poison through the protective layer

▷
Elasmucha grisea, a brood-protecting relative of the shield bugs, with her nymphs.

▷▷ and ▷▷▷
Cicadetta montana, shown in the left picture shortly after emerging from the empty nymphal husk (the exuvium).



ROSSO





















of cuticle. Insect control by contact poisons is thus no modern human invention; the bugs have been doing it for millions of years! That they are able to produce and spray out such dangerous substances without poisoning themselves is due to the special construction of their glands and exoskeleton; they are by no means immune to their own poison.

Families: Saldidae and Anthocoridae

Probably the most primitive Hemiptera are the small, egg-shaped SHORE BUGS (family Saldidae). Their large, conspicuous, protruding eyes identify them as predators. The adroitness with which they escape capture by leaping into flight is doubtless also of use to them in catching prey.

Other hunters equipped with large eyes are the MINUTE PIRATE BUGS family (Anthocoridae). Many of these feed on mites and small insects, and some have become specialists. For example, *Orius insidiosus* (L 1.8–2 mm) may be found throughout the Western Hemisphere living on the heads of various flowers, especially Compositae, where it feeds on plant lice, eggs, and small nymphs. Occasionally they bite humans rather painfully, but evidently that is only a mistake made in the search for food. Flower bugs are also not uncommonly found sucking out the protein-rich grains of pollen.

Family: Cimicidae

In contrast, the family Cimicidae, which includes the bed bugs, are genuine blood-suckers. Among the seventy-four species are three species parasitic on bats and one found on pigeons; the latter is capable of producing fertile offspring by mating with bed bugs and therefore probably should be considered only a subspecies. The SWALLOW BUG (*Oeciacus hirundinis* in Europe, and *O. vicarius* in North America) lives as a parasite in the nests of some swallows, of the common swift, and of some woodpeckers. Because of the long annual absences of these migratory birds, the bugs are obliged to undergo long fasts; they survive these quite well, although they occasionally break them by taking meals on humans. Of the true BED BUGS, *Cimex lectularius* (L 5–6 mm; see Color plate, p. 182) is mainly found in Europe and North America, while *Cimex hemipterus* is more common in southern Asia, Africa, and tropical America. In order to mature, they must suck blood at each stage of their five-molt development. Not every puncture opens up a source of blood, so the bed bug frequently bites several times in succession, producing a number of swellings at once. The bite itself usually goes unnoticed, and the swellings begin to itch only when the bug has long since returned to its hiding place. An adult bug, at ordinary room temperature, bites about once a week, but more often if it is warmer. It can live for more than a year and, if necessary, fast for over half a year. During its lifetime, a female lays 100–200 eggs—though a number as large as 541 has been observed. Development from the egg to the sexually mature animal, takes on the average, two months, though in a hot summer it can take only one month. At temperatures below 15°C, development is completely suppressed. Thus, under favorable circumstances, the infestation of a house with bedbugs can proceed quite rapidly. During the day these flattened animals rest in narrow crevices (behind skirting-

◁ Left, from top to bottom: three different species of fantastically shaped tropical treehoppers, and the froghopper *Cercopis sanguinolenta*. Right, top to bottom *Rhinocoris iracundus* (see Color plate, p. 187), an assassin bug, sucking out the body of a lady bug (see Chapter 13); the bed bug *Cimex lectularius* (see Color plate, p. 187), drawing blood from human skin; the nymph of a Brazilian hemipteran.

boards, pictures, and moldings, in light switches, in the channels for electrical cables, in tears in furniture, and beneath the wallpaper). But to hunt them down in these lairs requires professional experience, and one should also leave their eradication (by cyanide gas or fluid materials based on DDT and the like) to an expert.

Like other parasites which feed exclusively on blood, the bed bugs harbor bacteria to supply them with the essential B-vitamins lacking in blood. These symbiotic bacteria (see Chapter 1) migrate from the nutrient cells of the mother's ovary into the young egg and are thus passed on from one generation to the next. Similar means of bacteria transmission are observed in other blood-suckers. But the mating behavior of bed bugs and related families is unique among insects. The male does not introduce his sperm into the female genital opening, but rather punctures the body wall of one of the female's abdominal segments and deposits his sperm in a sac, the spermelege. From there, the spermatozoa actually migrate, through the body cavity and reach the seminal conceptacles, where they are stored for later fertilization. This method of fertilization, referred to as traumatic insemination, also occurs in Anthocoridae, Polyctenidae, and Plokiophilidae.

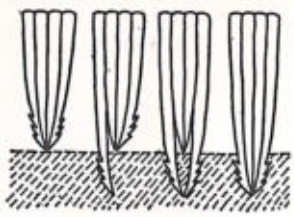


Fig. 10-2. Stylets of a bug, showing the sequence of positions during a bite; the outer stylets are the mandibles and the inner ones, the maxillae.

Families: Polyctenidae and Miridae

The bed bugs seek out and draw blood from their hosts only occasionally, but the tropical BAT BUGS of the family Polyctenidae are constant guests of their hosts, the bats. They are so extensively adapted to this permanent parasitism that they are practically unrecognizable as bugs. The head capsule, like that of fleas and some bird flies, is divided by a furrow running across the clypeus, so that the anterior part bearing the mouthparts can be firmly pressed onto the host. Like many other fur-dwellers, they have combs made of sturdy hairs which catch securely in the pelt of the hosts. They are wingless, like fleas, lice, and bird flies, though a remnant of the forewings has remained in the form of small scales grown together in the midline. As is typical for the other parasites mentioned, the antennae are short; long antennae would be a hindrance to an animal walking through a forest of hair. They are blind. Their forelegs are short, powerful gripping legs. The young are already at an advanced stage of development when they are born, and from the start they live in just the same way as the parents.

The hemipteran family with the greatest number of species (5000) is that of the PLANT BUGS (Miridae). It also includes the largest number of individuals native to North America; each sweep with an insect net through a summer meadow brings swarms of them to light. They are usually small and slender. They have compound eyes, but the ocelli are lacking. Most of them are plant-suckers, though a few are hunters. Of the roughly 5000 species in existence, several hundred live in the U.S.A. Some of them can damage cultivated plants by their injurious saliva. Among these are the four-lined plant bug (*Poecilocapus lineatus*; L 7–7.5 mm), which passes the winter as an egg on woody plants and in summer,



Fig. 10-3. Forewing of a hemipteran (*Calocoris hispanicus*; L 7 mm); 1. Corium, 1'. Cuneus, 2. Clavus, 3. Membrane.

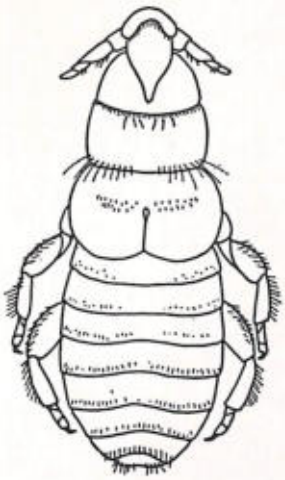


Fig. 10-4. The bat bug *Androctenus horvathi.*

in a second generation, sucks on gooseberry, rose, and many other shrubs, garden flowers, and herbaceous plants. The APPLE RED BUG (*Lygidea mendex*; L 6–6.5 mm) until recently lived on hawthorn (*Crataegus* spp.), where there injurious bites bothered no one. In the early years of this century, though, they underwent a hereditary change in taste and transferred their attentions to apple trees, although only certain varieties such as greenings. Nowadays this bug causes some damage to apples in northern U.S.A. Among the predatory mirids are many species of *Deraeocoris* (L 4–6 mm), which seek out colonies of aphids and suck out the aphids. Other species, as for example *Orectoderus obliquus* and *Coquillettia mimetica*, resemble ants, both for protection and perhaps to approach the aphids without alarming them. But it is doubtful whether those elements of their appearance which we regard as antlike actually deceive the ants. Their antlike movement and perhaps a similarity in smell are certainly a more effective camouflage. Ants receive impressions from the environment primarily with the organs of smell, so situated on the movable antennae as to point outward; they thus may even have a "three dimensional" sense of smell which we cannot imagine, since such sensations have been denied to us. Still other species of this group prefer honeydew from the aphids rather than the aphid blood.

Family: Nabidae

Other antlike bugs (from our point of view) are some larvae of the DAMSEL BUGS (family Nabidae). They even imitate the narrow waist of the ants by white spots on the back at the front end of the abdomen. Their movements are also antlike, though they evidently have nothing to do with ants.

Families: Reduviidae and Phymatidae

Most of the ASSASSIN BUGS (family Reduviidae; see Color plates, pp. 182 and 187) are quite large. The very movable head bears a long, curved, somewhat protruding proboscis; at the underside of the tip it is equipped with little teeth which produce a chirping noise when rubbed over a rippled ridge along the prothorax. Both sexes, as well as the larvae, chirp when they believe themselves under attack. The large black-and-red *Rhinocoris ventralis* suck out the bodies of insects. Similarly, the inconspicuous KISSING BUG (*Reduvius personatus*; see Color plate, p. 158) prefers to hunt flies and other undesirable insects in houses. Unfortunately, it is also attracted by sleeping humans, to whom it can inflict a painful bite, often on the lip; hence its name. The hairy nymphs disguise themselves with an overall covering of dust, so that they look like drifting dust balls, an excellent camouflage; as a result, the nymphs are known as masked hunters. Only the antennae, which carry the most important sense organs, are kept dust-free. Very much more dangerous are a number of South American predatory bugs of the subfamily Triatominae (*Rhodnius* spp., *Triatoma* spp.). These are blood-suckers which live in a way similar to that of bed bugs, but because of their wings they can spread much more easily from house to house. Certain individuals harbor flagellates of the species *Trypaonsoma cruzi* (see Vol. I and chapter 1 of this volume) in the gut.

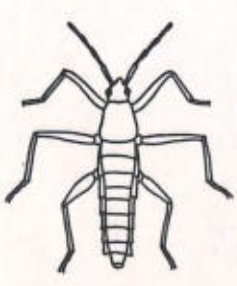


Fig. 10-5. Like all ripple bugs, *Velia currens* runs nimbly on all six legs.

While biting they generally discharge excrement, with which these dangerous protozoa may come onto the skin; the trypanosomes can then penetrate into the human body through wounded spots and particularly through the mucuous membranes around the eyes. Here they produce a syndrome known as Chagas' disease (see Chapter 1), in which the heart, thyroid gland, and nervous system are damaged; it usually occurs among children, and can be fatal. Species of bed bugs can also harbor this pathogen, but they do not pass it on when they bite because they do not defecate at the same time. The wheel bug, *Arilus cristatus*, occurs throughout the U.S.A. When disturbed it can inflict a painful bite, but it is not known to be a disease vector.

A chirping organ similar to that of the assassin bugs is found in the AMBUSH BUGS (family Phymatidae). The forelegs of these predatory bugs are prehensile; the tibia can be folded back against the femur, and the tarsus is regressed. Most species are tropical, only two having penetrated as far as Europe and only one of these (*Phymata crassipes*; see Color plate, p. 187) as far north as Germany. In the U.S.A., the ambush bug, *Phymata fasciata*, is the most commonly encountered species, though other species are also found here (for example, *Phymata erosa*, a yellowish ambush bug which may be up to 12 mm long); they are common in the fall, lurking in flowers for their insect prey.

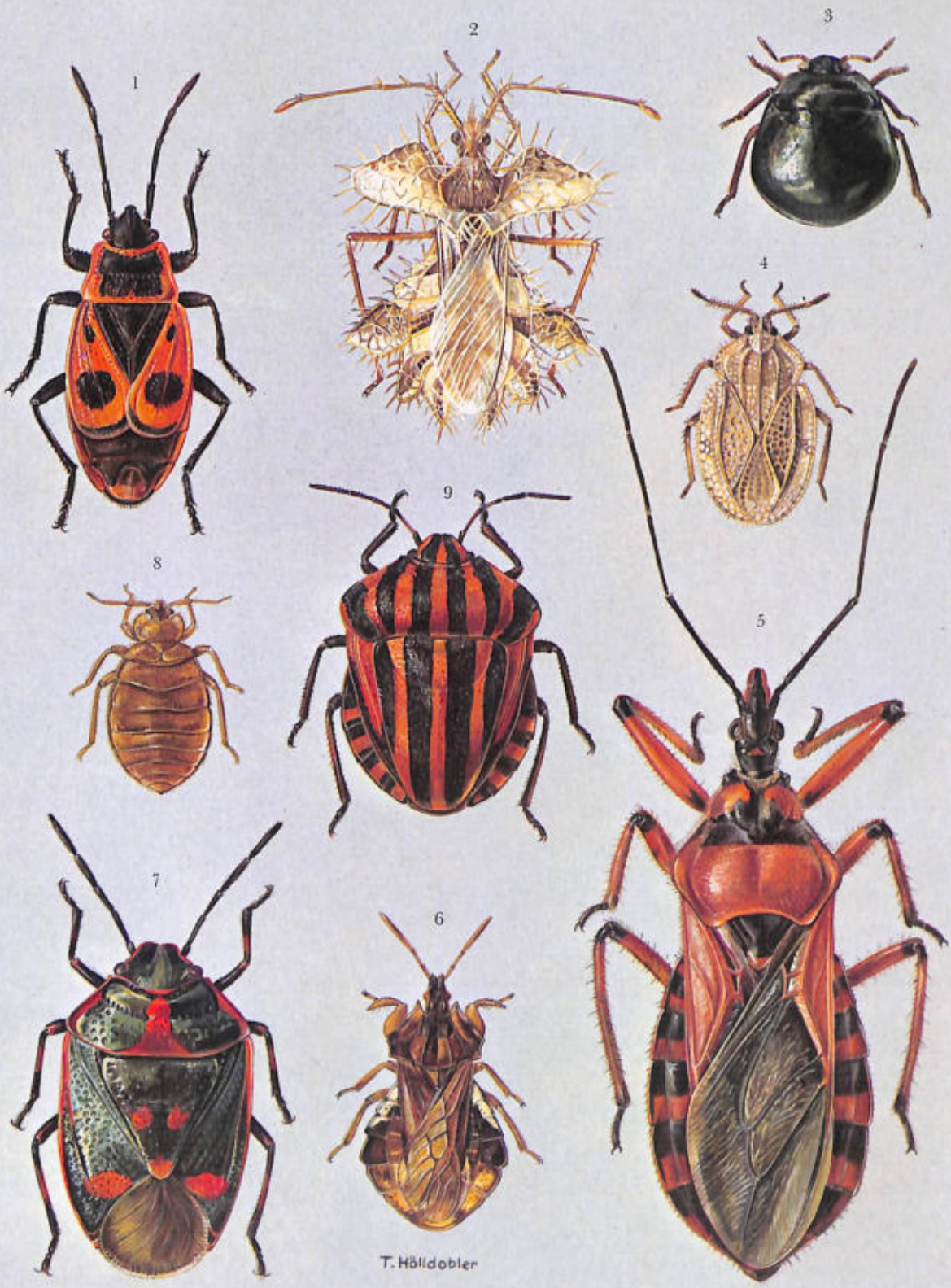
Terrestrial hemipterans of several groups have become adapted to life on the surface of water. Their tarsi are so constructed that they do not break through the surface, and they even permit walking on it. Among these water striders (in the broadest sense) are the true water striders, the ripple bugs, water treaders, the water measurers, and the velvet water bugs.

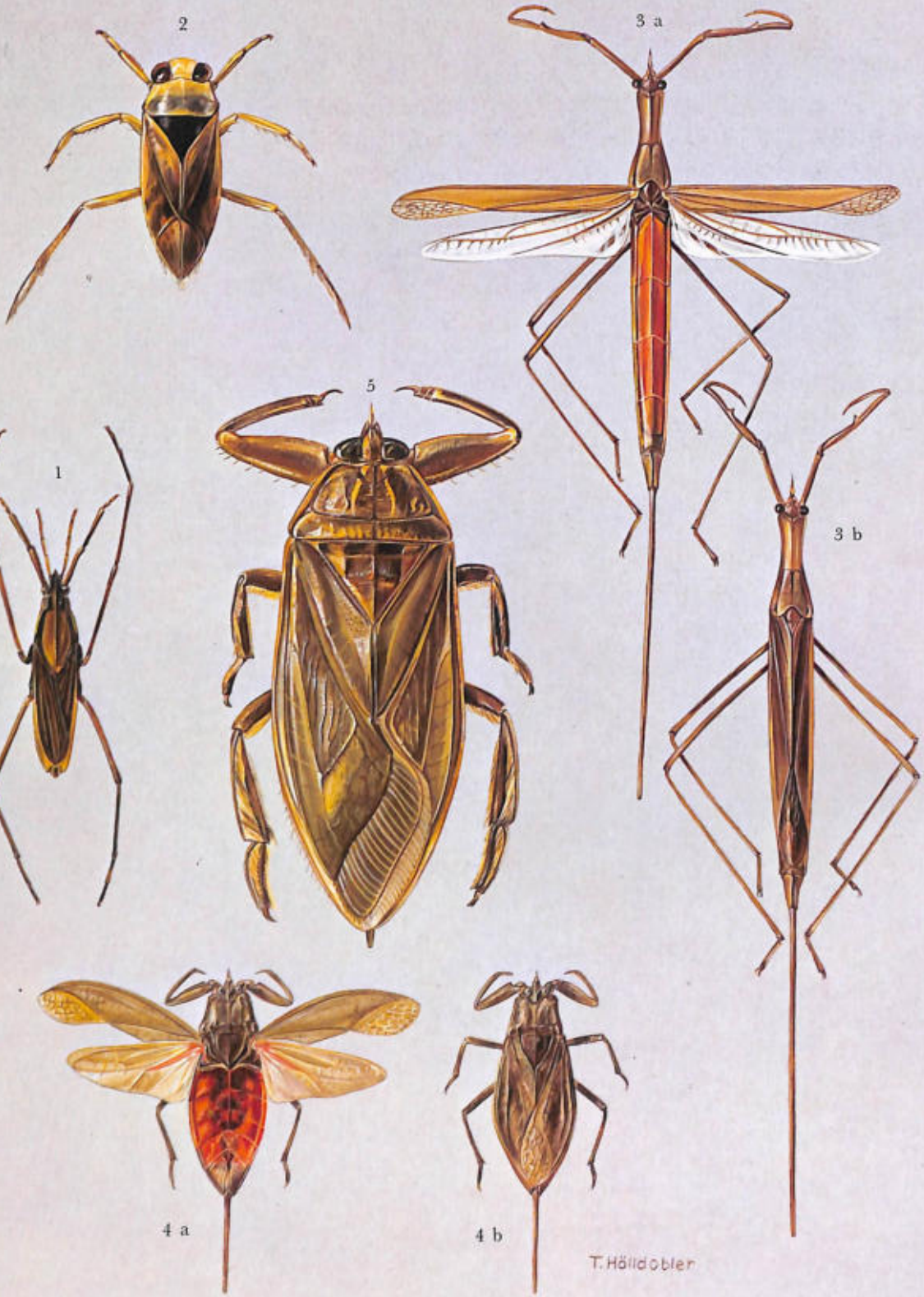
The highest level of adaptation has been achieved by the WATER STRIDERS (family Gerridae; see Color plate, p. 188). They progress by making rowing motions with the middle legs, laid flat on the water, and steer with the hindlegs; the forelegs are reserved for catching prey. The body is covered, in particular on the underside, with a silvery, water-repellent coat of hair, but only the undersides of the rowing legs rest on the water. The water striders move in jerks, and often even make considerable jumps; but neither on takeoff nor on landing do they ever break through the water surface. Some water striders live on the ocean; species of the genus *Halobates*, the only known marine insects, can even be found on the high seas. These "ocean striders" lay their eggs on drifting seaweed and on the violet snail (see Vol. III). They feed on the drifting bodies of dead marine animals.

The RIPPLE BUGS (family Veliidae) are short-legged; they run on the water with the legs bent. Since they hunt on flowing waters, they must compensate for drift. Species of tropical ripple bugs of the genus *Rhagovelia* even run against the current in rapidly flowing waters; they are able to do this because of the large fan of plumed bristles on the tarsi of the middle legs. Their locomotion differs from the rowing stroke of the water striders

▻
Terrestrial hemipterans: 1. *Pyrrhocoris apterus* (L 9–11 mm); 2. *Phyllomorpha lacinata* (L 9 mm), from Spain; 3. *Coptosoma scutellatum* (L 4 mm); 4. *Tingis reticulata* (L 4.5 mm), a lace bug; 5. *Rhinocoris iracundus* (L 18 mm; see Color plate, p. 182); an assassin bug; 6. *Phymata crassipes* (L 8 mm), the only European ambush bug; 7. The brassica bug (*Eurydema oleraceum*; L 5–7 mm); 8. A bed bug (*Cimex lectularius*; L 5–6 mm; see Color plate, p. 182); 9. *Graphosoma lineatum* (L 8–11 mm).

Family: Gerridae, and related families


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Water strider: 1. *Gerris costai*. Other aquatic hemipterans: 2. Backswimmer (*Notonecta glauca*; L 14–16 mm); 3. Water stick insect (*Ranatra linearis*; L 30–35 mm), with opened (a) and closed (b) wings; 4. A water scorpion (*Nepa rubra*; L 18–22 mm), with opened (a) and closed (b) wings; 5. *Belostoma cordoanum* (L up to 11 mm).

in that the legs of the ripple bugs move alternately; they cannot jump on the water, but they can hunt by diving underwater.

The WATER TREADERS (family Mesoveliidae) are represented in the U.S.A. by only one of the four genera, with four species. Their wings are usually regressed.

The VELVET WATER BUGS (family Hebridae), also very small animals, often creep along with the back upward under the water surface. According to the observations of K. H. Jordan, they are plant-suckers and also frequently sink their rostra into the mud of the bottom.

A quite different shape is presented by the WATER MEASURERS (family Hydrometridae), which walk slowly over the water on all six legs as though on stilts. They feed on small insects which have fallen into the water, by sucking out their bodies. Occasional adults possess wings, though the majority are wingless. Cross-breeding experiments demonstrated that this characteristic is inherited. The dainty "sculptured" eggs are about a fifth as long as the mother; they are laid singly on shore plants or on aquatic plants above the water level, attached by a stalk.

Family: Aradidae

With the FLAT BUGS (family Aradidae), we return to the terrestrial type. These are found under tree bark, in cracks in wood, and in fungi on trees (for which reason they are sometimes called FUNGUS BUGS). They are adapted to life in these narrow spaces by their greatly flattened, compact shape; they resemble bed bugs. They feed, however, in quite a different way. They are fungus suckers, inserting the extremely fine stylet bundle into the single threads of a fungus network and sucking out the contents. In this process, the stylet bundle follows the tortuous course of the fungus thread; it must therefore be very long and flexible. But what happens to this fragile structure, six times as long as the body, when it is not in use? It is formed into a loop, rolled up, and hidden inside the front part of the head, in a pocket under the labrum.

Family: Lygaeidae

The SEED BUGS (family Lygaeidae) constitute a family of over 2000 species, distributed throughout the world. In North America there are about 200 species in about sixty genera. The majority are plant-juice suckers, and many are pests. For example, *Blissus leucopterus*, the chinch bug, is one of the most serious agricultural pests in North America, where it has caused extensive damage to corn for over 200 years. It previously lived on the wild grasses in South America and was of no economic importance there; it then began to move northward in the mid-1700s, and became dispersed as far north as Canada. By the turn of the century had destroyed grain crops valued at a third of a billion dollars. A European species, *Nysins senecionis* causes great damage to grapes in southern France. A peculiar annual cycle of generations is found in a northern African ground bug, *Oxycarenus hyalipennis*. It does considerable damage to cotton, and also feeds on other malvaceous herbs, such as the marsh mallow. Depending on the plant it uses as food, the bug begins to reproduce at different times, but multiplication is always ended by a dor-

mant period (diapause) after the fourth generation, so that this annual number of generations is never exceeded, even under the most favorable conditions.

Families: Pyrrhocoridae and Coreidae

The RED BUG species (family Pyrrhocoridae) are few in number, and most of these live in the Old World. Only the COTTON STAINER (*Dysdercus suturellus*) has reached the Americas, where it is much feared because of the damage it does to cotton. Although these bugs, like the last-mentioned lygaeids, are called cotton stainers, it is not they which stain the cotton; rather, it is a fungus (*Nematospora*), which the bugs carry and introduce into the seed capsule when they suck. Of the two species native to Europe, *Pyrrhocoris apterus* (L 9–11 mm; see Color plate, p. 187) often lives in associations at the foot of old lindens, sucking the nuts of the tree. But it does not refuse other food, such as the fruits of mallows, dead insects, and insect eggs. The species epithet *apterus* (wingless) refers to the regression of the wings, but there are in fact three forms of these bugs: 1. hindwings regressed, forewings lacking membranes; 2. hindwings regressed, forewings fully developed; and 3. hindwings and forewings fully developed. It can also happen that the wings are dissimilar on the two sides. The pronotum and the sturdy inner part of the hemelytron (the corium), which is never regressed, are a pretty red with black markings, and the sharp-edged lateral folds of the abdomen are red.

The LEAF-FOOTED BUGS (family Coreidae) are of considerable size; there are over 1600 species, mostly tropical. Of the approximately 100 species native to the U.S.A., the best-known is the stately, clay-yellow SQUASH BUG (*Anasa tristis*). Imago and nymph both suck the green and succulent leaves of species of squash, cucumber, and melon plants, severely damaging the plants with their injurious saliva. The spectacular *Leptoglossus phyllopus* (L 18–20 mm) is found throughout eastern North America, and is a true leaf-footed bug. Many other species occur in western North America.

Other families of terrestrial Heteroptera

The STILT BUGS (family Berytidae) are fragile, slender animals with long, thin legs, the femora of which are thickened like clubs toward the knee. In the eastern U.S.A., *Jalysus spinosus* damages peaches, corn, and especially tomatoes.

The few species of ASH-GRAYLEAF BUGS (family Piesmidae) primarily suck various plants such as beets, goosefoots, pigweed, sycamore, buckeye, beech, etc. One of the ten American species, *Piesma cinerea*, was paid little attention until it was reported to feed on the leaves and flowers of grapes. In Europe, species of this genus (called beet bugs) attack sugar and fodder beets in Silesia, and today the area of destruction by beet bugs reaches from Poland across central Germany to the Weser and beyond. Southern Germany has so far been spared this damage. Even in the areas where it is a pest, the beet bug feeds on wild plants in the spring until the beets are planted, and often does not start in on them until the second generation. The real damage is not produced directly by the bite, but by a virus which is thereby transmitted and which produces a curly-leaf disease of the beets, though, remarkably, not in all areas where they are cultivated.

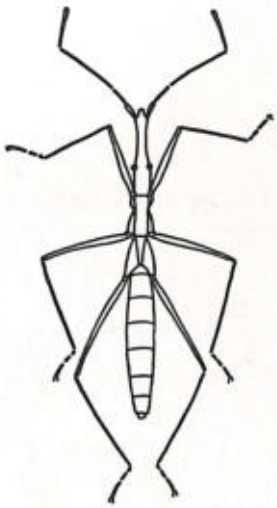


Fig. 10-6. Like all water measurers, *Hydrometra stagnorum* walks slowly on six legs, whereas the water striders (e.g., *Gerris*; see Color plate, p. 188) walk slowly on only four legs.

The LACE BUGS (family Tingidae; see Color plate, p. 187) received their name because of the extremely delicate lacy sculpturing of the pronotum and hemelytra. Anyone who thinks of bugs simply as repulsive vermin should take a look at one of these "natural art forms," either alive or from a collection, under a strong lens. The roughly 1820 species of lace bugs live in both the tropical and temperate regions of the world. The species *Stephanitis pyri* is distributed throughout Europe, and it may be found in the warmer locations around the Mediterranean, where it is a pest of fruit trees. Another species, the RHODODENDRON LACE BUG (*Stephanitis rhododendri*), is a native of Japan, feeding on rhododendrons in the open as well as in greenhouses. In 1877 it appeared in North America, around the turn of the century in Holland, in 1910 in England, 1913/14 in France, 1915/16 in Switzerland, and 1925 in Cape Province (South Africa), and since then it has even taken up a home in several locations in Germany.

The SHIELD BUG (family Pentatomidae), with about 2500 mostly tropical species, is among the largest hemipteran family. About 180 species are native to the U.S.A. Most of these are in large part confined to the warmer parts of the country. Their name comes from the prominent scutellum. In the pretty, black-and-red-striped *Graphosoma lineatum* (L 8–11 mm; see Color plate, p. 187), which is from the Mediterranean region, the scutellum reaches back to the end of the abdomen, almost completely covering the hemelytra. Several related species in the genus *Podops* occur in North America. Most of the shield bugs feed on plant juices, and some share our preferences. For example, the ONE-SPOT STINK BUG (*Euschistus variolarius*); L 11–11.5 mm) and species of the genus *Thyanta* make themselves unpopular by sucking berries and other fruit and in the process imparting their own odor to the fruit. On the cruciferous plants cultivated in the U.S.A., such as cabbage, radishes, and turnips, there often live large numbers of the brilliant red-and-black HARLEQUIN BUG (*Murgantia histrionica*; L 9–11.5 mm). In Europe, the BRASSICA BUGS (*Eurydema oleraceum*; L 5–7 mm; see color plate, p. 187) have similar habits. The coloration of these animals is unusually variable, changing even in the imago; the original white background becomes dyed by the accumulation of careotenoids (pigments contained in the plants eaten), first yellow and then red, and the black patterning of spots expands so that the ventral surface, which before the winter is light-colored with few if any spots, is completely black by spring. Since the systematists cannot discern this sort of long-term morphological color change in their dead museum specimens, Latin names were at one time given not only to the varieties but even to the various transitional colorations through which an individual animal passes. Great damage is done in the midwestern U.S.A. by the bright green stink bug, *Acrosternum hilare*; they suck out the milky contents of both the pods and seeds of soybeans. In addition to the numerous vegetarians, there are also some hunters among the shield bugs. *Stiretrus fimbriatus* (L 10–11.5 mm) lives throughout eastern North America. It is dull

yellow with reddish-brown markings, and is commonly found on plum and sumac trees. A rapacious predator on various larvae, it may be considered a useful collaborator with the fruit-grower. In Europe the females of *Acanthosoma grisea* are known to protect their eggs and nymphs. After hatching, the nymphs are led about by the mother much as a hen conducts her chicks.

The Plataspidae form a small family of unusually shaped Old World bugs. One common species is *Coptosoma scutellatum* (L 4 mm; see Color plate, p. 187); the high arch of its dorsal surface gives it almost the appearance of a ladybug. Just behind the broad pronotum is the scutellum, which in this case really does not deserve this diminutive term, for it is large enough to cover the wings and abdomen. Nevertheless, it corresponds entirely to the small triangular scutellum of the other bugs. *C. scutellatum* sucks the juices of the sicklewort and other papilionaceous plants; other bugs in the same family are fungus-suckers like the flat bugs.

The aquatic Hemiptera

It has doubtless happened several times in evolution that hemipterans have become adapted to life in the water. The associated transformations in body structure were largely the same each time: shortening of the antennae, modification of the walking legs into swimming legs, loss of the adhesive devices at the ends of the tarsi, and loss of the poison glands. These common characteristics of aquatic bugs therefore can be no indication of close relationship. Unfortunately, the fossilized remains of prehistoric aquatic bugs give us no information about their relationships to one or another family of terrestrial bugs, since the oldest finds (from the Jurassic) are similar to present-day animals. The transition to the aquatic life is still evinced today by the ripple bugs, described earlier. The creeping water bugs, water scorpions, giant water bugs, backswimmers, and water boatmen are completely adapted to the water.

Family: Naucoridae

The CREEPING WATER BUGS (family Naucoridae) are represented among the North American fauna by twelve species of very different habits. The larger species (L 8–21.5 mm) is the beetlelike *Ambrysus mormon*, an agile swimmer from northern and central California. Usually it is seen swimming with the back upward, but it often creeps along with the ventral side up just below the water surface. It is covered both dorsally and ventrally with fine hairs, and it this layer of hairs which retains the air it breathes, giving large parts of the animal a silvery sheen. The first pair of legs is modified into prehensile legs, the tibia and tarsus of which can be folded into a groove in the femur like the blade of a pocket knife into the handle. Of course, this blade lacks a sharp cutting edge, since is it used only for holding the prey. Not only prey animals are stabbed by the stylets; it can happen to humans as well, if they take these bugs into their hands. The bite is quite painful. The Danish fresh-water biologist Wesenberg-Lund reports that it caused him nerve pains in his whole arm which lasted for days. Another species known from Europe is the wingless *Aphelocheirus aestivalis* (L 9–10 mm), which inhabits the gravelly bottoms of

flowing waters. The animal is covered with extremely fine hairs formed from the outermost layer of the cuticle alone. There are two million of these hairs in a square millimeter! They are water-repellent, and under their curved tips they hold a coat of air around the bug, which is never used up because the gas pressure of the oxygen dissolved in the surrounding water continually replaces the respired oxygen (plastron breathing, see Chapter 1). These water bugs therefore need never rise to the surface. Nor do they swim; their three pairs of legs are walking legs. Thus the appropriateness of classifying these extreme specialists as swimming bugs is at least questionable.

Family: Belostomidae

The GIANT WATER BUGS (family Belostomidae; see Color plate, p. 188) are among the largest insects (L 8–11 cm). The 100 or so species live primarily in North America, South Africa, and India. *Lethocerus americanus* (L 50–55 mm) lives in ponds and streams throughout North America east of the Rocky Mountains. On the posterior end these bugs have two extensible and retractable semicylindrical appendages which, when held together, form a breathing tube. These are used only for underwater breathing, for in flight the air is exchanged through the spiracles in the thorax. Some species display a unique type of brood care, carried out by the males at the instigation of the females: the female climbs onto the violently struggling male and uses a water-insoluble glue to attach her eggs to his hemelytra. Even though one male is loaded with 150 to 175 eggs, the female needs two to four males to carry her entire supply of eggs. After a few days, when the larvae on his back have hatched, the male can take on another brood. In this case the female first carefully removes all the empty eggshells. The giant water bugs are as good flyers as they are swimmers; this is a great help in their search for new bodies of water, when the old one can no longer satisfy their hunger. They feed primarily on salamanders and frogs, but also frequently suck out the bodies of fish. They can even overpower fish twice their own size. In hatcheries, these fish killers often do great damage.

Family: Nepidae

There are about 150 species of WATER SCORPIONS (family Nepidae), only about a dozen of which are native to the U.S.A. The water scorpion *Nepa rubra* (L 18–22 mm; see Color plate, p. 188) is a European species, and *N. apiculata* of the eastern U.S.A is its American counterpart. The WATER STICK INSECT (*Ranatra linearis*; L 30–35 mm; see Color plate, p. 188) represents the other common genus, with *R. fusca*, of the eastern U.S.A., a common New World species. Species of both genera can bite quite painfully with their stylets, which is the basis for the common name of the family. Like the giant water bugs, they have abdominal appendages which are joined to form a breathing tube by means of hook-shaped bristles. This conducts the air to the single respiratory opening on the abdomen; those on the thorax are used only in flight. The spiracles of the fourth to sixth abdominal segments have taken on a new function. Near them are sense organs with sensory hairs spread out in the form of a shield under

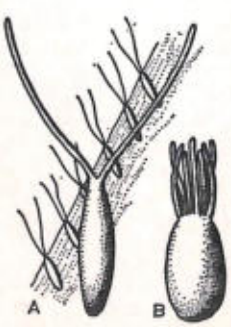


Fig. 10-7. Eggs of the water stick insect (left) and a water scorpion (right).

which there is a layer of air in communication with the tracheal system. The buoyancy of this bubble causes the hairs to be displaced in various ways depending on their orientation, and these stimuli tell the bug whether it is walking upward or downward along the bottom underwater. This is vital information for the water scorpion; as a walking and non-swimming bottom-dweller it must occasionally find its way to the surface to renew its air supply. To wander down unknowingly to too great a depth would therefore be disastrous. The nymphs, too, have sense organs of identical function but simpler structure. The water scorpions are predators which lie in wait for the prey, like dragonfly naiads. They seize their victims with a swift stroke of the forelegs. The middle and hind legs are walking legs. Since they hunt from a fixed station, they must be well camouflaged. *Nepa rubra* of Europe covers the tile-red upper surface of its abdomen with the mud-gray wings, which in addition are usually covered with mud from the bottom. The yellowish-red water stick insect, on the other hand, resembles in both color and shape a bit of a dead plant. *N. rubra* has wings but cannot fly, since its flight muscles have degenerated; members of the genus *Ranatra* are skillful flyers. The water scorpions lay their eggs in the soft, rotting parts of plants; it is typical of the family that the eggs also have breathing tubes, which one can see sticking out of the plant material. The egg of the *Nepa* spp. usually has seven (at least six, and at most nine) such appendages, and that of *Ranatra* spp., only two. These V-shaped structures, projecting in long rows from decaying reed stalks, betray to the skilled observer the presence of the water stick insect in a pond, even if he cannot see the well-camouflaged bugs themselves.

Families: Notonectidae and Pleidae

The streamlined BACKSWIMMERS (family Notonectidae) are in every respect opposite to the water scorpions. The dorsal surface is peaked like a roof, while the ventral surface is flat. As their name implies, they swim with the back down; the back, like the ventral surface of fish, is the lighter side, and viewed from below it contrasts very little with the sky. The ventral, top side is dark, like a fish's back, and when viewed from above is difficult to see against the dark background of the water depths. The long hindlegs row with powerful sweeping strokes. Most of the air for breathing is stored in two grooves on the ventral surface. The resultant buoyancy holds the animal in the upside-down position, and makes it lighter than water, so that it is usually found slightly below the surface. The backswimmer is also adept at flying, but of course it is unable to take off from the swimming position beneath the water. It must first crawl to land, where it turns over so that the ventral side is down; it takes off only when it has become sufficiently dry. The backswimmers, the most common of which are *Notonecta glauca* (L 14–16 mm; see Color plate, p. 188), from Europe, and *N. undulata* (L 10–17 mm), from North America, are all hunters. They attack aquatic insects and also tadpoles, salamander larvae, and fish spawn, and suck out their bodies. Like the water scorpions,

they also defend themselves against humans by biting rather painfully, so that in Germany they are colloquially referred to as water bees.

There is another group of smaller backswimmers closely related to the Notonectidae, the Pleidae. Only two American species are known. The most common is *Plea striola* (L 1.8–2.2 mm), which lives throughout North America. Though these bugs also swim on their backs, the back is not roof-shaped but highly arched. The hindwings are regressed, and only the corium remains of the forewings. Nevertheless, these bugs are capable flyers. They live in associations, and are said, as is appropriate to their size, to feed primarily on water fleas.

Family: Corixidae

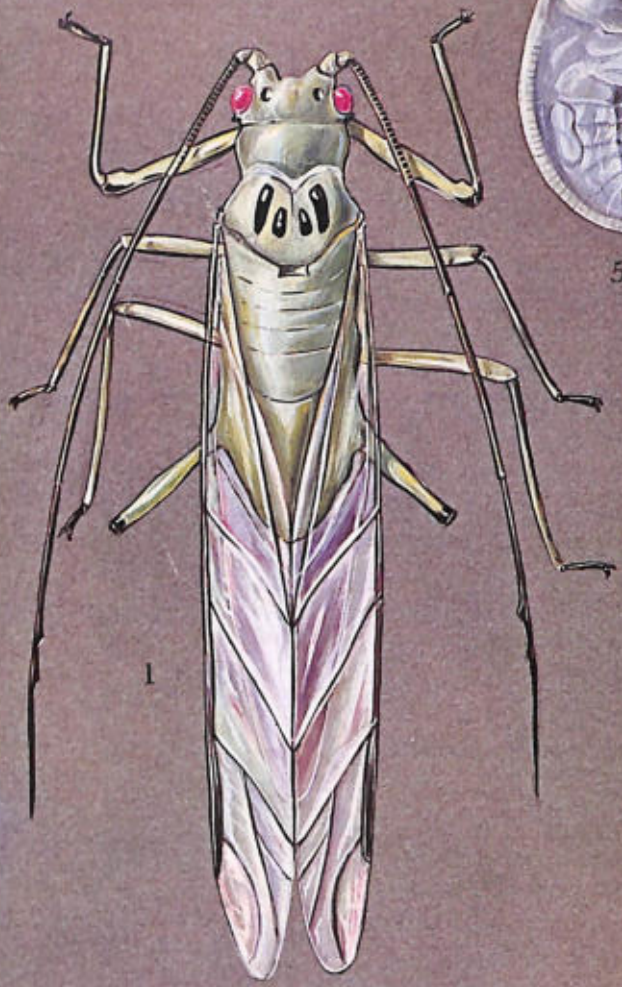
The WATER BOATMEN (family Corixidae) are the last hemipterans to be mentioned, because their habits differ most widely from those of all their relatives. In form, they resemble a backswimmer and, like them, the water boatmen are lighter than water and thus tend to float. But they live on the bottom, and make use of this tendency only to rise occasionally for air. The rest of the time they spend anchored at the bottom by their gripping legs. In contrast to the backswimmers, the water boatmen obtain air at the surface not with the underside of the end of the abdomen, but with the dorsal surface, between the head and prothorax, and most of the air is stored dorsally under the wings. They are thus in a stable position with respect to buoyancy when the back is up. A special ability, which gives them an advantage over all the other water bugs, is that of taking off into the air from the water. Their buoyancy, supplemented by the activity of the powerful rowing legs, causes them to break through the surface head first so that the strong wings can be brought into play immediately. The water boatmen also feed in a way different from that of the other bugs. They eat algae, which they shovel toward the broad mouth with their paddle-shaped legs. They are the only bugs which do not use the mouthparts as a sucking proboscis. The short stylets serve as tools to spear filaments of algae, the contents of which they consume. In addition, they feed on the organic debris which has sunk to the bottom and been caught in the cushions of algae. The water boatmen are the best musicians among the aquatic bugs and are often called water cicadas for this reason. *Corixa* spp. sing by stroking a bristly area on the anterior femur over parallel ridges on the front of the head. The male saucer bugs and both sexes of the pleids have other sound-producing organs. Several of these bugs have also been found to have auditory organs. Over 300 species are distributed throughout the world, with over fifty species. in the eastern U.S.A. *Arctocoxisa interrupta* (L 10–11 mm) occurs throughout northern North America.

11 The Cicadas, Hoppers, Whiteflies, Aphids, and Scales

Order: Homoptera
by P. Rietschel

All the true bugs not belonging to the Hemiptera are grouped in the order Homoptera. This name, in implying that the wings are identical, refers not to their size—for the hindwings are always smaller than the forewings—but rather to the fact that the forewings are no thicker than the hindwings and are not divided, like those of the Hemiptera, into stronger and more fragile sections. All the homopterans are vegetarians, and most of them suck the juices of plants out of the sieve tubes of the vascular bundles. To do this, they need only pierce a sieve tube with the bundle of stylets, and the pressure of the fluid saves the insect the work of sucking. The animal may even find it necessary to limit the influx of food if it is not to be burst by the considerable pressure. The juice of plants, however, contains much more carbohydrate (sucrose, invert sugar, and dextrins) than the insect needs for its sluggish way of life. The juice suckers cope with this surplus in two ways. First, the sugar can be passed out of the body in the fluid excrement (honeydew), dropping onto the leaves or the ground, or being milked from the anus by ants hungry for sugar. The second method of disposing of sugar is to convert it into wax within the body; this is then secreted by glands on the body surface, as threads or as an overall covering. Some of it can also be stored in blood cells; aphids use their waxy blood as a means of defense against enemies. The wax coatings secreted onto the body surface also provide protection to many homopterans. It was long believed that their extravagant consumption of plant juice was necessary on account of its low protein content; but it has now been shown that honeydew has very little less, or even more, protein than does the juice from sieve tubes. This is the more surprising since the homopterans have a huge protein requirement for the generation of progeny. The amount of protein needed by a female aphid in one day for twenty births is equivalent to that in her own body. The homopterans must therefore have access to other sources of protein. Wherever the nitrogen required for the synthesis of protein is lacking in the food, it must be obtained from the air—four-fifths of which, after all, is nitrogen.

▷
Aphids: 1. *Drepanosiphum platanoides* (L 3 mm); 2. Summer nymph of *Periphyllus villosus* (L 0.75 mm); 3. Summer nymphs of *Periphyllus acericola* (L 0.65 mm); 4. A beech aphid (*Schizodryobius pallipes*; L 4 mm), a lachnid with winter eggs (L 1.5 mm).
Whiteflies: 5. *Aleurochiton complanatus*, (a) summer puparium (L 1.8 mm), (b) winter puparia (L 2 mm).
Scale insect: 6. *Eulecanium coryli* (L 6.5 mm).

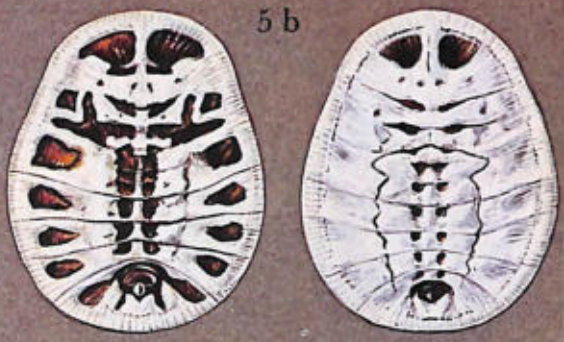


1



5a

5b





2



3



4



6



T. Hölldobler


1
4
5 a
5 b
5 c
2 a
2 b
2 c
3 a
3 b
3 c
T. Hölldobler

But only bacteria are capable of converting it. In fact, all homopterans living on plant juices harbor such bacteria in special organs, the mycetomes. L. Tóth, using bacterial cultures from species of aphid and cicada, demonstrated that these are capable of fixing the nitrogen in the air.

Suborder: Auchenorrhyncha

The order is divided into three suborders, the Auchenorrhyncha, the Sternorrhyncha, and the Coleorrhyncha, based on features of the mouthparts. Members of the first suborder differ from the other homopterans in that the stylet sheath (the labium) on the underside of the head appears to arise from the throat. They are therefore called Auchenorrhyncha (throat-beaked) to contrast them with the Sternorrhyncha (thorax-beaked), whose stylet sheath looks as though it projects from the thorax between the forelegs. This second group includes the psyllids, whiteflies, aphids, and scale insects. A third group, the Coleorrhyncha (sheath-beaked), is sometimes considered to be separate from and of equal rank to the first two. The Coleorrhyncha are regarded as close relatives of the Paleorhyncha which lived in the Permian (280 to 225 million years ago). There is only one family of Coleorrhyncha, the Peloridiidae, the twelve species of which are found in Australia, New Zealand, and South America. They are the only present-day homopterans which live on plants lacking vascular tissue, the mosses. The prothorax still has lateral folds like that of their primitive ancestors, and they bear a greater resemblance to lace bugs than to the cicadas, so they used to be classified as Heteroptera.

The cicadas and related families (superfamily Cicadoidea) are insects of small to quite considerable size. The largest species native to Europe, the blood-red cicada *Tibicen haematodes*, can grow to a L of almost 4 cm. In America, the periodical cicada or "locust" is *Magicicada septendecim*. They are often inconspicuously colored, but some are among the most striking insects, owing to their brilliant coloration or grotesque shape. At rest, the wings are carried like a roof above the abdomen. The hindlegs are often modified for jumping, but they are not so markedly thickened as those of the grasshoppers, since the cicadoideans jump by extending the leg at the coxal joint, and the jumping muscles lie in the coxa and in the metathorax. The cicadoideans may easily be distinguished from the somewhat similar psyllids by their short antennae ending in a thin flagellum. The antennae of the primitive Coleorrhyncha, in contrast, lack flagella and consist of only three segments of equal thickness.

Not all the Cicadoidea are chirping insects, as one might infer from the name of the superfamily. It is necessary to visit some place like southern Indiana in summer to become acquainted with the piercing cry of the cicada, which hardly deserves to be called a "chirp." Only the males produce this noise; this was known even to Xenarchos of Rhodes, who wrote, "Happy are the cicadas, for their wives are mute." But in 1949 the Swedish zoologist Ossian-Nilson discovered that the small planthoppers (superfamily Fulgoroidea) in more northern regions also sing, and in 1959 H. Strübing reported her observations on nineteen German

◁ Galls formed by aphids on deciduous trees: 1. That of *Baizongia pistaciae* on a southern European pistachio (L up to 40 cm); 2. Those of poplar aphids *Pemphigus bursarius* (a), *P. spirothecae* (b), and *P. populinigrae* (c); 3. Those of the elm aphids *Byrsocrypta ulmi* (a), *Schizoneura lanuginosa* (b), and *S. ulmi* (c).
Galls formed by aphids on fir trees: 4. Small pineapple gall of *Adelges lacris*; 5. *Sacciphantes abietis*, fundatrix, covered by woolly wax, in the spring (a), large pineapple gall, still closed (b), and later in the year with opened chambers (c). The white spots on the needles in (5c) are the exuvia of the nymphs which emerged from the chambers; the nymphs themselves have transferred to larch trees.

species of the families Delphacidae and Jassidae. In these species both sexes sing, though the song is imperceptible to the unaided human ear. During their antiphonal song the male searches out the female, who remains in one place.

No other group of insects houses so great a number of symbiotic fungi and bacteria as does the Auchenorrhyncha. Here, too, the Peloridiidae (Coleorrhyncha) with one pair of mycetomes in each of the fifth and sixth abdominal segments in which lives the so-called A-symbiont (a bacterium), represent the most primitive situation. By 1951 the researcher H. J. Müller had investigated 369 species of Auchenorrynchans from fifteen families. He succeeded in tracing the evolutionary course of the symbiotic relationship between these insects and eight different microscopic organisms. Next after the A-symbionts of the Peloridiids must have come the colonization of the PRIMITIVE CICADAS (Procicadidae) by a form of yeast. Other organisms came and went, and finally two of the treehoppers (Membranacidae) he studied managed to acquire six different sorts of symbionts. On the other hand, the family Typhlocybidae completely discarded its symbionts; its different feeding behavior (puncturing the cells of the host plants and sucking out the protein-rich content) had made them unnecessary. But the close reciprocal relationships are not just between the Auchenorrynchans and the microorganisms they harbor; the symbionts influence one another. Thus the bacteria crowd out the yeasts, and the later forms are all bacteria. In providing shelter for their guests, the Auchenorrynchans do not all behave the same; the more primitive Fulgoroidea offer each new arrival a home of its own, while the more highly evolved Cicadoidea attempt to keep them all in one place. In the case of the treehoppers (Membranacidae), which house up to six different sorts, this gives rise to all kinds of difficulties. The accumulation of new symbionts by this family is still in process.

Superfamily: Fulgoroidea

The more primitive families of Auchenorryncha, distinguished by peculiarities of structure of the head, are grouped in the superfamily Fulgoroidea. This is named after the family of the LANTERNFLIES (Fulgoridae), very large tropical insects with bulbous heads and lively coloration. The Latin name (*fulgor* means flash of lightning) is not really justified, since the reputed ability of the lanternlike cephalic process to shine has been proved nonexistent. But not all members of this family have such a fantastic appearance. Most species are confined to the tropics; there are no common species of lanternflies found in the U.S.A. or Canada. They do occur in Mexico and Central America.

The DELPHACIDS (family Delphacidae) are represented in the U.S.A. by many species; the members of this family are characterized by a large, sawtoothed spur at the tip of the hind tibia. The notorious SUGARCANE LEAFHOPPER (*Perkinsiella saccharicida*) was inadvertently introduced to Hawaii around the turn of the century, where it did millions of dollars worth of damage to the sugarcane plantations. At that point the first con-

cern was to discover its homeland. Once it had been established that this leafhopper came from Queensland, a search was made there for the parasites of its eggs and for other enemies which kept its reproduction in bounds. These were found and imported to Hawaii. Two decades later they had settled in so well that the threat was eliminated. At that time, it was only when parasite-free fields were first attacked, and during periods of high humidity (more injurious to the parasites than to the leafhoppers), that instances of damage occurred. This biological pest control could succeed only if simultaneous chemical control was avoided, for the spreading of poison would have interfered disastrously with the delicate process of establishing the natural enemies. Another species, the rice delphacid *Sogota orizicola*, is also a pest in the U.S.A., and the corn planthopper *Perigrinus maidis* is a pest in some regions.

The families Cixiidae and Issidae are represented by many species in the U.S.A. The Tettigometridae are unusual in appearance, with heads flattened in front. They are usually found among ants. One of them, *Tettigometra obliqua* (L 4 mm), became a pest in grain fields in Europe. The family is not represented in North America.

Superfamily: Cicadoidea

The second superfamily, the Cicadoidea, is at a higher stage of evolution than the Fulguroidea. This superfamily includes the cicadas and their relatives. In contrast to the Fulguroidea, the coxae of the middle legs are short and close together, while those of the hind legs are movable. The largest and most impressive animals in this superfamily are the CICADAS (family Cicadidae; see Color plates, pp. 180-181). The males of the large types produce a loud cry, whereas in species with small males the sound is rather quiet. Their stridulatory organ can be best observed if one raises the abdomen of a captured cicada a little and looks into the two cavities enclosed laterally by large projections of the abdomen and ventrally by the opercula of the metathorax. At the bottom one sees an arched plate, stiffened by parallel ribs, the tymbal. A living cicada male usually continues to produce single cries even when so observed, and one can see that the tymbal oscillates each time with a rapid reversal of the direction of curvature of the surface. This produces 120–600 rasping noises per second; they sound like the clicks made by depressing and releasing the arched lid of a metal box. The frequency of repetition determines the pitch of the call, and it can also be modulated by raising and lowering the abdomen. The two tymbals are activated by a pair of muscles originating midventrally and inserting on the tymbals by way of short tendons. A huge air sac which crowds all the abdominal organs toward the back, and is separated from the lateral cavity by a thin, shimmering membrane, no doubt contributes to amplification of the sound. Lateral to the tympani on either side are the auditory organs; these are inactivated by a special muscle when the cicada is about to chirp.

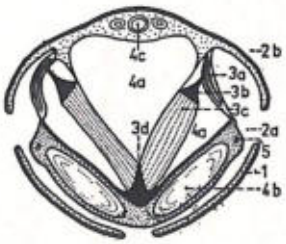


Fig. 11-1. Cross section through the anterior abdomen of a cicada, showing auditory and stridulatory organs. 1. Operculum, 2a. Tympanic cavity, 2b. Tymbal cover, 3a. Tymbal, with reinforcing ripples, 3b. Tymbal tendon, 3c. Tymbal muscle, 3d. Origin of the tymbal muscle, 4a. Air sac, 4b. Tympanic membrane, or mirror, 4c. Internal organs displaced dorsally by the air sac, 5. Auditory organ.

It is not only by their noise that the large cicadas of warm countries make themselves unpopular. The females lay their eggs with the strong

ovipositor deep in the woody parts of plants above the ground; the larvae which hatch from them move directly into the soil and suck the juices from the roots. Their forelegs are modified into digging tools, the shovels being formed particularly by the femora. The development of cicadas usually extends over several years; the American SEVENTEEN-YEAR CICADA (*Magicicada septendecim*; improperly called seventeen-year locust) requires thirteen years in the south and southwest, and seventeen years in the north and northeast, to develop from egg to imago. After this long period of damaging various cultivated plants the imago, in the four to six weeks of its existence, does not eat. Of the cicadas of southern Europe, *Lyristes plebejus* is largest, with a wingspan of 10 cm, and the somewhat smaller *Cicada orni* is the most common. Another southern species is the pretty, red-veined *Tibicen haematodes* (L 26–38 mm), which has spread into the warm vineyard regions of Europe. The habitat of *Cicadetta montana* (L at most 2 cm, wingspan 5 cm; see Color plates, pp. 180/181) extends still further.

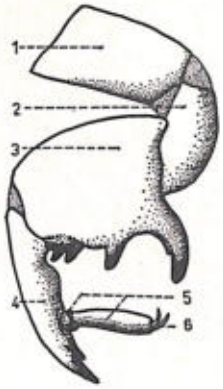


Fig. 11-2. Digging leg (foreleg) of a cicada larva. 1. Coxa, 2. Trochanter, 3. Femur, 4. Tibia, 5. Tarsal segments, 6. Claws (pretarsi).

The largely tropical family of the TREEHOPPERS (Membranacidae; see Color plate, p. 182) is distinguished by the pronotum, which extends backward to cover the abdomen, but attains its full size only in the imago. In tropical species it is often fantastically shaped and even the related American BUFFALO TREEHOPPER (*Strictocephala bubalus*; L 7–10 mm) provides only a feeble indication of such extravagance of design: its pronotum has a long, backward-pointing tip on the anterior margin, with two horns directed laterally. But there is no trace of the glorious coloration of its tropical relatives; it is green with transparent wings.

The many species of FROGHOPPERS (adults) or SPITTLEBUGS (nymphs) (family Cercopidae) have been given their colloquial names, spittle insects in America, cuckoo's spittle in Europe, because it is characteristic of the nymphs to cover themselves with foam. This serves as protection against dessication and probably against enemies as well, although it has been observed that thread-waisted wasps manage to fish them out of their foam. Of course, defense mechanisms which provide absolute security are unknown in nature. Evolution makes it possible for a species to maintain itself against others which prey upon it, but at the same time it can provide the predator with a means of coping with this protective device. The way the foam is produced has not yet been satisfactorily explained. Its water content arises largely from the gut, whereas the viscous element which gives the foam its stability comes at least in part from the excretory tubules, as Licent discovered. Osborn's investigations demonstrated that this substance is formed by the lateral glands of the seventh and eighth abdominal segments. According to Šulc, this glandular secretion is a wax, saponified by substances in the gut fluid and then dissolved in the fluid. The intestinal contents of this animal contain no sugar and can be discharged in large quantities by some froghoppers. Of a Madagascan species, Goudot reports that sixty animals filled a bottle with this fluid excrement in half an hour.

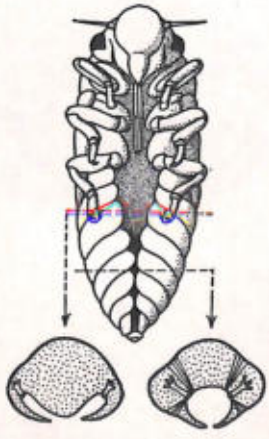


Fig. 11-3. Froghopper nymph (exemplified by *Aphophora salicina*). Above, ventral aspect; below, schematic cross sections. Note the air channel along the abdomen, which supplies the nymph with air through the surrounding foam.

But there is no need to draw on exotic examples; the nymphs of the American SPITTLEBUG (*Propsapia bicincta*; L 9–11 mm) put on a similar show in summer: their excrement is produced in such profusion that if one walks through the grass in which they live, one's garments become completely soaked. All agree that the air bubbles in the foam represent expelled respiratory air. In order to take in respiratory air while enveloped in foam, the nymph needs a special structure; the terga of the abdomen have incurved lateral margins which almost meet in the ventral midline, forming a groove, almost a closed canal, open at the end of the abdomen. The respiratory channels open into this groove. Now it suffices for the nymph to extend the end of the groove a little beyond the foam layer, so that it can take in fresh air. These foamy masses containing spittlebug nymphs can be found on many plants.

In contrast to the sluggish nymph, the froghopper imago is an agile jumper. It is assisted in the take-off by arrays of strong spines on the hind-legs, since these give the jumping legs a good purchase on the substrate. The most common meadow spittlebug, *Philaenus spumarius* (L 5–6 mm), occupies meadows in great numbers when the hay is mowed. The prettiest, *Cercopis sanguinolenta* (L 8–10 mm), from Europe, is patterned in black and red; its foamy masses cannot be observed, since the nymphs live underground. Most froghoppers are of no economic importance, but species of the genus *Tomaspis* do severe damage to sugarcane plantations in Trinidad, and the meadow spittlebug *Philaenus spumarius* can cause serious stunting of hay when the populations are large enough.

All the Auchenorrynchan families named so far are excelled by the LEAFHOPPERS (family Cicadellidae) in number of species and individuals. About 5000 species belong to this family, and every sweep of an insect net through grass, herbaceous plants, or bushes captures crowds of these small, dainty animals, usually greenish in color. But though they are caught so easily, they escape with equal ease by leaping or flying out of the opened net. The leafhoppers are distinguished from the froghoppers by their more slender, posteriorly tapered shape and by the long tibiae of the hind-legs, which lack spurs. But a strong lens is required to reveal their variety of form. Only the Indo-Australian species *Ledra aurita* is large enough (13–18 mm) to be studied with the unaided eye. Despite—or perhaps because of—its amazing shape, this animal is easily overlooked when it sits motionless on a tree trunk. The front of the head is broadened into a roof-like plate, and the pronotum bears an earlike appendage at either side over the bases of the wings. Furthermore, the network of veins on the thickened forewings stands out from the surface. Brown to dark olive, this animal is excellently matched in both form and color to the tree bark on which it usually sits. Early in their development the leafhoppers are food specialists, concentrating on certain plants; but as adults they no longer specialize. In their great numbers, they are doubtless injurious to plant growth, though the damage they do is difficult to estimate. Some species can cause

quite appreciable damage; one such species is *Carneocephala sagittifera* (L 4.5–5 mm), which is often quite abundant on pasture and turf grasses, causing discoloration, stunting, and protein loss as a result of its feeding activities. It occurs throughout the southern U.S.A. and the Caribbean area. The CLOVER LEAFHOPPER (*Aceratagallia sanguinolenta*; L 3–4.5 mm) is also a pest dreaded by farmers. Rather than feed on the juice from sieve tubes, the ROSE LEAFHOPPER (*Edwardsiana rosae*) sucks the cellular tissue, which it liquefies with its saliva. This gives the affected leaves yellow spots. The rose leafhopper attacks other members of the rose family as well —for example, plum and apple trees and strawberries—and even red-currant bushes, which are not closely related to the roses. The POTATO LEAFHOPPER (*Empoasca abrupta*; L 4 mm) can damage grain, potatoes and other root plants, and various herbs. Many other species of leafhoppers cause severe damage to crops. For example, *Eutettix tenella* is considered by sugar-beet growers in the western U.S.A. as their greatest enemy. *Erythroneura comes* does damage to grapevines second only to that done by the grape phylloxera. In Africa, *Chlorita facialis* is much feared in cotton plantations.

Suborder: Sternorrhyncha, superfamily Psylloidea

The PSYLLIDS (superfamily Psylloidea), with about 1000 species, are a less extensive group than the Cicadoidea, and are the first family of the suborder Sternorrhyncha. They are considered as a single family, the Psyllidae. The adults resemble some Cicadidae, but they can be distinguished by the long psyllid antenna, a slender, eight-segment flagellum with two basal segments. Their wings have fewer veins than those of the Auchenorrhyncha and almost always lack cross veins. The psyllids are as good as the Auchenorrhyncha at jumping, and they use the same technique of extension at the coxal joint; in fact, the psyllid method may be even better, since the coxae of their jumping legs do not move relative to the metathorax. The jump usually marks the beginning of a short flight, but the psyllids never fly very far at a time. The nymphs of the psyllids differ from the cicadoidean type more markedly than do the adults. They are unusually flattened creatures with three pairs of grasping legs. They secrete wax and produce large amounts of honeydew, the drops of which are covered with wax.

Behavior and life history have been most intensively studied in the psyllids which are pests. The APPLE SUCKER (*Psylla mali*; L 4 mm) is found mainly in neglected orchards. The females use their ovipositors to lay the yellow eggs in the bark at the tips of apple-tree twigs, where they spend the winter. In spring the flat nymphs hatch out and are then found, along with their abundant honeydew, among the leaves and blossoms. Soon sooty mold settles on the honeydew, covering the plants with a slimy black coating which is no less harmful than the loss of juice. The winged adults do no further damage. A closely related and similar species in Europe is *Psylla costalis* (L 2–2.5 mm); this leaf sucker, however, spends the winter as an imago, and the eggs thus develop later, so that the nymphs'

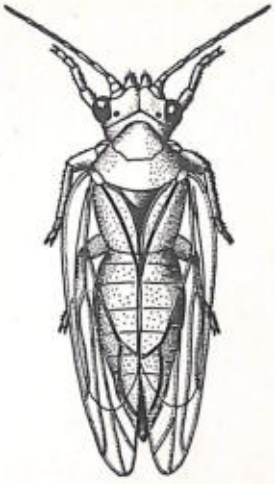


Fig. 11-4. The spotted pear psyllid (*Psylla pyricola*).

sucking and honeydew production do no harm to the blossoms. This is also true of the EUROPEAN PEAR PSYLLID (*Psylla pirisuga*) and AMERICAN PEAR PSYLLID (*P. pyricola*; L 3 mm). The females of *P. pirisuga* lay their eggs as late as April and May. The nymphs first suck the leaves, then the young shoots, and finally they congregate to suck the shoots from the previous year. In the process, they produce very much more honeydew than the apple psyllid, and it is this that does the main damage. *P. pyricola* behaves similarly, but with one difference; in the north of Europe it is limited to one generation per year, but after its accidental introduction to North America the annual number of generations increased to three or even four. The dangerous Mediterranean olive-tree pest *Euphyllura olivina* also has three or four generations per year.

All the psyllids named above belong to the subfamily Psyllinae; the European species *Trioza viridula* (L 1.7 mm), recognizable by the breadth of its head compared with the pronotum, belongs to the Triozinae. The yellow-green imagines, with dark red eyes, spend the winter on conifers and hedge bushes. In early summer they fly into the nearby carrot fields and cause curly leaf disease. They continue laying eggs into July, by which time the female has generated about 400–700 progeny, which even as nymphs also cause damage; they grow to adults in only a month. Another species, the PERSIMMON PSYLLA (*Trioza disapyri*) occurs in the U.S.A.

Superfamily: Aleurodoidea

The WHITEFLIES (superfamily Aleurodoidea) include the smallest number of species of any homopteran superfamily, again, the species are so similar that they are all classified as one family, the Aleurodidae. The adults are small, winged, and covered all over with waxy dust. This substance comes from glands on the underside of the abdomen; the legs distribute it over the whole body and even onto the surface of the wings. The antennae resemble those of the psyllids, the wings have only a few veins, and the hindwings are only slightly shorter than the forewings. At rest, the wings cover the abdomen like a roof. Unlike the wings of the hemipterans, Cicadoidea, psyllids, and aphids, those of the whiteflies are not coupled to form a unit during flight. Most species are tropical, and some are serious pests. At least six species, however, occur as far north as New York State.

The development and metamorphosis of whiteflies proceeds in a very strange manner. Although the newly hatched nymph can move about freely, the second-stage nymph (after the first molt) retains only the stumps of legs, so that it is immobilized during further development through the third and fourth stages. The nymph sucks juices up to the beginning of the fourth stage, and then it stops and undergoes an inner transformation to the imago. This is the most thorough transformation to occur in the entire insect class, exclusive of the holometabolous orders. Ordinarily the typical adult organs, such as the wings and the copulatory appendages, are gradually developed from one nymphal stage to the next; at the latest, primordia are laid down in the last nymphal stage (in the case

of complete metamorphosis, in the pupal stage). The last nymphal stage of the whiteflies is a dormant one, similar to a pupa, but at the beginning it displays not the slightest hint of the adult form. It is during this stage that the drastic transformation takes place. Finally the upper surface of the puparium, like a tiny box, opens in a T-shaped crack through which the winged insect emerges.

Of the few species of whiteflies native to Europe, the most commonly found, on the leaves of the Norway maple, is the last nymphal stage (the puparium) and the imago of *Aleurochiton complanatus* (see Color plate, p. 197). Here the puparium appears in two completely different forms: the summer puparium and the winter puparium. Both are pear-shaped in outline as seen from above. The summer form is smaller but thicker, and is surrounded by a wax border, while the larger, flatter winter form is dark brown and more or less covered on the upper surface by white waxy secretions which emphasize its pattern of segmentation. Day length determines which of the two forms appears. The summer puparium hatches in a few days at temperatures around 20°C, while lower temperatures delay its development and finally kill it. In contrast, the winter puparium is in a state of diapause (see Chapter 1); no amount of heating can arouse it unless it has previously rested at low temperature (0–10°C) for six to eight weeks. Summar puparia cannot survive such a period of cold, whereas the winter puparia require it for survival. The Homoptera researcher J. H. Müller, who made these discoveries, also found that although day length determines the form of the puparium, once a winter puparium has been produced, the day length no longer has any influence on it. It is only the sequence of a cold period followed by warmth that can wake it from its slumber.

In warmer countries, whiteflies are of considerable economic significance. In South Africa and NorthAmerica (particularly Florida), the CITRUS WHITEFLY (*Dialeurodes citri*), since its immigration from its Indian homeland, has become an arch foe of the citrus grower. Another emigrant from India is the CITRUS BLACKFLY (*Aleurocanthus woglumy*). With its five generations annually, it now despoils citrus orchards in the region of Panama and in the Antilles. On the other hand, the GREENHOUSE WHITEFLY (*Trialeurodes vaporarium*; L 1–3 mm), now established in North America, Europe, and Australia, probably originated in Central America. In those climatic zones where there is winter frost, this whitefly cannot survive in the open, but it finds in greenhouses a dwelling place where it can continue to reproduce regardless of the season. Since it is not at all particular about what it eats, it attacks all sorts of ornamental plants as well as tomatoes, cucumbers, and melons. The main damage is done not by the sucking itself, but by the superabundance of excrement. Remarkably, this is not sugar-containing honeydew; instead, it contains nitrogen compounds. The greenhouse whitefly lays about 130 eggs in its lifetime, and even the eggs of unmated females can develop. From the fertilized eggs come

progeny of both sexes, but the unfertilized eggs hatch out only males in the American form, and in the European form, only females.

Superfamily: Aphidoidea

In contrast to the whiteflies, the superfamily Aphidoidea (APHIDS) includes a great number of species. C. Börner estimated in 1951 that a total of 3000 species was known, 831 of them in central Europe. In the U.S.A. over eighty species are considered to be pests. All are small insects; they may or may not have wings. The wings, if present, are coupled together in flight, and at rest are carried like a roof over the abdomen. The antennae consist of three to six segments, and are equipped with olfactory sense organs called rhinaria. The lateral eyes are composed of three or more facets; in the latter case, three of the facets are often separated from the rest (forming the ocular tubercles). Only the winged forms have three ocelli. On the back of the fifth abdominal segment is a pair of tubules (cornicles) through which the animal can, when threatened, exude blood with wax-filled blood cells. Smeared onto the jaws of the attacker, this mass is said to be an effective weapon of defense.

The little aphids, quite unimpressive when seen with the naked eye, appear at first not very attractive, and in fact are viewed with dismay by gardening enthusiasts. Even amateur entomologists will probably never regard aphid colletions as competitive with collections of beetles or butterflies. The uniformity and small size of these animals also makes determination of species more difficult, so that they are almost the only insect group for which few keys have been published. But anyone who ignores these problems and takes up a detailed study of the aphids will find that they offer a greater abundance of fascinating puzzles than almost any other insect group. The usual rule is that children resemble their parents, but among the aphids there are sequences of generations which differ both in appearance and in behavior. This alternation of generations is frequently associated with an alternation of hosts, but it is more than just a change of menu. For example, one series of generations of the GREEN PEACH APHID (*Myzus persicae*) lives exclusively on peach trees; this is followed by another sequence which sucks the juices of plants from sixty-nine families, including ferns. The method of reproduction (bisexual or parthenogenetic) also changes with the generations in a regular way. At first the biologist may be bewildered by this complex of generation cycles; only the evolutionary history can offer a key to understanding. Efforts are being made to reconstruct this history; and since aphid development is still proceeding rapidly, the study of aphids provides intriguing insights into evolutionary processes among present-day insects.

Alternation of generations

If we are to understand this exceedingly complicated process of alternation of generations, we cannot avoid some of the special terms used by aphidologists. The animal hatching from a fertilized egg is always female and is called the fundatrix, or stem mother. She produces daughters, fundatrigeniae, by parthenogenesis, and these also reproduce parthenogenetically; for this reason they are also called virgins. Several generations of

virgins can follow one another; the aphids in the last such generation are called sexuparae, because their offspring are both male and female, and the latter cannot reproduce unless inseminated by the males. Their offspring are called sexuales, and the term female is sometimes reserved for those of this generation, even though the parthenogenetic aphids are also female. Whereas the fundatrix and virgins of most aphid families (with the exception of the adelgids and phylloxerids) are viviparous, bearing the young alive, the female sexuales always lay eggs. All of these generations differ from one another, and the variety is further increased by the fact that within one generation the virgins may be winged or wingless, may grow rapidly or slowly (even entering diapause), and may even have siblings which reproduce bisexually. The complete cycle of development, or holocycle (from the Greek $\delta\lambda os$ = whole) can become an incomplete cycle (anholocycle) by dropping out particular parts of the sequence, or a separate incomplete cycle (paracycle) may go on simultaneously, merging with the holocycle from time to time.

It may be assumed that the ancestral aphids were less particular about their host species and resembled the present-day primitive Lachnidae, Chaitophoridae, and Callaphididae. Nowadays the aphids are very much dependent upon the juice of particular plants on which they feed. In summer, however, the high pressures of the juices, typical of the trees in spring, decrease sharply. For this reason, many species acquired the habit of transferring to herbaceous plants in early summer, where they were provided with a rich supply of juice for a longer period. Here they stay until autumn, when the aphids in the last virginal generation return to the trees; there their inseminated female offspring lay the winter eggs. This is how alternation of hosts arose among the higher aphids. The evolutionarily older host is the tree: this is called the primary host or, in the terminology of parasitologists, the definitive or final host. The evolutionarily younger hosts of the higher aphids are then secondary hosts or, in the terminology of parasitologists, intermediate hosts. But the alternation of hosts was for some of the higher aphids not the end of their development; they returned by two separate paths to the condition of host constancy. One path involved disappearance of the generations on the primary host, so that the aphids are restricted to the secondary host; in the other, the generations on the secondary host are dropped out, so that the original evolutionary condition of restriction to the primary host is restored. We have seen that the sexuales and their offspring, the fundatrices, live on the primary host. If this part of the holocycle is omitted, only the virgins on the secondary host are left, and the part of the cycle which remains is composed only of parthenogenetically reproducing aphids. In some cases the sexuparae, sexuales, and fundatrices are all taken over onto the secondary host, and then the entire holocycle can proceed there. Of the more than 800 aphid species in central Europe, barely a fifth have retained the original condition in which all generations live on the primary host; a

Alternation of hosts

good four-fifths alternate hosts or have become settled on the secondary host or, as a recent development, on the primary one again. Without knowledge of their evolutionary background, one could not interpret this enormous variety.

As an inheritance from their ancestors, the aphids originally had wings in all generations. Among the present-day species, this is still the case for the Californian species of *Drepanosiphum*, *D. californicum*, whereas females of the German *D. platanoides* are without wings. In the next stage, the fundatrix lost her wings. In subsequent stages of this line of development individual virgins and finally whole virginal generations became wingless. The beech aphid native to Germany (*Phyllaphis fagi*) produces winged virgins only in the two generations following the fundatrix generation; then the wings vanish and only reappear in the males, several generations later. In the Saltusaphidinae, a subfamily of aphids which feed on sedges, the virgins still have wings, but the males have forfeited them. The virgins need wings to disperse the species and to migrate away should the host plants become overpopulated, and in species which alternate hosts the first virginal generation requires them for flight to the secondary host and the sexuparae need them to fly back to the primary host. Possession of wings allows the males to move to other colonies of the same species, so that sibling incest (and, among the aphids, incest between uncle and niece) is prevented. What, then, determines whether a virgin larva grows wings or not? Wing formation in the virgins is brought about by the lowered pressure of the juices in the vessels of the host plant and the resultant shortage of food. Here it is literally true that hunger gives wings. This generally occurs in early summer, but it may happen even sooner if the plants are overpopulated with aphids. Since the winged individuals fly away immediately after the last molt, the whole process is an example of a negative-feedback system. Production of the winged sexuparae which return to the original host is a consequence of a shorter period of daylight and a reduced temperature. The two migratory forms differ from their predecessors not only in the possession of wings; there is also a thorough transformation in their behavior. These animals have known as food, since the larval period, only that kind of plant on which they were born; but after the last molt they reject it completely and, at a stroke, switch to the plant which fed their ancestors, a most puzzling phenomenon.

The fundatrix usually develops from a fertilized egg; the other generations arise from unfertilized eggs in the case of the adelgids and phylloxerids, and are born as larvae (viviparously) in all other aphid families. Species which have lost the bisexual part of the cycle cannot pass the winter as fertilized eggs and cannot therefore survive in the open where the winters are cold. These anholocyclic species are therefore found in such regions only in greenhouses, cellars, and other protected places, though in the tropics they can pass the whole year outdoors. Only the adelgids, which lay eggs in all generations, can endure the cold winter

even on the secondary host, in the dormant first larval stage. Thus they can extend the complete cycle of development so that it spans two years; in addition, this family can form anholocyclic species and races which are confined to the secondary host.

The superfamily Aphidoidea contains four families, the aphids proper, or plantlice, APHIDAE, the woolly aphids and gall-making aphids, ERIOSOMATIDAE, the pine and spruce aphids, CHERMIDAE, and the phylloxerans, PHYLLOXERIDAE.

Family: Aphidae, subfamily Lachninae

Of the four subfamilies of Aphidae, one is distinguished as primitive by the fact that its species live on trees without alternation of hosts. In the subfamily Lachninae, the tribe Cinarini comprises aphids which feed on conifers. Some of these, while not changing their host, do regularly change their position on the host, descending to the roots in the summer, where the ants build earth-roofed barns for them and collect the sweet fluid excrement, the honeydew, as a favorite food. But not all Cinarini are visited by ants. The honeydew of some species is rejected by the ants even though these species may feed on the same host plant as another species whose honeydew is avidly collected. For example, *Buchneria pectinatae* receives no attention from the ants, but its copious excretions are highly prized by honeybees; this honeydew forms the basis of the famed fir honey, the most expensive of all. During the period of greatest honeydew production by this aphid in the German Black Forest, beekeepers travel there from far away with their bee colonies, and, unless storms destroy the aphids, they reap rich harvests. On mountain slopes the aphid *Cinaropsis piceae*, feeding on spruce and fir trees, also delivers an abundant yield. The population fluctuations of these and other honeydew producers of the forests are closely followed by expert apiarists, so that collection by the bees can be begun as soon as conditions are appropriate. Of course, an increase in a forest's aphid population hinders the growth of the wood, but in overall terms this damage is more than compensated by the value of the harvested honey. In the wooded mountain regions the Cinarini may well be counted among the useful animals.

The lachnines living on deciduous trees belong to the tribe Lachnini (see Color plate, p. 197). They are large, dark long-legged animals. Sitting in furrows of oak bark, *Stomaphis quercus* must drive its stylets all the way into the vascular bundles of the wood. Its rostrum is three times as long as the body! The large quantities of honeydew produced by this aphid attract the ant *Lasius fuliginosus*, which then often establishes a colony in the roots. A third lachnine tribe, the Tramini, propagates entirely parthenogenetically, with no bisexual generation; these aphids live in the ground about the roots of herbaceous plants, where they are cared for by ants.

Subfamily: Aphinae, tribe Chaitophorini

Among the aphid subfamily Aphinae, the tribe Chaitophorini (the species of the genus *Periphyllus*), has followed an unusual path of development. One, the NORWAY MAPLE APHID (*P. lyropictus*) feeds on the underside of maple leaves. Whereas other aphids in the same place continue to pro-

duce countless virgins all summer long, the *P. lyropictus* nymphs enter a dormant state in the spring and do not emerge from it until late summer. The bristly dormant stages of the European *P. acericola* (see Color plate, p. 197) often form large areas of closely packed larvae on the underside of leaves, while those of *P. villosus* (see Color plate, p. 197), with lamellate marginal hairs, are distributed singly and, due to their small size and green color, are difficult to find on most leaves. But on the red undersides of the leaves of a variety of Norway maple (*Acer platanoides*) they are quite obvious. By giving up the opportunity of summertime reproduction but at the same time avoiding the losses produced in summer by an army of enemies, this aphid species preserves itself just as effectively as do those which reproduce in the ordinary way.

Tribe: Callaphidini

The aphine tribe Callaphidini is the third group of tree-dwelling aphids which does not alternate hosts. It, too, includes a remarkable species, *Drepanosiphum platanoides* (L 3 mm; see Color plate, p. 197), also found on the undersides of maple leaves. Here they sit, often in great numbers, in a notably uniform distribution. Even a minor disturbance causes them to jump down and fly away; but if one carefully turns over a leaf occupied by these aphids, so that they are now sitting on the upper surface, they cannot jump off. They run over the edge of the leaf to its underside, and only then are they successful in jumping into flight. Their inability to jump upward lies in the fact that their jumping legs are the forelegs, and they propel the animal backward in a very flat arc. Thus when they are sitting on top of a leaf they are prevented by gravity from leaping free. In contrast to other, more sluggish species, this aphid is capable of fleeing from an enemy, even if it has already been seized by one leg; it simply lets the leg break off at a special place between trochanter and coxa. The structure at this place is such that the wound closes quickly, and the loss of one or two legs makes little difference to the locomotion of this winged aphid. Whereas *D. platanoides* is found in great numbers on maple trees until well into autumn, its relative *Phyllaphis fagi*, with its white, waxy "wool," is only apparent for a short time in spring. Shortly thereafter these aphids disappear, and for a long time where they had gone was a mystery. Now it is known that the winged second generation of virgins seeks out the crowns of beech trees, where subsequent wingless virgins, with a low rate of reproduction, pass the summer in seclusion.

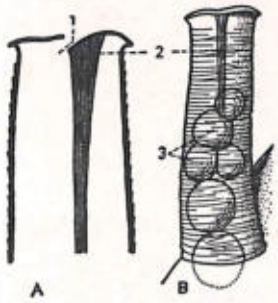


Fig. 11-5. Cornicle on the abdomen of an aphidid. A, longitudinal section; B, as seen from the side. The opening (1) is controlled by a muscle (2). Through it emerge wax-containing blood cells (3) intended to make the mouthparts of an attacker slippery.

Subfamily: Aphidinae

Of the four aphid subfamilies, the Aphidinae comprise by far the greatest number of species. Almost two-thirds of all species belong to this subfamily, and in it are represented all the transitions from restriction to one host to alternation of hosts, from complete to incomplete cycles on the primary and on the secondary host, and from the greatest variety in food to limitation to one host plant. A peculiarity of those which alternate hosts is the two-stage bisexual generation; the siblings of the males are virgins which bear parthenogenetically the females with which the males, their uncles, rather than their brothers, mate. This means that the males are

born on the secondary host and, as adults, fly to the primary host, where mating occurs. Only two economically important species will be mentioned here: the bean aphid and the green peach aphid. The BEAN APHID (*Aphis fabae*), known to and disliked by every gardener, spends the winter on its primary hosts, the spindle-tree genus *Euonymus*; the secondary hosts, occupied during the summer, are an enormous variety of herbaceous plants of different families. These aphids are industriously milked by ants, which increases the rate of production of honeydew and thus of juice intake. A consequence of this is a more rapid rate of growth and hence a greater multiplication of the aphids. A bean field from which the ants were excluded yielded twice as many beans, due to the smaller aphid population, than did an equally large field kept under the same conditions except that ants were allowed free access. The only primary host of the GREEN PEACH APHID (*Myzus persicae*) is the peach tree, whereas the countless secondary hosts belong to sixty-nine different families. These secondary hosts include many cultivated plants, but the main injury to these is not caused by the sucking of their juices: the peach aphid transmits pathogenic viruses to them. This aphid affects particularly potatoes (leaf-roll disease) and root vegetables (the mosaic and yellows of sugar beet), but it is not the only one involved; more than one-third of the animal species which transmit virus diseases to plants are aphids!

Subfamily: Thelaxinae, and family: Eriosomatidea

Of the subfamily Thelaxinae, only one forest pest, the BALSAM TWIG APHID (*Mindarus abietinus*) will be named. The family Eriosomatinae includes the WOOLLY APPLE APHID (*Eriosoma lanigerum*), an American species carried to Germany in 1802; there it reproduces exclusively by parthogenesis on its secondary host, the apple tree. In contrast, its close relative *Schizoneura languinosa* (see Color plate, p. 198) goes through the full cycle of generations. Its primary host is the common elm, and the secondary hosts are the pear tree and, more rarely, the quince. The fundatrix converts the leaf buds of the elm into large, closed sacs in which the virgins grow up. They cover the drops of honeydew with a thin layer of wax so that they can live among them without getting wet. Aphid galls of various sorts (spiral thickenings of the leaf stalks, saclike thickenings of the leaf ribs, in-rollings of the leaf margins) are frequently encountered on poplars (see Color plate, p. 198); they are produced by members of the genera *Pemphigus*, *Pachypappa*, *Thecabius*, and others. If one cuts open one of the elm or poplar galls to reveal the virgins inhabiting it, one can see that though these aphids are surrounded by tissue on all sides, they are not within the plant tissue itself but always outside the epidermis. This is also true of the gall-forming members of the two families to be discussed below. In contrast, the larvae of the gall wasps live within the plant tissue forming the gall.

Family: Chermidae

The last two aphid families, the Chermidae and Phylloxeridae, have no viviparous generations. All the virgins, like the inseminated females, lay eggs. The CHERMIDS (the pine and spruce aphids) are characterized by the fact that the fundatrix produces a gall on the red fir, from which the

winged virgins emerge. They fly to the secondary host, again always a conifer, where they lay their eggs. The secondary-host virgins which hatch from these spend the winter as juvenile larvae and eventually also lay their eggs on the secondary host. These develop into winged individuals which return to the primary host and, it was thought, lay eggs which hatch out both males and females. But the most recent investigations of A. W. Steffan have shown that some of the mothers produce only males and others, only females. Not all the individuals return to the primary host, however; some enter a dormant state in which they pass the winter, and others form several summer generations of secondary-host virgins and then become dormant for the winter. The male and female animals are the fifth generation of this five-step, two-year cycle. The incomplete paracycles which occur on both the primary and the secondary hosts have in some cases given rise to new species which can no longer merge with the holocycle. Of all these possible forms, the walker in the woods is most likely to note the pineapple-shaped galls on the twigs of spruce trees (see Color plate, p. 198). As a result of the bite of the fundatrix in the spring, the bases of the needles on the young shoots swell and expand. Between these expansions, chambers are created into which the first-stage nymphs move after they hatch from the eggs. The large galls made by the species of *Sacchiphantes* can be recognized by the long, unswollen tips of needles which remain; those of species of *Adelges* end in short tips. The secondary-host virgins of these chermids can be found all summer long in large numbers on the twigs of larches, especially in the vicinity of gall-bearing spruce trees. They are coated with woolly secretions of wax, as are their eggs. The trunks of white pines (*Pinus strobus*) growing in unsuitable places are also frequently covered with a white layer of waxy secretions. This actually consists of wax-coated secondary-host virgins of the PINE BARK APHID (*Pineus strobi*), an adelgid aphid native to the U.S.A. Its primary host is the silver fir. This aphid has been carried to Germany, where no silver firs live; in this case they are restricted to anholocyclid development on the secondary host. The same is true of *Gilletteella cooleyi*, the American primary hosts of which (various pines: *Pinus sitchensis*, *P. pungens*, and *P. engelmanni*) are not cultivated by foresters in Europe. The white flakes of wax are often to be seen on the primary host (the Douglas fir) in Europe, and in parks where one of the primary hosts happened to be standing near an infested Douglas fir, galls have been found on the pine; that is, the aphid will go through the holocycle even in Europe, if it is given the opportunity.

Family: Phylloxeridae

The family Phylloxeridae includes holocyclic species as well as species consisting only of the fundatrix and bisexual generations, or only of winged and wingless virgins. As in the chermid family, all generations come from eggs; in contrast to the chermids, there is no alternation of hosts, or at most only the initial stages. For example, in the southern OAK PHYLLOXERIDS both hosts belong to the same genus; the primary host, in winter, is an evergreen oak, and the secondary, summer, host is a

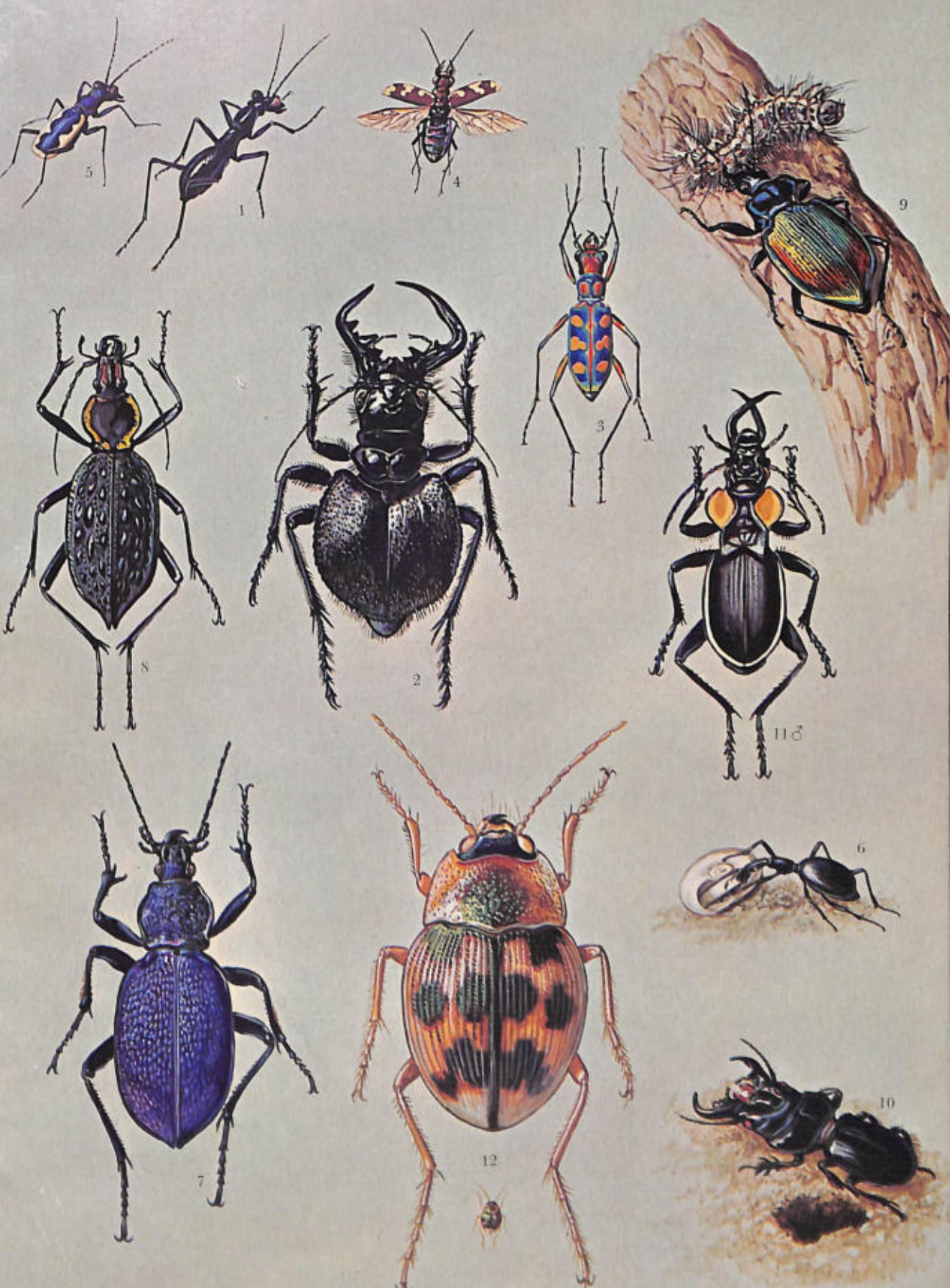
deciduous oak. The best-known phylloxerid originated in North America and was carried to England in 1863 and to France and Germany in 1874; this is the GRAPE PHYLLOXERID (*Phylloxera vitifoliae*). Here the primary host is the leaves of a grapevine and the secondary host, the roots of the same vine. But the alternation between the two involves more than just a change of position (an indication of this complexity has already been seen in the Cinarini): the leaf virgins differ from the root virgins. Not only the fundatrices, but all the leaf generations produce galls on the vine leaves, open at the top and with a wrinkled bottom where the eggs are laid. If a population increase requires it, they can also attack shoots and the stems of leaves and flowers. The root generations produce craterlike tuberosities on the young, still-elongating roots; the tuberosities then decay and can kill the roots. The way that saliva produces the galls has been explained by W. Kloft: in strong concentrations the poison in the saliva inhibits cell growth, but if the concentration is weak it encourages growth. Thus at different distances from the puncture there are zones growing at different rates. The generation of sexuparae is born on the roots and the adults migrate to the top of the vine and fly away. Partly under their own power, and partly blown by the wind, they reach other vines; there the tiny, wingless aphids of the bisexual generation develop above ground. From the fertilized eggs laid by these females a new fundatrix generation is produced, and these aphids produce leaf galls. This is the holocycle, which occurs primarily on American grapevines. On the European vines there usually are only root-gall generations. They generally spend the winter dormant, in the first nymphal stage. Unfortunately, the European vine cannot withstand root infestation as well as the American species can. The remedy for this is to graft the European vine, the leaves of which are resistant to infestation, onto American rootstocks. Moreover, the root aphids can be killed if one puts carbon disulphide in the soil.

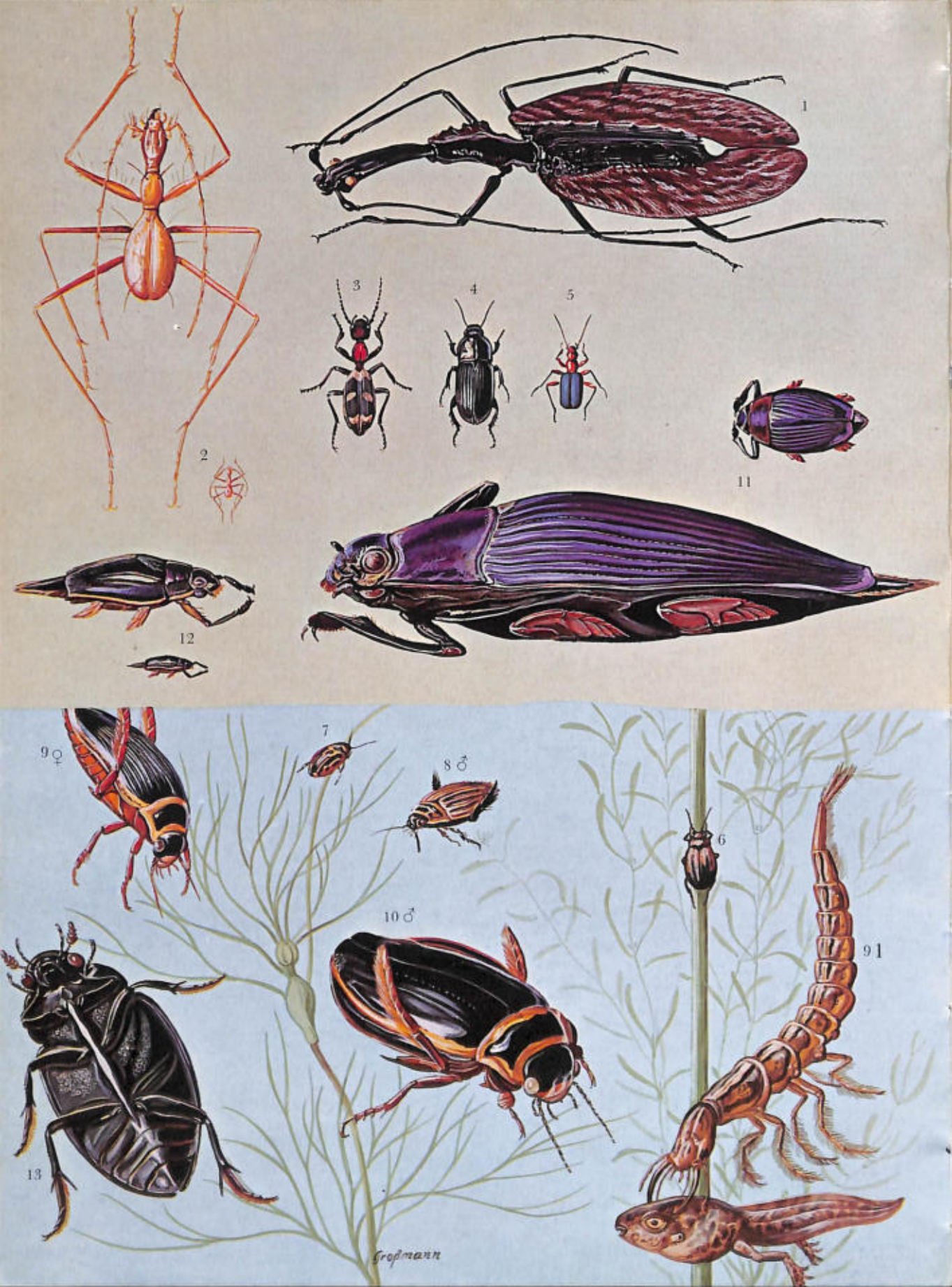
The large numbers of progeny and short generation span of aphids endow them with an enormous reproductive capacity. This would soon lead to overpopulation if it were not held in check by a long list of enemies. Many of these are encountered almost routinely among the aphid colonies of heavily infested plants: ladybugs and their larvae, green lacewings and their larvae (aphid lions), and the green hoverfly larvae, pointed in front and broad in back, are the most conspicuous of these. The army of wasps which parasitize aphid colonies operates more secretly, but the empty mummies and swollen aphids to be found in any older aphid colony betray their activity. Aphids are also attacked by other insects and many birds; the chickadees are masters at finding their winter eggs. But aphids are most vulnerable to the weather, which kills them either directly or indirectly by damaging the plants on which they feed and on which the sluggish, wingless generations are effectively imprisoned.

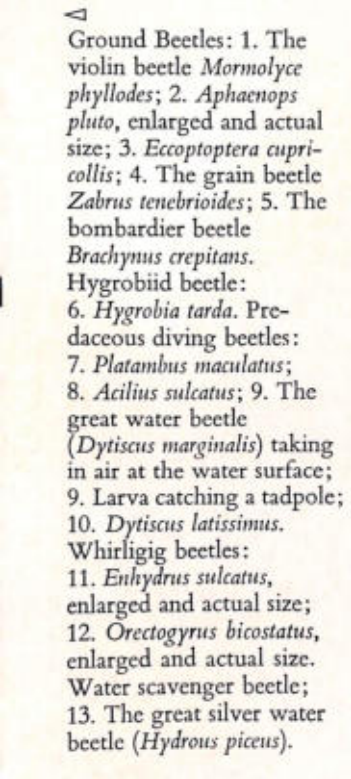
The homopteran superfamily Coccoidea is characterized by the great difference between the two sexes. The males are typical winged insects,

▷
Tiger beetles: 1. *Tricondyla aptera*; 2. *Mantichora scabra*; 3. *Cicindela octonotata*; 4. *Cicindela hybrida*; 5. *Cicindela galeata*. Ground beetles: 6. *Cychrus cylindricollis*; 7. *Carabus scabrosus*; 8. *Carabus angulicollis*; 9. The caterpillar hunter *Calosoma sycophanta* attacking a black arch caterpillar; 10. *Scarites buparius*; 11. The desert ground beetle *Anthia thoracica*; 12. *Omophron limbatum*; enlarged and actual size.

Superfamily: Coccoidea


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Ground Beetles: 1. The violin beetle *Mormolyce phyllodes*; 2. *Aphaenops pluto*, enlarged and actual size; 3. *Eccoptoptera cupricollis*; 4. The grain beetle *Zabrus tenebrioides*; 5. The bombardier beetle *Brachynus crepitans*. Hygrobiid beetle: 6. *Hygrobia tarda*. Predaceous diving beetles: 7. *Platambus maculatus*; 8. *Acilius sulcatus*; 9. The great water beetle (*Dytiscus marginalis*) taking in air at the water surface; 9. Larva catching a tadpole; 10. *Dytiscus latissimus*. Whirligig beetles: 11. *Enhydrus sulcatus*, enlarged and actual size; 12. *Orectogyrus bicostatus*, enlarged and actual size. Water scavenger beetle; 13. The great silver water beetle (*Hydrous piceus*).

though their hindwings are reduced to halteres like those of the Diptera, and they lack the proboscis so distinctive of the true bugs, so that they cannot eat. They are not uncommon among the coccids which often infest house plants, but they easily escape notice because they are so small. The females, on the other hand, are widely known as motionless plant parasites, quite unlike insects, and are very difficult to dispose of. The development of these homopterans is initially the same as that of the whiteflies: from the egg there hatches a freely moving young nymph, the crawler, which functions to disperse the species and to find a suitable place for further development. This accomplished, the crawler attaches itself firmly, grows, and molts, producing a second nymphal stage in which the sexes are still only slightly differentiated. After the next molt, in the third nymphal stage, the sexes develop in completely different directions. The males cease to feed and begin to lay down the primordia for the wings and copulatory organs, molt twice more, and after the final, fourth, molt are winged, sexually mature males. The sexually mature female, however, is produced immediately following the third (or sometimes even the second) nymphal stage. She, like the nymph, is usually firmly attached to the plant and otherwise resembles the previous nymphal stage, so that this is doubtless a case of neoteny.

The classification of the Coccoidea is based on the females, which differ from one another much more than do the males. The most primitive family, the ENSIGN SCALES (Orthezidae), move freely during their entire lives. *Orthezia urticae* attacks numerous plants, in Europe preferring the stinging nettle. This approximately 3-mm-long animal appears much larger because of the egg sac attached to its rear end. Both the back of the animal and the eggs are covered by white plates of wax, so that the bug is quite conspicuous on the green nettle leaves. But the inexperienced seldom notice it, assuming that it is a bird dropping.

Family: Orthezidae

Even in the family Margarodidae the females are free-moving. The COTTONY-CUSHION SCALE (*Icerya purchasi*) can take the credit for the initiation of biological pest control, as a result of its mass outbreak in California's citrus orchards. Its original home is Australia or New Zealand. There the German-American Koebele searched for its enemies and found them, particularly the lady bug *Rodolia cardinalis*. Of the beetles he sent to California, only a few arrived alive, but about 100 of those he brought back with him survived. They thrived on the ample supply of scale insects they found in California, and multiplied so that soon there were hundreds of thousands of lady bugs, which in a few years ended the plague. This scale insect has also penetrated as far as the Mediterranean countries, where it lives on species of *Genista* and other plants. The reproductive mechanism of the Californian form of this scale insect is noteworthy: males are very rare, and true females are altogether lacking, almost all individuals being independently fertile hermaphrodites!

Other families

The family Dactylopiidae includes the COCHINEAL INSECT (*Dactylopius*

coccus). Because it is the source of carmine dye, it is considered a valuable insect, but where it is not used for this purpose it is a pest on the prickly pear, cacti of the genus *Opuntia*. Competition from the synthetic dye industry has greatly diminished the value of these insects, but carmine is still highly prized in histology as a stain for nuclei. Originally a native of Mexico, the cochineal insect became established in India, northern and southern Africa, on the Canary Islands, Madeira, and Malta, and in Spain and southern France, always accompanied by its host plant, the cochineal cactus (*Nopalea coccinellifera*).

The GALL-LIKE COCCIDS (family Kermidae) all belong to one genus, *Kermes*. A common species in both North America and Europe is *Kermes quercus*, a kidney-shaped or heart-shaped animal, reddish-brown with black stripes, large numbers of which are often found in the crevices in oak bark. Here they produce an abundant flow of mucus, which reveals their presence even at a distance; it ferments and then attracts a variety of insects.

The PIT SCALE INSECTS (family Asterolecanidae) include another pest, the GOLDEN OAK SCALE (*Asterolecanium variolosum*). This scale insect leaves walled pits, like smallpox scars, in the bark, and can even be lethal to young oaks.

More species are found among the SOFT SCALE INSECTS (family Coccidae; see Color plate, p. 197). The coccids are flattened on the underside but have highly arched backs. The EUROPEAN FRUIT LECANIUM (*Eulecanium corni*) has many host plants which it can harm: plum and peach trees, grapevines, red-currant bushes, walnut trees, oaks, alders, elms, and ash and black-locust trees. The SPRUCE-BUD SCALES (*Physokermes hemicryphus*) and *P. piceae*) are of little importance to forestry, but their honeydew often offers a rich harvest to the beekeeper.

The last family to be mentioned, but by no means the least important, is that of the ARMORED SCALE INSECTS (Diaspididae). The hard dorsal shield is not discarded during molting, so that the sexually mature females of the third larval stage carry a stack of three shields on their backs. These shields may be circular, oval, pear-shaped, mussel-shaped, or elongated, may or may not be arranged concentrically, and may be white, yellow, brown, or black. The abdomen of the armored scale insect is clearly segmented only in the anterior section; the posterior, fused, section is called the pygidium. The pygidium may be bordered by lobes, plates, glandular horns, spurs, or bristles which are different in each species and thus are the most convenient characteristics for classification. Of course, one needs a microscope to make an identification. The most common and widespread armored scale insect is the mussel-shaped OYSTERSHELL SCALE (*Lepidosaphes ulmi*); it occurs in both a parthenogenetic and a bisexual form. This scale insect attacks a great variety of deciduous trees and occasionally fir trees as well. But the main damage is done to fruit trees, by *L. ulmi* and also by the two disc-shaped fruit scales, *Quadraspidiotus ostreaeformis* and *Q. pyri*.

Their close relative, the SAN JOSE SCALE (*Q. pernisciosus*), is much more dangerous. Originally from China, it first appeared as a pest in California and then was rapidly dispersed throughout the world. By enforcing strict controls at the borders, Germany succeeded for a long time in keeping it out, and as late as 1915 R. Heymons, in the fourth edition of *Brehms Animal Life Encyclopedia*, rejoiced that "fortunately the concern felt then has proved to be exaggerated, for the severe central European climate is so unsuited to the San Jose scale that its long-term establishment in Germany is little to be feared." But since 1946 it has found a suitable climate in the warmer regions, such as around Heidelberg and in the Palatinate, and has probably become permanently established there. The number of armored scale insects which feed on citrus plants is large. One can learn to know them without traveling at all; we find quite sufficient numbers of these small, dark, rounded or elongated formations on the peel of the oranges and lemons we buy.

12 Dobson Flies, Lacewings, Snakeflies, and Antlions

Order: Neuroptera, by H.Wundt

When it grows cold in the autumn, a greenish shimmering insect with sparkling gold eyes comes into the house. With its transparent wings, it looks as fragile as a piece of delicate glass. This animal, called the GOLDEN EYE (*Chrysopa oculata*), is a lacewing, and belongs to the superorder Neuroptera. For a long time the group was a sort of "junk drawer" for systematists—Linnaeus (1707–1778) himself lumped under this heading almost all the insects with transparent forewings and hindwings in which the dense network of veins can be seen. As late as the beginning of this century the Neuroptera were considered to include such different groups as the mayflies, stoneflies, Odonata, termites, book lice, alder flies, snakeflies, Planipennia (lacewings and antlions), scorpionflies, and caddisflies.

But the course of development in the first five of these groups is fundamentally different from that in the others. In all ten groups the juvenile stage is wingless and without genital appendages, but in the first five the small juvenile more or less resembles the imago, and the wings and external reproductive organs develop gradually during the process of growth. These animals are hemimetabolous (they have an incomplete metamorphosis; see Chapter 1). In contrast, the juvenile form (or larva) in the last five groups is radically different, internally and externally, from the adult, winged, reproductive form. Here the larval stage is entirely specialized for feeding and growing; once it has reached a certain size, it suddenly ceases to eat. Then it makes a protected place for itself in or on the ground, curls up, and, after an apparently dormant period, bursts its "skin"; what looks like a completely different animal appears. In one step the larva has transformed itself into a pupa, which is already very similar to the winged form. This complete metamorphosis is also called holometabolism (see Chapter 1). In this type of development there is first a period of growth and then a time of change; there are no smaller offspring which resemble the parents, but only two quite differently constructed forms, the larva and the full-sized reproductive animals.

The distinction between these two types of development is determined



Fig. 12-1. A single tracheal gill of a megalopteran larva, genus *Sialis*.

by heredity and is a fundamental factor in insect classification. The dividing line runs right through the ten groups listed above, formerly called Neuroptera.

Now we include only the following three suborders in the order Neuroptera: 1. the Megaloptera (alderflies, etc.), 2. the Raphidiodea (snakeflies), and 3. the Planipennia (antlions and lacewings). The Mecoptera and Trichoptera (caddisflies and scorpionflies, respectively; see Chapters 14 and 16) belong to separate orders related to the Lepidoptera (butterflies and moths; see Chapter 15), Diptera (flies; see Chapters 19 and 20), and Siphonaptera (fleas; see Chapter 21).

Suborder: Megaloptera

One suborder of Neuroptera, the Megaloptera, has scarcely changed since it first appeared. These are the most primitive members of the order, and the most primitive of all holometabolous insects. Here the processes of internal and external metamorphosis are all compressed into the final, long-lasting larval stage. In the brief pupal period, usually occupying only a few days, these processes are simply completed. The imago which emerges, the reproductive form, often lives only a few days more. Since the development of the Megaloptera involves almost exclusively the larval stages, the operation of natural selection on the reproductive individuals has relatively little chance to produce evolutionary change. Therefore the Megaloptera have kept their original body structure and their manner of metamorphosis for many millions of years. There are only about 100 species, most of which belong to the family Corydalidae.

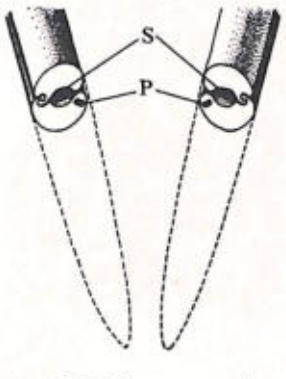


Fig. 12-2. The two suction stylets of an osmylid (genus *Osmylus*), showing the suction channel (S) and the salivary (poison) channel (P). The cut-off tips are indicated by dashed lines.

Some of the CORYDALIDS are real giants (see Color plate, p. 301). The genus *Acanthocorydalis*, from China and Japan, is 7 cm long from head to tail and has a wingspan of 16 cm. This and the American DOBSONFLY (*Corydalis cornutus*; wingspan up to 13 cm) are appropriate representatives of the order Megaloptera ("large-winged"). Many of the tropical corydalids are distinguished by their striking appearance: the mandibles of the males are so much elongated that they—like those of the stag beetles (see Chapter 13)—can equal half the body length. These clasping organs, like curved sabers, are used by the male to seize the female during copulation.

There are only two members of the Megaloptera in Europe, both of which are ALDERFLIES (family Sialidae). These are small, with a wingspan of only 3 cm. *Sialis lutaria* (see Color plate, p. 301) is commonly found in central Europe in the spring or summer, sitting on shore plants by still or slowly flowing waters. The second species, *Sialis fuliginosa*, is usually rather more dusky in color and differs from the first in the wing venation and the structure of the hind end of the body. The SMOKY ALDERFLY (*Sialis infumata*), of the U.S.A., with brownish-black wings, is similar in size and habits to the European species. At rest, the alderflies lay their wings together over the body like a roof, as do almost all the Neuroptera. They are hunters, both as adults and as larvae. The larvae, however, are aquatic (see Color plate, p. 301), and are adapted to this way of life by their closed tracheal system, which receives its oxygen supply through special tracheal

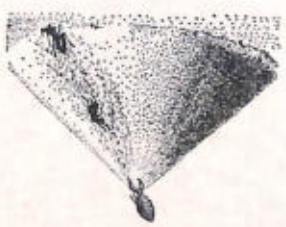


Fig. 12-3. An antlion in its funnel, catching ants.

gills (see Fig. 12-1 and Chapter 1). These segmented abdominal appendages are closely associated with limb primordia, which in the ancestors of the insects actually developed into limbs.

Even before the larval period is over, the alderflies change their way of life: they crawl to land. The spiracles at the sides of the body, previously closed and inoperative, now open so that the insect can take oxygen into the tracheal network directly from the air. The larva seeks out a place in the ground suitable for pupation. Once this stage has been completed, the pupa crawls back out of this chamber and the imago emerges. The imago is very like the larva in appearance, except that it lacks the tracheal gills.

Suborder: Raphidides

In the shady region at the edge of a wood, one can often see an insect with an unusually long "neck," sitting on twigs. The neck is held up at an angle, like that of a dinosaur. This is the SNAKEFLY *Raphidia ophiopsis* (L 10–20 mm; see Color plate, p. 301) or one of its close relatives. Its glassy wings are laid together over the abdomen like a roof. The illusion of a neck is produced by the greatly elongated prothorax. *Agulla adnixa* is a common species in the western U.S.A. The snakeflies belong to the suborder Raphidioidea.

Snakeflies, like the Megaloptera, are a very old branch of Neuroptera. Remnants of fossil snakeflies have been found at all levels, from the coal deposits of the Permian (about 280 to 240 million years ago) up to the amber of the Tertiary period (about 35 million years ago). These fossils show us that this order must have reached its peak in the Mesozoic era. In all stages of development, the snakeflies have retained primitive characteristics. Though their metamorphosis is complete, it is as primitive as that of the Megaloptera. The snakeflies are almost entirely restricted to the northern hemisphere.



Fig. 12-4. The larva of a green lacewing (*Chrysopa sp.*) hatching out of the long-stalked egg.

Using her long, curved, movable ovipositor, the female snakefly feels about in cracks in bark and rotting wood to find a suitable place to lay her eggs. In July and August the small larvae emerge; even they have part of the anterior body elongated to form a distinct neck, though it is not as long as in the imago. The small larvae are very active hunters, devoted to finding food and always ready to attack. They soon separate from their conspecifics of the same age, so that the danger of cannibalism is reduced. They live alone under loose bark, preying on other small insects as well as on spiders and their eggs. With their elongated, flexible bodies, they readily invade the tunnels of wood- and bark-burrowing insects.

With the onset of winter, the larva chews out a shallow depression in the bark, camouflaging it with chips of wood, and there remains until spring. The pupa which emerges, shortly before the molt to the imago, is already able to stand and to run about as rapidly as the larva. It leaves the hiding place, attaches itself to the bark of the tree, and bursts the case. That is, the imago has actually been walking about during this free-moving final part of the pupal stage, within the loosely fitting puparium.



Fig. 12-5. The larva of a green lacewing (*Chrysopa sp.*) after it has covered itself with the remains of aphids.

The adult snakefly is also a hunter. In stalking prey, it finds the long,

necklike prothorax a particular advantage. When an insect is within reach, the snakefly suddenly jerks the neck down, so that the head shoots forward with open jaws and seizes the prey. The neck and head are immediately pulled up again. If the captured insect is not too heavy, it hangs there helpless, and very soon it has been chewed up except for the legs and wings.

Suborder: Planipennia

The order Planipennia (antlions and lacewings), too, existed in the Palaeozoic. But in contrast to the Megaloptera and, even more, to the Raphidioidea, the planipennid larvae are fundamentally different in structure from the adults. Although the larva, even in this group, lives many times longer than the imago, development is not entirely restricted to this stage. That is, the imago in this group is not simply a "flying reproductive machine," serving only for propagation and dispersal of the species. In its longer lifetime it can better exploit the various habitats available. Because of this, the Planipennia have been able to take advantage of unusual opportunities for dispersal and for the evolution of new forms.

It is not surprising, then, that selection has played a significant role, particularly in view of the great age of the Planipennia. A number of different evolutionary paths have been followed, and these have led to the development of many specialized forms. Today there are more than 4500 species—more than the number of present-day species in both of the other suborders of Neuroptera. They are distributed throughout the world. There are eighteen planipennid families, of which eleven are represented in North America. Most species, as is the case with the other Neuroptera, live in the tropics and subtropics, but some diurnal members of the family Hemerobiidae have been able to advance as far as the Arctic.



Fig. 12-6. The pupa of a green lacewing (*Chrysopa sp.*) in its cocoon.

What do these families, so different in external appearance, have in common? Above all, the larvae; they have all retained the characteristic elongation of the mandibles and maxillae, with the adjacent surfaces of the two appendages grooved so that when joined they form a tube, pointed at the tip, on each side of the body. The mouth of the larva is not open in front, but rather is connected with the tubes at the sides. The mandibles thus serve as piercing and sucking tools for these predatory animals. A poison gland in the maxilla causes the prey to be paralyzed as soon as it is stabbed, even though it is frequently much larger than the hunter. Furthermore, the gut of the larva has no opening to the exterior at the posterior end. In most insects the dividing wall between midgut and hindgut is broken through in the embryo, but here it remains intact until after the larval period, which often lasts for several months; during all this time the feces accumulate. Not until the pupal stage do the two gut cavities become joined. When the imago emerges from the pupa, its first act is to discharge the months-long accumulation of feces.

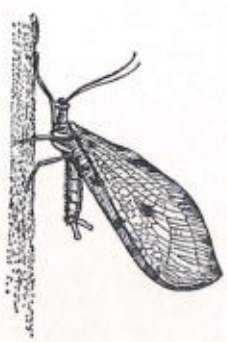


Fig. 12-7. The male of an osmylid (*Osmylus sp.*) positioned so as to attract the female with the everted scent sacs at the end of the abdomen.

But even in the full-grown larva the hindgut has a function. The associated structures which ordinarily serve to excrete metabolic waste products into the hindgut, at this stage produce threads of silk; together with the hindgut, they form a spinning apparatus. The larva uses this silk

gills (see Fig. 12-1 and Chapter 1). These segmented abdominal appendages are closely associated with limb primordia, which in the ancestors of the insects actually developed into limbs.

Even before the larval period is over, the alderflies change their way of life: they crawl to land. The spiracles at the sides of the body, previously closed and inoperative, now open so that the insect can take oxygen into the tracheal network directly from the air. The larva seeks out a place in the ground suitable for pupation. Once this stage has been completed, the pupa crawls back out of this chamber and the imago emerges. The imago is very like the larva in appearance, except that it lacks the tracheal gills.

Suborder: Raphidides

In the shady region at the edge of a wood, one can often see an insect with an unusually long "neck," sitting on twigs. The neck is held up at an angle, like that of a dinosaur. This is the SNAKEFLY *Raphidia ophiopsis* (L 10–20 mm; see Color plate, p. 301) or one of its close relatives. Its glassy wings are laid together over the abdomen like a roof. The illusion of a neck is produced by the greatly elongated prothorax. *Agulla adnixa* is a common species in the western U.S.A. The snakeflies belong to the suborder Raphidioidea.

Snakeflies, like the Megaloptera, are a very old branch of Neuroptera. Remnants of fossil snakeflies have been found at all levels, from the coal deposits of the Permian (about 280 to 240 million years ago) up to the amber of the Tertiary period (about 35 million years ago). These fossils show us that this order must have reached its peak in the Mesozoic era. In all stages of development, the snakeflies have retained primitive characteristics. Though their metamorphosis is complete, it is as primitive as that of the Megaloptera. The snakeflies are almost entirely restricted to the northern hemisphere.



Fig. 12-4. The larva of a green lacewing (*Chrysopa sp.*) hatching out of the long-stalked egg.

Using her long, curved, movable ovipositor, the female snakefly feels about in cracks in bark and rotting wood to find a suitable place to lay her eggs. In July and August the small larvae emerge; even they have part of the anterior body elongated to form a distinct neck, though it is not as long as in the imago. The small larvae are very active hunters, devoted to finding food and always ready to attack. They soon separate from their conspecifics of the same age, so that the danger of cannibalism is reduced. They live alone under loose bark, preying on other small insects as well as on spiders and their eggs. With their elongated, flexible bodies, they readily invade the tunnels of wood- and bark-burrowing insects.

With the onset of winter, the larva chews out a shallow depression in the bark, camouflaging it with chips of wood, and there remains until spring. The pupa which emerges, shortly before the molt to the imago, is already able to stand and to run about as rapidly as the larva. It leaves the hiding place, attaches itself to the bark of the tree, and bursts the case. That is, the imago has actually been walking about during this free-moving final part of the pupal stage, within the loosely fitting puparium.



Fig. 12-5. The larva of a green lacewing (*Chrysopa sp.*) after it has covered itself with the remains of aphids.

The adult snakefly is also a hunter. In stalking prey, it finds the long,

necklike prothorax a particular advantage. When an insect is within reach, the snakefly suddenly jerks the neck down, so that the head shoots forward with open jaws and seizes the prey. The neck and head are immediately pulled up again. If the captured insect is not too heavy, it hangs there helpless, and very soon it has been chewed up except for the legs and wings.

Suborder: Planipennia

The order Planipennia (antlions and lacewings), too, existed in the Palaeozoic. But in contrast to the Megaloptera and, even more, to the Raphidioidea, the planipennid larvae are fundamentally different in structure from the adults. Although the larva, even in this group, lives many times longer than the imago, development is not entirely restricted to this stage. That is, the imago in this group is not simply a "flying reproductive machine," serving only for propagation and dispersal of the species. In its longer lifetime it can better exploit the various habitats available. Because of this, the Planipennia have been able to take advantage of unusual opportunities for dispersal and for the evolution of new forms.

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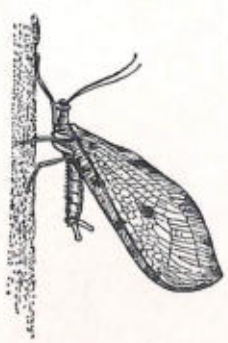


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But even in the full-grown larva the hindgut has a function. The associated structures which ordinarily serve to excrete metabolic waste products into the hindgut, at this stage produce threads of silk; together with the hindgut, they form a spinning apparatus. The larva uses this silk

to spin itself into a cocoon for pupation, and there, protected from the outside world, it undergoes the vast transformation from larva to pupa to imago.

Family: Myrmeleonidae

The best-known members of the suborder Planipennia, apart from the golden-eye lacewings which fly into houses for the winter, are the ANTLIONS (family Myrmeleonidae). The name is really applicable only to the broad-bodied larvae of this family (see Color plate, p. 301). The slender imago is like a damselfly, flitting among low shrubs in the warm summer months. But it is seldom seen, because it becomes active only in the evening; during the day it rests, motionless, well camouflaged by its transparent wings and dusky body. The larva, however, deserves our attention. Its hindlegs have been modified by fusion, to form digging tools. In temperate latitudes one can see them working with these, in dry, sunny spots sheltered by elevations of the ground from wind and rain, particularly on south-facing slopes. The soil must be light and easy to shift. Pushing itself backward, the larva first draws a circle on the ground; then, digging deeper and deeper, it spirals in toward the center. The excavated soil is thrown out energetically with the head. After only a quarter of an hour the antlion has made a funnel-shaped crater in the earth. It buries itself at the bottom so that only the head, with opened jaws, is to be seen, and there it waits for its prey.

When ants or other small insects come up to the edge of the crater, the soil slips and they slide down, straight into the large, curved, piercing-sucking mandibles of the hunter. It seizes the victim, paralyzes it with the poison injected at the first bite, and then sucks out its vital juices. If the prey manages to stop itself from sliding all the way down the crater, and tries to climb up again, the antlion accurately hurls a rain of sand at it, invariably causing the captive to lose its grip and fall to the bottom. Often quite powerful animals fall into the trap. Even then, the small hunter grasps them immediately, and the forward-pointing bristles on its buried body anchor it so firmly that the violently struggling prey cannot pull the antlion out. On the contrary: the antlion makes movements which tend to pull the prey deeper into the ground. Even with such large animals, the injected poison takes effect very quickly. Once it has finished sucking out the prey, the antlion uses the same throwing motion of the head to fling the empty body out of the crater. The size of the crater is related not to the size of the antlion, but to its hunger; the longer the animal has gone without food, the larger it makes its crater.

These spectacular events can all be observed very easily if one keeps an eye out for the conspicuous funnels when walking by suitable locations. Frequently whole colonies of them are found together. The main European species are *Myrmeleon formicarius* (see Color plate, p. 301) and *Euroleon nostras*. *Myrmeleon obsoletus* is a common species in the U.S.A. If one catches such an animal, takes it home, and puts in in a bowl of dry sand, the little "lion," called the "doodlebug" in the U.S.A., sets to work im-

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Hister beetles: 1. *Oxysternus maximus*; 2. *Saprinus maculatus*.
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Catopid beetle: 5. *Leptodirus hohenwardi*, enlarged and actual size.
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Net-winged beetle: 9. *Chlamydolycus trabeatus*.
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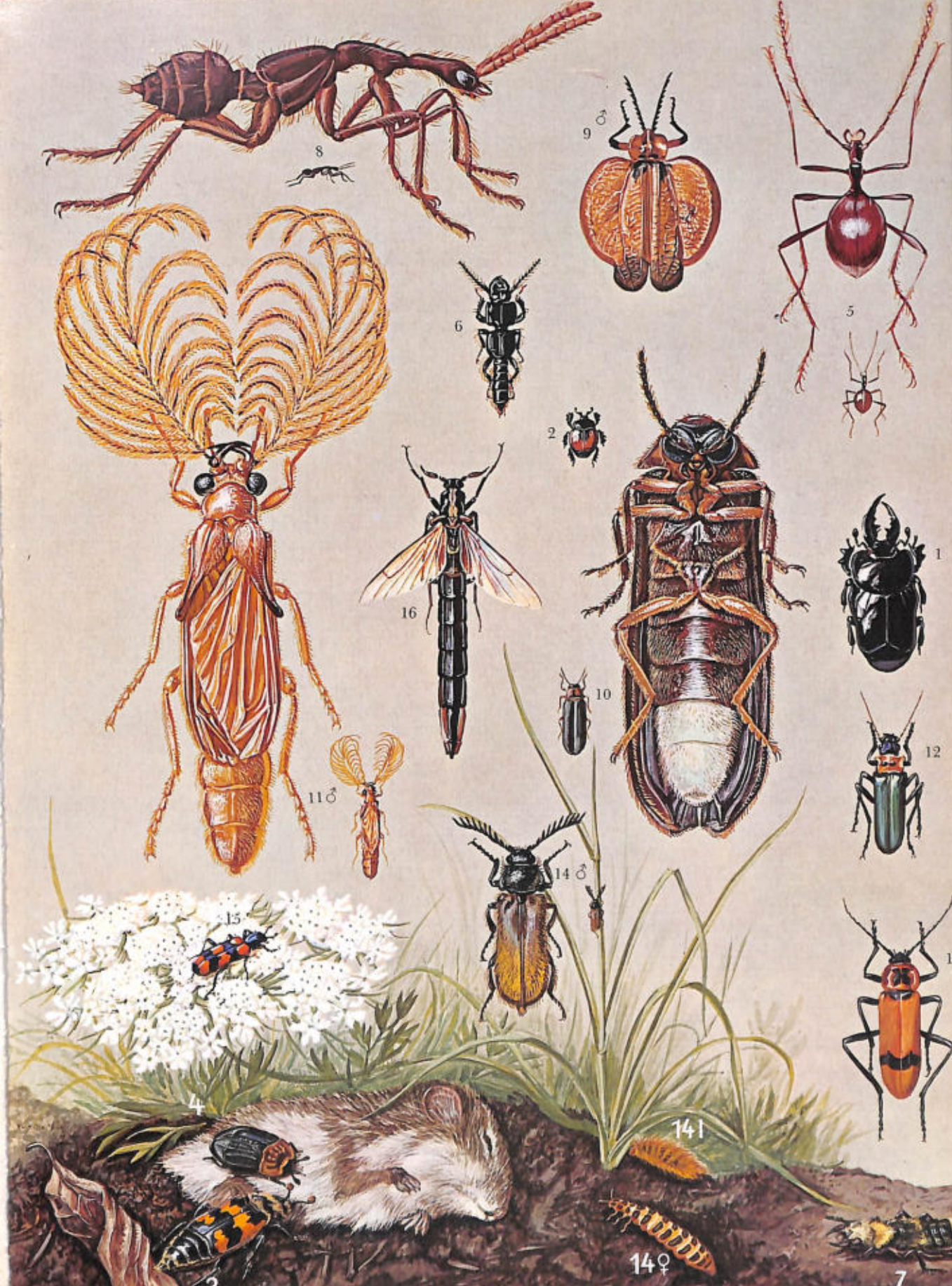
Family: Myrmeleonidae

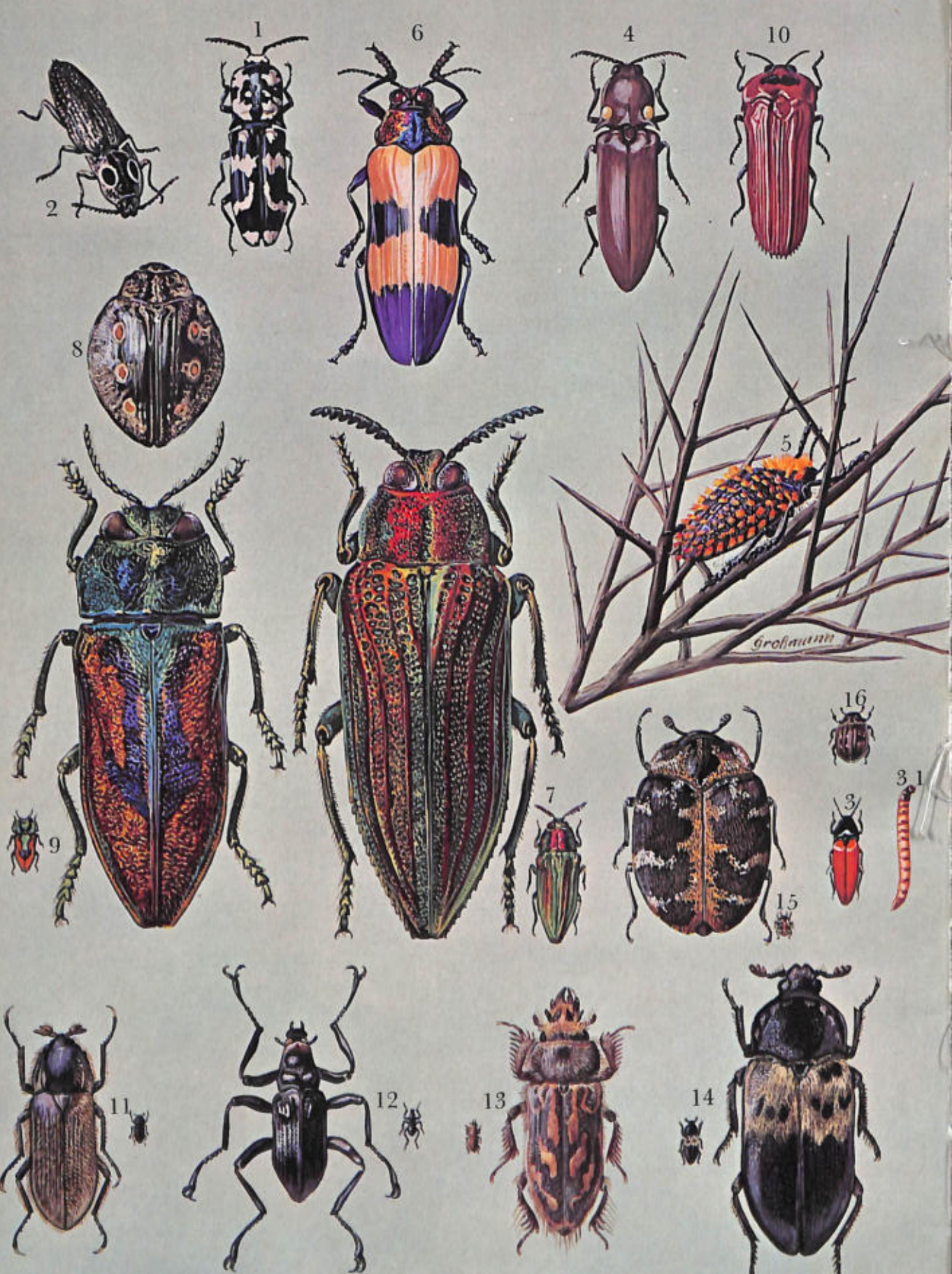
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Click beetles: 1. *Lycoreus hacquardi*; 2. *Alaus oculatus*; 3. *Elater sanguineus*; 3. Larva ("wireworm"); 4. *Pyrophorus noctilucus*
Metallic woodborers: 5. *Julodis mellyi*; 6. *Chrysochroa buqueti*; 7. *Evides elegans*, enlarged and actual size; 8. *Polybothris sparsuta*; 9. *Anthaxia candens*, enlarged and actual size; 10. *Hyperantha testacea*.
Long-toed water beetles: 11. *Dryops auriculatus*, enlarged and actual size; 12. *Macronychus quadrituberculatus*, enlarged and actual size.
Variegated mud-loving beetles: 13. *Heterocerus parallelus*, enlarged and actual size.
Hide beetles: 14. The larder beetle (*Dermestes lardarius*), enlarged and actual size; 15. The carpet beetle (*Anthrenus scrophulariae*), enlarged and actual size.
Pill beetle: 16. *Byrrhus pilula*

Family: Chrysopidae

mediately, building a funnel and waiting for prey. It accepts any small insect one throws to it. In a warm room it stays active even in winter, as long as it is given food. If several antlions are kept in the same container, they eat one another until only the strongest remains. Outdoors, the larva withdraws deeper into the ground as soon as the weather becomes cold in the autumn; it passes the winter in a dormant phase. Often they do not pupate until the third year of life. Then they build cocoons in the ground, hard on the outside and with a soft inner lining for the pupa (see Color plate, p. 301), and the thin-bodied imago emerges from this.

By no means all antlions build funnels. The approximately 2000 species of this family are distributed throughout the world, particularly in the warmer regions. The largest forms are found in the predominantly African genus *Palpares*; these have a wingspan of 16 cm. By contrast, a very small form in Arabia has a wingspan of only 2 cm. The largest European species is *Acanthaclisis occitanica*, with a wingspan of 11 cm. The rest of the ten or so species native to central Europe are about a third smaller. In half of these species the larvae do not build funnels, but rather simply bury themselves in the loose soil for concealment during the day. After dark they run about on the ground looking for prey. They can run forward as well as backward, whereas the funnel-building larvae can only move backward and, correspondingly, have legs angled sharply toward the front.

The GREEN or COMMON LACEWINGS (family Chrysopidae) are distinguished by their gauzy, transparent, shimmering wings, cross-hatched with green, yellow, or a darker color. They have evolved an extraordinary variety of forms, in about 2000 species. Their wingspan ranges from 8 to 65 mm; that of the European forms is 30 mm on the average. Like most Neuroptera, the common lacewings are twilight animals. In summer and autumn, masses of them are often attracted by the lighted show windows of city streets. Ordinarily the species involved is the well-known GOLDEN-EYE (*Chrysopa oculata*; in Europe, *Chrysopa carnea*; see Color plate, p. 292). This is the only species which, as an imago, spends the winter in human houses. During this dormant period the insect, otherwise greenish in color, becomes reddish, owing to the decrease in metabolism which leads to the accumulation of certain red pigments. When the animals become active again in the spring, they regain their greenish coloration.

Some green lacewings release an unpleasant smell of putrefaction when they are touched. Experienced collectors can tell simply by using their noses what species are in the net. These scent glands have sometimes caused these delicate animals to be called "stink flies." Presumably the smell serves a protective function, as, perhaps, does another peculiarity of various green-lacewing larvae; these slender little creatures with inwardly bent suction pincers cover their bodies with all sorts of objects—for example, the empty shells of their victims, moss or bits of bark, sand grains, and so on (see Fig. 12-5). If one keeps such a larva as a pet, one can

offer it small pieces of paper, and it will attach them to the hooked hairs on its back. Like the adults, the larvae feed on small insects and insect larvae, especially aphids. For this reason they, like the very similarly built larvae of the brown lacewings (family Hemerobiidae), are called "aphid lions." The eggs of the green lacewings have a remarkably funguslike appearance; in fact, they were at one time thought to be fungi and were given the scientific name *Ascophora ovalis*. Each egg sits on a very long, thin stalk, closely resembling the fruiting bodies of ascomycetes (see Color plate, p. 292; and Fig. 12-4).

Family: Osmylidae

Some of the OSMYLIDS (family Osmylidae) also make use of odoriferous substances. The male *Osmylus*, when ready for mating, attracts the female with two eversible scent sacs at the end of the abdomen. The name of the group (from the Greek ὀσμύλοζ = "strong-smelling") reflects this behavior. The family is distributed throughout the world, but only one species, *Osmylus chrysops*, with brown-spotted wings spanning about 4.5 cm (see Color plate, p. 301), lives in Europe. This family does not occur in North America. When the larva hatches, it opens the hard eggshell with a knife-like structure on the front of the head, formed especially for the purpose. A few other lacewings also have this larval structure; it is repeatedly pushed against the shell until it breaks through. In these cases, the first molt occurs simultaneously with emergence from the egg, and the egg-cutter remains behind with the cast-off exuvium.



Fig. 12-8. The larva of a nemopteran (*Nemoptera sp.*).

Osmylid larvae (see Color plate, p. 301) hide during the day on the shores of clear, shady brooks; they are hunters, with long, almost straight, daggerlike sucking mouthparts (see Fig. 12-2). During pupation, the larva in its cocoon does a surprising thing; it breaks these daggers off to only a quarter their original length. The purpose of this is unclear, since a short while later the entire exoskeleton will be shed in any case. No other planipennid does such a curious thing, though certain members of other insect groups cast off parts of the body they no longer need (for example, ants and termites discard the wings after the nuptial flight).

Family: Hemerobiidae

The BROWN LACEWINGS (family Hemerobiidae; see Color plate, p. 301) have evolved a considerably greater number of species than the Osmylidae. One-tenth of the 750 species are native to Europe. *Hemerobius stigmaterus* is a common species in the U.S.A. The small, very lively, predaceous larvae are diligent hunters of aphids, earning—like the larvae of the common lacewing—the name "aphid lion." When danger threatens they pull in their appendages and "play dead." Other members of the order, such as the antlions, can also do this. This cramped position can be maintained for many hours, and one may well wonder why the animals do not become exhausted. The reason is that there are various types of muscle, some of which have a high metabolic rate and tire more readily, and others which have almost negligible metabolism and therefore do not tire.

Family: Ascalaphidae

The most beautiful of the European Neuroptera are those of the family Ascalaphidae (see Color plate, p. 291). Their transparent, triangular wings

span about 50 mm; they are conspicuous because of the yellow, brown, and white pattern which makes them look like butterflies when they fly in the sunshine. In fact, they were once considered to be Lepidoptera. This family, too, occurs primarily in the tropics. Many of its members have long, narrow wings and an abdomen of the same shape; with their often-glassy wings they are reminiscent of damselflies rather than butterflies. They fly very rapidly, and in flight the male seizes the female for copulation.

Families: Nemopteridae and Mantispidae

In India, Australia, and South America, as well as in the Mediterranean region, there lives a neuropteran family, the Nemopteridae, which often possesses yellow-and-brown patterned wings. The hindwings of these NEMOPTERIDS (see Color plate, p. 302) are unusual in form, each consisting of a long, narrow band or, in some species, of only a thin thread. Bandlike wings of this sort occur nowhere else in the insect kingdom. The nemopterids are graceful animals of moderate size. In some species the larvae have an elongated prothorax, forming a "neck" as long as the rest of the body.

Anyone who has seen a praying mantis, with its striking prehensile forelegs, will surely think that he is seeing another, smaller mantis if he encounters a member of the genus *Mantispa* (family Mantispidae). But the two animals are not even distantly related. Only the forelegs have been modified in an identical way, producing a device for the capture of prey. The relationship of *Mantispa* (BL 16 mm) to the lacewings, etc., can be discerned by the fact that its larvae have the characteristic sucking mouthparts. *Climacella brunnea* occurs in western North America.

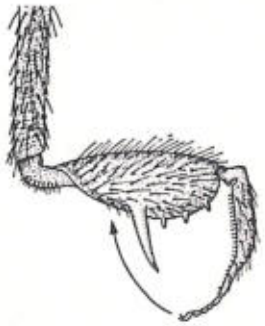


Fig. 12-9. Prehensile leg of a mantispid (*Mantispa sp.*)

But it is not at all easy to catch sight of a MANTISPID larva; for a long time the larval form of these insects was entirely unknown. The reason for this was that there are actually two larval forms (see Color plate, p. 302). Only the tiny, freshly hatched larva runs freely about; soon it crawls into the egg cocoon of a certain spider, becoming almost completely inaccessible to observation. Only this first-stage larva has the tiny piercing-sucking mandibles characteristic of the suborder. It molts within the spider's cocoon, becoming a parasite on the spider's eggs. As in almost all parasitic insects, the body has lost all its characteristic traits; it is unsegmented and swollen, no longer needing to expend any effort in obtaining food. The appendages have degenerated to small vestiges, and the animal wiggles about awkwardly like a maggot, between the remains of the eggs it has eaten and the young spiders. While still in the cocoon of the spider, the larva builds its own cocoon in which it pupates. Like an alderfly or snakefly pupa, the mantispid pupa which emerges is extremely active; it breaks through all the materials encasing it and crawls about for a time before molting to produce the imago. There is also a South American mantispid which undergoes metamorphosis in a wasp's nest.

The imagos of all members of the family have the forelegs modified into prehensile organs. The two distal, spur-bearing segments can be folded back like the blade of a pocketknife against the next segment, which is also

spurred. There is essentially no escape for an animal caught in this apparatus. Only one species of these animals, usually more at home in the tropics, can be found in southern Europe.

Family: Sisyridae

Members of the family Sisyridae (see Color plate, p. 301) are sometimes called by the unusual name SPONGILLAFLIES. It seems odd that they should be associated with fresh-water sponges, which of course are found only underwater, but in fact the larvae of these planipennids do live fully submersed in the water. Like the megalopteran larvae, they breathe by means of tracheal gills on the abdomen. With their long, straight, very fine suction stylets, they feed on the juices of fresh-water sponges. The larvae move onto land only when they are ready to pupate. The eggs from which they hatch are also deposited there. The reproductive form of the spongillaflies is easily overlooked, since (in the few European species) it is only 2–3 mm long. *Sisyra vicaria* (L 6–8 mm) is found in sponge-infested lakes in the U.S.A. Though there are just 50 species, the family is represented throughout the world.

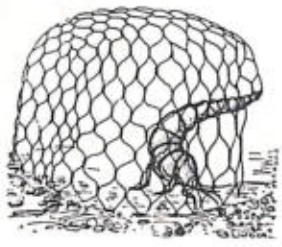


Fig. 12-10. The larva of a spongillafly (*Sisyra sp.*) building a cocoon.

Family: Coniopterygidae

The tiny DUSTY-WINGS (family Coniopterygidae; see Color plate, p. 301) are the smallest of the Neuroptera, measuring only 2 mm. Their common name comes from the fact that a powdery dust is distributed over the body and wings; it consists of fine scales of wax and gives the animals a characteristic mealy white appearance. The only other insect family to display such a phenomenon is that of the whiteflies (Aleurodidae; see Chapter 11). Both larvae and adult dusty-wings live on trees, deciduous as well as coniferous, and fossil forms have been found enclosed in amber. The larvae feed on all sorts of small insects and their eggs; with their mouthparts, transformed into sucking stylets, they can even pierce the shields of the scale insects. Anyone who has tried in vain to rid his house plants of scale insects would be glad to have the presence of a few dusty-wings! Thirty-six species occur in North America.

13 The Beetles, Weevils, and Stylopids

Order: Coleoptera, by R. zur Strassen

To many people, all sorts of small creeping things are "beetles." Some of these are really isopods, ticks, or insects such as silverfish, cockroaches, and bugs. The real beetles are a quite distinct group of insects, the main characteristic of which is the possession of hard wing covers, or "elytra." The name of the group comes from the Old English *bitan*, to bite, and refers to their tendency (shared, of course, with other kinds of "vermin") to chew and gnaw. The original German word for beetle, *Wibel*, has been taken over into English as the designation for a particular kind of beetle, the weevil.

The unimaginable variety in their forms has made the beetles (order Coleoptera) the insect order with by far the greatest number of species. So far nearly 290,000 species have been described, which corresponds to more than two-fifths of all the insects which have been named. The number of beetle species is about six times as large as that of all vertebrate species. Unfortunately, in a single chapter we can give only a hint of the variety of forms and habits to be found in the group. In order to illustrate some of the unusual structures among beetles, our pictures will concentrate on forms less well known than, say, the June beetle or the lady beetle (the latter is commonly called a "ladybug" in the U.S.A. and "ladybird" in Britain, but of course it is neither). Descriptions of behavior, too, must be limited to a few examples. Most of the chapter will be devoted to a general discussion. Not all of the families described will be included in the systematic section which occurs near the end of the chapter; but all the beetle families mentioned can be found in the Systematic Classification near the end of the book.

Distinguishing characteristics: Trunk

Most entomologists now group the beetles with the Strepsiptera as the family Stylopsidae in the superorder Coleoptera. The superorder includes insects 0.25 mm to 16 cm in length, weighing 0.4 mg to 30 g. Even within a family the body shape may be variable (for example, among the darkling beetles; see Color plate, p. 245); the basic type is cylindrical, but departures from this shape range from extremely thin rods through boxlike or

hemispherical forms to flat, leaflike animals. The upper side is usually more strongly arched than the underside, the latter usually being a smooth flat surface (a bearing surface), particularly in short-legged species. The body is unmistakably divided into head, thorax, and abdomen, but when viewed from above only the dorsal plate of the prothorax (the pronotum) and —strictly speaking—part of the second thoracic segment (the elytra, which attach to the mesothorax) are visible. The other parts of the thorax are hidden under the elytra, except in a few short-winged forms, where the end of the abdomen can be seen. In many beetles another part of the mesothorax is also visible; this is the scutellum, a triangular plate in the midline behind the pronotum (see Fig. 13-1). The most conspicuous parts of the mesothorax are the elytra, laid protectively over the soft dorsal surfaces of mesothorax, metathorax, and abdomen. The elytra are the strongly sclerotized forewings, no longer used for flight. In the ROVE BEETLES (family Staphylinidae; see Color plate, p. 225) the elytra are much shortened; short elytra are also found in beetles of a number of other families, such as the CARRION BEETLES (Silphidae), the FIREFLIES (Lampyridae), the SOFT-WINGED FLOWER BEETLES (Melyridae), the BLISTER BEETLES (Meloidae; see Color plate, p. 236), and the LONG-HORNED BEETLES (Cerambycidae; see Color plate, p. 255). In some of the SHIP-TIMBER BEETLES (Lymexylonidae) small scales are all that remain of the elytra (see Color plate, p. 225). The scientific name Coleoptera for the beetle order can be translated as "sheath-winged insects"; it refers to the protective function of the elytra.

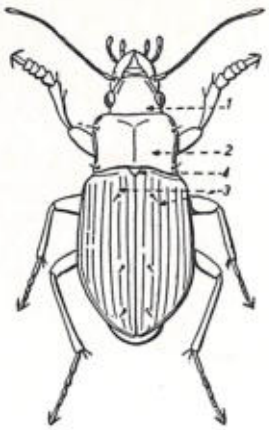


Fig. 13-1. Dorsal aspect of a ground beetle (family Carabidae): 1. Head, 2. Pronotum, 3. Elytra, 4. Scutellum.

External appearance

The external appearance of the DARKLING BEETLE (*Tenebrio molitor*; see Color plate, p. 245), a cosmopolitan pest, particularly in stored cereals, represents what most people imagine as typical of a beetle. None of its parts is excessively enlarged or reduced, there are no outgrowths or unusual appendages, and one can immediately tell the front end from the hind end. This body-form type is repeated in almost all families and appears countless times in the darkling beetle family. But the majority of beetles depart from it most remarkably; our twenty color plates give at least a suggestion of these startling adaptatations.

The bodies of many beetles are characterized by ridges, humps, or even hornlike formations. These are most often on the head and the pronotum (see Color plate, p. 250), less commonly on the elytra (see Color plate, p. 255), and sometimes even on the legs (see Color plates, pp. 236 and 249). These curious projections are formed by a bulging outward of the cuticle which covers the insect, and are hollow, even where they are as long as those of the COLUMBIAN RHINOCEROS BEETLE (*Golofa porteri*; see Color plate, p. 250). In the males of certain species the mandibles are lengthened and transformed into "horns" resembling those of antelopes or the antlers of stags. The best-known of these in Europe is the male STAG BEETLE (♂ *Lucanus cervus*; see Color plate, p. 266; other examples are given in the Color plate on page 250). This is very similar to the North American GIANT STAG BEETLE (*Lucanus elaphus*).



Fig. 13-2. Male of the rhinoceros beetle *Oryctes nasicornis*; actual size 40 mm.

Coloration and patterning

This abundance of forms is matched by the striking spectrum of coloration and patterning. The examples in the color plates on pages 226 and 246 give only a suggestion of the frequently glowing colors seen in nature. A particularly interesting aspect is the color change which takes place in living beetles. One is reminded of the chameleon, which can change its color within a few minutes. The color change of a beetle occurs in quite a different way from that of a reptile, but it proceeds equally rapidly. In the TORTOISE BEETLES (subfamily Cassidinae) of the genus *Charidotella*, which live in Central America and in northern South America, it requires only twenty minutes. This phenomenon was observed in the 6-mm-long species, *Charidotella sexpunctata*, which occasionally is found in shipments of bananas. The golden-colored tortoise beetle or GOLD BUG (*Metriona bicolor*) is a common North American species living on bindweed. It, too, is capable of changing its color from a dull yellow to a polished brass or gold, or tints of pearl.

In the most decorative phase, the upper side of these beetles gleams a lustrous gold, with no patterning to break up the uniform sheen of the surface. One can see oneself reflected as in a Christmas-tree ball. Once the color change has begun—for reasons as yet unknown—a gradually expanding area around each of the tiny pores on the elytra becomes metallic green. These pores are arranged in longitudinal rows on the outer surface of the innermost layer of chitin, the endocuticle. They shine through the two layers above that, the epicuticle and exocuticle, which in this species are colorless and therefore transparent. The process of color change thus goes on "inside" the elytra, between the endocuticle and epicuticle, and can be observed as though under a plate of glass. As the change progresses, over the surfaces of the pronotum and scutellum as well, the green spots gradually coalesce. The golden glow gives way to a metallic green, and that in turn to a dull greenish-blue, which brightens and takes on a brownish tone with a sheen like mother-of-pearl. Finally, all the shininess disappears, and the beetle has changed into the dowdy yellow-brown phase. During the color change three spots appear on each elytron, blurred at first but finally sharply outlined. Blood pigments probably participate in the transformation, perhaps by way of a light-refracting effect. In the reverse change, from dull yellow-brown to radiant gold, air is presumably pumped into the elytra.

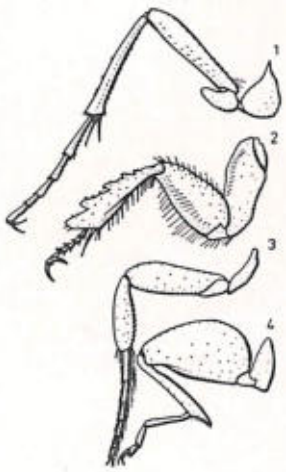


Fig. 13-3. The leg shapes of beetles reflect their different habits: 1. Walking leg of a ground beetle (genus *Carabus* sp.), 2. Digging leg of a dung beetle (genus *Geotrupes* sp.). 3. Rowing leg of a diving beetle (*Dytiscus* sp.), 4. Jumping leg of *Psylliodes* sp.

Distinguishing characteristics: Legs and wings

The legs are normally segmented but quite variable in shape, occasionally being greatly elongated as in the tropical HARLEQUIN BEETLE (*Acrocinus longimanus*) and another long-horned beetle, *Gerania bosci* (see Color plate, p. 255). The basic type has walking legs, but these may be modified into digging, rowing, jumping, and even climbing or clasping legs. The tarsi usually consist of five segments, but not uncommonly there are four, three, or occasionally just two.

There are always two pairs of wings; only in a few cases are both pairs entirely regressed—for example, in certain females which have retained

the larval form, those of many FIREFLIES (Lampyridae) and of the families Drilidae (see Color plate, p. 225) and Phengodidae. The anterior pair is modified into wing covers which are usually hard; the posterior pair is membranous and is used for flight.

Manner of flight

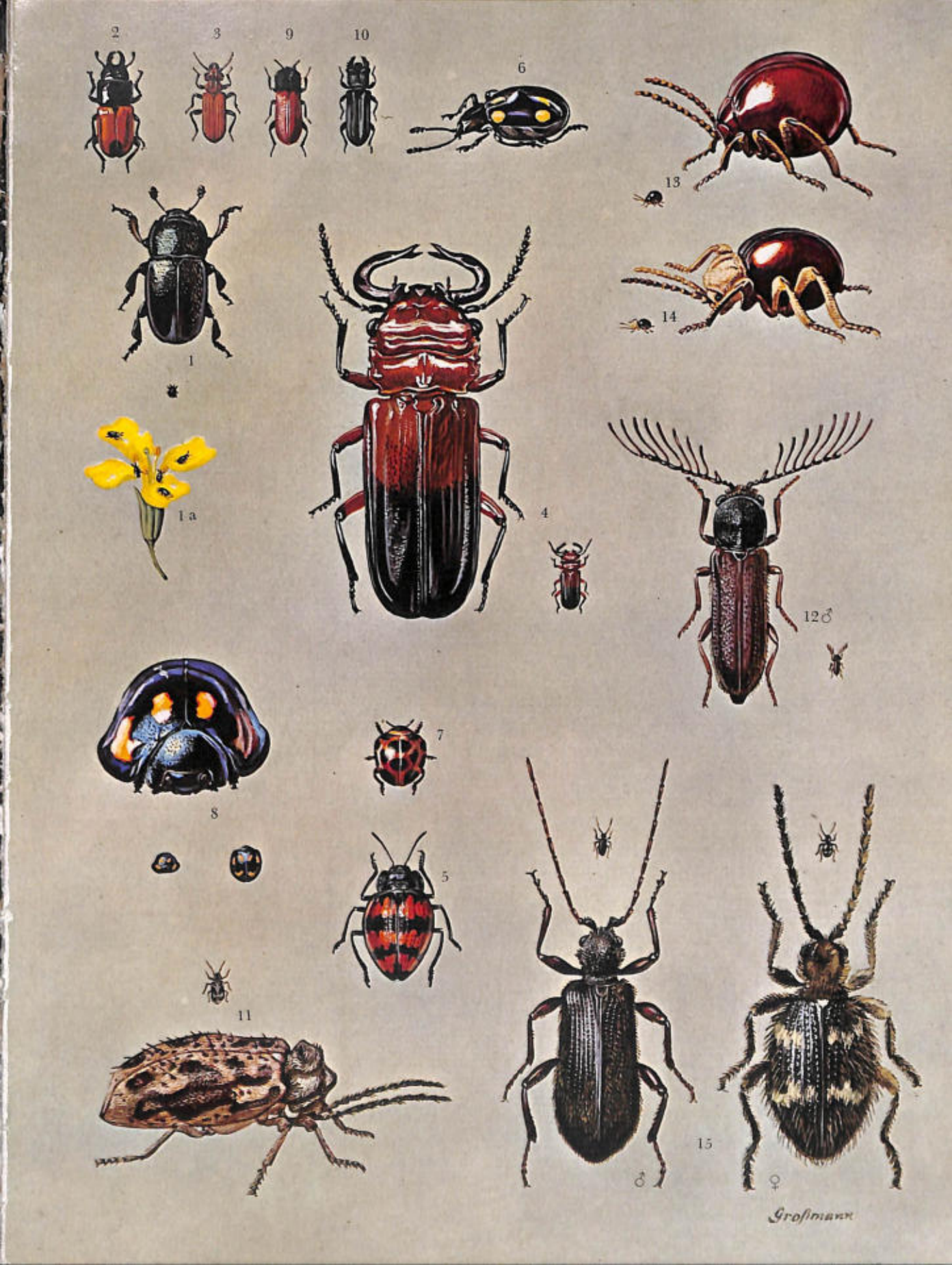
The elytra are held out to the sides during flight, angled slightly upward. They are said not to participate in the mechanics of flight; at most they oscillate a bit along with the hindwings. But in the FLOWER BEETLES (Cetoninae) the elytra are raised only briefly, to allow unfolding of the hindwings, and are then laid over the abdomen again, even during flight. Just behind the point of attachment the flower beetles' elytra are indented at the sides so as to allow the hindwings room to beat. Because of this adaptation, the flower beetles are among the beetles with the greatest skill and endurance in flight. The hindwings of all beetles are longer than the elytra. To fit beneath the protective covering, therefore, they must be folded according to a predetermined pattern and held in this position by a complicated arrangement of joints in the wing veins. Before takeoff the beetle unlocks these joints, whereupon the hindwings unfold automatically and spread out to the side.

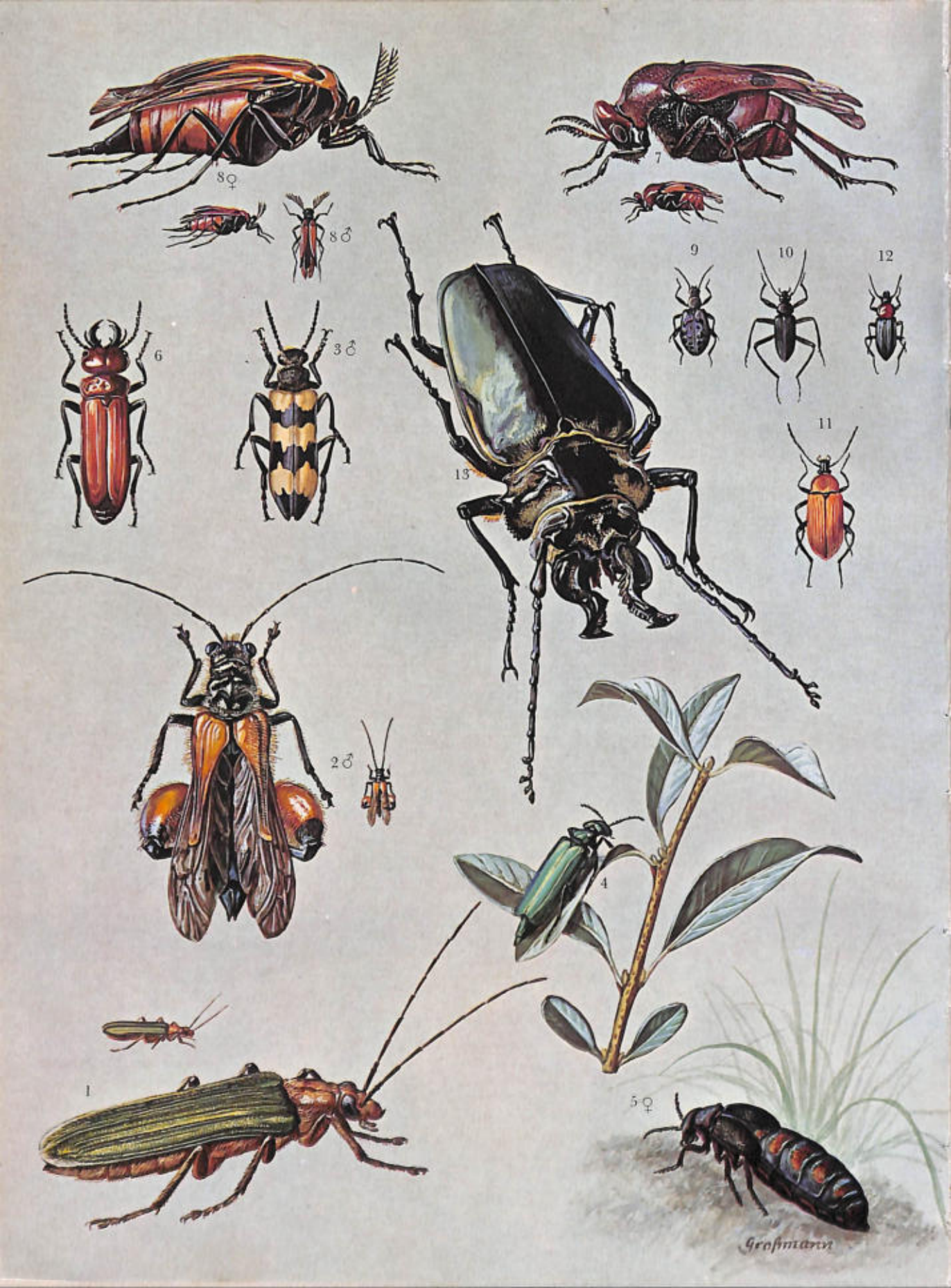
The hindwings of beetles are not operated by muscles attached directly to them, but are activated indirectly (see Chapter 1). When the set of muscles running from the back to the ventral surface of the metathorax contracts strongly, these two surfaces are pulled together somewhat, pushing the sides outward. The dorsal plate of the metathorax is slightly recessed between the lateral plates, and this displacement pulls it below the upper edges of the lateral plates, like a too-small lid sliding down into a pot. Now if the dorso-ventral muscles relax and, instead, the dorsal longitudinal muscles (running from front to back) contract, there is another deformation of the metathorax which pushes the dorsal plate upward again. At a certain place on either side, where the edges of the dorsal and lateral plates slide past each other with a narrow gap, there is a flexible "snapping" joint between the two edges. It is to these joints that the hindwings are attached. With each "snap" the wings are jerked upward (when the dorsal plate snaps down) or downward (when the dorsal plate snaps out again). Actually the whole process is even more complicated than this.

In comparison with certain other insects—some flies, moths, and bees, for example—the beetles are not really very good flyers. Whereas hawk moths (see Chapter 15) can reach a flight speed of 54 kph, species of JUNE BEETLES of the genus *Phyllophaga* can achieve barely 8 kph. In LADY BEETLES (family Coccinellidae) and SOLDIER BEETLES (family Cantharidae) the number of wingbeats per second is around seventy to ninety and in the June beetle only forty-five to fifty, while the mosquito beats its wings 280–310 times per second.

Not all beetles which fly well have entirely membranous hindwings. In the very smallest ones, such as the FEATHER-WINGED BEETLES (family Ptiliidae; see Figs. 13-4 and 13-5), the membranous part of the hindwings is

▻
Sap-feeding beetles: 1. *Meligethes aeneus*, enlarged and actual size; (a) on a rape flower; 2. *Paromia dorcoides*. Flat bark beetles: 3. *Cucujus cinnaberinus*; 4. *Palaestes freyreissi*, enlarged and actual size. Pleasing fungus beetle: 5. *Erotylus varians*. Handsome fungus beetle: 6. *Eumorphus marginatus*. Lady beetles (cf. Color plates, pp. 182 and 275): 7. *Solanophilus insignis*; 8. *Orcus australasiae*, from the front, enlarged and actual size; dorsal aspect, actual size. False powder-post beetles: 9. *Bostrichus capucinus*; 10. *Bostrychoptlites cornutus*. Death watch beetles: 11. *Hedobia imperalis*, lateral aspect enlarged and dorsal aspect actual size; 12. *Ptilinus pectinicornis*, enlarged and actual size. Spider beetles: 13. *Gibbium psylloides*, enlarged and actual size; 14. *Mezium affine*, enlarged and actual size; 15. *Ptinus rufipes*, enlarged and actual size.


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reduced to a narrow bar. The capacity to generate lift has been retained, however, since the bar is bordered by a long, thick fringe, similar to that on the wings of the thrips (Thysanoptera; see Chapter 9) and of the tiny wasps (Mymaridae; see Chapter 17).

Surfactant swimming

A quite different and peculiar method of locomotion is "surfactant swimming." This is done by the large-eyed species of ROVE BEETLES of the genus *Stenus* (see Fig. 13-6), using glands at the end of the abdomen; the glands secrete a substance which lowers the surface tension of the water. These species live on the shore and often accidentally get onto the water, from which they must escape as soon as possible. Once the glandular secretion has touched the water, there is an area of reduced surface tension around the end of the beetle's body; the higher surface tensions at the other points where the beetle touches—the tarsi—act to pull the animal forward, and the direction of movement is controlled by bending the abdomen.

Distinguishing characteristics: mouthparts

The mouthparts of beetles are of the chewing type; they are directed more or less precisely forward, along the body axis, or may be angled downward. The mandibles are usually strong pincers, often toothed on the inner edge; less commonly, they can be sickle-shaped, and occasionally they are greatly lengthened, in which case they have lost their original function (an example is the male stag beetle; see Color plates, pp. 246 and 266). In the STRAIGHT-SNOUTED WEEVILS (Brenthidae) and the WEEVILS or SNOUT BEETLES (Curculionidae) the head is extended anteriorly into a proboscis (see Color plates, pp. 256 and 277), with the mouthparts at its tip. In rare cases, the mouthparts are strongly modified and adapted to special functions. The galeae of the maxillae are often somewhat elongated, as in many members of the Scarabaeidae, or even extremely elongated and provided with sharp tips as in some of the Nemognathini. In both cases these galeae are thickly covered with hairs and during feeding are held close together, so that they form an apparatus for licking and sucking.

◁
Oedemerid beetles:
1. *Xanthochroa waterhousei*, enlarged and actual size;
2. *Oedemera brevipennis*, enlarged and actual size.
Blister beetles: 3. *Mylabris syriaca*; 4. The Spanishfly (*Lytta vesicatoria*); 5. The oil beetle *Meloe variegatus*; 6. *Cissetes cephalotes*.
Rhipiphorid beetles:
7. *Macrosiagon tricuspidatum*, enlarged and actual size;
8. *Metoecus paradoxus*, ♀ enlarged and actual size, ♂ actual size.
Lagriid bark beetle:
9. *Lagria pulchella*.
Comb-clawed beetles:
10. *Allecula fuliginosa*;
11. *Cistellomorpha costatipennis*; 12. *Heliotaurus sanguinicollis*.
Trictenotomid beetle:
13. *Autocrates aeneus*.

An amazing transformation is exhibited by the labium of certain species of the ROVE BEETLE *Stenus*. It can be shot far out to capture prey (see Fig. 13-6) in a way reminiscent of the tongue-flick of chameleons, particularly since there is a sticky cushion at the tip in both cases. The apparatus is everted by an increase in the internal blood pressure, and drawn back again by contraction of four pairs of muscle bundles. Another remarkable modification is the formation of a hollow pincers by the mandibles of DIVING BEETLE larvae (Dytiscidae; see Color plate, p. 216); it functions as an injection device.

Carnivorous beetles which live by hunting do not tear the prey into bite-sized pieces; they simply slightly enlarge the wound they have made as soon as the prey is caught, and vomit the juices from their midgut into it. These digestive juices contain enzymes which decompose protein and fats, and they rapidly liquefy the soft parts of the victim. That is, the food is predigested outside the beetle's body and the resulting "soup" is lapped up. Aquatic predatory beetles can feed in this way only if they are able to

inject the saliva and suck out the food; otherwise everything would be diluted by the water. This injection is made possible by a channel on the inner edge of the mandible. Beetles which prey upon snails (especially those of the family Drilidae) also use the injection technique, since the snail defends itself by secreting mucus which would dilute the digestive juice and render it ineffective.

Feeding behavior

As is the case among the mammals, carnivorous beetles have shorter intestines than those which feed on plants; in the latter the intestine can be as much as ten times as long as the body. It is very important for certain vegetarian beetles, in particular for their larvae, to have symbiotic bacteria. These are housed in special organs, the mycetomes (see Chapter 1), or in protruding bits of tissue at certain places along the gut. The beetles themselves cannot digest cellulose; the bacteria, of which there are various kinds, are capable of chemically decomposing the cellulose components of the food so that they can be handled by the enzymes in the digestive tract of the beetle. The larvae of the DEATHWATCH BEETLES (Anobiidae), STAG BEETLES (Lucanidae), LONG-HORNED BEETLES (Cerambycidae), and many SNOUT BEETLES (Curculionidae), all of which live or burrow in wood, are especially dependent upon the collaboration of these organisms. But there are also snout beetle larvae which have their own cellulose-digesting enzymes.



Fig. 13-4. Hairy wing of a feather-winged beetle (family Ptiliidae).

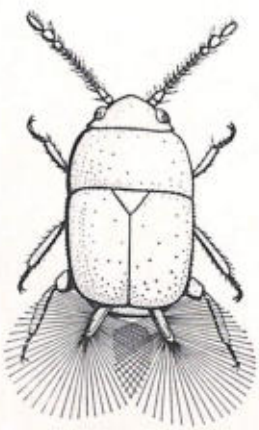


Fig. 13-5. Dorsal aspect of the feather-winged beetle *Acrotrichis sericans*, with wings extending from beneath the elytra (L 0.7 mm).

Not all of the carnivorous species hunt living prey. Many beetles feed on dead animals, some on fresh carrion just beginning to decay, others on old, dry corpses, and still others on all sorts of animal remains, such as hair, feathers, horn, flakes of skin, bone, fat, and even processed materials like hides, wool, dried meat, and prepared gut. The same is true of the vegetarian beetles; they are not at all limited to the fresh, green parts of the plants. Adults and larvae of the most varied sorts eat the petals and bases of flowers, pollen, seeds at all stages of ripeness, stems, roots, algae, fungi, and molds. A number of species mine within the leaves, and others burrow in the fibrous tissues; there are even some which act as gall producers. And all sorts of dead plant materials provide certain beetles with their necessary nutrients. Apart from wood (building timber and furniture) beetles feed on dry leaves, fruits and seeds (including those which have been dried by humans for their own consumption), bakery products, raisins, chocolate, tea, tobacco, drugs, and many other materials. Thus many beetles have become pests in pantries and warehouses. Finally, the "refuse consumers" should be mentioned; these seek their food in mud, humus, and—above all—in the excrement of the vegetarian mammals.

Malpighian tubules, glands

Usually only four or six Malpighian tubules (see Chapter 1) are present in a beetle. The excretions from these are used by many larvae to spin a cocoon before pupation. GROUND BEETLES (Carabidae), CARRION BEETLES (Silphidae), Paussidae, and some other forms have a pair of glands (pygidial glands) in the posterior abdomen, opening at either side of the anus. The special function of these is to secrete substances, repellent in taste or

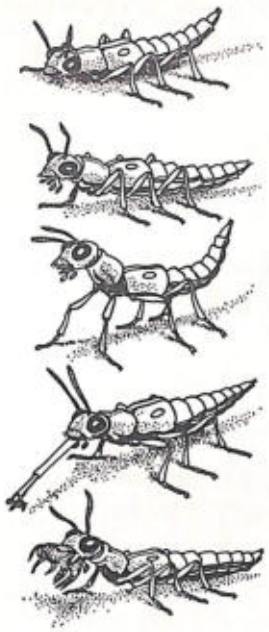


Fig. 13-6. Rove beetles (*Stenus* spp.; L 6 mm) catch their prey with a sticky prehensile apparatus which can be shot forward.

smell, which serve as defense mechanisms when they are squirted at enemies. In some species—for example the nimble desert ground beetles of the genus *Anthia* (see Color plate, p. 215) and the VIOLIN BEETLES (*Mormolyce phyllodes*; see Color plate, p. 216)—these secretions also have a corrosive action. Therefore one must take great care not to allow such beetles to spray one's eyes.

Such protective devices are developed to an astonishing degree in the BOMBARDIER BEETLES (Carabidae subfamily Brachyninae). Here the pygidial glands produce two different chemical substances, which are stored in separate chambers closed off by muscular valves. The gland cells of one chamber secrete two hydroquinone compounds, and those of the other, hydrogen peroxide at a concentration of twenty-three percent. When a bombardier beetle such as *Brachinus crepitans* (Color plate, p. 216) or the widespread North American species *B. fumans* is attacked, it opens the valves of the storage chambers, causing the contents to flow into an especially thick-walled space which serves as a reaction chamber. The instant the two substances come together there, an enzyme catalyzes an explosive reaction involving the decomposition of the hydrogen peroxide. The oxygen thus released supplies the gas pressure which forces out the quinone solution. The fine spray of this solution has such a deterrent effect on most pursuers that they immediately give up their attack. Even reptiles and birds spit out a bombardier beetle as soon as this corrosive substance comes into contact with the mouth. Under favorable conditions, the "explosion" of the larger bombardier beetles *Aptinus* spp. and *Pheropsophus* spp. (L more than 12 mm) can actually be audible. There are occasional reports that a small veillike cloud is formed simultaneously.

Luminescent organs

The luminescent organs of the well-known FIREFLIES (Lampyridae), as well as those of some members of other beetle families which produce light signals (the Phengodidae and Elateridae) are regarded as derivatives of the fat body. The light is completely cold—no heat is generated as in incandescent light sources. The origin of the light, whether pulsed or continuous, is in localized organs which—to describe them simply—consist of three layers. The innermost cellular layer acts as a reflector. The protoplasm of these cells is packed full of microscopically small crystals of a uric-acid salt, the surfaces of which reflect light outward. The middle layer contains the actual "light cells," richly supplied with nerves and very fine terminal branches of tracheae. These light-producing cells are filled with rounded or elongated particles—not luminescent bacteria, as was previously thought, but rather the cell's own mitochondria—which supply the energy required for the operation of the system. The actual light production and the control of the pulses is based upon a complex chemical system. The third layer of the organ is the skin, which here is transparent like a window, entirely lacking in pigment. The light produced contains no infrared or ultraviolet rays. The wavelength range of the COMMON GLOWWORM of Europe (*Lampyris noctiluca*), for example, is 518–656 nm,

that of the North American *Photinus pyralis*, 520–650 nm, and that of the South American *Pyrophorus noctilucus* (family Elateridae), 486–720 nm (a nanometer, nm, is one-millionth of a millimeter, or 10 Ångstroms). As an example of the intensity of the light, 6000 females of the common glowworm can, together, produce a light as bright as that of a normal candle. But only thirty-seven to forty *Pyrophorus noctilucus* produce the same amount of light.

Distinguishing characteristics: Trachae

The tracheal system is well developed; it communicates with the outside world through one or two pairs of thoracic spiracles and at most eight pairs in the abdomen. Frequently some pairs are regressed, in particular where individual abdominal segments have been modified for some special purpose. The best-flying beetles are provided with air sacs (tracheal vesicles; see Chapter 1).

The respiration of aquatic beetles

Even aquatic beetles like the SCREECH BEETLES (Hygrobiidae; see Color plate, p. 216), the CRAWLING WATER BEETLES (Haliplidae), the PREDACEOUS DIVING BEETLES (Dytiscidae; see Color plates, pp. 216 and 264), the WATER SCAVENGER BEETLES (Hydrophilidae), and their relatives, as well as most of their larvae, are dependent upon air respiration. All of them have open spiracles, and to renew the tracheal air they must swim to the surface at regular intervals. The same is true of the WHIRLIGIG BEETLES (Gyrinidae; see Color plate, p. 216), but not of their larvae, which meet their oxygen requirements by means of tracheal gills. Each of the first eight abdominal segments of the whirligig beetle larva has one such featherlike gill on each side, and the ninth segment has two per side. Even the larvae of species of the hydrophilid genus *Berosus* and those of many species of LONG-TOED WATER BEETLES (Dryopidae; see Color plate, p. 226) are equipped with tracheal gills; in the dryopids, though, they are found only in the last segment of the abdomen, from which they can be extended and retracted.

When a dytiscid beetle comes to the surface for air, it stretches the tip of its abdomen only slightly above the surface, lifts the elytra slightly, and immediately thereafter dives again. This sort of up-and-down maneuver can often be observed from the shore, particularly with the larger species such as the GREAT WATER BEETLE (*Dytiscus marginalis*; see Color plates, pp. 216 and 264) of Europe, and *D. fasciventris* of North America. By pumping movements, the beetles squeeze the used-up air out of the tracheae at the water surface and draw oxygen-rich air in again. This exchange of air takes place entirely through the slitlike opening between the end of the abdomen and the tip of the slightly raised elytra. Through this crack, the fresh air enters the space between the elytra and the dorsal surface of the abdomen. This cavity can be closed to form a water-tight chamber into which the tracheae open, the spiracles having migrated dorsally in this family. Now when the beetle dives again, it takes with it under the elytra a bubble of air which serves both as a reserve supply and as a source of buoyancy. The large dytiscids, such as the European *Dytiscus latissimus* (see Color plate, p. 216) and its American relatives, cannot swim to the

water surface without the buoyancy of the air bubble they carry with them. The small species can remain underwater for a relatively long time, particularly if the oxygen content of the water is high. They push the air bubble a little way out from the elytra, but not so far that it can escape. Gas exchange with the water can now occur by way of this bubble, so that the beetles can stay under longer than would be possible if they had only the limited amount of oxygen originally in the bubble. Because of differences in concentration, oxygen dissolved in the water moves into the bubble, while carbon dioxide in the "used" air moves in the opposite direction.

Certain very small dytiscids (L barely 2–3 mm) can actually live under water for weeks or months. Their replacement supply of oxygen is that produced by the plants, in the form of tiny bubbles of gas. Other very small aquatic beetles of various families breathe under water in a way similar to the dytiscids; but, rather than a bubble under the elytra, they carry with them a film of air (the plastron), which either envelopes the whole body or is restricted to certain regions, depending on the species. It is held in place by a dense array of short hairs. In some species the individual hairs are bent at the tip, forming a layer beneath which the plastron lies; the body surface between the hairs stays quite dry. The plastron, like the air bubble protruding from under the elytra, serves both for gas exchange and for regulation of buoyancy.

The *Dytiscus* sp. larvae obtain air by hanging head-down at the surface; only at the posterior end of the body do they have a functional tracheal opening. A quite different procedure for obtaining air has been developed in beetles of the family Hydrophilidae. When such a beetle—for example, the SILVER WATER BEETLE (*Hydrous piceus*; see Color plate, p. 216) or *Hydrophilus triangularis* of North America—needs fresh air, it brings the front of the body, not the abdomen, to the surface. As soon as the top of the head and the pronotum lie just below the surface, the beetle bends the antennae back so that they lie beside the eyes; the first segment of the terminal club (the fourth segment from the end of the antenna) barely emerges from the water, and the other three club segments curve so that the underside faces the anterior edge of the prothorax. All four club segments are covered with velvety hairs and are thus not wetted by the water, and at the back of the head they adjoin a groove, both edges of which have a thick border of hairs. In this position, a sort of "snorkel" is effected, through which air can flow into the water-repellent cushion of hairs on the thorax. From there it proceeds under the elytra and on into the tracheal network.

Heart and blood

The tubular heart of the beetle (see Chapter 1) extends from the first to the eighth abdominal segment; more anteriorly it is prolonged into the aorta, which traverses the thorax and opens into the head. In each of the two posterior thoracic segments a sort of bladder (the dorsal ampulla) branches upward from the aorta.

Beetle blood is usually yellowish or light orange, but may be of a

greenish hue. A number of species—for example, some of the SOLDIER BEETLES (Cantharidae), LADY BEETLES (Coccinellidae), BLISTER BEETLES (Meloidae), and LEAF BEETLES (Chrysomelidae)—are able to squirt out their blood at special places between femur and tibia when they are disturbed. Colored droplets then appear at these "knee" joints. In such species the blood is charged with defensive substances which smell or taste objectionable to an attacker, or are poisonous or corrosive. This reflex bleeding thus has the same significance as other beetles' defensive spraying from the pygidial glands. Many beetles are protected to a certain extent by their bad-tasting or corrosive body fluids even though they do not exude them from the body. They bear "warning coloration," which is said to repel would-be attackers which have already had unpleasant experiences with identically colored, bad-tasting insects (but see Chapter 1).

Bad-tasting and poisonous beetles

Warning patterns of this sort usually consist in the juxtaposition of very dark (dark blue or black) regions and glaring ones (yellow or orange) in the form of spots, bands, or stripes on the upper side of the body. For example, most of the NET-WINGED BEETLES (Lycidae) are equipped with this sort of coloration, especially those living in the tropics and subtropics. Their elytra are relatively soft; they fly in a sluggish and awkward manner; moreover, many species are rather large (15 mm or more), so that they may well make a rewarding and easy-to-catch morsel for certain diurnal birds and monkeys. Probably the most effective poison in beetle blood is cantharidin, found mainly in the BLISTER BEETLES and the SPANISH-FLY (both members of the family Meloidae). Remarkably, this substance (an anhydride) does not harm the insectivorous vertebrates such as frogs, hedgehogs, bats, and birds. But a dose of as little as 0.03 g of cantharidin taken internally is fatal to humans.



Fig. 13-7. The whirligig beetles (family Gyrinidae) have an eye separated into two parts.

Distinguishing characteristics: Sense organs

The compound eyes are quite variable in form; usually they are rounded or oval, sometimes large and bulging as in the TIGER BEETLES (Cicindelidae) and some METALLIC WOODBORERS (Buprestidae). Occasionally the eyes are markedly kidney-shaped in outline, and in the WHIRLIGIG BEETLES (Gyrinidae) they are actually divided into two, each upper half (see Color plate, p. 216) adapted for vision on or above the water surface, and the lower half, for underwater vision. The eyes of subterranean and cave-dwelling beetles may be largely or completely regressed. Such blind beetles are particularly numerous among the GROUND BEETLES (for example, *Aphaenops pluto* of Europe; see Color plate, p. 216) or *Neaphaenops tellkampfii* of Mammoth Cave in the U.S.A. and the Leptodiridae (for example, *Leptodirus hohenwardi* of Europe; see Color plate, p. 225; or *Adelops* spp. of the eastern U.S.A.). But even among the PREDACEOUS DIVING BEETLES (Dytiscidae), MAMMAL-NEST BEETLES (Leptinidae), FEATHER-WINGED BEETLES (Ptiliidae), ROVE BEETLES (Staphylinidae), and the Pselaphidae there are blind forms. Ocelli are very rare, occurring only among the SKIN BEETLES (Dermestidae). The larvae have only single eyes (stemmata), usually in groups of up to six on either side.

The antennae are usually made up of ten or eleven segments, but there may be twelve, nine, or eight. Exceptions to this rule include the Paussidae, which have only two segments, and some long-horned beetle genera in the subfamily Prioninae, in which the antennae of the males can have several times the usual number of segments. The record in this respect is held by the northeastern African beetle *Polyarthron pectinicornis* (see Color plate, p. 255), with up to sixty-four segments in its antennae. Firefly species of the South American genus *Amydetes* have as many as forty antennal segments. But the number of segments is no indication of length. The antennae of the African long-horned beetle just mentioned are far from the longest found among beetles. Males of the European TIMBERMAN (*Acanthocinus aedilis*) or *A. medosus*, from the eastern U.S.A., have antennae five times as long as the body, and in the Solomon Island *Batocera kibleri* males they are up to 23 cm long. On the other hand, extremely short antennae are found in, for example, the WHIRLIGIG BEETLES (Gyrinidae), many LADY BEETLES (Coccinellidae), and some Dryopidae.

The best-developed senses

The structure of the antennae is greatly varied among the beetles, as it must be to correspond to the variety of habits. Their primary function is to house the sense organs of touch and smell. These two sorts of stimuli are associated with finding food and sexual partners, the identification of objects, and the detection of vibrations and currents. The sensitivity of some beetles to vibration is quite impressive. Probably most people have noticed how beetles play dead, drop to the ground, or withdraw into holes as soon as one approaches, no matter how carefully this is done. Other beetles prefer rapid flight to hiding. In either case, though other stimuli may also be involved, the decisive factor eliciting such behavior is usually some form of vibration.

Even greater sensitivity and more rapid reactions are exhibited by WHIRLIGIG BEETLES (Gyrinidae) as they rush in zig-zag paths past one another on the water surface. Within a small area—50–100 cm in diameter—dozens of them may be bustling about, and in the tropics there may be many hundreds of individuals in an area only slightly larger. But they never bump into one another. They can perceive the wave "echo" reflected by an object on the water, and can take instantaneous evasive action. On the other hand, they are also capable of localizing and catching a prey animal swimming on the water in the dark. The organ which guides the whirligig beetles so efficiently and reliably during these maneuvers is located in the ear-shaped second segment of the very short antennae. As mentioned above, in some WATER SCAVENGER BEETLES (Hydrophilidae) the antennae, remarkably, are used for renewing the respiratory air; the ordinary function of these antennae has been taken over by the strikingly long mandibular palps.

Sense organs may also be located on almost any other part of the body. One rather peculiar location, for example, is the edge of the coxal pit on the middle legs. Here, lying in a depression, some of the METALLIC WOOD-

BORERS (Buprestidae) have an infrared-sensitive organ—that is, it responds to wave lengths longer than those of visible light (radiant heat). These enable such beetles to tell when they are near a source of heat. The blue beetle *Melanophila acuminata*, widespread in Asia, Europe, and North America, has become particularly well known for such behavior, flying toward forest fires.

Distinguishing characteristics: Reproduction

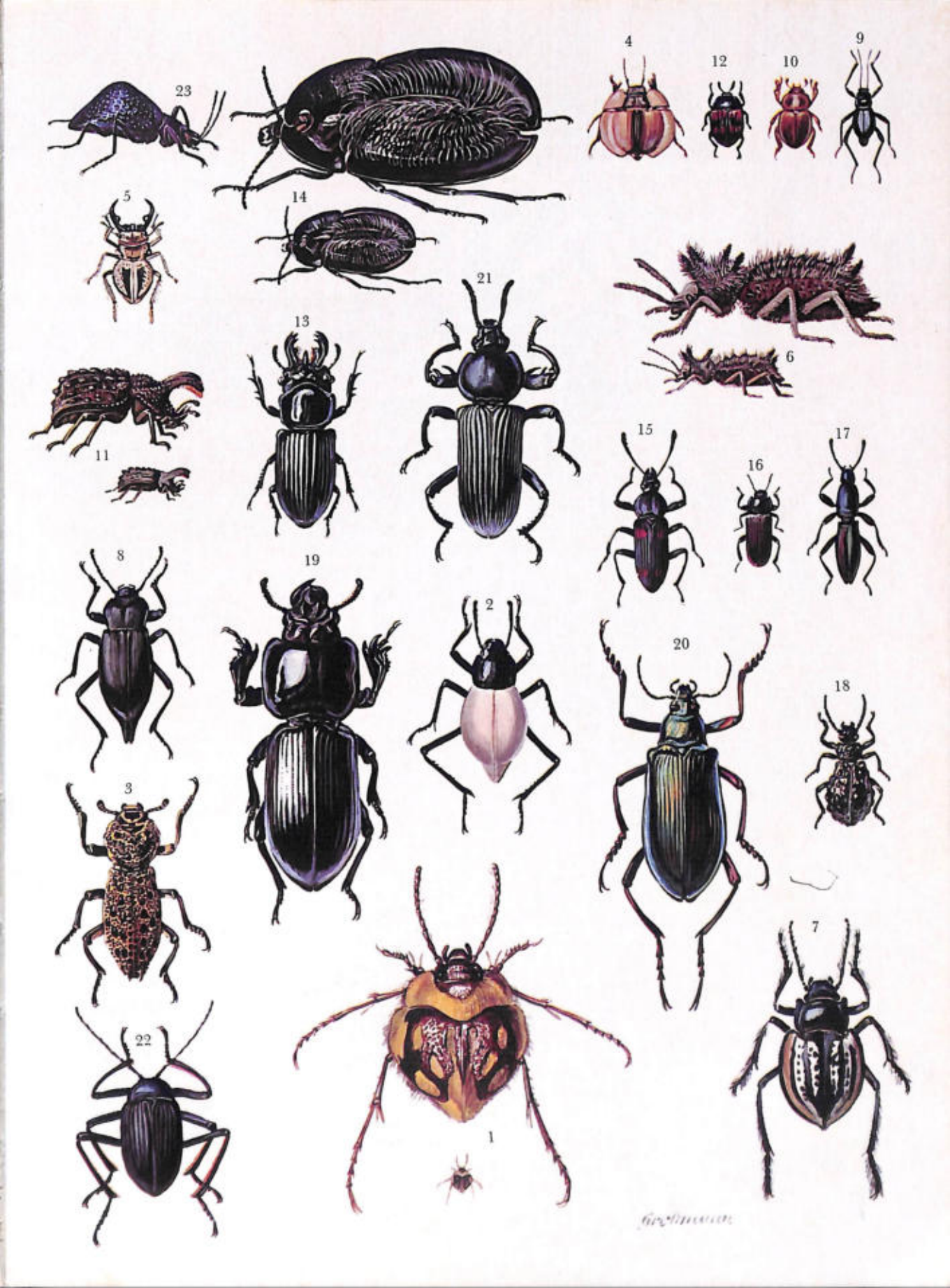
Among beetles, sexual reproduction is the rule; with very few exceptions, the females lay fertilized eggs. But the copulatory position is not always the same. In many species the male sits on the back of the female, holding tight with his legs; occasionally the situation may be reversed. The forelegs are often specially modified for this purpose, particularly by broadening of the tarsi and provision of an adhesive pad of hairs on the underside, or even of suction discs as in the dytiscids. In other species there are teeth or hooks on the tibiae, which serve to anchor the animal on the edges of the pronotum or the elytra of its partner.

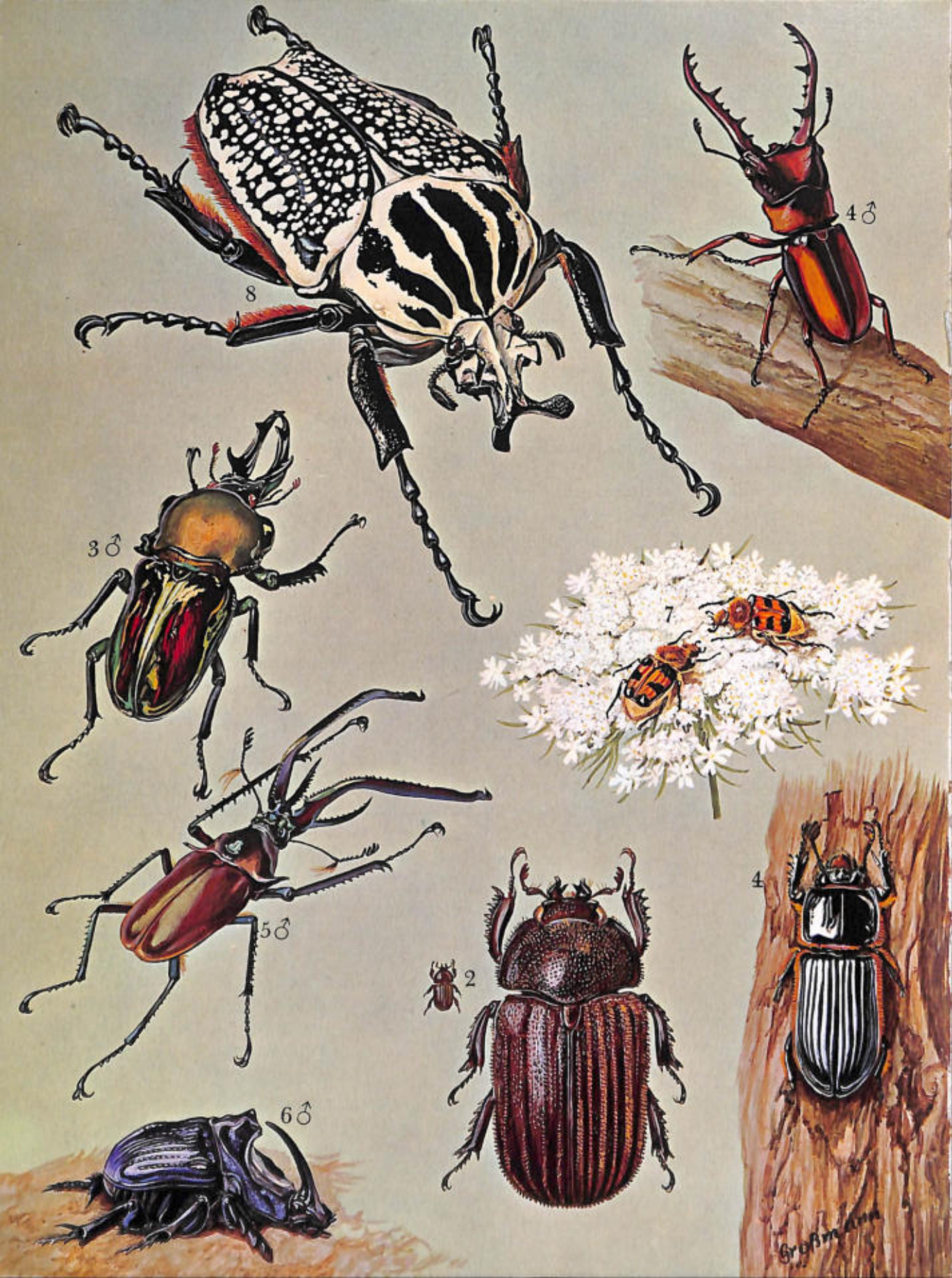
Courtship and mating behavior

Some males also use their mandibles to hang on to the female. The "piggy-back" position is not maintained during the entire process of copulation by all these beetles. Not uncommonly the male lets himself slip off to the side and stays there, usually on the right of his partner. Other males, like those of the Scarabaeidae and especially species of the JUNE BEETLE genus *Phyllophaga*, eventually let themselves fall over backward. Then the *Phyllophaga* spp. males are dragged about on their backs by the females. Frequently the two partners are turned away from each other, hind ends together. SOLDIER BEETLES (Cantharidae) copulate in this way, the male attaching his abdomen to that of the female by means of a special clasping apparatus. Copulation may last only a few seconds, a minute (in the case of the rove beetles), or even several hours (as in the June beetles).

Quite often the actual copulation is preceded by a sort of courtship. In the simplest, and probably the most common, cases the male taps his partner with the antennae, or performs some other species-specific movements while touching her; but there are also much more complicated behavioral patterns. As examples we shall mention two of the more striking courtship ceremonies. Flying FIREFLY males (Lampyridae) send out species-specific light signals, often rhythmically, when they are ready to mate. Receptive females answer with a "matched" pattern of flashes, also characteristic of the species. This "code" ensures that only members of the same species come together. The females usually are sitting near the ground, on stalks of grass or on plants. Their wings may be regressed, so that they cannot fly. The males, in general, have large, often protruding eyes, with which they detect the females' signals. Usually the flashes of the females are brighter than those of the males. If a male of the North American firefly *Photinus pyralis* detects a signal exactly two seconds after his own was given, he flies toward the source. In other species the characteristic interval between the two signals may be different, or it may be the intensity or the duration of the flash which is the essential element in recog-

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Darkling beetles: 1. *Cardiosus namtibensus*, enlarged and actual size; 2. *Onymacris candidipennis*; 3. *Zopherus mexicanus*; 4. *Lepidochora eberlanzi*; 5. *Calognathus chevrolati*; 6. *Sepidium muscosum*, enlarged and actual size; 7. *Sternodes caspicus*; 8. The cellar beetle *Blaps mortisaga*; 9. *Philorea setipennis*; 10. *Choerodes trachysceloides*; 11. *Bolitotherus cornutus*, enlarged and actual size; 12. *Diaperis boleti*; 13. *Phrenapates bennetti*; 14. *Helaeus perforatus*, enlarged and actual size; 15. *Zophobas tibialis*; 16. *Tenebrio molitor* (the larva of this beetle is the well-known "mealworm"); 17. *Macellocerus dimidiatus*; 18. *Phymatestes denticollis*; 19. *Hemipristis muelleri*; 20. *Camaria fruhstorferi*; 21. *Pycnocerus passerini*; 22. *Eupezus spinicrus*; 23. *Cuphotes cyaneus*.


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◁ Betsy beetle: 1. *Passalus punctiger.* Stag beetles (cf. Color plate, p. 266): 2. *Aesalus scarabaeoides,* enlarged and actual size; 3. *Phalacrognathus muelleri*; 4. *Prosopocoilus savagei*; 5. *Chiasognathus granti.* Lamellicorn beetles (cf. Color plates, p. 249f.): 6. *Phanaeus lancifer*; 7. *Trichius fasciatus*; 8. The Goliath beetle *Goliathus meleagris,* actual size.

nition. Once the male has found his partner, he touches her with his antennae to confirm that she has the proper smell; in many cases both partners do this. Only if this test is passed do the animals proceed to copulate.

This characteristic touching, to identify the partner, is also practiced as a rule by the Melyridae, our second example of relatively highly developed courtship behavior. Touching with the antennae is a preliminary to the courtship display of these lively little beetles. Immediately thereafter the male either brings his head close up to the mouthparts of his partner, or he turns tail and holds the tips of his elytra out to her. Other parts of the body may also be put in a particular position before the female's head. In each case there is a special organ, which contains a secretion, on the part presented. In the different genera these organs may lie either on the front of the broadened head (in groove between the antennae), in infoldings at the ends of the elytra, in certain aberrantly constructed segments of otherwise normal antennae or palps, or in depressions in the pronotum, the underside of the metathorax, the tibiae, or the abdominal segments. The female bites into the tufts of hair, bristles, skin folds, or swellings of the organ, receiving the flavored secretion of her partner. Then the two insects turn head to head again and repeat the process, first touching with the antennae and then offering the male organ, which is bitten. Often this sequence is repeated countless times; it goes on until the excitation on both sides has become great enough to lead to copulation.

Parthenogenesis does occur in some species, for example in the SKIN BEETLES (Dermestidae), DARKLING BEETLES (Tenebrionidae), LEAF BEETLES (Chrysomelidae), and SNOUT BEETLES (Curculionidae). A form of viviparity has been observed in a few ROVE BEETLES (Staphylinidae) and some LEAF BEETLES. In these cases eggs are in fact laid, but the larvae hatch immediately, sometimes with a delay of only a few minutes.

Distinguishing characteristics: Eggs

The shape of the eggs varies greatly, usually being more or less oval; but there are also rounded, cylindrical, spindlelike, or rodlike (Lyctidae) forms. The number of eggs laid by a single female also varies greatly from species to species and from family to family. Females of the large dung beetles of the genus *Scarabaeus* produce about six to ten eggs, those of the dung beetle genus *Copris*, five to seven; the STAG BEETLES (Lucanidae) produce thirty to seventy, some LEAF BEETLES (Chrysomelidae), up to 400, and the BLISTER BEETLES (Meloidae), 2000–10,000.

Development and metamorphosis

All beetles undergo a complete (holometabolous) metamorphosis during their development from egg to imago. The number of larval stages in many families is three, but it can be four to six and, in rare cases, even more, Under special culture conditions in the laboratory, forty stages or molts have been induced. Usually the larval stages resemble one another externally except that they become larger with each molt. But in some beetle species there are larval states of different appearance, due to differences in the way of life during these stages—usually associated with a

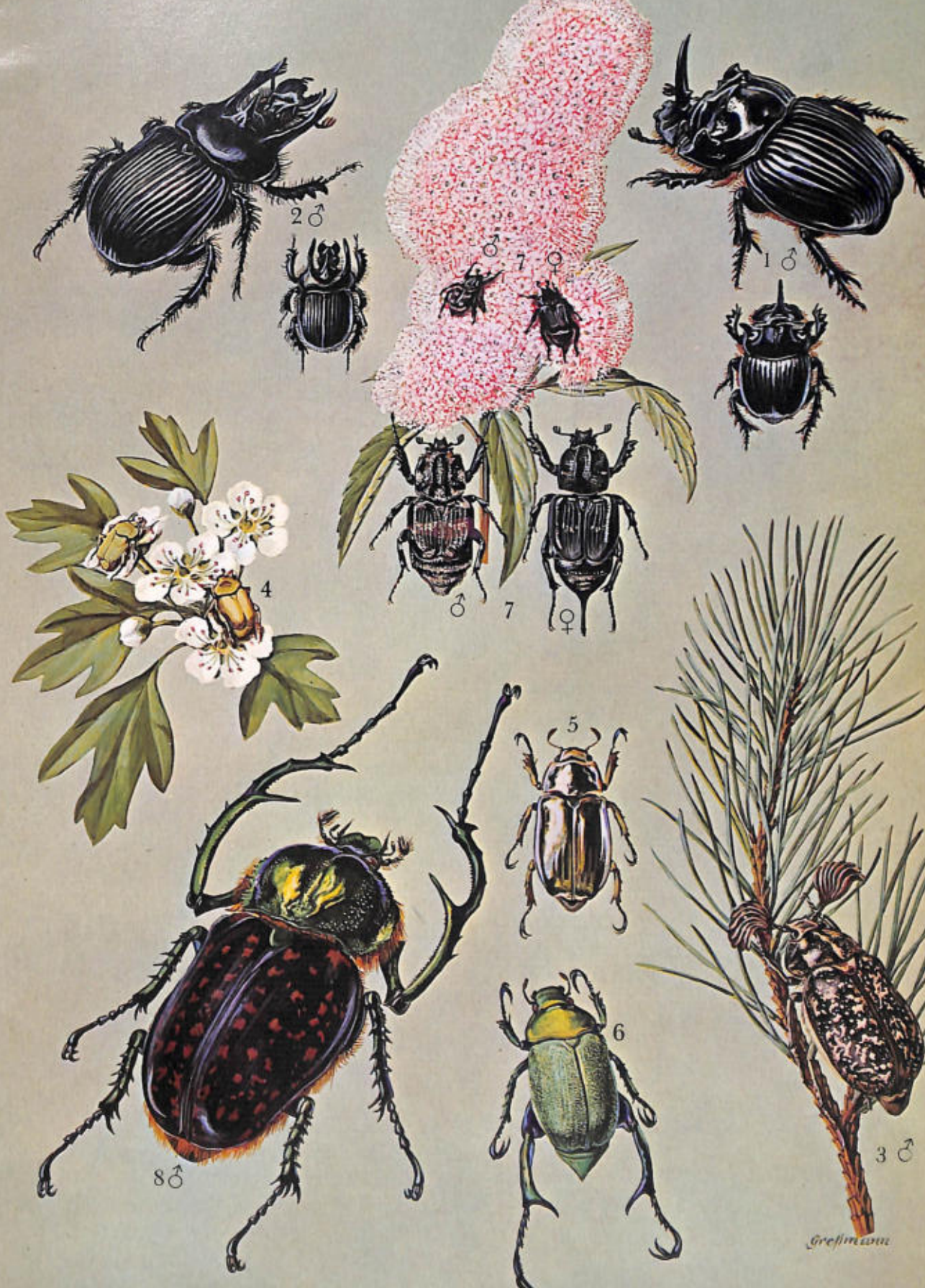
transition to parasitism. The first larval stage of such a beetle is always lively and active; from the second or third stage onward the larvae take on a different, usually more awkward, shape and lose the ability to move about. This change in form and habits during development (heteromorphosis) is known to occur in the GROUND BEETLE *Lebia grandis*, some species of the ROVE BEETLE genus *Aleochara*, in the Drilidae, the Rhipiphoridae, and the SHIP-TIMBER BEETLES (Lymexylonidae).

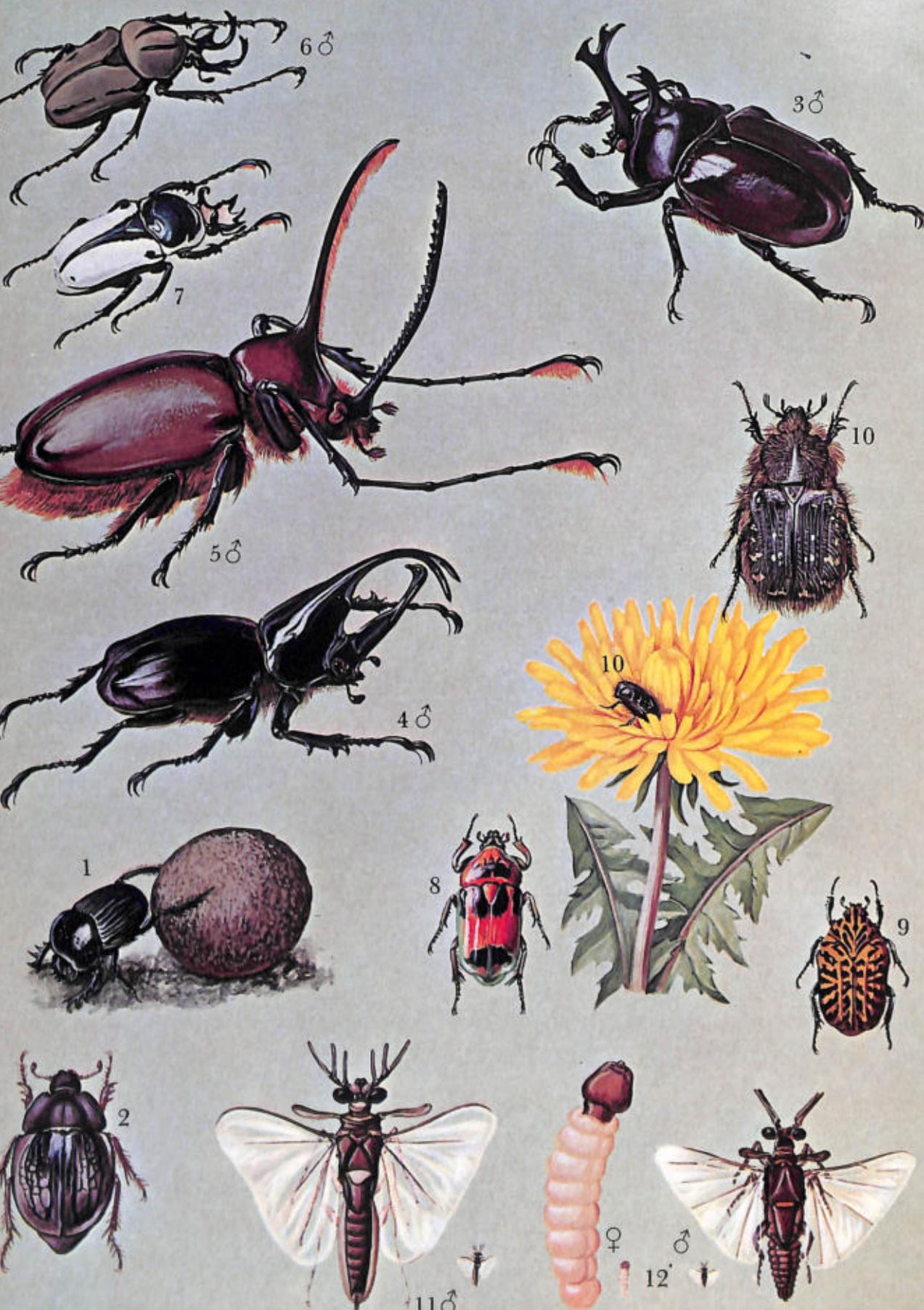
The development of the BLISTER BEETLES (Meloidae) is even more complicated. The first larval stage (called the triungulin, or "three-clawed larva," since the last segment of each tarsus has three claws; see Fig. 13-13) is slender and very active. It is followed by a fat, maggotlike second-stage larva and then by a dormant stage (pseudopupa). The pseudopupa is followed by another maggotlike larva capable of movement and then by the pupa, from which the adult beetle emerges. This remarkable (hypermetabolous) type of metamorphosis, with an interposed dormant stage, occurs in no other insect family.

In the order Coleoptera there is just one known example of alternation of generations. The North American beetle *Micromalthus debilis* reproduces both in the ordinary bisexual way and by way of the larva (paedogenesis). This species spends the winter as a legless, wormlike larva. When the winter dormant period is over, some of the larvae pupate, and from these pupae emerge female beetles. The other larvae retain their larval form, and each of them gives birth either to a single egg or to several young larvae with legs. From the egg there hatches a legless larva which eats up the mother larva, grows rapidly, enters a prepupal stage, and pupates. A male beetle emerges from this pupa. The larvae borne by the mother larva move about actively, and eventually molt into the wormlike larval forms which again carry the species through the winter.

The duration of larval development may vary within a wide range, depending not only upon the eventual size of the adult, but also to a great extent upon the size and nutritive value of the food supply, and upon the temperature. Many of the small beetles need only a few weeks to complete their development, so that several generations follow one another during the course of a year. In warm countries, as a rule, there are more generations per year than in cooler ones, even within a single species which occupies both climatic zones. The majority of beetles in the temperate zones have one generation every year (in the case of many metallic woodborers, the blister beetles, and certain long-horned beetles), or two per year (ground beetles, lady beetles, etc.) But there are a considerable number of beetles which require two years to develop, and others needing three years, four, or even more. For example, the larval period of many DEATHWATCH BEETLES (Anobiidae), which are only a few millimeters long, lasts for two to three years, and so does that of the FLOWER EATER (*Cetonia nitidia*), which grows as long as 20 mm. It is common knowledge that the most widespread European June beetle species, the WHITE GRUB (*Phyllo-*

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Lamellicorn beetles (cf. Color plates, pp. 246, 250, and 266); 1. *Copris lunaris*, enlarged and actual size; 2. *Typhoeus typhoeus*, enlarged and actual size; 3. *Polyphylla fullo*; 4. *Hoplia farinosa*; 5. *Plusiotis chrysargyrea*; 6. *Chrysophora chrysochlora*; 7. *Valgus hemipterus*, enlarged and actual size; 8. *Choirotonus macleayi*.


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phaga anxia), has "flight years" separated by two or three years during which flying animals are not observed; it requires about this time for their development. The larval period of the European cerambycid *Cerambyx cerdo* lasts three to five years, and that of the GIANT STAG BEETLE (*Lucanus elaphus*) five to eight years, whereas a small (L only 7 mm) relative of the latter beetle, the European *Aesalus scarabaeoides* (see Color plate, p. 246), develops in only one to three years. The developmental period of a pest belonging to the Cerambycidae, the OLD HOUSE BORER (*Hylotrupes bajulus*), in central Europe and eastern North America requires six to eight, or under unfavorable circumstances even twelve to fifteen, years, whereas the same animal matures in two to five years in South Africa.

The pupal stage

Most beetle larvae move to the ground to pupate, if they do not already live there. According to species, they dig pupal chambers in the earth at depths of 5 cm to 1.5 m. Larvae which pupate in crumbly materials such as compost heaps, ant nests, rotting tree trunks and stumps, or galleries in wood containing a lot of bore dust, usually use these materials to construct their pupal chambers or "puparia." There are only a few species which pupate in the open air, hanging head-down from plants (as do, for example, lady beetles and some leaf beetles). The pupal chambers are lined either with fine crumbs of the surrounding soil or with rotten wood, particles of excrement, or even a substance excreted by the Malpighian tubules. The beetle pupa is "exarate"—that is, the cases in which the adult appendages (antennae, legs, and wings) lie are not fused along their length to the body. The pupal period often lasts for several weeks and frequently for many months. Exceptionally short periods of only a few days do occur, and rarely pupae may remain dormant for years.

Life span of adult beetles

The maximum age achieved by beetles also fluctuates widely from one species to another. The boring beetle *Hylocoetus dermestoides* lives just a week, and some species of rhipiphorids of the genus *Rhipidius* survive for no more than three to four days. Countless beetles live for several weeks or months, including those which, after emerging from the pupal case, remain in the puparium or cocoon until the months of unfavorable weather (winter or dry season) have passed. *Lucanus elaphus*, for example, spends seven to nine months in the pupal chamber before emerging in June; thereafter it lives about three to five weeks more. RHINOCEROS BEETLE species of the genus *Oryctes* live in the open for six to nine months without eating. The longest-lived are probably some of the SNOUT BEETLES (Curculionidae); for example, the PALES WEEVIL (*Hylobius pales*; L 10–13 mm), as an imago, can live as long as three years. In laboratory conditions, *Dytiscus* sp. have been kept alive for five years, and *Copris* sp. and the BOLL WEEVIL (*Anthonomus grandis*), for three years.

Even remote and inhospitable islands beyond the polar circles have been colonized by beetles. On continental land masses, there are no regions or habitats which have not been conquered by beetles, except for the high mountain glaciers and the eternal ice in the polar zones. In fresh water

◁ Lamellicorn beetles (cf. Color plates, pp. 246, 249, and 266): 1. *Scarabaeus laticollis*, rolling a dung ball to the right; 2. *Hexodon reticulatum*; 3. *Allomyrina dichotomus*; 4. *Dynastes gideon*; 5. *Golofa porteri*; 6. *Dicranocephalus wallichi*; 7. *Ranzania bertolinii*; 8. *Heterorrhina imperatrix*; 9. *Gymnetis hieroglyphica*; 10. *Tropinota hirta*. Stylopidae: 11. *Mengenilla kaszabi*; 12. *Xenos vesparum*, enlarged and actual size.

there are hundreds of species, even in cold, rushing mountain brooks. Although they have avoided the open seas, countless forms inhabit the spray zone along the coast. Some of these, such as the small hydrophilid species of the genus *Ochthebius*, can even exist in tiny pools in the rocks where the salinity of the water is considerably greater than that of sea water. Living conditions in the deserts of the world are no less unusual, but beetles are found there, sometimes represented by great numbers of species.

Distribution and adaptation to the environment

The larger, more important families are almost all distributed worldwide, though they may not have invaded all possible habitats. The 1300 species of STRAIGHT-SNOUTED WEEVILS (Brenthidae), though, are limited to the tropical zones, and the 550 species of BETSY BEETLES (Passalidae; L up to 8 cm) are distributed only in Africa south of the Sahara, in southeastern Asia, in Australia, and in North and South America. In families consisting of very many species, subfamilies or groups of genera are frequently restricted to particular regions of the earth, such as eastern Asia or South Africa. The smaller the systematic unit (genus, subgenus), the more narrowly circumscribed, as a rule, is its area of occurrence. The same is true for subfamilies or families with few species: the twenty-five species of the ground beetle subfamily Migadopinae are to be found only in Australia, New Zealand, and southern South America, while the fifteen species of the family Trictenotomidae, some of which may be 8 cm long, are restricted to tropical southern Asia. Conversely, some large genera, with countless species, occur in all parts of the earth.



Fig. 13-8. Female of the old house borer (*Hylotrupes bajulus*; L 20 mm).

The beetle is in a sense the most successful of all animal types. It has managed to invade essentially all habitats that the land can offer. To be sure, there are some regions so completely hostile to life that even the beetles have avoided them. The order Coleoptera has a greater abundance of forms than any other, even without taking advantage of the oceans to encourage different life-form types; the basic beetle habitat is the land, even though they have in some cases found the way back to the water. How, then, did they arrive at this peak of success? Which of their abilities and characteristics paved the way? We can be sure that it was no single special characteristic, but rather that success depended upon the "right" combination of certain properties of insects in general. At least two characteristics seem of particular importance. One of these is the preservation of simple biting-chewing mouthparts, not modified into complicated proboscises for piercing, sucking, or sponging. The great variety of solid food which must be torn into bits is more regularly and abundantly available than fluid food, which must be sucked up. Nevertheless, many beetles are also able to consume fluids, by licking. The second special property is the transformation of the anterior pair of wings into solid elytra; this gives the abdomen greater protection, in many respects, than is available to other insects.

The most successful of all animal types

The substances on which beetles feed were listed earlier in this chapter.

Habitats and food



Fig. 13-9. Range of the beetle family Trictenotomidae.

Such a list is in itself an indication of where the beetles occur and how they live. By far the greater proportion is vegetarian, feeding on plants crisp or soft, fresh or rotted, juicy or dry, natural or processed by man (groceries and drugs). The rest eat animal materials, usually hunting their own prey but often scavenging animal refuse. Plants are to be found almost everywhere, on land and in water; they thrive even in the desert, where they survive the dry periods as seeds or dormant subterranean shoots, and at intervals of several years sprout and bloom after it has rained. Both the subterranean parts and the desiccated plant remains above ground are fodder for beetles. Moreover, vegetable debris is distributed widely over the surface of the ground by the wind; some of these bits are caught under stones or in crevices. At night the humidity is high in deserts adjoined by ocean coasts. Thus even these austere conditions are adequate for appropriately adapted beetles.

Beetles in the desert

A few years ago it was discovered, surprisingly, that the sand dunes of the Namib Desert in southwestern Africa—supposed to be devoid of insect life—are the home of a considerable number of beetle species, many of the family Tenebrionidae. No one had suspected how many beetles lead a hidden existence in the sand, and how lively the dunes can become at night. Scientists also discovered that the windward slopes of the dunes can house different species than do the lee sides (away from the wind). Furthermore, the beetles living in the sand near the ridge of the dunes are different from those near the foot, and those in the valleys between the dunes differ from both. In many cases one can infer the desert habitat directly from the appearance of these beetles. Regardless of their family relationships, they have many external characteristics in common. For example, the upper side of the body of some species is light in color, either due to a whitish covering of hair, to white waxy cuticular secretions, or to the absence of melanin (black pigment). This sort of lightening minimizes the absorption of radiant heat by the body. Other beetles have much more strongly arched elytra than do their relatives outside the desert; this produces a large insulating air space between the elytra and the abdomen, which also offers protection from the strong sun. Still other beetles escape the high daytime temperatures by burrowing in the sand, as one can guess from their broadened anterior tibiae. Many sand-dwelling beetles have long legs, often with a dense coat of hairs on the tarsi; they are thus properly equipped to move across dry, fine-grained sand. The Namib Desert provides an example of the ability of beetles to live even where life appears impossible; it also shows that even regions which seem most monotonous and desolate can offer several quite distinct types of habitat, with a particular fauna associated with each.

. . . in the semidesert

The next habitat to be considered, in which beetles are somewhat more abundant, is the semidesert, with an average of 50–100 mm precipitation per year. Here there is a more or less stable flora, consisting of scattered woody and usually thick-leaved cushion plants, small shrubs, and thorn

bushes. Between these, the ground is barren and baked by the sun; there is no layer of humus and only scattered hillocks with hard grasses. It is easy to imagine how many more opportunities the semidesert offers for beetle life than does the desert. Here the beetles regularly find green foliage, fallen and dried leaves, green and dead wood, and for short periods even flowers, ripening and fallen fruits, and seeds. As a consequence, the number of beetle species is larger here; it becomes greater depending on the density of plant cover, the number of plant species, and the diversity of the landscape and the weather, since changes in these variables increase the number of distinct habitats.

Saprophagous beetles, tree dwellers

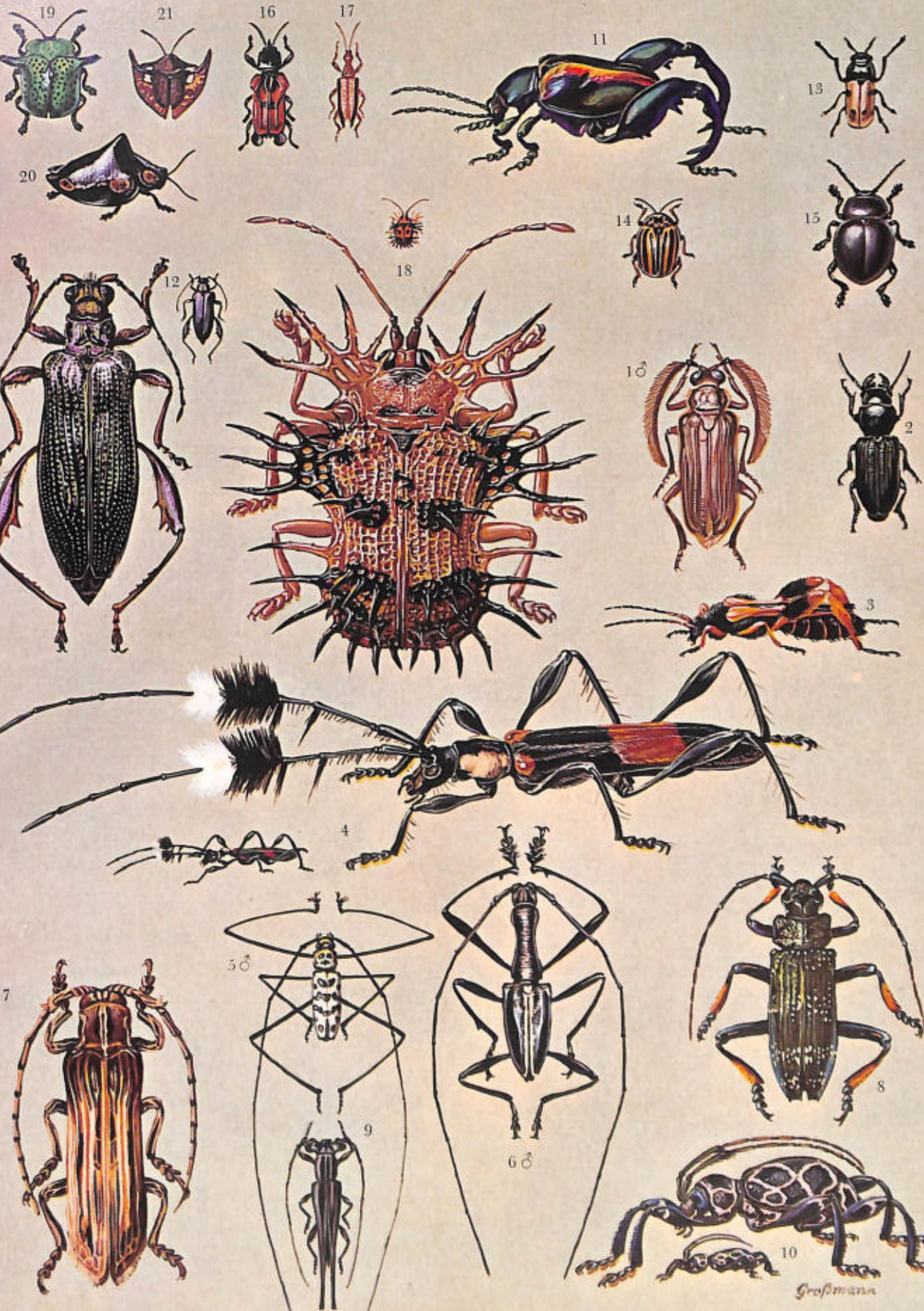
One varied set of habitats, to be found wherever there is sufficient plant life, is that offered by rotting vegetation; there are many stages of decay, levels of humus, and degrees of humidity. Correspondingly, there are many saprophagous (decayed-plant consuming) beetles, forming a sequence of adaptations to each sort of food. Most of these are dependent on a specific degree of decomposition and/or humidity, and appear only when conditions are exactly right. Molds, another food source, attract various beetles. Trees, such as those on the edge of a mixed wood, offer shade which keeps the soil damp, and here there grow plants quite different from those in the unshaded area a hundred yards away. There is a corresponding difference in the composition of the beetle populations in the two localities. The trees themselves harbor many beetle species of their own, different beetles for almost every different species of tree. The leaves are mined by the larvae of small METALLIC WOODBORERS (Buprestidae), LEAF BEETLES (Chrysomelidae), and SNOUT BEETLES (Curculionidae); in the wood of the twigs there burrow, depending on its condition, metallic woodborers, FALSE POWDER-POST BEETLES (Bostrychidae; see Color plate, p. 235), DEATHWATCH BEETLES (Anobiidae), LONG-HORNED BEETLES (Cerambycidae), some weevils, BARK BEETLES (Scolytidae; see Color plates, pp. 256 and 276), and Platypodidae. Various species burrow in the phloem tissue, and still others live under the bark, the type of beetle depending on the bark's state of preservation.

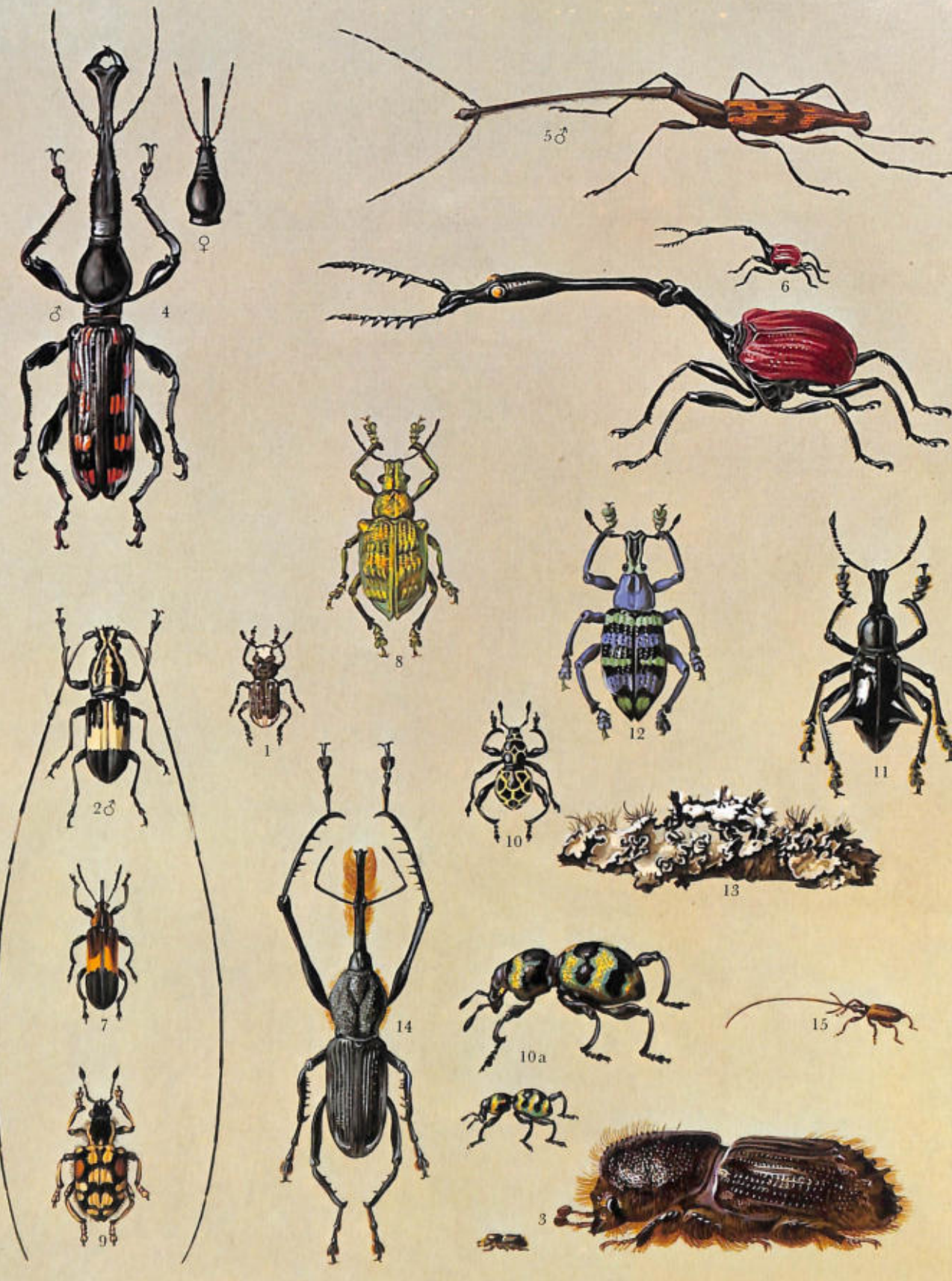
Fungi on dead branches and agaric fungi are occupied by specialist beetles: SHINING FUNGUS BEETLES (Scaphidiidae), PLEASING FUNGUS BEETLES (Erotylidae), SILKEN FUNGUS BEETLES (Cryptophagidae), HAIRY FUNGUS BEETLES (Mycetophagidae), HANDSOME FUNGUS BEETLES (Endomychidae), MINUTE TREE FUNGUS BEETLES (Cisidae), Serropalpidae, and others. Even animals as large as the VIOLIN BEETLE (*Mormolyce phyllodes*; L up to 10 cm; see Color plate, p. 216) live on or in agarics in southeastern Asia. Dead tree trunks house a similar abundance of beetles, again of types specific to the particular state of decomposition of the wood. The same is true of the dung of vegetarian mammals, which contain their own sort of beetle fauna, as one may infer from the name "dung beetle"; most of these belong to the family Scarabaeidae.

Thus one can readily visualize the vast range of beetle habitats, bounded

▷
Long-horned beetles: 1. *Polyarthron pectinicornis*; 2. *Spondylis buprestoides*; 3. *Callisyphris macropus*; 4. *Cosmisoma ammiralis*, enlarged and actual size; 5. *Gerania bosci*; 6. *Gnoma agroides*; 7. *Xylorhiza adusta*; 8. *Sphingonotus albertisi*; 9. *Enicodes montrouzieri*; 10. *Doliops pachyrrhynchoides*, enlarged and actual size. Leaf beetles (cf. Color plate, p. 278); 11. *Sagra busqueti*; 12. *Donacia crassipes*, enlarged and actual size; 13. *Lachnaea vicina*; 14. The potato beetle *Leptinotarsa decemlineata*; 15. The bloody-nosed beetle *Timarcha tenebricosa*; 16. *Xenarescus monocerus*; 17. *Aproida balyi*; 18. *Platypria coronata*, enlarged and natural size; 19. *Tauroma casta*; 20. *Mesomphalia sublaevis*; 21. *Selenis spinifex*, a tortoise beetle.

Fungus-eating and coprophagous beetles


19
21
16
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1♂
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5♂
6♂
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9
10
Großmann


♂
♀
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3

at one extreme by the desert and at the other, by the zone at the edge of a mixed forest. The range encompasses savannas, prairies, heaths, bogs, swamps, marshes, mountain meadows, boggy woods, deciduous forests, mangrove swamps, rain forests, coniferous forests, salt flats, brine pools, and the shore zones of brooks, rivers, lakes, and oceans. Beetles also occupy the artificial habitats created by men throughout the world—the cultivated forests and agricultural lands. And, of course, one meadow is not the same as another, nor one wood identical to the next. Soils differing in friability, drainage, heat capacity, acidity, and chemical composition support different plant communities which are further modified by the altitude and slope of the ground—and in each case different beetles exploit them.

Carnivores

Actually, the interactions between members of an ecological community are more complicated than has been indicated, even if one considers only the beetles, for wherever vegetarian animals live, carnivores are usually present. This is as true among the beetles—and in the insect world in general—as it is for the fish, birds, and mammals. Of course, the herbivorous beetles are not only slaughtered by hunters of their own order; other insects, particularly Hymenoptera (digger, thread-waisted, roller, and parasitic wasps) and predatory and parasitic Diptera prey upon them. Conversely, carnivorous beetles prey not only upon their herbivorous relatives, but more often upon other insects. Thus, the prey of the GROUND BEETLES and ROVE BEETLES are predominantly lepidopteran caterpillars, the larvae of sawflies, fly grubs, springtails, thrips, bug larvae, and even small worms. The larvae of certain STONE BEETLES (Scydmaenidae) hunt mites, while the LADY BEETLES and their larvae hunt thrips, scale insects, and aphids. The larvae of species of the BLISTER BEETLE genus *Epicauta* consume the eggs laid by grasshoppers. Some hunting forms of the FUNGUS WEEVIL (Anthribidae) feed on scale insects, and those of the STRAIGHT-SNOUTED WEEVILS (Brenthidae) eat various wood-boring insects.

The number of prey animals which can fall victim to a single hunter is surprisingly large; in certain species of small LADY BEETLES each larva destroys in its lifetime up to 3100 scale insects or their larvae. Certain beetles specialize in the pursuit of other beetles. The GROUND BEETLE *Lebia vittata* feeds on the eggs and larvae of the fleabeetle *Disonycha alternata*, while its relatives hunt those of other leaf beetles (species of *Chrysomela*, *Phytodecta*, *Galerucella*). The HISTER BEETLE (*Hister sextriatus*) stalks the nearly mature larvae of the moth *Agrotis upsilon*, a black cutworm. Some of its relatives pursue bark beetles (Scolytidae) under the bark of trees, and others capture the larvae of many other species of beetles. Various CHECKERED BEETLES (Cleridae) consume deathwatch beetles (Anobiidae), small long-horned beetles (Cerambycidae), and especially bark beetles. Several species of the family Rhizophagidae also feed on bark beetles, and some also eat wood-boring snout beetles (Curculionidae). The 9-mm-long *Rhizophagus dimidiatus* is the main enemy of the sctoylid *Dendroctonus obesus*, which breeds on the Sitka spruce.

◁
Fungus weevils: 1. *Platyrrhinus resinosus*; 2. *Xenocerus semiluctuosus*.
Bark beetle (cf. Color plate, p. 276): 3. *Ips sexdentatus*.
Straight-snouted weevils: 4. *Eutrachelus temmincki* male; next to it, the head of the female;
5. *Lasiorrhynchus barbicornis*.
Snout beetles (cf. Color plate, p. 277): 6. *Trachelophorus giraffa*; 7. *Homalocerus lyciformis*; 8. *Lamprocyphus augustus*;
9. *Trichaptus mutillarius*;
10. *Pachyrrhynchus reticulatus*;
10a, *Pachyrrhynchus* sp. from the islands of southeastern Asia; 11. *Gymnopholus weiskei*; 12. *Eupholus magnificus*; 13. *Lithinus nigrocristatus*, camouflaged like tree bark; 14. *Rhina barbirostris*; 15. *Antliarrhinus tamiae*.

Eaters of animal refuse

In addition to all these "fresh meat" eaters, there are many species which feed on dry animal refuse, usually long-dead, desiccated corpses or parts of them. They also eat all kinds of natural waste products found in nests and the burrows and other sleeping places of warm-blooded animals —scales of skin, feathers, hairs, and shed scabs, as well as the remains of sucked-out insect bodies and the exuvia of larvae and pupae. Finally, these animal materials also include those processed by humans, such as dried meat, tallow, grease, bone, wool, hides, furs, and instrument strings of gut. Dried-up corpses lie about in the open more commonly than one supposes, though there are fewer in humid zones than in dry ones. These are a source of food for various species of BONE BEETLES (Corynetinae) and especially the SKIN BEETLE *Dermestes* spp (Dermestidae; see Color plate, p. 226), as well as some DARKLING BEETLES (Tenebrionidae). Where there are bone remnants containing fat and suet, beetles of the subfamily Troginae appear. And where garbage is infested with fly maggots, one finds predatory beetles, primarily ROVE BEETLES (Staphylinidae) and HISTER BEETLES (Histeridae; see Color plate, p. 225).

Bird nests attract an amazingly rich beetle fauna. The location of the nest is often of critical importance, as is the extent to which it is protected from wind and weather, and its present or past inhabitants. The humidity and amount of shade depends upon whether the nest is on fallen leaves on the ground, between bundles of grass, in piles of brush, or in niches of rock; accordingly, each such nest has different beetle occupants. This is also true of nests in burrows and caves. Nor is it irrelevant whether the nest belongs to songbirds, water birds, or birds of prey. The same holds for the nests and sleeping places of rodents, insectivores, small predatory animals, and other mammals. These may be placed above or below ground, in the forest or in the open, in sand, clay, or turf. The beetles most characteristic of such places are the HISTER BEETLES (Histeridae), Leptodiridae, MAMMAL-NEST BEETLES (Leptinidae), FEATHER-WINGED BEETLES (Ptiliidae), many of the small ROVE BEETLES (Staphylinidae), some SKIN BEETLES (Dermestidae), SILKEN FUNGUS BEETLES (Cryptophagidae), Troginae, and others. Many of these beetles are remarkably adapted to this sort of habitat. For example, the CARPET BEETLES (species of *Anthrenus*) and some of their relatives are able to digest keratin—hoofs, claws, hair, wool, feathers, etc. Their digestive juices contain special materials which reduce the disulfide groups in the keratin, freeing the chains of protein so that they can be attacked by the ordinary enzymes.

Insect cadavers are a ubiquitous source of food for the beetles. These are found, for example, under or even in deserted spider webs, at places where such nests are frequently constructed, and where crab spiders choose to lie in wait. Insect remains also accumulate in all sorts of hollows they use as retreats, or into which they are dragged by their captors. The bodies of insects are hidden under bark and stones. Again, these are more common in dry climates than in more humid ones. The beetles which feed on dry

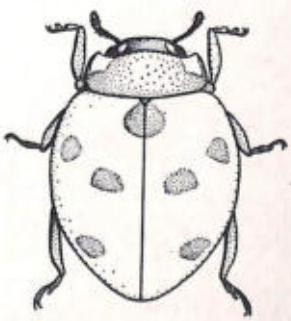


Fig. 13-10. The lady beetle *Coccinella septempunctata* (L 7 mm) is a zealous aphid hunter.

animal materials include most of the hordes of beetle pests which invade wool, hides, and other human possessions of animal origin. Any amount of wool is available to them in human habitations, in the form of clothing and carpets, while tons of skins and furs are bundled in warehouses and the holds of ships; feathers and hair hang as trophies in the homes of countless hunters and travelers. These treasures are usually protected from the vagaries of climate and from most predaceous or parasitic animals, but the beetles occasionally find conditions here ideal for development and multiplication.

Association with ants

There is yet another special beetle fauna in the nests of ants; the species concerned are more or less dependent on this symbiosis and are modified accordingly. In such associations between ants and other insects ("myrmecophily," see Chapter 18), the ants always play the role of hosts, and the associated insects (in this case, beetles), that of guests. Since ants always make vigorous efforts to defend their structures against alien intruders, the guests must evidently take special steps in order to be tolerated. In the simplest case, the guests help themselves, without opposition, to the eggs and larvae of the ants; this is done by some staphylinids. Other beetles—for example, other staphylinids and hysterids—clean up the sick and dead workers in the nest. Even more useful are the small staphylinids which pull parasitic mites off the ants and devour them. In Europe and western Asia, the staphylinid *Dinarda dentata*, together with its larvae, has adopted this role in the nests of forest ant species of the genus *Formica* (see Chapter 18), and in addition the beetles consume dead ants. In the course of adaptation to the differently sized species of this ant genus, the beetle has developed five separate varieties, distinguished not only by coloration, size, and certain aspects of body structure, but also in the manner of their association with the host ants. On occasion, *Dinarda* spp. beetles even follow the ants when they move to a new nest.

A more complex association is found between ants and beetles of the family Paussidae, which are found in all warm countries, but primarily in Africa. They are ravenous hunters, almost always appearing singly, wandering in and out of the nest and attacking the young. The hosts, mainly ant species of the genus *Pheidole* (see Chapter 18), put up no resistance—on the contrary, they seem to value the beetle's presence. The beetles produce a secretion which the ants eagerly lick up; it is produced by glands and accumulates in bundles of hairs within pits, irregular depressions, or peculiarly twisted transverse grooves on the pronotum. Nevertheless, there are often battles between the ants and a beetle which has just invaded the nest. The beetle always wins, either because it is too large and hard for the (often very small) workers, or because it sprays them with an iodine-containing fluid from its pygidial gland. Eventually the ants discover the thoracic secretion and leave the beetle in peace. In any case, the beetle in time takes on the smell of the nest and is then tolerated for that reason. Some particularly small (L only 2–3 mm) paussids of the African

genus *Hylotorus* have a body so smoothly cylindrical and highly polished that all attempts by the ants to get a firm hold on it with the mouthparts are in vain. There is no sharp corner or protruding edge; all the parts of this minute body lie absolutely flush, and even the head is smoothly rounded in front like a hemisphere. This invulnerability allows the beetle to stay in the ant nest long enough to be accepted.

Communal life with the ants becomes even more complex in cases where the hosts actually feed and care for their guests. Here, too, staphylinids offer examples. Those in Europe are *Lomechusa strumosa* and some species of *Atemeles*, while in North America this role is played by *Xenodusa cava*. Since the ants "beg" one another for food, the beetles also beg from the ants—with the same sort of vibration of the antennae and tapping with the forelegs. The ants (species of the genus *Formica*) then regurgitate a drop of food juice, which the beetles accept. These staphylinids are welcomed as guests because, like the paussids, they produce secretions avidly eaten by the ants. The corresponding bundles of hairs are in this case found on the dorsal surface of the anterior abdominal segments, near the lateral edges. The beetles are no more dependent on being fed by the ants than are the ants on the beetles; the beetles, especially their larvae, feed copiously on eggs and ant larvae.

The ant workers even take care of the staphylinid larvae. They treat the guests just as they do their own brood until they reach the pupal stage, feeding and licking them and if necessary carrying them along with their own offspring to another part of the nest. Their instincts account for this behavior, since the beetle larvae beg for food just as their own larvae do; they push the labium against a worker, causing reflex regurgitation and offering of the crop contents. The body surface of the beetle larvae also exudes substances which release the same brood-care behavior as do the substances on the ant larvae. It is not an uncommon occurrence that *Formica* nests are inhabited by many beetles at once, which can lead to a corresponding diminution in the ant population. Furthermore, female ant larvae are often damaged in such a way that they develop into useless cripples rather than reproductive queens. The reason for this is an excessive intake of the beetle secretions. Degenerative phenomena of this sort can contribute to the decline—and sometimes to the fall—of the ant "State."

The Pselaphidae have developed their association with ants to a similar degree. They, too, feed on the offspring of the host, demand food by antennal vibration and secrete from the first abdominal segment a substance much desired by the ants. But in constrast to the much more active *Atemeles* beetles, which leave the ant colony in the autumn, the clavigerids, blind and sluggish animals, remain with the hosts for their entire lives and cannot survive outside the nest. The technique of begging ants for food by antennal vibration has been mastered by various other beetles, some of which never or only occasionally enter an ant nest. One North American example is the broad, flat, dappled, nitictulid *Amphotis ulkei* (L 4–5

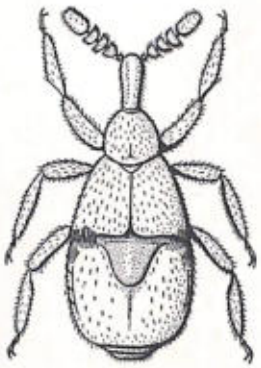


Fig. 13-11. This blind beetle, *Claviger testaceus* (L 2.5 mm), lives in an ant colony.

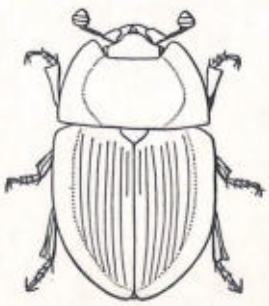


Fig. 13-12. A sap-sucking beetle which begs from ants, *Amphotis marginata* (L 4.5 mm).

mm) of the eastern U.S.A. From time to time this beetle visits the nests of a black ant (probably *Lasius* spp.; see Chapter 18), but it just as frequently begs in the open on a tree trunk, accosting a worker on its way back to the nest.

A particularly remarkable adaptation by a guest to the social organization of the hosts has been found in the species of the African genus *Doryloxenus*, rove beetles. Some species of this genus live in association with army ants (Dorylinae, see Chapter 18), which at regular intervals go out on hunting expeditions. They never return to their previous nest, but at each stage of their migratory life they build a new one. The beetles participate in these marches, each clinging with legs and mouthparts to the back of one of the ants, and thus being transported from the old nest to the new. In South America, there are a number of other rove beetles which live in a similar way among the New World army ants (*Eciton* spp. and others, see Chapter 18). Often host ant and beetle bear a striking resemblance to one another in color, size, and manner of movement. Unless one looks closely, one would not realize that the migrating ants are carrying a number of beetles with them. Some such beetles have elongated heads, like *Ecitophytes coniceps* (see Color plate, p. 225).

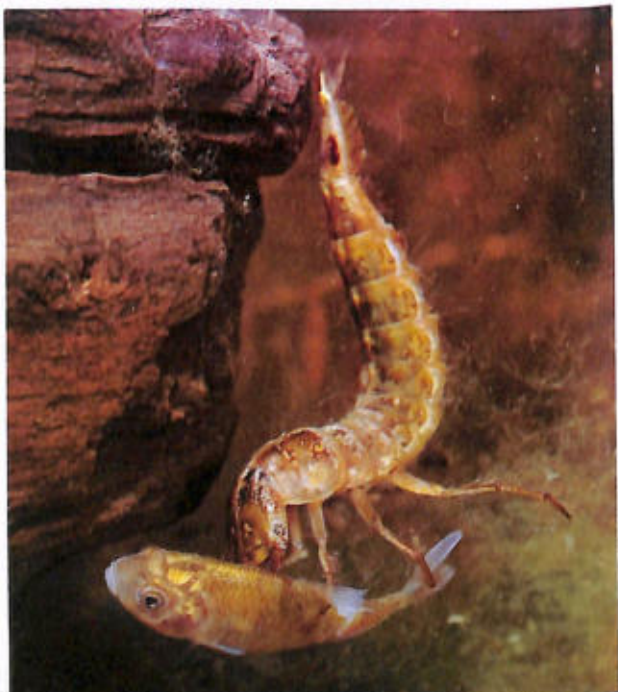
The beetle fauna in ant nests comprises hundreds of species. And by no means all species of ants—especially in the tropics—have yet been investigated in this respect. The majority of these guest-beetles are the paussids and staphylinids already mentioned. Other well-represented families are the Pselaphidae, the Thorictidae, and the Histeridae. These five families are the real "ant beetles." Other beetles which appear in ant nests are less closely associated with the ants themselves, even though they may have reached a high degree of specialized adaptation to life in an ant nest, feeding primarily on plant remains they find in the nests, on the fruiting bodies of molds, and on mycelia. They belong to several families, among others the BROWN SCAVENGER BEETLES (Lathridiidae), the FLAT BARK BEETLES (Cucujidae), the DARKLING BEETLES (Tenebrionidae), the LEAF BEETLES (Chrysomelidae), the STRAIGHT-SNOUTED WEEVILS (Brenthidae), the SNOUT BEETLES (Curculionidae), and the LAMELLICORN BEETLES (Scarabaeidae). One would not expect that the larvae of one Asian and European species of flower beetles, *Potosia cuprea*, develops in the nests of forest ants. These grublike larvae eat only the chips of wood collected there. The species of the American genus of scarabs, *Cremastocheilus*, are obligate predators of the larvae of species of the ant genus *Myrmecocystus*.

Association with other social insects

Not only the ants have beetles as guests; beetles inhabit colonies of wasps, bees, bumblebees, and termites. The American *Macrosiagon flavipenne*, of the family Rhiphoridae, is a parasite in the nest of species of wasps of the genus *Bembex* and bees of the genus *Prosopis* (see Color plate, p. 236; European *M. tricuspidatum*.) In central and southern Europe, in the nests of the common wasp (*Paravespula vulgaris*; see Chapter 18), is a predatory beetle, *Metoecus paradoxus* (see Color plate, p. 236), also of the family























. . . and with solitary Hymenoptera

The non-social bees are molested by beetles to a far greater extent than are the honeybees. For example, the larvae of the *Trichodes* species just mentioned make their way into the bee nests, usually located in the soil. The larvae of the many BLISTER BEETLE species (family Meloidae) even allow themselves to be carried there by the bees. The first larval stage (the triungulin, barely 1 mm long) of the blister beetles is very active; it climbs up the plants and in the process many happen upon flowers. As soon as a hairy insect arrives there, the triungulin scrambles onto it, grasps it firmly, and is carried away. If it turns out not to be a bee, or to be the "wrong" species, that is the end of the triungulin—it can develop no further and must perish. This high mortality is partly compensated by the large number of eggs laid by the female blister beetles. In species of the OIL BEETLES (genus *Meloe*), 4000–10,000 eggs are laid at a time. The beetle larvae which happen to hit the "right" target eventually drop off the bee in its nest and consume the eggs. Soon thereafter they molt; the second larval stage is quite different in appearance—pale, fat, soft-skinned, with stumps of legs and without the long bristles in which the triungulin abdomen terminates. In this second stage they feed on plant matter, the more or less viscous soup of pollen and nectar which the host bee has prepared for its own offspring. The beetle larva grows steadily and molts two more times without changing shape. Finally, it leaves the nest, buries itself in the ground, and molts into the dormant form, the pseudopupa, in which it passes the winter. In the spring there is a further molt, producing a larval form similar to the second-stage larva, and a few days later the insect pupates. Four weeks thereafter, the adult beetle emerges, the culmination of a most complicated course of development!



◁ Ø Above: The male stag beetles (Ø *Lucanus cervus*) use their mandibles, enlarged into hard antlers, as a weapon in battles with rivals. The much shorter mandibles of the female (lower right in the picture) are also very strong; the beetles can bite with them so sharply that they cause bleeding wounds. Below: a forest dung beetle (*Geotrupes stercorarius*) is used as a means of transport by nymphs of the mite *Parasitus* (see Vol. I). In this way the mites move to a location favorable to their further development.

Hosts of the OIL BEETLE (*Meloe*; see Color plate, p. 236) include, among others, species of the bee genera *Halictus*, *Andrena* (mining bee), *Eucera* (long-horned bee), *Anthophora* (hairy flower bee), and *Osmia* and *Chalicodoma* (mason bees). Like the abovementioned *Trichodes* species larvae, many blister beetles (for example, species of the genera *Lytta*, *Apalus*, and *Zonitis*) seek out the earthen nests of the solitary bees. The SPANISHFLY (*Lytta vesicatoria*) undergoes its development in the nests of mason bees, leaf-cutter bees (*Megachile* spp.), and bee species of the genus *Colletes* and others; the *Apalus* and *Zonitis* species choose host bees both from the above genera and from *Andrena* and *Anthophora*. The larvae of some *Apalus* beetles hatch in autumn but remain clumped together under the egg shells during the winter. Since the eggs are laid in the nest tubes of the bees, contact with the host is assured; when the newly hatched bees crawl out of the nest in the spring, the beetle larvae cling to them.

Association with termites

Termites do not act as hosts to beetles as often as do the ants, and accordingly the number of "termitophilous" beetle species is much smaller than that of the myrmecophilous species. Beetles associated with termites include certain GROUND BEETLES (Carabidae), ROVE BEETLES (Staphylinidae), HISTER BEETLES (Histeridae), BROWN SCAVENGER BEETLES (Lathridiidae),

DARKLING BEETLES (Tenebrionidae), and DUNG BEETLES of the subfamily Aphodiinae. The different species feed either on the young stages and workers of the termites or on the plant debris or fungus gardens available in the nest. Like the beetles associating with ants, several of those found among termites offer their hosts special secretions to lick. In this case, too, the secretions may be accumulated in bundles of hair, or the termites may lap them up directly from the openings of the glands on the surface. Some of these staphylinids are fantastically shaped. For example, the anterior part of the body may be disc-shaped, as the generic names indicate (*Discoxenus*, *Termitodiscus*); the pronotum is enlarged and, together with the elytra, forms a protective shield under which the rest of the body can be hidden. Other species have a greatly swollen abdomen (the "physogastric" condition), sometimes covered with secondary swellings and paired limblike appendages. An even greater departure from normality is represented by the appearance of the staphylinids with the abdomen bent upward and forward over the back, held like a balloon over the body.

The associations between beetles and Hymenoptera or termites is in general more advantageous to the beetles than to the hosts. To be sure, the beetle frees its hosts from parasitic mites, but the host society pays for this by affording the guests a hospitable refuge and a steady food supply. A rather doubtful "advantage" for the host is the association with those beetles which offer glandular secretions, in return for which they receive not only a home but the "right" to prey on the young and steal from the food stores. Of course, the insect colony is not usually disrupted in any other way. On the other hand, some relationships are entirely one-sided—for example, in the case of beetle larvae which are carried to the nest by the host, and even protected while devouring the host's young. Some beetles are true parasites; that is, they live on or in the body of their hosts and feed on them without killing them directly. Such a relationship exists between the larvae of small staphylinid species of the genus *Aleochara* and flies, between the larvae of certain Rhipiphoridae and cockroaches, and between the larvae of species of the blister beetle genus *Cerocoma* and grasshoppers. How do these associations work out in practice, for the beetle larvae and their hosts?

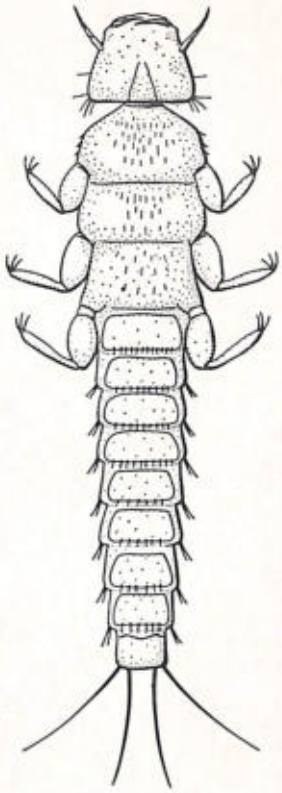


Fig. 13-13. The triungulin larva of an oil beetle (genus *Meloe*; L 0.5 mm).

Beetles as true parasites

In the case of *Aleochara* spp., the beetle larva wanders about searching for the puparia of flies; finding one, it enters and after feeding on the pupa for a time, it molts. The second larval stage is of quite different appearance, a grub with withered legs and antennae, and entirely without eyes. During the remainder of its larval development it eats up the rest of the fly pupa. Some *Aleochara* species molt again without a change in form before pupating, still inside the fly puparium. Other species leave the puparium and bury themselves in the earth to pupate; these change in form at the second molt, so that the third larval stage regains the eyes, antennae, and legs of the first stage.

The process is more complicated among the Rhipiphoridae, and is best

known in the case of the European *Rhipidius quadriceps*. Here the triungulin larvae hatch in summer and crawl about on the floor of the forest; when one of them encounters a newly hatched nymph of the wood cockroach *Ectobius* spp. (see Chapter 6), it clings tightly, working its way to a thoracic joint membrane or an equally thin place on the abdomen and holding itself there with the mandibles. After one or two days it bores a hole so that its entire head can penetrate and the beetle is partly inside and partly outside the roach larva. Within two to three weeks it has burrowed completely into the host, assisted to some extent by the movements of the roach; on the dorsal surface of the parasite's abdominal segments are posteriorly directed bristles, which presumably act as barbs. It often happens that several beetle larvae burrow into a single roach larva at one time. After the parasites have been at work within the host's body for a few days, usually in the abdomen, they molt to form a limbless, grublike larval stage which soon enters diapause. This dormant stage survives the whole winter within the living cockroach.

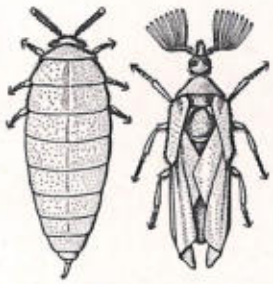


Fig. 13-14. Female (left) and male (right) of *Rhipidius quadriceps*, which develops as a parasite in wood cockroaches (L 5 mm).

In spring the next molt occurs, and now—surprisingly—this endoparasitic larva regains antennae, sensory palps, and legs. At this point the *R. quadriceps* larva begins to grow in earnest, and so does the roach. After one or two more months the beetle larva molts to produce the fourth stage, with even-better-defined limbs, and in three or four days it breaks open the end of the host's abdomen and emerges. This fourth-stage beetle looks for a suitable place for pupation: a crack in the bark of a tree, a leaf lying on the ground, or a similarly secluded spot. In May and June the adult beetles emerge, the female wingless and very like a larva, the male with elytra gaping widely to leave the hindwings free. The female rapidly swells up until she resembles an egg-filled sack; the 1500–2200 eggs are laid shortly after copulation. Neither sex feeds in any way, and both die within four days. The closely related *Rhipidius pectinicornis* develops very similarly within the cockroach *Blatella germanica* (see Chapter 6); both species are distributed throughout the world.

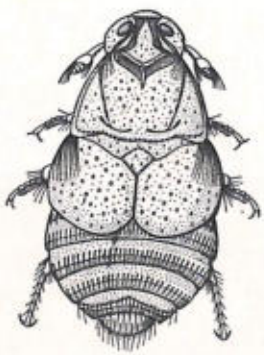


Fig. 13-15. The name "beaver louse" for this beetle, *Platypsyllus castoris* (L 2.5 mm), is misleading; it does not parasitize the beavers, but rather frees them from parasitic mites.

The third example of true parasitism among beetles is the blister beetle species of the genus *Cerocoma*; it marks a transition to what might be called "food parasitism." The triungulin larvae of *Cerocoma* sp. burrow into the bodies of grasshoppers and develop there; they do not find the grasshoppers in the open, but rather in the tubes dug in the earth by wasp species of the genus *Tachytes*. The wasps drag grasshoppers into the nest, still alive but paralyzed by a sting, and lay eggs next to them. The grasshoppers are meant as a food store for the larvae of the wasp, but the beetle larvae share the benefit.

This sort of "cuckoo" behavior appears even more clearly in the SNOUT BEETLE (*Lasiorrhynchites sericeus*), which parasitizes the young of a somewhat smaller snout beetle, the oak-leaf-rolling weevil *Attelabus nitens*. Even as the female leaf roller works to curl up a leaf (see Fig. 13-18), the parasite flies up and attempts to lay eggs between its folds. If prevented

from doing this, it later drills into the finished roll and lays its eggs in the holes. These eggs are larger than those of the host. The larvae of both species feed on the dried tissue of the leaf roll.

There are no beetles living as true parasites on vertebrates, although it was long thought that there were. The small, pale yellow beetle species of the genus *Leptinus* have often been found in the pelts of mice and were therefore thought to be parasitic on rodents. But it has been known for some time that these little blind beetles are simply residents of the nests of small mammals, and only accidentally get into their fur. Occasionally the beetle remains when the host leaves its home. Another species of beetle, *Platypsyllus castoris* (see Fig. 13-15), seemed even more clearly to be a mammalian parasite like fleas or lice, and for that reason was called the "beaver louse," an interpretation supported by its appearance. These 2–3-mm-long, greatly flattened animals and their larvae do live on beavers, but they are hunters. Their prey are the mites which occur only on beavers, preferentially in the corners of the mouth, the external ear, and the genital area—and that is where the beetles are also found. Up to forty "beaver lice" have been found on a single beaver. The beetle lives on both European and Canadian beavers. An Australian species of beetle is highly adapted to life on mammals, also in an unsuual way; *Macropocopris symbioticus* (L 4–5 mm), of the family Scarabaeidae, is often found in the anus of the wallaby (a small to medium-sized kangaroo; see Vol. X), where it feeds on the feces. Its closest relatives are the widespread dung beetle species of the genus *Onthophagus*.

Reproduction

The average number of eggs laid by a female beetle in her lifetime ranges from six or eight to 10,000. This does not mean that small numbers of eggs are always laid by small beetles and vice versa. Rather, there is a relationship between the number of eggs and the location where they are laid (and thus also to the prospects for larval development after hatching). Eggs deposited in the open are much more vulnerable to predators, parasites, and environmental influences such as the weather, than those laid in sheltered hiding places. Therefore preservation of the species can be ensured in the first case only by providing eggs in great numbers. Conversely, fewer eggs are necessary if they are laid directly in the feeding place of the future larvae, and more if it is a matter of chance whether a young larva will ever find the place where it is to carry out its development, as is the case for the blister beetles. Furthermore, the mortality rate is usually higher for the younger larval stages than for the more advanced, and this effect is again more marked among larvae which live in the open than among hidden larvae. Among the most important of these factors is temperature, which acts both on the state of the female (the degree of activity and life span) and on the day-to-day opportunities for egg laying. Amount and quality of food also play a role, even in the larval stages of short-lived forms, and in the adults of longer-lived species. Malnourished larvae become feeble beetles, and females unable to find a sufficient food

supply produce fewer eggs than their sisters which have eaten their fill.

Provision of food and shelter for the young

In laying their eggs in some sort of hiding place, or directly at a source of larval food, female beetles perform a type of "brood care." This behavior is developed in various ways by different beetles, ranging from rather simple actions to quite complicated procedures. If the female goes so far as to watch over the eggs until the larvae emerge, or if the parents remain with the young while they grow up, they have reached the level of true brood care; some examples will be described later. At all levels, the behavior is instinctive (or inborn) and is released automatically by certain key stimuli.

The eggs are given some protection if they are buried in plant tissue by the female or pushed under scales or into crevices in bark. Other beetle species bury their eggs in the ground, singly or in groups, or they place them in holes or cracks in the earth which they then plug up. Another protective measure is to cover or encase the egg(s) with excrement or glandular secretions. Sometimes the fecal pellets are glued onto the eggs by secretions. TORTOISE BEETLES (subfamily Cassidinae; see Color plate, p. 225) are true masters in the construction of camouflage coatings for their eggs, making them blend into the background or look like natural irregularities on a plant stalk, or droppings or galls on a leaf. Some of the many tortoise beetle species of the genus *Aspidomorpha* produce stalked packets of eggs which hang down from the undersides of leaves in a way reminiscent of the egg capsules of the mantids (see Chapter 6). Protective cases for single eggs are also made by many other LEAF BEETLES (Chrysomelidae) which glue small fecal particles to the shell in a densely packed array. The external appearance of such structures, in general resembling tiny pine cones or seeds, is characteristic of each species. Eggs equipped with these fecal cases (scatoconches) may be fastened singly or in groups directly to the substrate or suspended by a thread. In some leaf beetles (the subfamily Clytrinae and the genus *Cryptocephalus*) the fecal coating is carried along for protection by the newly hatched larva, which enlarges the case as it grows by cementing bits of soil and new fecal pellets into place. The larvae of the leaf beetle *Clytra* spp., which grow up in the nests of the red ant, could not survive without their protective sacks.

Another kind of shelter for the eggs is used by the European leaf beetle *Pyrrhalta viburni* and the North American *P. luteola* (on elm). The female gnaws a row of holes in a viburnum twig, one under the other, extending into the pith. In each of these she lays three to eight eggs, and then closes them in with a special cover consisting of her own excrement and chewed-out splinters of wood, all held together by a glandular secretion which becomes very hard. One female can make up to ninety nests, spending two to three hours on each one.

AQUATIC BEETLES of the families Hydraenidae and Hydrophilidae also make protective cases for their eggs. They use threads of silk produced by a special arrangement of glands at the end of the female's abdomen. The actual spinning is done by an organ of complex construction, which is

very movable and can be pushed far out from the abdomen. Beetle species of the genus *Hydraena* weave quite simple egg covers, amounting to a dense layer of threads. And the threads of the *Ochthebius* species, laid loose over the eggs, can hardly be considered as woven at all. By contrast, many aquatic species build proper containers for the eggs. Females of the TURNIP they MUD BEETLE (*Helophorus* spp.) spin a long, bottle-shaped cocoon which hide in moss or under algae. The egg-holder of *Laccobius* species is round and bears a silken flag. Females of *Enochrus* species use roots of duckweed or threads of algae to build their cocoons, and other beetles fasten the containers to the undersides of water plants drifting on the surface.

The most elaborate containers are made by WATER SCAVENGER BEETLES, the small species of *Hydrophilus* and the larger species of *Tropisternus* and *Hydrous*. The females spin a cocoon that looks like a ship, with a slender "smokestack" to let air in. Such a ship, up to 2 cm long depending on the species, is fastened to the underside of a floating leaf, covered with duckweed, or anchored to an aquatic plant by silken threads. But in all cases the smokestack extends into the air. In the "hold" of the ship are the eggs, arranged in rows; those of the European species number about fifty, while North American species place up to 100 in each vessel. Over the eggs is a layer of wadding, continued in the upper part of the container into a loose, airy tissue. Because of this manner of construction, the center of gravity of the ship is low, preventing it from overturning. It takes the beetle about three hours to build such a cocoon.

Another factor in brood care is the placing of the eggs in the immediate vicinity of, or directly upon, the material which will feed the future larvae. Often this is accomplished by very simple means, but it can require quite involved operations. The simplest solution is to lay the eggs on or in the food eaten by the mature beetles. Many beetles feeding on plants, in particular the LEAF BEETLES (Chrysomelidae), lay their eggs on their own food plants. Usually they are placed on the undersides of the leaves, either glued on without protection (sometimes side by side, forming a plate) or covered by a protective secretion; in some cases they may be buried in the tissue of the plant, occasionally even in a hole specially made for the purpose (as by the *Pyrrhalta* species discussed above). The same is true of numerous beetles which feed on fungus and mold; they lay their eggs on exposed layers of mold, in moldy hay or fallen leaves, or under bark. A similar behavior is found in species living in dung.

When eggs are laid in holes in stems, buds, fruits, or seeds, the larvae remain in this protective cavity after hatching, eating the plant tissues which surround them or chewing out a tunnel along which they progress. *Meligethes aenus* (see Color plate, p. 235) inserts one egg each into the still-closed flower buds of the rape plant. Better known are the HAZELNUT WEEVIL *Curculio neocorylus* (see Color plate, p. 277) and the COTTON BOLL WEEVIL (*Anthonomus grandis*); these lay their eggs in the young, soft hazelnuts and in the small flower buds of cotton, respectively. Other weevils

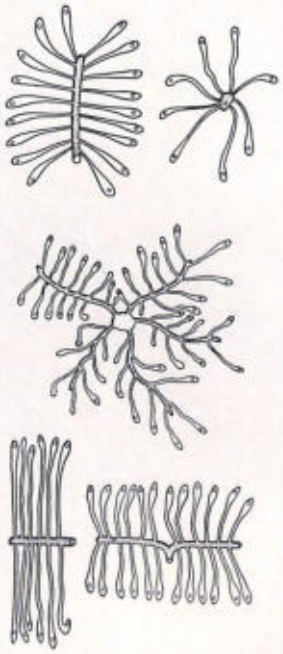


Fig. 13-16. Types of brood structures built by various species of bark beetles (family Scolytidae); egg galleries dotted, larval galleries not shaded.

burrow into apples and pears before they are ripe, and still others, into cherries and other fruits.

Besides the simple cavities produced for protection of the eggs and larvae, tunnels of various shapes are made—even branching tunnels such as those of the ENGRAVER BEETLES (Scolytidae). A female engraver beetle, after being inseminated on the surface of a tree trunk, spends hours boring into the bark. Just beneath the bark the female gnaws out a central passage and a number of small niches, in each of which an egg is laid (see Color plate, p. 276). She first produces an entrance channel which usually rises slightly as it proceeds inward, and in general passes all the way through the bark. In many cases it is the male that selects a suitable (usually sickly) tree for his brood and burrows into it, After entering, he builds a larger chamber in which two or more females gather. In these species copulation occurs here, and then each female bores her own tunnel, branching away from the nuptial chamber, and lays her eggs in it. The length of these egg galleries varies from species to species, with a mean value characteristic of each species. It is influenced by the physical state of the female, the condition of the wood, the weather, the population density, and other things. The females of some species dig tunnels 50–60 cm in length. The arrangement of the egg chambers is characteristic of each species, as is that of the extensions made later by the larvae as they eat. Foresters can tell from these patterns alone which scolytid species is involved, without ever seeing the animals.

A still-higher form of brood care has been achieved by the beetles which both construct protective chambers for their offspring, and in some way, ensure a food supply. For example, this may be accomplished by interrupting the supply of sap to the healthy parts of the food plant selected for egg deposition. As a result, these parts usually die and may dry out rapidly, becoming both shelter and suitable fodder for the larvae. Other beetles dig galleries or systems of galleries in the earth and then carry food into them for the future larvae. The first group (those which cause parts of plants to dry up) includes primarily SNOUT BEETLES (Curculionidae) and some LONG-HORNED BEETLES (Cerambycidae); the second group (those which provision galleries) includes predominantly LAMELLICORN BEETLES (Scarabaeidae) and a few ROVE BEETLES (Staphylinidae).

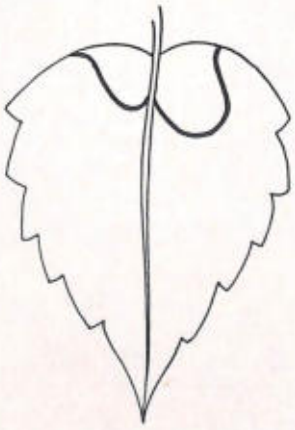


Fig. 13-17. The birch-leaf roller *Deporaus betulae* begins by making two cuts (dark curves) in a leaf, the lower parts of which are then rolled together into a funnel (see Color plate, p. 265).

The SNOUT BEETLES of this type prefer tender, juicy tissues like those of flower and leaf buds, the tips of young shoots, fruits at an early stage of development, and young leaves. For example, female STRAWBERRY WEEVILS (*Anthonomus signatus*, subfamily Curculioninae) burrow into the flower buds of rosaceous plants like strawberries, raspberries, and blackberries, laying an egg in each bud. The stalk of the future flower is then gnawed almost in two, so that the blossom wilts and cannot open. Buds within which the larvae are developing hang from the stalks and eventually fall to the ground.

The following species, all of which use the first of these two brood-care

techniques, belong to the subfamily Rhynchitinae. Early in the spring, female weevils of the species *Coenorrhinus aeneovirens* burrow into the point of attachment of the leaf buds on deciduous trees, biting through the vascular bundle. The female gnaws a second hole below the tip of the bud; just inside its opening she lays an egg and then pushes it in deeper with the snout. Sometimes a third hole is drilled in the middle of the bud, to receive a second egg. Although the buds wilt, they do not fall off. Related species, such as *C. interpunctatus*, usually make a hole in the midrib at the base of a leaf of a rosaceous plant, so that the leaf curls up, wilts, and finally falls to earth. When the larvae hatch, they burrow in the midrib. Other species of *Coenorrhinus*, as well as of *Rhynchites*, seek out the young shoots of various trees, gnaw holes extending into the pith at several points, insert an egg into each, and then cut through the shoot, beneath the lowest egg hole, so that only a thin fiber remains. Naturally, these heavily damaged shoots wilt and are eventually torn off by the wind; the developing larvae burrow in the pith. Still other species of these two genera attack young, developing fruits of certain trees; one Mediterranean species (*Coenorrhinus cribripennis*) specializes in the fruit of the olive tree. The females of these fruit weevils lay eggs 1–4 mm deep in the fruit and then chew almost through its stem. After a while, the fruit falls to the ground, and it is then that the larva hatches and feeds on the drying fruit. Some related weevils, such as the North American *Coenorrhinus bicolor*, proceed differently; they lay several eggs in a single fruit, sealing the holes with a plug of glandular secretion, but do not bite the stem. Nevertheless, the injury to such fruits is sufficient that they, too, dry up.

These examples illustrate four types of egg placement by the piercing of holes: in buds, leaf ribs, young shoots, and fruits. A different sort of behavior is shown by the LEAF-ROLLING WEEVILS. Each of them rolls up leaves in a certain, species-specific manner, having prepared the leaves either by notching the stem or the main rib, or by cutting into the vane of the leaf. The leaf rolls thus produced house the eggs. By the time the larvae hatch, the leaf tissue is drying up and serves as food. The precision with which the female leaf-rolling weevils carry out their task is striking. They cut into the stem, not just anywhere, but at a quite specific point, and their cuts across the vane of the leaf are not positioned at random, but follow the only possible course—sometimes a complex curve—which will allow subsequent rolling of the leaf. One receives the impression that each of the cutting and rolling activities is worked out carefully in advance, according to a predetermined program. These achievements of instinct are among the most highly developed in any of the beetles. The males of these weevils lack such instincts. Leaf rollers belong to the subfamily Rhynchitinae and to the two related subfamilies Attelabinae and Apoderinae. There are two main techniques: "longitudinal" rollers use the midrib as an axis around which the leaf is rolled like a cornucopia, while "transverse" rollers separate the vane of the leaf and roll it up with the axis perpendicular to

▻ Above: *Chilomenes lunata*, a lady beetle (family Coccinellidae) from southern and eastern Africa, laying eggs. Below: the large firefly *Lampyris noctiluca*; the small winged male is inseminating the larger, wingless female (left); the larva (right) is attacking a snail (see Vol. III).

▻▻ The passages made by a bark beetle (family Scolytidae) with white larvae (exposed by removal of the bark).

▻▻▻ Above: yellow-striped flea beetles (*Phyllotreta nemorum*) on a cabbage leaf almost destroyed by the beetles. Center: the female of the hazelnut weevil *Curculio neocorylus* deposits her eggs in young, still-soft hazelnuts. The larva hollows out the nut and fills it with its feces, then leaves the nut through a large drilled hole and pupates in the ground. Below: *Acanthoscelides obtectus* (family Bruchidae), like many of its relatives, has become a "storehouse pest," because humans, by accumulating stores of food, made available unusually favorable living conditions.



















the midrib, producing a cylindrical or barrel-shaped roll. In both groups there are species which roll the leaf without making any initial cuts, and others which always begin the work by cutting.

An example of the longitudinal rollers which do not cut the leaf is *Byctiscus betulae*, a metallic green or blue beetle 6–9 mm long. In Europe and Asia it prefers grapevines for egg deposition, but it also makes use of beeches, hazelnut trees, poplars, lindens, willows, and fruit trees. First, the female gnaws a hole in the petiole, near the twig, and then leaves the leaf alone for a while. Soon it is sagging limply, and the upper surface begins to fold in around the main vein, so that the edges of this surface come closer and closer together. After three to four hours, the leaf is sufficiently wilted that the beetle can begin the actual work of rolling it up. The two halves are twisted irregularly around one another, the underside always outward, until a loosely rolled cigar-shaped structure results. A sticky substance produced by a gland at the end of the abdomen is applied to the folds and edges of the leaf, to glue the roll together. The four to fifteen eggs are either laid during the rolling process, in the spaces between the layers of leaf, or else the female makes holes after the container is completed and pushes the eggs into them. Sometimes, when several leaves hang close together as on a beech or pear tree, she works them all into a single roll. If many such weevils attack a vineyard, the plants are appreciably weakened.

In contrast to this weevil, the European and Siberian *Deporaus betulae* (L 3–4 mm; see Color plate, p. 265, and Fig. 13-17) is a longitudinal roller which begins by cutting the leaf. This black beetle is also not confined to its main breeding tree, the birch, but works with beech, hornbeam, alder, and hazel leaves as well. In sunny weather, the female makes a sharply curving S-shaped cut in the top part of the leaf vane, beginning at the edge and proceeding to the midrib. The opening of the first curve of the S is always facing away from the midrib, and that of the second, facing toward it. Now the rib is given a slanting notch at the point where the cut meets it. After that the second cut is made, from the midrib to the opposite edge of the leaf; this is also S-shaped, but the curves are much more gradual. As soon as she is finished, she rolls up the part of the leaf separated by the first cut like a funnel, with the underside inward; then the other separated section is rolled around this, with the upper side inward. The next step is to lay the eggs. The female chews out two to five small pockets in the leaf tissue inside the roll, and each of these receives an egg. Then she pulls down the tip of the outside funnel and fastens it by pushing it through several layers of leaf with her snout. Finally, she closes the opening of the funnel, which hangs downward, by covering it with the unused portion of the leaf. After about an hour the structure is complete.

The "transverse" rollers, on the other hand, roll the leaf up from the tip. The "cylinder rolling" types manage to do this without making a preparatory cut; an example of these is the Japanese weevil *Taiwanobyc-*

◁ Leaf beetles (family Chrysomelidae) in copulation. Above: A large poplar-leaf beetle (*Melasoma populi*). Below: *Chrysomela varaians*.

tiscus paviei. The female rolls up the whole leaf, beginning at the tip and stopping just short of the petiole. First she makes several notches in the midrib and the lateral veins, so that they bend more readily. Among those species which do make a cut first, some make it only on one side of the vane, either straight or curved. These weevils are almost all representatives of the subfamily Apoderinae. The best-known is *Apoderus coryli*, a little (L 4–6 mm) black and red beetle, distributed from northern China across Siberia as far as western Europe. The female constructs her rolls primarily of hazel leaves, but she also may use those of alders, beeches, hornbeams, aspens, or oaks. But to meet the requirements of this beetle the trees must always be shrublike. The female begins her cut not far from the petiole and continues it in an irregular arc to the midrib. Then she chews all the way through the rib and carries the cut a bit further into the other half of the leaf. Now she makes several notches in the thicker end of the cut-off section of midrib, as well as in the thicker lateral veins. Meanwhile, the leaf has become wilted and limp. The part of the vane hanging loose is folded over onto the other part, still connected with the petiole, and the two are rolled up together, beginning at the tip of the leaf. Now and then the female folds in a part of the edge which stickes out, thus closing the roll at one end. The other end is closed almost automatically by the remaining part of the leaf. While rolling, the female lays two to four eggs at the lower end of the innermost layers. Finally, she connects the outer layers of the roll by boring holes through them; the jagged edges of the top layers are pushed through the openings below, providing an effective attachment.

A somewhat similar technique is used by those transverse rollers that make a cut on two sides rather than just one. They bite all the way across the leaf at a certain spot, leaving only the midrib intact. Species of the subfamily Attelabinae proceed in this way. The OAK-LEAF-ROLLING WEEVIL (*Attelabus nitens*; see Fig. 13-18) is found throughout Europe, in Turkey, and in northern Asia. The females seek out leaves in oak shrubbery or on low-hanging branches of slightly older trees. Occasionally they work with leaves of alder and European chestnut. The beetle begins its task in the upper third of the leaf, by making a straight cut from the edge to the midrib. Then it moves to the opposite edge and from there, at just the same level, bites out a second cut toward the midline, where the two cuts usually meet. Now the beetle makes a notch in the rib itself, slightly toward the stalk from the place where the two cuts meet, and then makes a number of notches in the thicker parts of the midrib and lateral veins. Meanwhile, the end section of the leaf has become limp and easy to work with; the beetle folds it in half along the midrib. To do this, the female goes to the tip of the leaf, takes up a position astride the midrib, and moves along it toward the cut; with every step she presses down the two halves of the leaf, and the closer she comes to the cut, the closer the halves approach one another, until finally they touch. The rolling is also begun

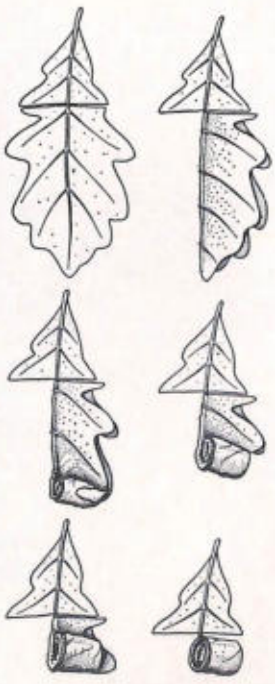


Fig. 13-18. Stages in roll construction by the oak-leaf-rolling weevil (*Attelabus nitens*).

from the tip of the leaf. The beetle lays up to seven eggs singly in the folds, without sticking them in place. Sometimes another, somewhat larger, weevil, *Lasiorrhynchites sericeus*, appears at this stage and, with the cuckoo-like behavior discussed previously, smuggles its eggs into the roll being made by *Attelabus* spp.

A second method of drying out the selected plant tissue has been developed by some weevils of the subfamily Mecininae and certain of the Cerambycidae. They "ring" branches or cut curved lines in the bark. In Africa, the weevil *Alcidodes brevirostris* attacks cotton plants, chewing a deep groove all around the stem, or, on larger plants, the branches. The part of the plant above the wound dies and later falls over, under its own weight or blown by the wind. After ringing the plant, the female bores one or more holes into the wood, and in each she lays one egg. The larvae develop inside the dead piece of plant.

Among the long-horned beetles, species of the New World genus *Oncideres* (average L 2.5 cm) have become notorious for ringing the branches of cultivated trees. These beetles bite the bark off piece by piece. Usually they also gnaw out a more or less thick layer of wood. Some species are satisfied to make a groove passing only half or three-quarters of the way around the branch, but others encircle it completely. In any case, the ringed part of the twig dies. The female lays between three and forty eggs there, each in its own specially made hole in the bark. Usually she closes the openings afterward with a rubberlike mass; this is done, for example, by the North American fruit-tree pest *Oncideres cingulatus*. In general, the beetles avoid the thinnest twigs; branches 3–5 cm thick are bitten into so deeply that sooner or later they break off. In Brazil, *Oncideres dejeani* actually manages to kill eucalyptus and acacia branches 12 cm in diameter.

Whereas the larvae of all the above species develop in the drying part of the plant, those of the European hazel longhorn *Oberea linearis* live in the remaining, living part. The females of this species do ring the young shoot selected on a hazel bush (or less commonly on a walnut or linden tree), but the circumferential cut is made toward the end of the shoot from the place where the eggs are deposited, not proximal to it as with the previously mentioned species. Furthermore, the female performs the ringing operation only after the egg has been laid. She drills a hole in the bark with her ovipositor and pushes the egg between it and the wood. The bark covering the egg later wilts, but below it are formed swellings of wound tissue which completely surround the egg. This tissue may well be the first food of the newly hatched larva, which later burrows up through the wood to the ring made by its parent. Although this beetle does cause parts of the plant to die off, the wound in the bark acts as a stimulus for the growth of new tissue.

The production of pathological plant growth plays a much greater role in the behavior of the poplar longhorn *Saperda calcarata* (L up to 1.5 cm).

The main brood tree of this beetle is the poplar, but its larvae thrive in the branches of other species of the willow family. Its range of distribution is large, from Siberia through Turkey to western Europe, and northern North America. As soon as a female of this species has found a favorable place for egg deposition, she stands head-down at this spot and bites a few superficial grooves crossways in the bark; below them, she makes a deeper hole, extending into the sapwood. To the left and right of the hole she digs out a curved furrow leading upward. These, together with the hole, make a horseshoe-shaped figure, half framed by the cross grooves made at the start. Sometimes the beetle proceeds to make still more cross grooves within the semicircle; if not, she lays an egg, positioning herself head-upward and putting the ovipositor in the hole so that the egg rests in a small cavity deep under the bark. To make one such brood chamber requires about half an hour; once it is finished, the female begins on the next.

The egg in the hole is at first pressed flat under the bark. In the next few hours the space around it gradually increases, for the furrowed bark over it loses its turgor and the horseshoe-shaped groove reduces the transport of fluids to the area. At the same time, the fluids discolor the walls of the egg cavity, changing it from yellowish-white or greenish-white to brown and then to black. After about two days the full effect of the wound becomes apparent. The plant tissue begins to grow like a tumor, pushing toward the egg on all sides. This raises the bark over the egg so that a swelling is visible from outside. When the weather is warm and dry, the tumors grow more slowly and the beetle larva develops more rapidly; in cool, damp weather the situation is reversed. Thus there is a sort of competition between the tumor growth and the egg or larva of the beetle. If conditions are favorable the rate of development of the embryo and growth of the larva are great enough that the larva can eat up the plant tissue—the only available food—before so much has formed that it suffocates or squeezes the young beetle to death. Later, the larva burrows between the phloem tissue and the sapwood, and enters the tubes in the pith for pupation.

A quite different group of beetles which provide food for their young is those species which dig galleries in the earth for the eggs. In this case food is brought to the brood place, while in all cases previously discussed the brood (as an egg) is brought to the food. These beetles use both fresh plant materials and dead plant and animal substances as food. Fresh plants are employed, for example, by ROVE BEETLE species of the genus *Bledius*, the LAMELLICORN *Lethrus apterus*, and some UNICORN BEETLES (Dynastinae); dead plants are imported by many coprophagous (dung-eating) scarabaeids of the subfamilies Coprinae and Geotrupinae, while other members of the Coprinae bring dead animal remains to the brood hole.

Almost all of the species of *Bledius* beetles live in sandy strips of shore directly adjacent to the water, whether on seacoasts, lakes, rivers, or brooks. Many prefer clay or loam, so that some of these 3–8-mm long beetles are also to be found on the edges of the puddles in clay pits. All of

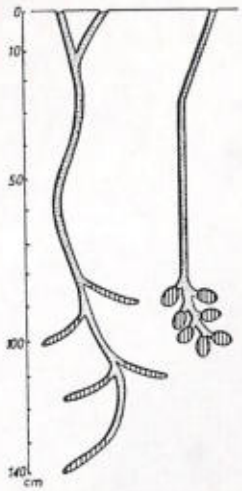


Fig. 13-19. System of brood tunnels of *Typhoeus typhoeus* (left) and *Lethrus apterus* (right). The tunnels are dotted and the brood chambers filled with dung, cross-hatched; the egg chambers lie outside the brood chambers.

them build tubes to live in—straight or bent, narrow or enlarged, simple or multiple tunnels extending in some cases as much as 50 cm down. The food of these staphylinids consists of living blue algae (as, for example, in species of *Oscillatoria* and *Anabaena*) or green algae (*Oocystis*, *Ankistrodesmus*, *Tribonema*) growing on single grains of sand in the damp layer just beneath the soil surface. These algae are collected by the beetles and stored along the walls of the galleries or in special storerooms, where the young larvae find them. The larvae of some species, such as *Bledius arenarius*, must do the searching themselves, for the mother beetle has simply laid the eggs in sand rich in algae. On the other hand, the female of *B. fuscipes* deposits her eggs on a pile of algae in an egg chamber; after hatching, the larvae fall right into their food.

Lethrus apterus brings fresh bits of plants to its tubes, which can be as much as 1 m deep. This beetle shapes leaves, buds, and shoots into a little ball for the larvae; the plant matter may come from grapevines, rape, hemp, spurge, sunflowers, tulips, wheat, or other plants. The male gathers the food and hangs it over to the female in the tunnel; she carries it down to the terminal chambers of the lowest "side galleries." These side galleries are found only at levels below 80 cm. Beginning at the bottom, the beetles construct them in sequence, each being built after the preceding one has been filled and closed. Each side gallery terminates in an oval chamber about the size of a pigeon's egg, just behind the wall of which there is a small chamber where the female lays an egg. Then she packs the larger chamber with plant material, bit by bit, pushing it in until the chamber is quite full. Thereupon she plugs up the lateral gallery with dirt, and begins on the next. Altogether, she does this six to eleven times. The food pellet ferments, increasing its nutritive value.

The South American RHINOCEROS BEETLE (*Diloboderus abderus*) digs only a short, slanting tunnel barely 20 cm long, adjoined by a horizontal chamber. This brood chamber is filled up with fresh, green plant materials, usually young leaves and tender stalks of grass, which are then pressed together. After filling it, the female distributes five to seven eggs regularly throughout the ball of food, which is just sufficient to feed the young larvae. When the ball of food has been consumed, the larvae crawl out of the tunnel and feed on plant roots. Other South American rhinoceros beetles fill cavities in tree trunks, up to the size of a human fist, with small bits of wood on which the young larvae later feed. The OX BEETLE (*Strategus antaeus*) of eastern North America makes a chamber about 12 cm long, reached by a tunnel descending for 20 cm, into which it carries an enormous quantity of bits of rotting oak leaves. It lays only a single egg in the middle of this mass of leaves.

A quite unusual location for the construction of brood places has been chosen by the Brazilian *Choeridium granigerum*. This beetle finds its way into the subterranean structures of leaf-cutting species of ants of the genus *Atta* (see Chapter 18), and in the oldest (lowest) refuse chambers it dis-

covers food, consisting of rotted leaf mold. From the floor or side walls of such chambers the beetle digs out irregular passages, 10 to 12 cm long. Starting at the lower end, it fills up approximately half of each tunnel with finely shredded leaf remnants, and the rest is stuffed full of earth. One larva can develop in each tunnel. Sometimes the soil under large nests of leaf-cutting ants is penetrated by hundreds of such brood tunnels, made by a large number of beetles.

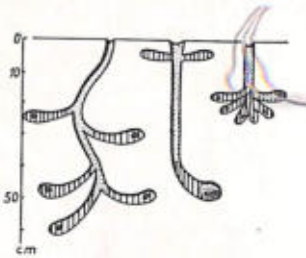


Fig. 13-20. System of brood tunnels of *Geotrupes stercorarius* (left), *G. vernalis* (middle), and *G. spiniger* (right); passages dotted, brood chambers filled with dung cross-hatched. The egg chambers are within the brood chambers.

The beetles last mentioned provide their larvae with plant materials which, though no longer fresh, have at least not been eaten previously by another animal. In contrast, many species of beetles live in the dung of herbivorous mammals, which of course consists of dead plant materials. Some species live in fresh dung and others in dung which is slightly or thoroughly dried. Certain beetles have arrived within the first twenty-four hours after the feces have been deposited; thirty-six hours later they have been replaced by others, and after a few days, by still others. Often several species may be found simultaneously in the dung. Many of these, in particular the coprophagous scarabaeids, carry out brood care. They bring pieces or prepared pellets of dung into specially constructed tunnels, either filling up the brood chambers completely with dung, like a sausage skin filled with ground meat, or fashioning it into egg-shaped or pear-shaped balls for their young.

The subterranean structures and systems of galleries of the various species hardly ever resemble one another. Even within one genus the structural forms are variable and characteristic of each species. Like the previously mentioned *Lethrus apterus*, the beetles living on dung usually dig out a main gallery from which several lateral galleries branch off; each lateral gallery terminates in a brood chamber. Sometimes the lateral galleries themselves are branched or are so long that there can be several brood chambers leading off from them. Many species make only a simple, unbranched tunnel, at the end of which there is a single brood chamber.

Remarkable achievements in digging are made by the New World dung beetle *Peltotropes youngi*, from the southeastern U.S.A.; its tunnels extend down for over 2 m. The THREE-HORNED DOR BEETLE (*Typhoeus typhoeus*; see Color plate, p. 249), which occurs in central and western Europe and the most northern part of Morocco, is an equally skilled digger. In this species, the two parents work together to make a gallery up to 1.5 m deep (see Fig. 13-19). These are constructed exclusively in sandy soil, particularly in moorland where spruce or pine trees grow. With the female working inside the nest and the male outside, the brood galleries are provisioned with the dung of rabbits, sheep, or red deer. The egg is not laid in the food store, but rather outside the lateral gallery, a few centimeters away from the wall closing it off. Species of the dung beetle genus *Geotrupes* also dig deep tunnels; in the western Asian and European *Geotrupes stercorarius* they are up to 65 cm deep (see Fig. 13-20). In the course of making these tunnels, a single pair can in its lifetime bury a quite considerable quantity of dung

—for example, in *Geotrupes spiniger* it amounts to 2000 times its body weight. The females of this and related species lay their eggs in small chambers built within the food matrix. The same behavior has been observed in species of the genus *Onthophagus*, the many species of which are distributed worldwide. The pellets of dung prepared by these small beetles are not clublike or sausage-shaped like those of the other Geotrupinae, but rather form rounded or oval balls which fill up the whole brood chamber. According to the body size of the different species, the length of these brood pellets ranges from 8 to 30 mm, and their volume is between 1 and 4 cc.

A rather more elaborate method of producing food balls is displayed by those coprophagous scarabaeids which knead a bit of feces into a sphere while still above ground, then roll it with them for a while and bury it in a suitable place. Thus the galleries of these beetles (subfamily Coprinae) have only one brood chamber each. In this chamber the sphere is molded into its final shape, sometimes becoming pear-shaped. In the upper part of this "pear" there is an egg chamber, narrow in some species and spacious in others, where the egg lies, stands, or hangs from the roof (see Fig. 13-21). Usually this egg chamber emphasizes the pearlike shape of the ball. Some species surround the ball with a coating of earth, which hardens. The brood chamber is usually large enough that the beetle has room to climb about on the ball. It appears that a few species do not bury their brood pellets but rather leave them lying on the surface; one of these is the slender South American *Eurysternus plebeius* (L 8–10 mm). In other species, the initial ball is not always large enough to make a brood pellet, so the beetle (for example, *Copris* spp.; see Color plate, p. 249) must go in and out several times until enough dung has been collected in the chamber.

In the New World genus *Phanaeus* (see Color plate, p. 246), many species of which are brightly colored, the passages extend down into the earth for 50–60 cm, and are usually formed by pressing soil to the side, forming the walls of the tunnel. The brood chamber is about as large as a small orange, and the dung pellet is 4 cm high. Some *Phanaeus* species coat their pellets with a 10-mm-thick layer of clay, leaving at the upper pole a small, flat cupola consisting of a layer of loosely piled fibers, permeable to air.

Especially famed are the dung beetles which roll their spherical dung balls along with them; the best-known species belong to the genus *Scarabaeus* and include the SACRED SCARAB (*Scarabaeus sacer*). Before starting on their travels, these animals must make certain that the ball will roll readily; no egg is placed in it at this stage. Once the ball has arrived in the brood chamber, its form is modified and an egg chamber is built into it, but this is done to only some of the balls—the others remain spherical and are left as food for the grown-up beetle. These food pellets consist of less carefully selected materials than the pellets containing eggs. The tasks of foraging

Transition to true brood care

In many cases the activities of the parents, and in particular of the mother, go beyond simply laying the eggs in a protected position and providing food for the larvae. Such beetles do not leave the brood area but rather stay with the brood, sometimes until the larvae have grown up. In what is probably the simplest case, the female watches over the eggs until the larvae have hatched. For example, some aquatic beetles carry the eggs about with them; the female *Helochares maculicollis* (family Hydrophilidae) covers the underside of her abdomen with a layer of threads and attaches the egg sack to it. This is a time-consuming process, in which the thirty-five to forty eggs are individually positioned in a specific sequence. Finally, the female covers the whole arrangement with another thick layer of threads. A similar egg-holder, in the form of a little basket, is made by the females of the European water beetle *Spercheus emarginatus*. It is anchored to the backs of the hindleg femora, and when it has been filled with about sixty eggs it is closed and then held with the hind tibiae until the larvae hatch. In an aquarium, one female produced six such cocoons within two months.

Among the terrestrial beetles, TORTOISE BEETLES (Cassidinae) have an effective way of watching over their eggs: they simply sit on them. This sort of behavior has been known for some time in the South American tortoise beetle *Selenis spinifex* (see Color plate, p. 255). The female bundles together about thirty eggs, each provided with a thread at one pole, to form something like an elongated bunch of grapes. This bundle is then attached to the midrib on the underside of a leaf, so that it hangs down. Then the female climbs onto her bundle and remains there. Mother tortoise beetles belonging to species of the South American genera *Omaspides* and *Neomphalia* are known to offer protection to the larvae as well, using their laterally broadened elytra as a shield. During the day, about a dozen larvae are gathered under this protective cover, with only the ends of their abdomens showing, and the few that cannot get in remain as close to the mother as possible, like chicks with the hen. During the hours of darkness they all go off hunting for food, and toward morning they gather again around the mother.

Other leaf beetles are not so constructed that they can offer shelter to the larvae, but they have their own ways of guarding them. In Europe and northern Asia there lives a small leaf beetle, *Gonioctena rufipes*, and in North America, *G. americana*, primarily on poplars. Twigs on which the leaves are just beginning to develop are chosen for egg-laying. Immediately after the eggs are laid, the larvae hatch; they stay together in groups while feeding. The mother stays on the twig below the feeding place, and when danger threatens she rocks her body from side to side. If ants, lady beetles, soldier beetles, or other enemies of the young larvae climb up the branch, the female presumably tries to chase them away. But after the second molt, the larvae are left alone.

Among the BARK BEETLES (Scolytidae), too, the females of several species

guard their young. A female sits at the entrance to the brood shelter, a hole drilled in the bark, which she plugs, as it were, with her body. But this is not the only brood-care behavior. These bark-beetle species usually brood in the sapwood; there the mother makes, besides the passages with the egg chambers, special larval passages on the walls of which she establishes fungus gardens. The tunnels of these species are directly within the wood, in contrast to those of the engraver beetles, which are in or just below the bark. Whereas the larvae of all bark-brooding species chew out their own passages, those of only a few of the wood-brooding species burrow for themselves, and their tunnels are very short. The food of wood-boring larvae is not wood, but the highly nutritious, spore-bearing parts of the fungi "planted" by the mother beetle. A fresh coating of fungus in the tunnels looks matte white, but in the course of time the tunnel walls turn deep black, and even the first millimeter of the adjacent wood becomes rather dark. When the females burrow into the wood, they bring the fungus along with them, in the form of spores. Some species have a brush of hairs on the front side of the head, where the fungus spores catch and are carried about. In some species they are found at certain places in the alimentary canal; they are brought to the outside either by vomiting or along with the feces. The spores are not digested by the beetles and thus can remain in the gut for months. Bark beetles even care for their fungus gardens, in part by "sowing" new spores when the coating has disappeared, and in part by eating up alien fungi, which spring up like weeds, and the bacteria and yeast colonies which would destroy the gardens. They also often remove the dust produced by their boring, to regulate the humidity in the passages and obtain fresh air, or they build barriers with it, to prevent drafts.

Females of another group of wood-brooding beetles, species of *Trypodendron*, even keep the passages clean by regularly carrying out the feces of the larvae. During copulation, the females of the European *Trypodendron lineatum* extend only the abdomen out of the entrance opening. The males ordinarily do not participate in the construction of the brood nest, but those of *T. signatum* carry the dust produced by boring out of the tunnel.

Species of the genus *Copris* (family Scarabaeidae) also show this highly developed brood-care behavior, in which the female performs certain services for the growing larvae. Both male and female cooperate in bringing a sufficient amount of dung into the prepared chamber (the crypt) underneath a pile of dung, and several spherical pellets are formed there. The chamber of the small *Copris lunaris* (see Color plate, p. 249), found in the southern parts of central Europe, is of impressive size—12–15 cm long and 6 cm high. Depending on the amount of dung brought in, the female kneads into shape six to ten, and occasionally as many as fifteen, pellets, all about the same size, and sets them in a row. The finished pellets are pear-shaped, the upper, smaller part being formed when the egg chamber is constructed and filled with an egg. After she has laid the eggs, the female

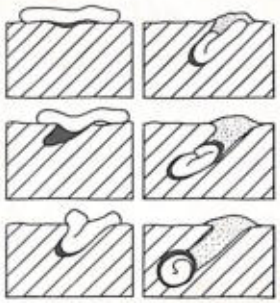


Fig. 13-22. In this way sexton beetles (*Nicrophorus vespillo*) bury animal corpses for their brood (schematic; cavity black, shifted earth dotted).

remains constantly in the brood chamber, repeatedly smoothing the surface of the pellets and removing any mold that may appear. The male is sometimes chased out of the chamber even before the brood pellets are prepared, but in many cases he is allowed to stay. The female does not leave the chamber until the young beetles crawl out, and then she goes with them. Other species build less spacious chambers, with fewer brood pellets.

Even a greater development of brood-care behavior is found in the SEXTON BEETLES (*Nicrophorus*; see Color plate, p. 225). Here the female beetle actually feeds the newly hatched larvae. This fascinating performance is carried out in a more or less rounded subterranean hollow, into which male and female together have brought a small animal corpse—an amphibian, reptile, bird, or mouse. The process of burying this animal takes about three to ten hours, depending on the nature of the soil. Even as they begin to dig, the beetles fold the animal together and as the slanting tunnel progresses, the compressed corpse is forced along it. By continually pushing against the corpse from all sides, the beetles shape it into a rounded mass. Finally, by the time the position selected for the brood chamber is reached, the corpse is almost a sphere. The final manipulations to make a completely round ball of carrion in the finished chamber are done by the female after the male has left.

The chambers of the small species of sexton beetles are 6–10 cm deep, while those of large forms like *Nicrophorus germanicus* (common to both Europe and North America) can be up to 60 cm deep. The female does not lay her eggs in or on the ball of carrion; but rather in small chambers in the earth; the female *N. vespillo* (also in Europe and North America) even digs a side tunnel leading away from the main chamber, and from there she pushes her eggs through the tunnel wall into the earth. When the young larvae come to the carrion, the mother beetle is sitting on it in a sort of funnel or crater she has made on top of the ball. She feeds on the ball by vomiting digestive juices which liquefy parts of the carrion so that it can be sucked in. With this liquid food, she feeds her young, drop by drop, as they crowd in front of her head. As the larvae grow older they become increasingly more capable of consuming the carrion independently. They are particularly dependent on feeding by the mother during the first hours after hatching and just after each molt.

Fossil beetles

The oldest fossil beetles known to us come from the Permian, and are thus around 280 to 230 million years old. But at that time, the end of the Paleozoic era, there were not yet many species of Coleoptera. The beetles really began to proliferate at the beginning of the Mesozoic era, increasing steadily through the Triassic period (about 225 million years ago) until the end of the Jurassic (about 180 million years ago). Most of the beetle species living then—to judge by the remnants of them which have survived—belonged to genera which have long since become extinct. But even then there were some representatives of present-day families: GROUND BEETLES

(Carabidae), WATER SCAVENGER BEETLES (Hydrophilidae), CLICK BEETLES (Elateridae), and METALIC WOODBORERS (Buprestidae). In subsequent epochs the number of species increased rapidly, and one more frequently finds fossils with the characteristics of genera of beetles alive today. Many of the fossil beetles from the Tertiary (65 to 2 million years ago) are embedded in amber or copal resin, so that the fine structure of the body can be studied in detail. For example, it has been established that some of the present-day species of TIGER BEETLES (family Cicindelidae) lived as much as 35 to 45 million years ago.

Good evidence has been presented recently to indicate that beetles and some Neuroptera are closely related and probably have common ancestors.

Classification of beetles

Traditionally the beetles are divided into two suborders, but recent studies indicate that four suborders are needed to provide a balanced classification. Of the 133 beetle families, only the most important can be treated briefly in the outline below. Other groups and species are listed in the Systematic Classification, and some of these are illustrated on the color plates on pages 215f., 225f., 235f., 245f., 255ff., and 275ff. The suborder Archostemata contains only one small family, the Cupedidae. The suborder Myxophaga contains four small families of rare fungus beetles.

Suborder: Adephaga

Suborder Adephaga (from the Greek *αδηφάγοζ* = voracious): The ventral plate (sternite) of the first visible abdominal segment is deeply indented to accommodate the coxae of the hindlegs, so that usually only the lateral parts of the sternite are to be seen. In the outer third of the hindwings there are cross veins between the longitudinal veins, forming at least one enclosed wing cell. These beetles are primarily carnivorous. There are ten families, including about nine percent of all beetles, of which the most important are as follows:

Families: Carabidae, Dytiscidae, and their relatives

1. The TIGER BEETLES (Cicindelidae; see Color plates, pp. 215, and 263) with fewer than 1400 species, are distributed throughout the world except for the cold regions. They are long-legged, usually agile, and quick to spring into flight. The elytra often bear vivid patterns. The larvae dig tubes for themselves in the ground, where they lie in wait for prey.

2. The GROUND BEETLES (Carabidae; see Color plates, pp. 215f. and 264) have recently been divided by some authors into several families; there are approximately 23,000 species, primarily in Asia, Europe, North America, and northern Africa, though many are also found in other regions of the world. They are 1 mm to 10 cm in length and quite variable in appearance, though usually black. Nimble runners, most of them are predatory; some live in holes and others frequent the nests of ants and termites. A few are vegetarian. More than 300 fossil species are known.

3. The PAUSSID BEETLES (Paussidae, of Carabidae) comprise 300 species found mainly in Africa, Madagascar, and Australia. Most are smaller than 10 mm. The upper body surface is smooth and brown, and the short antennae are peculiarly shaped. As associates of ants, they prey on the ant young.

▷ *Ascalaphus* (Ascalaphidae) is one of the most beautiful of Europe's Neuroptera.









The green lacewing *Chrysopa carnea* eagerly hunts aphids, both as a larva (above) and as an adult (below). Its eggs (below right) sit upon long, thin stalks.

4. The CRAWLING WATER BEETLES (Haliplidae) are at most 5 mm long. The 120 species are found in all parts of the earth. The body is boat-shaped with the hind coxae broadened into large plates. Both adults and larvae feed on aquatic plants, mainly green algae.

5. The PREDACEOUS DIVING BEETLES (Dytiscidae; see Color plates, pp. 216 and 264) are found primarily in the northern hemisphere, though a few of the 2500 species live in Australia. The hindlegs are flattened and equipped with hairs to facilitate swimming. The body often has the shape of a flattened disc. Only a few of these beetles are herbivorous; the rest are hunters, and the larvae have sucking pincers. One hundred and twenty fossil forms have been found.

6. The 450 species of WHIRLIGIG BEETLES (Gyrinidae; see Color plate, p. 216) are distributed worldwide; swarms of them often collect on the water surface, swimming in zig-zag paths past one another. The eyes are separated into distinct parts, and the forelegs are much elongated, while the other legs are shaped like paddles. Both larvae and adults are predators. There are about a dozen fossil species.

7. The WRINKLED BARK BEETLES (Rhysodidae), of which there are 150 species throughout the world, especially in southeastern Asia and South America, have slender bodies with the upper surface often rippled. The antennae are short, like strings of beads. Larvae and adults live in rotting wood or under bark.

Suborder: Polyphaga

Suborder Polyphaga (from the Greek πολύς = much or many, and φαγειν = to eat): The sternum of the first visible abdominal segment is not narrowed to accommodate the coxae of the hindlegs, so that its full width can be seen; the hindwings lack cross veins or, rarely, have one vein, but the veins never enclose a wing cell. About ninety percent of all beetles belong to this suborder, the 118 families of which may usefully be divided into several groups. We shall not discuss here whether any of these groups should be given the rank of superfamily.

Family: Hydraenidae, and its relatives

I. The group Palpicornia (see Color plate, p. 216) includes the two families of aquatic beetles: 1. the HYDRAENIDS (Hydraenidae), with 500 species, and 2. the WATER SCAVENGER BEETLES (Hydrophilidae), with 2000 species; many species of the latter family are terrestrial, feeding on dung, rotting plant materials, or fungi. There are about 100 fossil species.

Families: Silphidae, Staphylinidae, and their relatives

II. The group or superfamily Staphylinoidea includes many beetles with shortened elytra. Here we mention only some of the families:

1. The HISTER BEETLES (Histeridae; see Color plate, p. 225) comprise 4000 species of worldwide distribution. Predominantly bulky, short-legged forms which nevertheless are not slow-moving, they are predators, living in rotting materials such as dung, carrion, compost, decaying wood, under bark, and in some cases in ant and termite colonies.

2. The CARRION BEETLES (Silphidae; see Color plate, p. 225), with 600 species, are found mainly in the temperate zones of the northern hemi-

sphere. They are medium-sized beetles with short clavate antennae; the indentations for the coxae of the anterior legs are open toward the back. They feed primarily on carrion, but some species eat plants and are pests.

3. The SMALL CARRION BEETLES (Leptodiridae), including the cave dwellers (Bathycinae) which some scientists consider as a separate family, comprise about 550 species; they occupy all parts of the earth. These small, usually brown animals, with head narrowed to form a "neck," are found on animal corpses and fungi, in the nests of birds and mammals, and in some cases in ant colonies, while numerous species are specialized for living in caves (particularly those of the subfamily Bathyscinae; see Color plate, p. 225).

4. The ROUND CARRION BEETLES (Liodidae) comprise 600 species, found in all regions of the world. They are very small animals, strongly arched or even hemispherical in shape. They are associated with fungi (including subterranean types), particularly slime molds and moldy bark.

5. The STONE BEETLES (Scydmaenidae), with about 2500 species in all latitudes and climatic zones but especially in the northern hemisphere, are generally smaller than 2 mm. Both head and pronotum narrow toward the back. They are usually found in damp places such as rotting leaves, moss, and decaying trees; they probably hunt mites, and some species live among ants.

6. The FEATHER-WINGED BEETLES (Ptiliidae) are tiny insects, the 500 species of which are distributed throughout the world. The hindwings are very narrow with a fringed border. They feed on fungus spores, though a few species are found in the nests of mammals and in ant colonies.

7. The SHINING FUNGUS BEETLES (Scaphidiidae) comprise 300 species which live in all regions of the world. These are nimble animals, usually spindle-shaped with the end of the abdomen free, and almost all of them live on fungi.

8. The ROVE BEETLES (Staphylinidae; see Color plate, p. 225), with 28,000 species, are one of the few really large families. They are widespread, living even in the cooler regions. They are distinguished by the elytra, usually very short, and the elongated body. The abdomen is often bent upward. Most of the species, and their larvae, live as predators, many in anthills and some in the nests of termites. A few feed on plants. There are 200 fossil species.

9. The ANT-LOVING BEETLES (Pselaphidae; L 1–3 mm; see Color plate, p. 273) live in all parts of the world, especially the warm areas; there are 5000 species. The mandibular palps are relatively large, and the last tarsal segment usually bears only one claw. They are found in rotting trees, in moss, under fallen leaves, in refuse, or among ants. Presumably they hunt mites. Some of them live underground.

Several other families belong to the group Staphylinoidea.

III. The group Malacodermata includes slender beetles, usually with soft exoskeletons. There are eleven families, including the following:

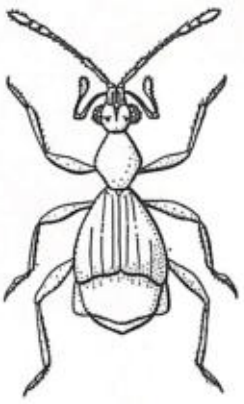


Fig. 13-23. An ant-loving beetle (*Pselaphus heisei*; L 1.8 mm).

1. The NET-WINGED BEETLES (Lycidae; see Color plate, p. 225), with 3000 mainly tropical species, often have the head extended into a beak, and the elytra are frequently yellow and black. These beetles live predominantly by hunting snails and insects.

2. The FIREFLIES (Lampyridae; see Color plates, pp. 225 and 275) comprise 1300 species of worldwide distribution, particularly common in the warm countries. There is a luminescent organ on the abdomen, even in the larvae. Some females (glow worms) are often unable to fly. They are nocturnal animals, the adults feeding on nectar or not at all, while the larvae are hunters.

3. The SOLDIER BEETLES (Cantharidae; see Color plate, p. 225), with 4000 species, are found throughout the world. These long-legged beetles are often brightly colored. The larvae have a velvety surface, and hunt like the adults.

4. The SOFT-WINGED FLOWER BEETLES (Melyridae) comprise 5000 species and live in all parts of the earth. The body is fragile and small, often with glowing colors. The males of many species possess glandular organs, usually paired, which function in courtship. The feed partly on captured animals and partly on pollen.

5. The CHECKERED BEETLES (Cleridae; see Color plate, p. 225) occur throughout the world; there are almost 4500 species. The body is slender, and the elytra are usually striped transversely; the beetles sometimes look like ants or mutillid wasps (see Chapter 18). They are predators, hunting anobiid and scotylid beetles, while certain of the larvae get into the nests of solitary bees and eat the young. Some species are pests, consuming stored dried materials of animal origin.

Families: Elateridae, Eucnemidae, and Buprestidae

IV. The group Sternoxia is distinguished by, among other characteristics, the prothorax, which is extended to form a posterior projection. There are seven families, of which the largest are the following three:

1. The CLICK BEETLES (Elateridae; see Color plate, p. 226). There are approximately 10,000 species distributed throughout the world. They can project themselves into the air with a hornlike appendage on the prothorax, which snaps into a groove in the mesothorax; otherwise there is little that is remarkable about their appearance. The larvae, elongated and compact (so-called wireworms), live in rotten wood or gnaw on the roots of plants, and often are destructive. Some South American species have luminescent organs. There are 150 fossil species.

2. The FALSE CLICK BEETLES (Eucnemidae) are widespread, with 500 species; they resemble the click beetles, except that the clypeus is much widened anteriorly, the larvae live in the wood of diseased and dead trees.

3. The 15,000 species of METALLIC WOODBORERS (Buprestidae; see Color plate, p. 226) are represented in all parts of the world. The prothorax and mesothorax are fused so that they cannot move, relative to one another. The beetles are often brightly colored, sometimes with a metallic sheen. The larvae have a broad prothorax and lack legs. They burrow in wood,

sometimes injuring the tree, though a few very small species are leaf miners. There are over 100 known fossil species.

Families: Dascillidae and Helodidae

V. The group Fossipedes includes four small families, two of which are the DASCILLIDS (Dascillidae), with 300 species, and the SOFT-BODIED PLANT BEETLES (Helodidae), with 350 species. Larvae of the latter family develop in the water. Some species are good jumpers.

Families: Dryopidae and Heteroceridae

VI. The group Macrodactylia contains few species. As adults they live in or on the water. There are two particularly important families:

1. The LONG-TOED WATER BEETLES (Dryopidae; see Color plate, p. 226), with about 300 species in all parts of the earth. The last tarsal segment is markedly elongated, with very large claws. Although the beetles live underwater, they cannot swim.

2. The VARIEGATED MUD-LOVING BEETLES (Heteroceridae; see Color plate, p. 226), with about 220 species found especially on shores in Asia and Europe. These small, marbled animals dig in the sand with their saw-toothed anterior tibiae.

Families: Dermestidae and Byrrhidae

VII. The group Brachymera includes small beetles, usually of compact shape and often with scales. The two most important families are the following:

1. The SKIN BEETLES (Dermestidae; see Color plate, p. 226), with 800 species in all parts of the earth. Many species have one ocellus, and the antennae have an enlarged, clublike terminal segment. The larvae often have a striking coat of hair, sometimes with brushlike tufts. They feed on dry animal substances, and some are pests throughout the world (carpet beetles and the like).

2. The PILL BEETLES (Byrrhidae; see Color plate, p. 226), with 300 species in most regions of the earth. The body is strongly arched and the legs are flattened. They feed on algae and mossy plants.

Families: Ostomidae, Nitidulidae, Coccinellidae, etc.

VIII. The group Clavicornia includes many species in fewer than two dozen families. Usually the beetles are small; though they may vary in structure, the antennae in general cannot be bent sharply and the terminal segments are often club-shaped. The most important families are the following:

1. The GRAIN AND BARK GNAWING BEETLES (Ostomidae). There are over 575 species, primarily in the tropics. The first tarsal segment is especially small, and the body may be cylindrical or disc-shaped. Many species hunt metallic woodborers, long-horned beetles, and bark beetles under bark and in tunnels in wood; others live among fungi; and a few are pests in storehouses.

2. The SAP-FEEDING BEETLES (Nitidulidae; see Color plate, p. 235). There are almost 2500 species in all parts of the earth; the body is often metallic in appearance and may have a mottled pattern. They are predominantly herbivorous, feeding on leaf tissue, pollen, sap, and fungi, or on dry materials, and some of them are injurious to stored products. Some are found in animal refuse and in the nests of ants.

3. The RHIZOPHAGIDS (Rhizophagidae). There are about 300 species, mainly in the northern hemisphere. The body is long and narrow. Both larvae and adults are found under bark; some hunt burrowing beetles and long-horned beetles, while others eat fungi.

4. The FLAT BARK BEETLES (Cucujidae; see Color plate, p. 235). There are at least 1200 species, occurring in all parts of the earth; the insects are small and flattened, occasionally attaining a length of 3.5 cm. They live primarily under bark and eat animal and vegetable refuse of all kinds; they are also found on moldy plant materials. A few hunt mites and small bristletails, while others are found among ants; some are pests throughout the world.

5. The PLEASING FUNGUS BEETLES (Erotylidae; see Color plate, p. 235). There are around 1900 species of worldwide distribution, mainly in the subtropics and tropics. They are quite varied in form, and intensely colored, with the upper surface lacking hair. Larvae and adults live in agaric fungi or under fungus-infested bark; some live in association with ants or termites.

6. The SILKEN FUNGUS BEETLES (Cryptophagidae). There are 1000 species in all parts of the world. They are very small beetles, oval or elongated, and covered with hair. They may be found everywhere in moldy areas, on rotting leaves or hay, decaying wood, fungus-infested tunnels made by insects, moldy combs of wasps and bees, and in barns, cellars, damp storerooms, etc. A few species burrow in healthy plants.

7. The BROWN SCAVENGER BEETLES (Lathridiidae). There are at least 500 species, especially in the more humid regions. They are very small, the tarsi have only three segments, and the elytra are often deeply ribbed. They feed on beds of fungus and fungus spores, so they are to be found on moldy plant materials, in damp rooms, and occasionally among ants or termites.

8. The COLYDIIDS (Colydiidae). There are 1800 species in all parts of the world. The body form is quite variable, often being elongated; the anterior coxae are small and spherical, the prothorax is rather long, and the tarsi consist of four segments. They are often encountered in moldy plants —for example, in rotting wood, loose bark, fallen leaves, and the deserted tunnels of other insects—and some live among ants. A few feed on lichens, and others are predators. Some blind beetles live underground.

9. The HANDSOME FUNGUS BEETLES (Endomychidae; see Color plate, p. 235). There are over 1500 species, primarily in the tropics. The pronotum usually has a line impressed on either side; the body seldom bears hairs. These beetles live on fungi, usually agarics but also puff-balls, molds, and fungus-containing soil. Twenty species have been found as fossils.

10. The LADY BEETLES OR LADY BUGS (Coccinellidae; see Color plates, pp. 182, 235, and 275). These are considered by some entomologists to be closely related to the leaf beetles. There are 4000 species throughout the world. The body is arched and usually brightly patterned; despite their

short legs they are good runners. Many species are very small. The majority of both larvae and adults are predators, eating scale insects and aphids, but some are herbivorous (the subfamily Epilachninae). The JACQUES LADYBUG (*Subcoccinella vigintiquatuorpunctata*), a European species, recently has been introduced into the eastern U.S.A., where it may become a pest on alfalfa. There are fifty fossil species.

Family: Lyctidae, and others

IX. The group Teredilia contains half a dozen families of beetles, usually rather small, with five-segment tarsi. The larvae are predominantly grublike, and most of them burrow in wood. The four larger or more important families are the following:

1. The POWDER-POST BEETLES (Lyctidae). There are about seventy species distributed worldwide, some having been introduced by accident. The body is small but elongated, with a hump on the clypeus on either side above the antennae. The eggs are often long and rod-shaped; the larvae burrow in starchy deciduous woods. Some species are pests, either on structural wood or on stored drugs.

2. The FALSE POWDER-POST BEETLES (Bostrichidae; see Color plate, p. 235). There are 600 species, representatives of which are found in all parts of the world. They are usually small, only rarely becoming as long as 3.5 cm; they have the form of a extended cylinder, with the pronotum drawn over the head like a hood. Ordinarily they burrow in dead wood, but some bore into living plants (coffee, bamboo, rice); a few species are pests, on structural wood or stored drugs, while some damage stored food products. There are about twenty-five fossil species.

3. The DEATHWATCH BEETLES (Anobiidae; see Color plate, p. 235). There are around 1500 species, occurring in all regions. All of them are small, and the antennae either bear sawteeth or have an elongated terminal segment. Both larvae and adults burrow in wood, usually dry (for example, dead branches), and often damage furniture as well as stored wood for carpentry and cabinetmaking. Some forms eat fungi, while others damage drugs. There are about fifty known fossil species.

4. The SPIDER BEETLES (Ptinidae; see Color plate, p. 235). There are 575 species distributed worldwide, especially in the warmer countries. They are small, with the antennae arising close together between the eyes; the pronotum is distinctly narrower than the abdomen. The females are often more slender than the paunchy males. Some species are wood-borers, while others feed on dried organic substances. A few are injurious, or at least troublesome, pests on drugs and groceries. Very occasionally they occur in the nests of vertebrates.

Families: Oedemeridae, Meloidae, Tenebrionidae, etc.

X. The group Heteromera is quite extensive, being represented by very many species in the subtropics and tropics. There are about two dozen families, very different in body shape, but as a rule with five-segment anterior and middle tarsi and four-segment hind tarsi. Nine families are chosen for mention here:

1. The OEDEMERID BEETLES (Oedemeridae; see Color plate, p. 236).

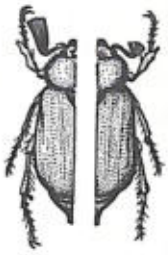


Fig. 13-24. The June beetle *Melolontha melolontha*; left, ♂; right, ♀.

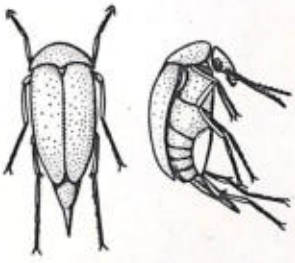


Fig. 13-25. The tumbling flower beetle *Mordella aculeata*, from above and from the side (L 6 mm).

There are about 1800 species distributed worldwide. The body is slender, with elytra often gaping at the back; the upper surface is frequently metallic in appearance; the antennae are long and thin. The larvae live in rotting wood and the stumps of trees, as well as in wood for construction; others mine in the pith of thin branches of deciduous trees. The adult beetles are often found on flowers. All species are obligate pollen feeders.

2. The NARROW-WAISTED BARK BEETLES (Salpingidae). There are 300 species, mainly in subtropical and tropical countries. The head is stretched out anteriorly and elongated, more or less like a proboscis. These beetles inhabit dead branches and brittle twigs, some feeding on fungi and others preying upon other insects, especially bark beetles.

3. The ANTLIKE FLOWER BEETLES (Anthicidae). There are approximately 2000 species, represented in all parts of the earth. In general, they are very small and slender, and most of them are hairy; many, as the name implies, have the exernal appearance of ants. They move with agility. Ordinarily they are found under piles of rubbish and brushwood or rotting plant remains, and they may even live underground in sand. Just twenty species are known as fossils.

4. The BLISTER BEETLES (Meloidae; see Color plate, p. 236). There are 3000 species distributed throughout the world; these are of two body types, the oil-beetle type (with shortened elytra and blunt mandibles) and the Spanish-fly type (with normal elytra and sharp mandibles). Often they are patterned in black and yellow. The larvae (the first stage of which is the "triungulin," shown in Fig. 13-13) live in the nests of solitary bees or eat the eggs of grasshoppers; the adults are vegetarian, sometimes becoming pests, particularly on solanaceous plants.

5. The RHIPIPHORID BEETLES (Rhipiphoridae; see Color plate, p. 236). There are about 300 species, concentrated in warm regions. The elytra gape open or are reduced, so that the hindwings can be seen beneath them. the antennae of the males bear striking combs. The females often look like larvae. The larvae are parasitic on cockroaches, wasps, bees, and beetles. The lifetime of the adults, as a rule, is short.

6. The TUMBLING FLOWER BEETLES (Mordellidae). There are over 700 species, in all zones of the earth but primarily in the subtropics and tropics. Slender animals, often laterally compressed, their tarsal segments are much longer than the tibiae, and in many species the abdomen is lengthened into a spine. The larvae are found in fungus-infested wood, or may feed themselves by hunting. The adults flit rapidly, jumping like fleas, among bright flowers. Twenty-five fossil species are known.

7. The LAGRIID BARK BEETLES (Lagriidae; see Color plate, p. 236). There are 600 species, mainly in the tropics. The body is usually covered with a woolly coating of hairs, and the antennae are like strings of beads. The horny larvae develop in plant debris; some of them are predators upon bark beetles.

8. The COMB-CLAWED BEETLES (Alleculidae; see Color plate, p. 236).

There are approximately 1500 species, distributed worldwide. Ordinarily they are slender, with long antennae and fine teeth on the pretarsal claws. The larvae live in the decaying parts of old trees, on agaric fungi, under moldy bark, or on the ground among plant rubbish; a few live with ants. The adults often injure cultivated plants.

9. The DARKLING BEETLES (Tenebrionidae; see Color plate, p. 245). There are around 17,000 species, distributed throughout the world and concentrated in the warm countries, where they prefer the dry regions such as steppe and desert. There is great variety in form, but the beetles are usually black, often with kidney-shaped eyes and string-of-beads antennae arising from beneath a lobelike protuberance on the side of the head. They are predominantly vegetarian, eating dead, rotting plant materials; they also live in decaying wood and fungi or below ground in the sand. Some (for example, the "mealworms") are pests in stored food, while others live in the colonies of ants or termites. Over forty fossil forms are known.

XI. The group Lamellicornia consists of three families, the beetles of which have geniculate (elbowed) antennae, with the terminal segments enlarged to form a leaflike structure:

1. The BETSY BEETLES (Passalidae; see Color plate, p. 246). There are 500 species, mainly in the southern hemisphere, but also in Central America and southeastern Asia and, rarely, in North America. They are large (L 1–8 cm), powerful beetles, almost all black, with grooved elytra. Preferring darkness, both larvae and adults are most commonly found in rotting wood.

2. The LAMELLICORN BEETLES (Scarabaeidae; see Color plates, pp. 246, 249f., and 266). Some entomologists regard this group as comprising up to a dozen families; with more than 18,000 species, it is one of the larger families, its members distributed throughout the world. The lamellicorns (L 1 mm to 15 cm) are quite variable in form, often with projections on the head or pronotum, and many of them are brightly decorated. The larvae and adults both feed on plant materials, frequently the dung of plant-eating mammals. Some are major pests. More than 100 fossil species have been found.

3. The STAG BEETLES (Lucanidae; see Color plates, pp. 246 and 266). There are 800 species, occurring in all parts of the world. They are large beetles, ranging in length (including the mandibles, which are more or less elongated in different species) from 7 mm to 10 cm. The larvae generally develop in rotting wood, and their development often requires several years.

XII. The group Phytophaga is distinguished by the deceptive segmentation of the tarsi, the fourth segment being very small and hidden in the third; the head is not elongated, nor are the antennae geniculate. There are three families:

1. The LONG-HORNED BEETLES (Cerambydicae; L 4 mm to 16 cm; see Color plate, p. 255). There are approximately 80,000 species, represented

Family: Scarabacidae, and its relatives

▷
Neuroptera, suborder Megaloptera (see Chapter 12): 1. *Corydalis* sp.; 2. The alder fly *Sialis lutaria*, enlarged and actual size, 3*l*. Larva of *Sialis fuliginosa*, enlarged and actual size. Rhaphidides (see Chapter 12): 4. The snakefly *Raphidia notata*, enlarged and actual size. Planipennia (see Chapter 12): 5. *Myrmeleon formicarius*, actual size, 5l. its larva, an ant lion, enlarged and actual size, 5k. pupal cocoon, enlarged; 6. The brown lacewing *Hemerobius nitidulus*, enlarged and actual size; 7. The dusty-wing *Semidalis aleurodiformis*, enlarged and actual size, 7l. its larva, enlarged; 8. The spongilla fly *Sisyra fuscata*, enlarged and actual size, 8*l*. its larva, enlarged and actual size, on a freshwater sponge; 9. *Osmylus chrysops*, enlarged and actual size, 9l. its larva, actual size.


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Families: Cerambycidae, Chrysomelidae, and Bruchidae

in all parts of the world. They are usually slender insects with long, thread-like antennae and tibiae with two terminal spurs. Some species are colored like wasps or bees. Some larvae develop in wood or under bark, while others mine in branches and the stalks or ovules of herbaceous plants; certain species are pests. There are about 100 fossil species.

2. The LEAF BEETLES (Chrysomelidae; see Color plates, pp. 255 and 278). Some entomologists divide these into several families. There are about 25,000 species, distributed worldwide. They are predominantly rounded or oval beetles, brightly colored, often with short antennae and usually lacking hairs on the elytra. The tibiae are without spurs; many species can jump. Both larvae and adults live on plants, and some larvae develop in plant stalks under water; others grow up in the nests of ants. Numerous species are injurious to plants. At least 160 fossil species are known.

3. The SEED WEEVILS (Bruchidae). There are about 1000 species, in all parts of the earth. The body is small and compact, and usually bears a mottled pattern of hairs; the antennae are often equipped with sawteeth. As adults, they are good runners. The larvae almost all develop in seeds, especially those of papilionaceous plants, while some are injurious to stored products.

XIII. The group Rhynchophora includes beetles with head more or less markedly elongated into a proboscis, with the rather small mouthparts at its tip. The antennae of most species are geniculate. There are five families:

1. The FUNGUS WEEVILS (Anthribidae; see Color plate, p. 256). There are 2300 species, in all parts of the world but particularly in the subtropical and tropical regions of the Old World. Not very gracefully shaped, they are 5 mm to 5 cm long and have broad heads with the labrum exposed; the antennae are not geniculate, but may be very long, in which case the beetles look like long-horned beetles. The larvae mine in the bases of flowers and in thin twigs, or burrow in seeds; some do damage to stored products, and others hunt scale insects.

2. The BARK, CONE, and ENGRAVER BEETLES (Scolytidae; see Color plates, pp. 256 and 276). There are about 1200 species, distributed worldwide but concentrated in the tropics of southeastern Asia and South America. The body is cylindrical, the legs are short, with delicate tarsi, and the downward-pointing head is narrower than the pronotum. They burrow in bark, in the phloem tissue, and in sapwood; in sapwood they feed on fungus cultures. Some species mine in the stalks of herbaceous plants. Numerous bark beetles are pests in forests, where foresters sometimes combat them by catching them on baited trees. More than sixty fossil species have been described.

3. The AMBROSIA BEETLES (Platypodidae). There are over 300 species in all parts of the earth, particularly in the warm countries. The body is shaped like an elongated cylinder, with head and pronotum of equal width and head stretched forward. Both larvae and adults burrow in wood and feed on fungus cultures.

Families: Scolytidae, Curculionidae, and their relatives

◁
Planipennia (see Chapter 12): 1. *Nemoptera sinuata*; 2. *Nemoptera ephemera*; 3. *Mantispa styriaca*, enlarged with prey and actual size, 3e. eggs (on stalks), 3l′. first-stage larva, enlarged and actual size, 3l″. first-stage larva on a spider cocoon, 3l‴. the subsequent larval stage, parasitic in a spider cocoon. Mecoptera: 4. The scorpionfly *Panorpa communis*, enlarged and actual size, 4l. its larva, enlarged and actual size; 5. The hanging scorpionfly *Bittacus* sp., enlarged with prey and actual size; 6. The snow scorpionfly *Boreus hyemalis* in the snow, enlarged and actual size.
Trichoptera (some enlarged; *l′*, larvae in cases; *l″*, larvae removed from the cases; g, nets spun by larvae): 7. *Phryganea grandis*, 8. *Limnophilus* sp.; 9. *Oxyethira costalis*; 10. *Helicopsyche* sp.; 11. *Stenophylax* sp.; 12. *Glyphotaelius punctato*; 13. *Sericostoma* sp. ; 14. *Crunoecia irrorata*; 15. *Leptocerus cinereus*; 16. *Holocentropus* sp.; 17. *Hydropsyche angustipennis*; 18. *Rhyacophila* sp.; 19. *Plectrocnemia* sp.; 20. *Neureclipsis* sp.

4. The STRAIGHT-SNOUTED WEEVILS (Brenthidae; see Color plate, p. 256). There are almost 1300 species inhabiting the warm latitudes, especially in the Indo-Malaysian region and the South American tropics. The body is long and slender, the antennae are not geniculate nor do they end in a club, and the head is extended in a straight line, like a proboscis. Most of them burrow in wood, but some are predators.

5. The SNOUT BEETLES (Curculionidae; see Color plates, pp. 256 and 277). With at least 50,000 species, this family exceeds all others in the animal kingdom. They are distributed throughout the world, with the majority in warm countries. There is considerable variety in form; often they are tear-shaped, the proboscislike extension of the head is usually bent downward, and the labrum is ordinarily invisible. They are herbivorous, often boring into plant tissue, including wood, seeds, and leaves; many are pests. Some forms can jump. About 500 fossil species are known.



Fig. 13-26. The larva of a June beetle (genus *Melolontha*); the full-grown larva is 48 mm long.

The Coleoptera, with more species than any other order of insects, present us with a great variety of forms which have become adapted to almost all imaginable habitats, food sources, and conditions for larval development. The number of species indicated for each of the families is an estimate only of the beetles which have been described so far; the true numbers are probably considerably higher, since by no means all regions of the world have yet been investigated thoroughly with respect to the insects, and in particular with respect to the beetle fauna. It must be acknowledged that, because of the variety of appearance and behavior the beetles exhibit, hardly any other group of animals can equal their prominent—even dominant—role in the cycle of natural phenomea.

Family: Stylopidae, by R. Kinzelbach

The systematic position of the TWISTED-WINGED INSECTS (family Stylopidae) is subject to further consideration, but most entomologists now place them as a highly specialized beetle family instead of treating them as a separate order, Strepsiptera, as was frequently the case in the past. They are placed near the Meloidae because of their parasitic habits. They are among those insects which undergo a complete (holometabolous) metamorphosis. Though only about 400 species have been described so far, one can expect that there will be about 1000 altogether. Here we shall follow the custom of many entomologists in combining the Strepsiptera with the Coleoptera in the family Stylopidae. It may be questioned whether the two groups are really closely related; evidently the Stylopidae separated from related families at an early stage and became adapted to a parasitic way of life. This view can be inferred from the degree of adaptation to their various host animals and the variety of animals which serve as hosts, their worldwide distribution, the large number of high-level subgroups within the family, and, not least, their body structure.

All the stylopids are parasites, undergoing at least part of their development in other insects. They are particularly noteworthy because of their sexual dimorphism (difference in external appearance between the sexes).



Fig. 13-27. *Lychnocolax mindoro*, male.

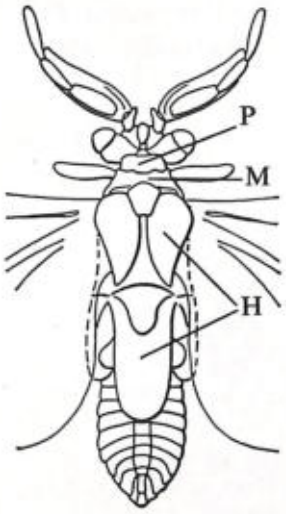


Fig. 13-28. Dorsal aspect of a *Stylops* male: P, prothorax; M, mesothorax with forewings; H, metathorax with hindwings.

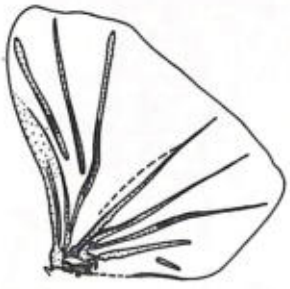


Fig. 13-29. Hindwing of a male of the genus *Stylops*.

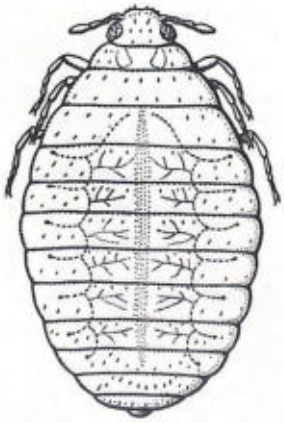


Fig. 13-30. Female of *Eoxenos laboulbenei*.

Whereas the males look like "real" insects with their sense organs, wings, and legs, in the females of most strepsipteran species these organs are largely regressed, so that the females look like larvae. The distinguishing characteristics of the two sexes must therefore be discussed separately.

1. Male: The overall length ranges from 1 to 7.5 mm. The head is broad, with compound eyes which often appear to be on stalks (the generic epithet *Stylops* means "stalk-eye") and look rather like blackberries. The head capsule of the more primitive forms is similar in structure to that of the Orthoptera, while in those which have evolved in certain directions it can be much altered. The antennae originally consisted of seven segments, but in many cases they have been simplified by fusion; at least the third segment is flabellate (bears a lateral projection), and in the fourth there is an olfactory pit. The mouthparts are of the biting type and are often fused. The mandibles, when present, are knife-shaped or conical; often they are provided with sense organs, as are the (usually two-segment) maxillae, and in many cases serve as olfactory sensors. The prothorax and mesothorax are small (see Fig. 13-28), and arising from the latter are the reduced forewings, which because of their function are often compared with the halteres of Diptera. The hindwings, attached to the well-developed methatorax, have only longitudinal veins; at rest they are folded longitudinally like a fan and laid back against the body. The trochanter is absent from the forelegs and middle legs. The tarsi consist of two to five segments; if there are five segments, the last bears claws, while in the other cases there can be hooklike processes (accessory claws) at the lower end of the tibia or on some of the tarsal segments. The anterior and middle coxae are free, but the hind coxae are fused to the metathorax. The abdomen consists of ten very movable segments, and at its end there is a hard copulatory organ, the aedeagus, which may be straight, hooklike, or anchor-shaped.

2. Female: These are free-living only in the subfamily Mengenillinae, members of which have completely functional compound eyes, antennae, and legs, but lack wings. Females of the remaining subfamilies spend their entire reproductive lives within the exuvium of the last larval stage, forming a functional unit with it, as we shall see below. This larva-shaped female, often with an awkwardly distended abdomen, lives permanently within the insect host, only the head and thorax—fused to form a "cephalothorax"—sticking out of the host like a hernia. Most organs are regressed; there remain mouth, mandibles, the spiracles of the metathoracic segment, and a transverse slit (see Fig. 13-32) on the ventral side (which is turned away from the host) between the head and prothorax. In a sagittal section one can see that this slit is continuous with a passage leading back between the pupal skin and the adult animal to form a brood chamber; into this chamber there open a number of tubes through which the larvae pass out from the body cavity of the mother.

In 1793 the Italian natural historian Pietro Rossi raised a small black

parasite with only one pair of wings. He had found it in the wasp *Polistes gallicus* (see Chapter 18), and he was surprised at some of the characteristics of this *Xenos vesparum* (as he called it, from the Greek ξένοζ = guest or stranger, and the Latin *vespa* = wasp.) But he was convinced that he had discovered a new species of parasitic wasp. The famous French zoologist Pierre Andre Latreille included *Xenos vesparum* in the classification of the insects he produced in 1809, but he was not quite sure where this odd little organism belonged, and called it an *animalculum animum excrucians* (a little animal which—because of its strange characteristics—torments the mind). But, he continued consolingly, time would surely bring insight to some other researcher. Finally, in 1813, W. Kirby assigned *Xenos*, along with the second genus which had meanwhile been discovered, *Stylops*, to an order of their own, and so it has remained, in essence, until recently.

The little animal that torments the mind

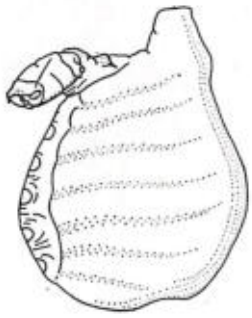


Fig. 13-31. Female of *Trizocera macrocysti*, from the side.

Of course, entomologists were not satisfied with this bare minimum of organization, and they have looked for evidence of relationships between the Stylopidae and the other beetles. In the last century, especially, some entomologists believed that these small parasites must be closely related to a beetle family also parasitic in insects, the Rhipiphoridae. However, the rhipiphorids are less well adapted to life as parasites in insects, though as a result of their similar way of life they do resemble the Stylopidae at first glance. On closer examination, it is apparent that this resemblance is somewhat superficial and that the Stylopidae differ considerably from the Rhipiphoridae in many respects. The shortened stylopid forewings are soft membranes showing the vestiges of veins; they oscillate rapidly during flight. Those of the Rhipiphoradae are hard and lack veins, and in flight they are spread out to the side and held still. Furthermore, the shape and functional design of the segments are different.

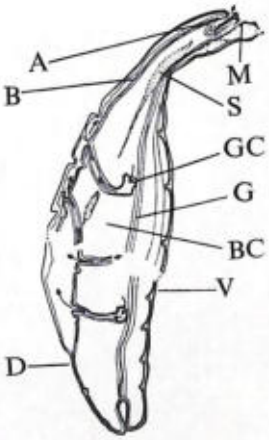


Fig. 13-32. The *Stylops* female in sagittal section: B, brood canal; A, aperture of brood canal; M, mouth; S, subesophageal ganglion; GC, genital canal; G, gut; BC, body cavity; V, ventral surface; D, dorsal surface.

The researchers of earlier times may be excused for not noticing such fine points; their acquaintance with these two rather rare insect groups was limited to pitifully desiccated museum specimens. And these museum relics give an entirely false picture of the Stylopidae; delicate and flexible in life, these animals become distorted in almost all dimensions when they dry up, so that the details of body structure can no longer be discerned. As we now know, the similarity between the Stylopidae and the Rhipiphoridae represents—as is so often the case in the animal kingdom—a case of convergent adaptation: two groups only distantly related phylogenetically have acquired similar appearance as a result of similar habits. It is now generally conceded that they form a superfamily by themselves, placed near the Meloidea.

Stylopid subfamilies

The Stylopidae are divided into two groups of subfamilies, together comprising nine subfamilies, each of which attacks quite specific groups of insects. The Mengenillinae live in bristletails (Thysanura; see Chapter 2); we find them in the western Mediterranean region, in eastern Asia, and in Australia. The Mengeinae are known only as a single fossil species, from Baltic amber. In the warmer zones of all parts of the earth, the Calli-

pharixeninae live in bugs (Hemiptera). The Halictophaginae, which also appear all over the world, parasitize bugs, cicadas, cockroaches, crickets, and flies. Only one species of Bohartillinae has been found, in Central America. The Myrmecolacinae, parasitic on ants, grasshoppers, mole crickets, and mantids, are found in the tropical zones of the earth. The Elenchinae, distributed worldwide, find their hosts among the cicadas. The Hylecthrinae attack bees of the family Colletidae in Europe, North America, eastern Asia, and Australia. Finally, hymenopterans of the most varied groups are the victims of the Stylopinae, which occur in all parts of the world except Australia.

Reproduction and development

The life span of the male stylopids is measured in hours. As adults, they search out the mature females by following the attractant smell the latter send out. This "pheromone" is detected by the males by means of two sorts of antennal sense organs, the sensilla and olfactory pits. The sensilla are often also strewn over the mandibles and maxillae, and in one *Halictophagus* species they are even found on the legs (see Fig. 13-34). Once the female has been found, either free-living or embedded in the host, she is inseminated in an unusual manner: the male sticks his copulatory organ, the aedeagus, into the female at any position and thus anchors himself. The sperm cells migrate to the eggs, large numbers of which lie free within the abdomen of the female. It is not always the case that one egg produces one larva; it has been demonstrated for species of *Halictoxenos* that the embryos split at an early stage, thus increasing in number (polyembryony).

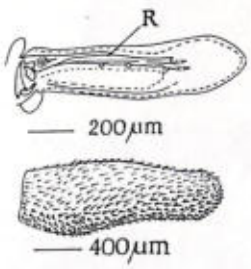


Fig. 13-33. Forewing of *Stylops* (above) and *Rhipiphorus* (below); R, remnants of wing venation.

These embryos grow into the first-stage (triungulin) larvae, 0.5–1.5 mm long; they are transported through the tubules into the brood chamber and from there to the exterior, by way of the brood slit behind the mouth of the female. Since they can move, and even jump with the long caudal bristles, they are able, for example, to reach the flowers being visited by the mother's host. Then they attach themselves to conspecifics of the host visiting the same flowers. But the triungulin does not burrow into this adult host; rather, it lets itself be carried into the host's nest. There, while the host cares for its brood, the triungulin finds an opportunity to move to the larvae and penetrate one of them. Within the host larva it molts, becoming a soft, grublike second-stage larva which sucks in the body fluid of the attacked animal by means of a powerful suction device in the mouth. The stylopid larva molts five times, and after the last molt it either leaves the host entirely (as is the case with the Mengenillinae) or, pushing out its anterior end, it pupates within the exuvium of the last larval stage. This exuvium hardens, becoming a puparium; that of the males is barrel-shaped, and that of the females, usually somewhat flattened. Respiration, which previously was accomplished by tapping off from the trachae of the host, now is done by way of the metathoracic spiracles, which are outside the host.



Fig. 13-34. Leg of *Halictophagus bidentatus*.

The molt following the pupal stage, only a trace of which appears in

the female, produces a stage corresponding to the "subimago" of the Mayflies (see Chapter 3). The presence of such a stage is further evidence for the great evolutionary age of the Stylopidae. The male imago emerges within the puparium, spreads out his wings, and waits—sometimes for days—for the proper moment to leave his "barrel." Then, on a bright morning, all the males in one place creep out simultaneously, presumably in response to the stimulus of light, detected through the transparent eyespots in the puparium.

This, in outline, is the life cycle of a stylopid parasitic on Hymenoptera, as are the members of the subfamily Stylopinae. For most other stylopids the life cycle is still unknown. We know only that in the Myrmecolacinae the male and female first-stage larvae, which differ in appearance, seek out different hosts, the males attacking ants and the females other insects—for example, grasshoppers. The males of most stylopid subfamilies fly to lights at night, sometimes in great numbers. In Mongolia, the Hungarian entomologist Z. Kaszab caught about seventy male Mengenillinae—a family which is considered particularly rare—in a single night. As adults the males do not eat, but frequently search out water or drops of resin on trees.

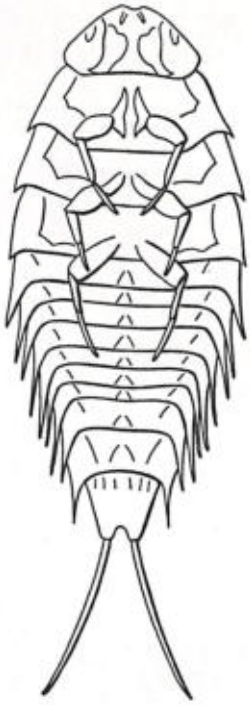


Fig. 13-35. First-stage larva of *Elenchus tenuicornis*.

14 The Caddis Flies

Order: Trichoptera, by H. Wundt

The order Trichoptera (see Color plate, p. 302) includes over 5000 species, distributed mainly over the northern hemisphere. Even Aristotle was familiar with the CADDIS FLIES, calling them "wood-destroyers" because some of their larvae burrow in wood. But it is more typical of these insects that the larvae build elaborate cases in which they live under water. The term "caddis" originally referred specifically to these larvae, used as bait by anglers at least since the middle of the 17th Century. The adults, which appear early in the spring, are characterized by hairy wings, the hind pair of which can be folded; they resemble inconspicuously colored moths.



Fig. 14-1. Net of a caddis larva (*Hydropsyche* sp.).

The caddis flies often appear in great numbers; then the larvae are sometimes collected and sold by the sackful as bird food. Swarms of adults are often attracted by lighted shop windows, and the number of larvae found in brooks is equaled by no other insect order—hence their familiarity to fishermen. Trout will swallow the larvae together with their cases, regardless of whether they are made of wood or stones.

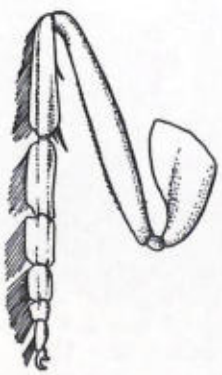


Fig. 14-2. Swimming leg of a caddis fly.

It is worth while taking the time to look for these remarkable creatures, in clear brooks or still waters. There one can see small tessellated tubes, up to a few centimeters long, sitting on or below stones and on aquatic plants, or moving along slowly. Inside, hidden up to the thorax, is a caterpillarlike animal, carrying the tube with it like the shell of a snail. Each species builds its case out of a characteristic material and in its own particular style. Some prefer sand, mud, or small pebbles, while others use dead or living plants. Still others search for live or dead snails and clams, and some are content with a hollow stalk (which they may hollow out themselves). The cases may be straight, curved, or spiralled, cylindrical or conical, only slightly arched or formed into a proper room. If plant materials are used, the animal bites them into many pieces of equal size, and as it builds the case it arranges them in a certain pattern, longitudinal, transverse, perpendicular to the body axis, or in the form of a helix. Larvae which stay on the bottom of a body of water may add ballast, in the form of stones attached

to the outside of the tube. Those which float at the surface need a light case, and often construct it of green leaves, which contain air. When the leaves die, they become saturated with water and thus heavier, and the larva replaces them with fresh bits of greenery. So that the sensitive abdomen does not rub against the rough materials of which the case is constructed—especially during respiratory movements—the inside of the case is lined with fine silk produced by the salivary glands. There are some species which construct their cases almost entirely of this silk. All these animals feed primarily on plants.

Another group of caddis larvae lives quite differently. They build no cases, but rather are quick-moving hunters. As in other predatory animals, the eyes are directed more toward the front of the head than to the side. The body is altogether of flatter construction. Often they lack even the external tracheal gills, which are more characteristic of the case-building members of the group. These hunters either swim about freely, looking for prey in every corner and crack between stones, or—in certain species—they adopt a method of prey capture quite well known, but in a different sphere: they build nets. In the same way that spiders "filter" the air, they filter the water.

There are a great many ways that this can be done; just as the spiders build webs in the form of snares, so do certain rare caddis larvae build snares in quiet waters. These are in the shape of a funnel, a few centimeters in diameter at the rim; one can often see them in running brooks, oriented so that the opening faces upstream. They capture all sorts of plankton (animals which drift with the water), as well as mosquito larvae, small crustaceans, and the like. Some of these nets look like the nests of swallows, while others are in the shape of a trumpet, and still others consist of sacks as long as a finger, attached, to a stone, only at the front (open) end. The larva sits in the closed floating end, as though in a hammock, and feeds on the small animals and bits of plants swept in. Even more complicated nets or systems of traps—often with several chambers—can be built.

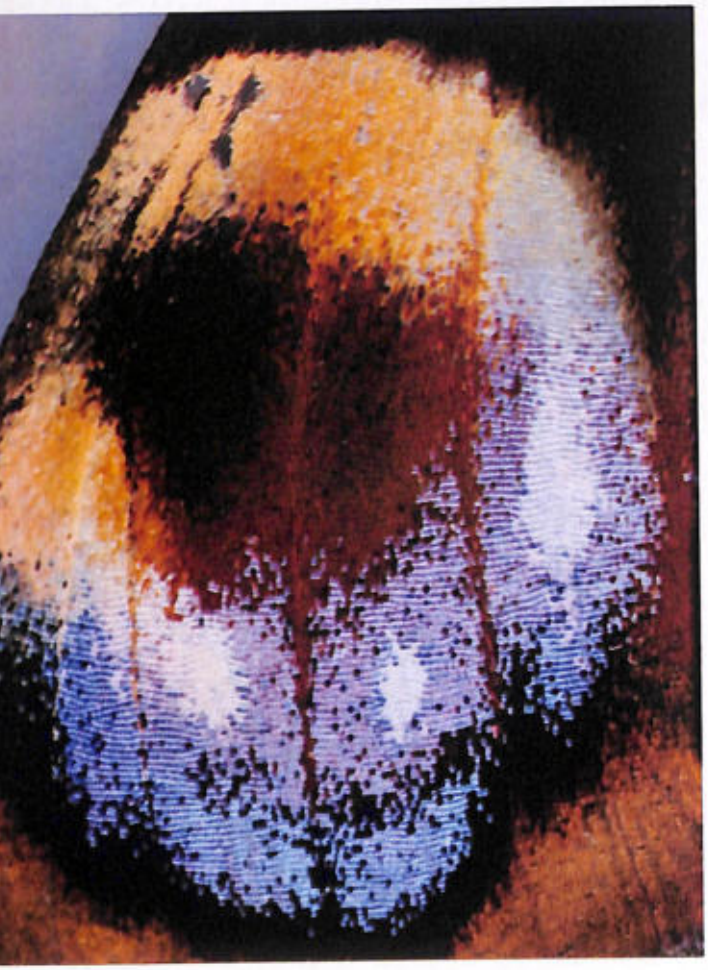
In still waters, where there is no current to carry prey into the net, one finds the threads stretched out in all directions. If, for example, a small crustacean bumps into a thread, the caddis larva flings itself with unbelievable speed along the thread and onto the prey, seizes it, and drags it back into its lair. When the time comes to pupate, these species, which do not build cases as larvae, make solid houses to protect themselves as pupae.

The species which do have cases as larvae fasten them onto wood or under stones for pupation, closing them at each end with a sieve. Only particular stones or wood meet all the requirements of an anchorage for these pupal chambers. There may be hundreds and even thousands of closely packed cases on one of these suitable sites, each housing a single pupa. Whereas in other insects the pupal period is a dormant one—at least to all external appearances—the caddis pupa in its case never really settles to rest. In order to maintain the current of fresh water it needs for

▻
The clouded yellow *Colias croceus* is a European butterfly of the family Pieridae.

▻▻
The eyespot of the peacock (*Nymphalis io*). Color and patterning of butterfly wings are produced by tiny scales.

▻▻▻
Depending on the direction of light and the angle of vision, the dark areas on the upper surface of the wing of the male purple emperor (*Apartura iris*) look dull dark brown or brilliant blue. These iridescent colors are caused by the fine structure of the scales (cf. Color plate, p. 338).









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Fig. 14-3. Gelatinous egg-mass of a caddis fly.

respiration, it must make breathing movements almost continuously, and in addition must clean the sieves at the ends of the case, removing the foreign bodies which accumulate. For the sieve at the back of the tube, the respiratory movements also serve as cleaning movements. But the front sieve must be repeatedly scrubbed with certain bristles and with the mandibles.

How does the winged reproductive insect escape from this underwater case? In some species, the pupa swims to land and there bursts its skin, so that the still-soft imago can climb slowly out. In others, the pupa swims only to the surface of the water, where it floats with the back of the thorax exposed. A tear suddenly develops here; the imago struggles out, leaps onto the water surface, and immediately runs or flies away.

The adults often live for months, feeding on plant juices. Anyone who observes caddis flies fluttering low over the water will often see them running on the surface as well, and they are even able to dive through it. Then they swim for a little distance, using their broadened middle legs. These are tricks that one would hardly expect from these delicate animals. It is the females which dive and swim, looking for suitable places to lay their eggs. The eggs are deposited under water, either glued onto stones, plants, or pieces of wood, or—in other species—embedded in a gelatinous mass like the spawn of frogs. This gelatinous spawn takes the form of lumps, strings, or even small rings. Soon countless small larvae hatch out and proceed to build their elaborate cases or delicate nets.

◁ Metamorphosis of the monarch butterfly (*Danaus plexippus*): 1. Ready to pupate, the caterpillar has attached the hind end to a twig with silk and has swollen up. 2. The skin of the caterpillar bursts and the pupa appears. 3. The pupa has stripped off the caterpillar skin. 4. Final form of the chrysalis. 5. About two weeks later: the imago is completely developed and has burst the transparent chrysalis in order to emerge. 6. The butterfly has emerged and hangs from the empty chrysalis. 7. and 8. By forcing blood into the hollow wing veins the butterfly stretches the still-soft wings. 9. With wings fully spread, the butterfly rests near the empty chrysalis until the wings have hardened.

15 The Butterflies, Skippers, and Moths

Order: Lepidoptera, by W. Dierl

The order Lepidoptera, along with the Coleoptera, Hymenoptera, and Diptera, is among the largest of the insect groups. With more than 112,000 known species of BUTTERFLIES and MOTHS, it is represented in all regions of the earth where plants grow and provide a source of food and shelter for adults and caterpillars alike. Antarctica is the only continent on which no lepidopterans as yet have been found. In comparison with the other insect groups, the Lepidoptera seem very uniform; those species which have evolved particular adaptations to special habitats and ways of life are the exception rather than the rule. The characteristics of the order combine both primitive and highly developed traits. Among the primitive characteristics are the structure and feeding behavior of the caterpillars, for they are almost all planteaters. A highly evolved characteristic is their complete metamorphosis (see Chapter 1) and, in many adult forms, a special development of the external body structure. Apart from a very few species, the Lepidoptera have remained terrestrial. Some genera and species, though very much in the minority, have adapted their habits to unusual environmental conditions.

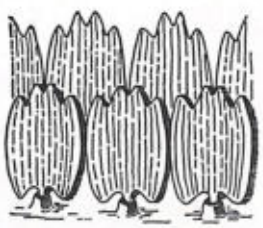


Fig. 15-1. The wing scales are attached by short pedicels which fit into sockets.

Size

Lepidoptera are probably the most popular insects among non-zoologists. The order includes animals of a great range of sizes; probably equalled among insects only by the beetles; this range is as great for caterpillars as for adults. The smallest adults are moths of the family Nepticulidae, with a wingspan of barely 2 mm; their caterpillars are also tiny. The wingspan of the largest lepidopteran, the South American owlet moth *Thysania agrippina*, amounts to around 32 cm—over a foot. But their wings are narrow, and their area is exceeded by that of the giant silkworm moth *Coscinocera hercules*; only slightly smaller in wingspan, this moth has a wing area of 300 cm^2. A southeastern Asian member of the same family, *Attacus atlas*, has a wing area nearly as great. Such giant moths, of course, also have particularly large caterpillars, in some cases more than 15 cm long.

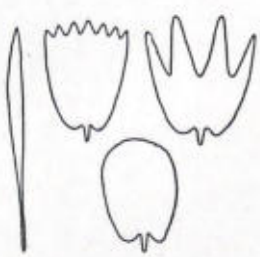


Fig. 15-2. Various forms of scales.

The distinctive broad wings of the Lepidoptera often appear to be

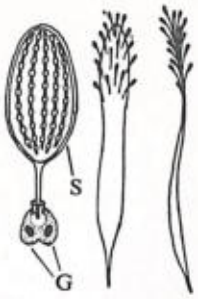


Fig. 15-3. The surface of scent scales is enlarged by irregularities or brushlike processes; at left is shown the connection between scale (S) and gland cells (G) producing the odor substance.

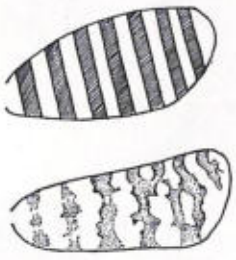


Fig. 15-4. Diagram of the basic seven-band wing pattern (above) and its actual appearance in a leaf roller (below).



Fig. 15-5. Diagram of a lepidopteran; the wings on the left side have been removed and their positions marked by black dots between the wing joints.

single structures; actually, they are composed of two wings on either side, covered above and below with very small scales overlapping like shingles. It is these scales that produce the magnificent colors and patterns often seen (see Color plate, p. 312). The actual wing membrane, which bears the scales, is colorless and as transparent as glass. Where limited areas of the wing lack scales, as in the emperor moths (family Saturniidae), the wing membrane is revealed in "windows." In some hawk moths (family Sphingidae) and clearwing moths (family Aegeriidae) the wings are transparent, being without scales except for narrow bands at the margin (see Color plate, p. 347). These moths thus resemble certain Hymenoptera, and because of this similarity they enjoy the same protection as these well-armed insects (mimicry; see Chapter 1). Body and legs of the lepidopteran adults are also densely covered with scales, which sometimes can take the form of hairs.

On the wings, on the body, or on the legs, the Lepidoptera bear specially shaped scales or bundles of scales associated with glands. These glands secrete odoriferous substances which serve as attractants and excitors for both sexes. In the males, the wing scales are often arranged in particular fields (androconia). In contrast, the scales or bundles of hairs on the abdomen of the female, which serve to diffuse sexual attractant substances, are usually recessed in pockets and are everted only when in use.

The scales covering the wings, which produce their coloration and patterning, contain either pigments of various chemical composition or are so constructed that, by purely physical means, they generate gloriously shimmering metallic colors (for example, in the moths *Urania* and *Morpho*, and in many other species of numerous families). The patterning of the wings consists of transverse stripes and spots in a regular array that is determined during embryological development, at the pupal stage. The basic plan may well be a sequence of seven bands which still occurs in a few very primitive lepidopteran families. In the more highly evolved families this sequence was transformed and duplicated in a way usually characteristic of the group, and thus arose the great variety in patterns we see today. Sometimes both pattern and color can be influenced by external conditions, such as temperature and humidity; this effect produces variations which are distinctly different depending on the climatic conditions associated with the time of year and are thus referred to as seasonal forms. In exceptional cases lepidopterans can be entirely black. These instances of melanism can also be caused by sudden changes (mutations) in the hereditary material. Day length can also affect the development of color and pattern. For example, in the brush-footed butterfly *Araschnia levana* the red spring form (levana) appears if the animal has developed while the days were short and the nights long, whereas the summer form (prorsa) is developed when the period of daylight exceeds that of darkness.

The scales, hairs, and general surface of the lepidopteran exoskeleton are covered by a thin layer of wax which makes them water-repellent.

The animals are thus protected from rain and often can even save themselves if they are unfortunate enough to fall into the water.

The predominant method of locomotion of the adults is flight; only certain species in a few families—for example, some female clothes moths—prefer to use their legs. There are quite distinct methods of flight, associated with differences in body structure, wing shape, and musculature. These fall into two basic categories. The more primitive method is probably fluttering, a technique in which the wings are moved up and down at a moderate rate and in which the maximum flight speed is severely limited. The large cabbage white butterfly (*Pieris brassicae*) has been shown to have an average flight velocity of 2 m/sec, which corresponds to something over 7 kph (4 mph). In flight, it beats its wings hardly more than ten times per second. Lepidoptera which fly by fluttering include almost all the diurnal types and numerous nocturnal ones from many groups—for example, the geometrid moths. It is characteristic of these lepidopterans are both forewings and hindwings are broad.

Fluttering is a particularly striking behavior in some small leipdopterans with delicate wings, the area of which is increased by a long fringe of hair, especially marked on the hindwings. Their flight resembles a slow hovering, and since they are moved more by the air currents than by their own power, this type of flight is sometimes called parachute flight. Flying in this inefficient manner, of course, they manage to cover no great distances.

The best flyers among the Lepidoptera, in contrast, beat their wings so rapidly that they are visible only as a blur and often produce a faint whirring sound. The extraordinary achievements possible with this whirring flight are due to a narrowing of the forewings and a reduction of the hindwing area, for this conformation is aerodynamically the most favorable. Furthermore, the forewings and hindwings are effectively connected by a special device so that they can easily be moved together. In the males of this sort, the connective device consists of a sharply curved bristle, the frenulum, at the base of the hindwing, which hooks into a bent lobe, the retinaculum, on the underside of the forewing. In the females, there are usually three finer bristles, held to the forewing by a sort of comb. These structures provide an easy way to distinguish the two sexes.

The hawk moths (Sphingidae) have the most highly developed form of whirring flight; their narrow forewings, small hindwings, and spindly body give them the appearance of a modern airplane. Some species have been clocked at speeds as great as 60 kph (37 mph). But in addition, hawk moths are capable of hovering in the air like helicopters, while they use their long proboscises to suck the nectar out of the depths of their preferred flowers.

This sucking proboscis is a further distinctive characteristic of the Lepidoptera. At rest it is carried between the labial palps, rolled into a spiral; to take in food, it is extended by means of muscular action and

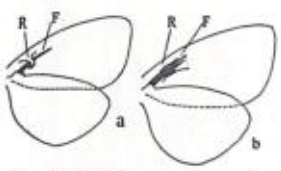


Fig. 15-6. Connection of forewing and hindwing by frenulum (F) and retinaculum (R): (a) in the male a strong bristle interlocks with a fold of cuticle; (b) in the female several thin bristles are anchored by a comb of bristles.

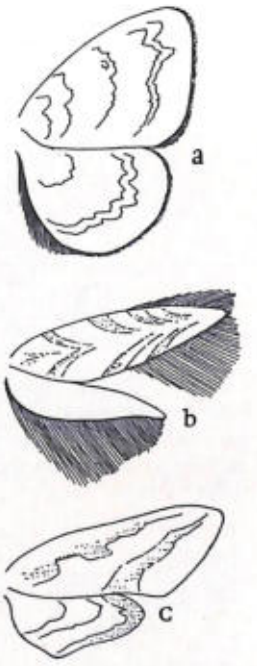


Fig. 15-7. Wing form and type of flight: (a) broad wing used for fluttering flight (geometrid); (b) narrow wing for parachute flight (the reduction of the wing surface is compensated by long, fringelike scales); (c) wing specialized for whirring flight (hawkmoth) with strong, narrow forewings and the aerodynamically advantageous reduction of hindwings.



Fig. 15-8. The sucking proboscis consists of two interlocking parts.

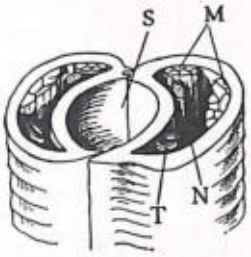


Fig. 15-9. Cross section of the proboscis: in the middle the suction tube (S), at either side of which is the cavity within the galea of the maxilla, containing muscle bundles (M), a nerve (N), and tracheae (T).

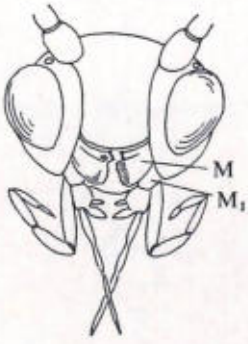


Fig. 15-10. The mouthparts of a primitive moth: well-developed mandibles (M) instead of a proboscis, and the maxillae (M_1) are normally segmented.

increased blood pressure. In the moths, particularly the hawk moths (see Fig. 15-38), it can be extremely long, often longer than the body; the greatest length measured is 28 cm. On the other hand, there are a number of moths in which the proboscis is regressed and nonfunctional. These animals, as adults, no longer eat, but rather live on the reserves stored up during the course of their development as caterpillars.

The sucking proboscis consists of the much elongated galeae of the maxillae, joined together along their length so as to enclose a tubular cavity through which fluids can pass. The two parts develop separately during the pupal stage, becoming joined only after the imago has emerged. In addition to the proboscis, there are other mouthparts on the head, which bear sense organs for taste and smell. These are the labial palps, possessed as a rule by all Lepidoptera, and the mandibular or accessory palps, which are well developed only in the more primitive groups and are absent or vestigial in the higher forms.

Although the majority of lepidopterans have a normally constructed sucking proboscis—or at least had one at some time in the course of evolution—there are a few small forms, the primitive moths (familyMicropterygidae), which have biting mouthparts used to eat the pollen of flowers. These animals no doubt provide us with a picture of the ancestors of all the Lepidoptera, which were provided with such biting mouthparts. The primitive moths are therefore usually placed at the base of the tree of lepidopteran evolution, though recently some zoologists have ranked them as a separate order, the Zeugloptera, between the Trichoptera (see Chapter 14) and the Lepidoptera.

The antennae on the lepidopteran head bear important sense organs, especially for the sense of smell. For the nocturnal flyers this sense is of crucial assistance in finding sexual partners and sources of food, since for these activities vision has been reduced to a subordinate role. The simplest lepidopteran antennae are threadlike, consisting of numerous individual segments. But often the surface is enlarged, permitting an increase in the number of sense organs and thus an improvement in the ability to detect stimuli. The simplest stage in this process is the formation of sawtoothlike projections on each antennal segment, but further elaboration can lead to paired feathery extensions which give the antenna the appearance of a plume. The peak of such development is represented by the giant silkworm moths (Saturniidae); each segment of their antennae bears two pairs of branchlets, each of which is covered with sensory hairs. With such elaborate structures, unimaginable achievements in sensory detection are possible (for example, by the silkworms of the family Bombycidae). The plumed antennae are usually much better developed in males than in females, for it is the males which must detect the sexual attractant, whereas the females need only use the sense of smell to find food plants, for themselves and for deposition of the eggs.

The compound eyes of lepidopterans are hemispherical. They provide

the insect with a rough, raster-type picture of its surroundings and permit the discrimination of different colors. In the diurnal species this ability is significant for recognition of both the sexual partner and the sources of food (particularly flowers). Nocturnal types, on the other hand, use their eyes primarily for general orientation by the weak light from the sky. The well-known fact that nocturnal lepidoptera so often fly to artificial light sources and can thus be caught and collected is ascribable to a misapplication of this orientation behavior. In contrast to humans, lepidopterans are capable of detecting even long-wave ultraviolet light; since this can be produced by modern lamps, it is possible to catch these insects with light sources we ourselves can hardly see.



Fig. 15-11. Various forms of antennae: A, filiform; B, clavate; C, serrate; D, bipectinate; E, plumose.

The most important organs for the sense of taste are located not on the head, but on the legs. These sensilla (see Chapter 1), on the terminal parts of the legs, the tarsi, detect not only the sweet substances produced by plants but highly unappetizing substances as well. Some species of Lepidoptera prefer to suck food from decaying or fermenting matter or even dung. When the females seek out certain food plants (those the caterpillars will eat) on which to lay their eggs, they test the plants for appropriateness with the tarsal sense organs, in the case of certain butterflies, beating the legs up and down.

In some lepidopteran families the tympanal organs are especially well developed. These auditory sense organs are located in the thorax or at the anterior end of the abdomen. In the basic form, they are depressions in the body surface equipped with tympanic membranes which oscillate in response to sound. In contact with the membrane are threadlike sense cells which respond to these oscillations and produce impulses in the sensory nerve fibers. Insofar as they are present, these organs are constructed in a characteristic way in each family, so that they are of great use in the classification of these insects. Their greatest value to the insects themselves lies in the detection of the ultrasonic tones produced by their worst enemies, the bats, for echolocation of their prey (see Vol. XI). By cleverly maneuvering in flight, turning suddenly, or simply letting themselves fall, the insects attempt to escape from the swoop of the bat.



Fig. 15-12. Various forms of eggs.

Reproductive organs

The cylindrical abdomen encloses important organ systems, not the least important of which are those for reproduction. At the end of the male abdomen are claspers, complex structures of chitin used in mating. Usually their shape is species-specific, so that they give the systematist another valuable criterion for classification. Many lepidopterans, otherwise identical in appearance, can be distinguished only by means of these organs. The external genitalia of the females ordinarily consist of an ovipositor which can be extended like a telescope and which is used to attach the eggs to various surfaces.

Metamorphosis

Lepidoptera undergo the complete metamorphosis characteristic of the higher insects. The eggs are usually very small; a caterpillar emerges and, in almost all species, feeds on plants and stores up proteins and fats as it

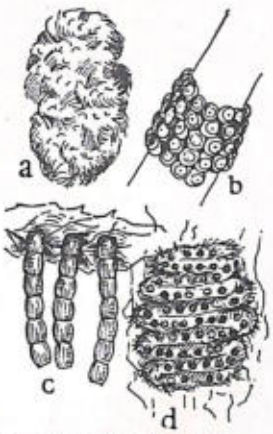


Fig. 15-13. Various egg masses: (a) that of the gypsy moth, covered with "wool"; (b) that of the common lackey, arranged in a spiral; (c) that of *Araschnia levana*, like little towers; (d) that of an Asian *Euproctis* species, in folded tubes made of woolly hairs.

grows. The fully developed caterpillar then transforms itself into a pupa, or chrysalis, a dormant stage that can hardly be seen to move at all. Within the pupa, however, drastic alterations occur, in the course of which the organs of the caterpillar degenerate completely. The materials of which the caterpillar was formed, including the stored substances, are employed to form the body of the future moth or butterfly. When the development of the flying insect is complete, it breaks through the shell of the chrysalis and frees its wings; at first small and soft, they are stretched out to their final size as blood is forced into the hollow veins. Finally, they harden in the air. The blood is then withdrawn from the wing veins, and the insect is ready to take off on its first flight.

The eggs of Lepidoptera are more or less spherical, often with the surface sculptured in a characteristic way, and their size ranges from 0.2 to 3 mm. The number of eggs one female can lay depends upon their size and can be anywhere from fifty to several thousand. The female deposits the eggs either individually, in small groups, or in large masses, gluing them the to substrate with the secretion of a gland; in many cases she covers them with a woolly substance consisting of the fine hairlike scales which form a wreath around the end of her abdomen. Species with long ovipositors push their eggs deep into crevices of various sorts or into seed capsules. Whereas most species select very carefully the place where the eggs are to be laid, a few scatter their eggs in flight; such random laying is done by the ghost moths (Hepialidae) and some meadow brown butterflies (Satyridae).

The caterpillars are animals of very simple construction. Their main task is eating, and they have no organs which are not associated with this function: they have no wings, no highly developed sense organs, and only short legs. They lack compound eyes; on either side of the head they have only a row of six ocelli which are barely able to distinguish light from dark. Nevertheless, they are capable of perceiving the trunk of a tree, so that they can proceed from the ground into the foliage of the tree on which they feed. Of the mouthparts, the mandibles are always large and powerful, admirably suited for chewing up plant food, even solid wood. As weapons of defense, though, they are of little use, and even less as aggressive weapons. The remaining mouthparts are small and poorly developed; they bear sense organs for touch and taste and serve to guide the caterpillar to an appropriate food plant. The caterpillars of many lepidopteran species are restricted to certain plants and would starve before accepting any other plant as food.

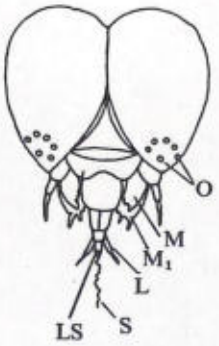


Fig. 15-14. Head of a caterpillar: O. ocilli; M, mandible; M_1, maxilla; L, labium; the labial spinneret (LS) extrudes a thread of silk (S).

In the middle of the labium of the caterpillar there is a small papilla, the spinneret, with the openings of the two silk glands. These glands are often very large, in some cases extending throughout the body (see Fig. 15-15). All caterpillars, without exception, are able to produce silken threads, though the amount they can produce varies. The thread extruded from a silk gland consists of two substances which harden on contact with the air.

The silk marketed commercially is this substance; true silk is produced by the SILKWORM (*Bombyx mori*), but the silk of other caterpillars is also used. The threads are usually white but often yellowish or, in the case of many large caterpillars, even dark brown.

These silk threads play a central role in the life of a caterpillar. Many caterpillars actually live on an endless string which they produce continuously; they attach it to the substrate and clasp it with their legs. Thus they can creep about on even the smoothest surfaces. If such a caterpillar falls from its position, it spins the thread out a bit more, still hanging from it, and then uses it like a rope to climb back into place. The same technique allows it to escape from enemy attacks. Species which live in hiding, and others which build communal nests, use the thread as a guideline to and from the feeding place. The caterpillar of course uses large quantities of silk to build cocoons and other woven structures, and the threads are also used to line mines in leaves and tunnels in wood.



Fig. 15-15. Diagram of a caterpillar; the large silk gland (S) is coiled throughout the body.

Each of the three thoracic segments bears a pair of short legs consisting of only one leg segment with one claw. On the caterpillar abdomen there are, as a rule, five fleshy pairs of prolegs which are not segmented, but rather represent evaginations of the body wall, at the apex of which there is a circle of curved hooks or crochets. Ordinarily these "abdominal feet" are on the third to sixth segments, and there is a similar appendage on the last. But in several families some pairs are missing—for example in certain owlet moths (Noctuidae) and all measuring worms (Geometridae). Among the prominents (Notodontidae) there are species in which the last pair is strongly modified.

The caterpillar's wormlike body is often decoratively colored and sometimes oddly shaped, with various outgrowths or with wartlike verrucae, thornlike scoli, or hairs on the upper surface. Presumably all these devices serve as protection from enemies, whether by camouflaging the caterpillar of frightening the predator. Some caterpillars also have organs specially designed for defense. One of these is the eversible osmeterium of the swallowtail caterpillars, which produces a repugnant smell. Other weapons of defense are urticating hairs (hairs which cause irritation when touched) and hard, sharp bristles, whose painful stab may be accentuated by poisonous substances.

Lepidopteran pupae are more or less rounded structures with hard shells, to which the primordia of the appendages are usually firmly attached along with the rest of the body. When they are located on or in the ground they are protected by hollows made of glued-together debris or by cocoons, often elaborately constructed of silk threads; in most of the diurnal species, however, the pupae hang free, suspended by small threads or in some cases by a silken girdle. Fundamentally the pupae are brown in color; only the free-hanging pupae are often brightly colored, sometimes with spots of a glowing metallic sheen which disguise the animal.

The life span of the fully developed adult butterfly or moth is depen-

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A male nymphalid butterfly (*Melitaea cynthia*).

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Caterpillar of the prominent *Cerura vinula*.

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Caterpillars: 1. The hawk moth *Deilephila elpenor*; 2. An African species of lasiocampid moth; 3. The shark *Cucullia artemisiae*, a noctuid moth; 4. The lobster moth (*Stauropus fagi*); 5. The saturniid moth *Aglia tau*; 6. The gypsy moth (*Porthetria dispar*), head of the caterpillar; 7. The pebble prominent (*Notodonta ziazac*), with a pseudo-head at the hind end of the body; 8. *Dasychira pudibunda*; 9. The scarce vapourer (*Orgyia recens*); 10. *Urapteryx sambucaria*, a species of geometrid; 11. The privet hawk (*Sphinx ligustri*) in defensive posture.

▷▷▷▷
A male saturniid moth (*Hyalophora cecropia*) seen from the front. The very feathery antennae enable the moth to locate the scent of a female from a great distance.







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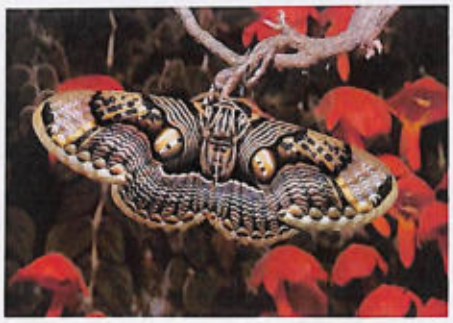


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dent upon its ability to eat and upon the inclusion of one or more diapauses. Those lepidopterans which eat as adults live, on the average, two to four weeks. Many need to be able to eat for a longer period if their eggs are to have time to ripen. If a dormant period is entered, particularly one which lasts the winter, the life span can be extended to several months, and by entering diapause in summer as well (as does the brimstone butterfly *Gonepteryx rhamni*, from Europe) they can attain a maximum life span of nine months. In contrast, lepidopterans which do not eat at all live, as males, only until they have mated or, as females, until the eggs have been laid—that is, a few days or even, in extreme cases, only a few hours.

The duration of the egg stage can amount to some days or even up to five months, if a dormant period is included. The caterpillars live at least a month and at most three years—depending upon the number of winter dormant periods and the abundance of the food supply. Caterpillars feeding on substances low in nutritive value, such as wood, usually require two years to develop. The pupal stage lasts at least a week, but it can be several months long, extending over one winter, and at most (as in the lasiocampid moth *Eriogaster arbusculae*) seven years. Often the length of the pupal stage is influenced by climatic conditions and thus can be quite variable.

At one time the Lepidoptera were divided into two groups on the basis of size, and the large lepidopterans were further subdivided according to whether they were active by night (the Heterocera) or by day (the Rhopalocera). According to modern systematists, such a classification is unjustified, for there are no distinguishing characteristics which adequately corroborate the separation of the small lepidopterans from the large ones. Many families were lumped together as "Microlepidoptera," the overall characteristics of which give evidence of a closer relationship to certain families of "Macrolepidoptera" than to others in the microlepidopteran category; two examples are the snout moths (Pyralidae) and the geometers (Geometridae). This earlier categorization was not even consistently applied in terms of size, since there were some very small and very large species in both the Microlepidoptera and the Macrolepidoptera.

Nor could the classification on the basis of nocturnal *vs.* diurnal habit be readily justified, since among the main group of Rhopalocera (the superfamily Papilionoidea) there are at least a few species active at twilight, whereas many of the Heterocera fly only when the sun is shining. Although outdated as a systematic classification, the distinction between the two groups is still reflected in the common terms "butterfly" and "moth." Butterflies, mostly diurnal, slender-bodied insects with threadlike antennae terminating in a club, belong to the family Papilionidae and those which follow it in the Systematic Classification section. All the other Lepidoptera treated here are known as moths (characterized in general by nocturnal habits, thicker bodies, and plumose antennae) except for the family Hesperiidae (known as skippers). In modern systematics it is considered useful

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Adult Lepidoptera: 1. The swallowtail *Papilio machaon*; 2. *Brahmaea wallichii*, a representative of the eastern Asian family Brahmaeidae, not mentioned in the text; 3. The luna moth *Actias selene*; 4. The eyed hawk (*Smerinthus ocellata*); 5. *Rotheschildia morana*, a saturniid moth; 6. The papilionid *Zerynthia hypsipyle*; 7. The "88" (*Callicore* sp.), a nymphalid butterfly; 8. *Aglia tau*, a saturniid moth; 9. *Rothschildia* sp. a saturniid moth; 10. *Morpho achilleus*, of the family Morphidae; 11. The hornet moth *Aegeria apiformis*; 12. The alder dagger (*Acronycta alni*), an owlet moth; 13. The red admiral (*Vanessa atalanta*); 14. and 15. An American saturniid moth, *Platysamia cecropia*.

Classification of Lepidoptera

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Above: the hawkmoth *Deilephila elpenor* flying to a campion blossom. Middle left: *Danaus aglea*, a relative of the monarch butterfly. Middle right: *Lobocraspis griseifusca*, an owlet moth from Thailand, sucking the lachrymal fluid from the eye of a banteng (*Bos javanicus*, see Vol. XIII). Below: In warm countries there are often many butterflies gathered at damp spots to drink. Here they are chocolate albatrosses (*Apias lyncida*) and at the left a papilionid (*Graphium sarpedon*) from southeastern Asia.

to distinguish 80–100 families of Lepidoptera, which we shall classify in two suborders according to the evolutionary level they represent: the Homoneura and the Heteroneura.

Suborder: Homoneura

The HOMONEURANS (suborder Homoneura-Jugatae) are distinguished by the similarity in structure of their forewings and hindwings. This is a very primitive characteristic of insects in general, and it is to this that their scientific name refers. The members of one homoneuran family, the primitive moths, even have functional mandibles and for that reason were considered by some entomologists as a separate order. In other families of this suborder functional mandibles do appear transiently during pupal development, but in the final adult form they have again been modified. In the ghost moth family, finally, the mandibles are completely regressed, so that these moths cannot eat. But this also occurs among the more highly evolved groups, and is to be considered as a secondarily acquired characteristic. The geographical distribution of this suborder is similar to that of other phylogenetically ancient groups: though they do occur in Europe, for example, they are primarily to be found in those parts of the world which separated early from the main land masses—especially Australia and New Zealand, where the group is represented in particularly large numbers. Only two of the four families of homoneurons are mentioned here, the primitive moths and the ghost moths.

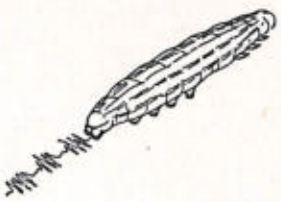


Fig. 15-16. In crawling along smooth surfaces, the caterpillar produces a ladder of silk which it grips.

Family: Micropterygidae

The PRIMITIVE MOTHS (family Micropterygidae) are distinguished by the above-mentioned functional mandibles. They are small insects, with wingspan no more than 6 mm. The coloration of many of them is very inconspicuous, but some species have a metallic sheen—blue, green, or purple—often with yellow spots. As moths they feed on the pollen of flowers and the spores of the lower plants. One of Europe's most common species is *Micropteryx calthella* (see Color plate, p. 341); small and metallic green, it is frequently to be found in spring sitting in the flowers of the marsh marigold (*Caltha palustris*) and avidly consuming the pollen. The genus is represented in the eastern U.S.A. by *M. auricrinella* (food plant unknown).

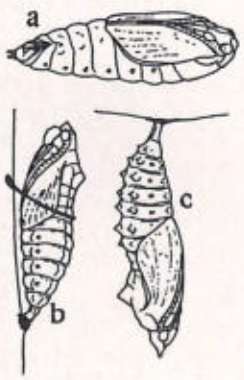


Fig. 15-17. Forms of pupae: (a) mummylike chrysalis of an owlet moth; (b) chrysalis fastened by a girdle of silk; (c) hanging chrysalis.

Caterpillars of this family live on mosses. They are also quite primitive in form; in contrast to all the other caterpillars they have true (though small) compound eyes. In addition, the young caterpillars have a row of separate appendages, large ovate, socketed scales on each side, a primitive characteristic lost in the full-grown animals. In some species the caterpillars are entirely without legs, while others have legs on all the abdominal segments, so that the average caterpillar leg number in this family is much higher than that of all other lepidopteran families. The moths fly only during the day when the sun is shining. The family is distributed throughout the world, but each of the several species occupies a limited area separate from those of the other species.

Family: Hepialidae

In contrast to the other families in this suborder, the GHOST MOTHS (Hepialidae) are of moderate to very large size. With a wingspan of up to



Fig. 15-18. Caterpillar of a ghost moth of the genus *Hepialus* sp. burrowing in a twig (part removed to show tunnel).



Fig. 15-19. Wing connection in the ghost moth by means of a jugum (Ju).

25 cm, they are among the largest of the Lepidoptera. They are very brightly colored, in some cases (for example, the large Australian species *Charagia ramsayi*; see Color plate, p. 359) with a mixture of numerous different hues. The caterpillars feed on the roots of plants; the moths usually fly in the evening or at night, though some species are active during the day.

Of the few species inhabiting central Europe, *Sthenopis argenteomaculatus* is the best known. Its caterpillars feed predominantly on the stems of alder, and if there are very many of them they do appreciable damage. The male moths have shiny, silvery-white wings and perform unusual swarming flights in the evenings, whirring up and down over a very small spot. The females, on the other hand, are spotted yellow and orange—that is, their general appearance is distinct from that of the males, a situation not uncommon among the Lepidoptera. They scatter their many small eggs while flying. One European species which flies at sunset is *Hepialus hecta*; here, too, the males perform oscillating swarming flights in one spot. During the dance they attract females with odoriferous substances secreted by glands on the hindlegs.

A peculiarity of these moths is the manner in which the wings are joined. The connecting device is a fingerlike lobe called the jugum, on the posterior margin of the forewing, which grips the anterior margin of the hindwing. Because of this unique structure, the Hepialidae have been regarded by some as a suborder (Jugatae), separate from all the other Lepidoptera. The mouthparts of the ghost moths are entirely regressed; the moths do not feed, but live on the reserve materials they stored up as caterpillars. For this reason, their life span is very short, amounting at most to a few days.

Suborder: Heteroneura

The suborder Heteroneura (Frenatae) includes all the other Lepidoptera —that is, the vast majority of the members of the order. The forewings of the HETERONEURONS are different in structure from the hindwings, and the latter vary greatly in form, usually being small, sometimes with notches, teeth, or prominent extensions, and sometimes even greatly regressed as in especially good flyers like the hawk moths. Opinions differ as to the number of families in the suborder; there are at most 100, of which about thirty-five will be described or at least mentioned briefly here.

Family: Nepticulidae

The smallest of all lepidopterans are the NEPTICULIDS (Nepticulidae), with an average wingspan of only 2 mm; even the largest of them are no more than twice that size. They are quite prettily and brightly colored, often with a metallic sheen. The caterpillars live in tunnels or mines, under bark or in leaves, and a few are gall makers. They eat out these galleries in a species-specific pattern. The choice of food plant in which to burrow is also characteristic of the species. Often the nepticulid species can be more easily identified by their galleries and the type of plant in which they are found than by the external appearance of the animals themselves Such "miners" and "borers" are also found in other lepidopteran families; they

all have in common a flattened body and mouthparts directed forward, characteristics which adapt them for life in constricted tunnels.

Although many of the Lepidoptera are called millers, we consider the TRUE MILLERS (family Tineidae) to be only the clothes moths and their close relatives. These are small, insignificantly colored species which. because of their peculiar way of life, damage human property. The caterpillars feed primarily on dead organic materials: fibers of animal and plant origin, horny materials, and the like. While inhabiting such human possessions, most tineid species have been inadvertently transported all over the world, so that nowadays they are very widely distributed.

The WEBBING CLOTHES MOTH (*Tineola bisselliella*) feeds on wollen material and on furs; it can easily be identified by its galleries, which consist of loosely woven tubes of silken threads. The CASE-MAKING CLOTHES MOTH (*Tinea pellionella*; see Color plate, p. 341), on the other hand, constructs small, flat, oval cases of threads and food remnants, and carries these about for its entire life as a caterpillar. This species, like the webbing clothes moth, feeds on fabrics and to some extent on furs. Another species which is often a pest is the CARPET MOTH (*Trichophaga tapetzella*), which can spin more capacious structures than its relatives.

As moths, members of this family are very reluctant to fly. Most of the moths which do fly about in houses belong to other, harmless families. But if there is a clothes moth among them, it is generally a male. The females, on the other hand, run very nimbly and when disturbed flee as quickly as possible to the safety of dark cracks. Hunting them is thus a rather ineffectual procedure. Today there are a number of highly effective chemical control methods, in which the threatened objects are impregnated, dusted, or treated with a vapor, to a large extent preventing their infestation by moths. There are numerous species of tineid moths which feed on dead animals or the rubbish in nests, and on rotting plants. The species which today are pests probably lived in the same way at one time, only later "taking advantage" of mankind.



Fig. 15-20. Bagworm in its case; it walks with only the thoracic legs.

Families: Tineidae and Psychidae

One of the most interesting lepidopteran families is that of the BAGWORM MOTHS (Psychidae). Most of its members are rather small, inconspicuous moths; there are 800 species, distributed throughout the world. As soon as they have hatched from the egg, even before eating anything, the caterpillars build a case, sometimes of threads alone but in other cases reinforced with bits of soil or plants. In this the bagworms spend their entire lives, up to and including pupation. It is built like a tube with both ends open; from the front end emerge the caterpillar's head and thorax, whenever it moves about, walking with the thoracic legs only. When at rest, during molting, and for pupation the caterpillar firmly attaches the front end of the bag to a substrate. The opening at the back is used for passing out feces and the exuvia after each molt. But the front-to-back orientation is not permanent; if prevented from walking forward, the caterpillar can turn around within the bag and move in the reverse direction.

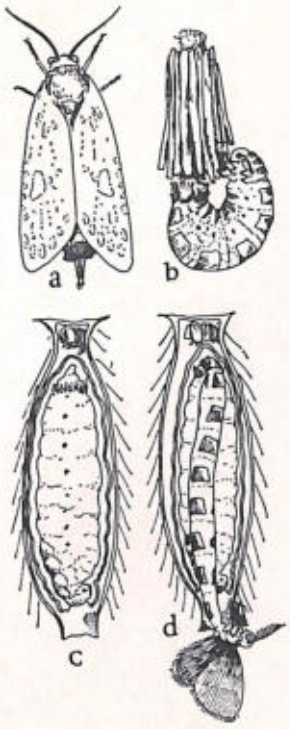


Fig. 15-21. Different forms of the female bagworm moth: (a) winged female of a *Melasina* species; (b) stubby-winged female of a *Fumea* species; (c) wingless female which never leaves her pupal case; she is inseminated by the male (d) when he pushes his very extensible abdomen into the case.

Bagworms continually enlarge and expand the case so that it fits them as they grow. The materials used and their arrangement, often elegantly designed, are usually characteristic of the species or at least of the genus. For example, the species of the tropical genus *Eumeta* select little sticks of equal length and lay them in parallel along the case, and the species of the northern African genus *Amicta* build rigid cases with four walls, each consisting of a stack of small pieces. In another genus a similarly constructed case can be twisted helically.

After the pupa pushes its way out of the case, the moth emerges. The males fly in search of females only during a few specific hours of the day; their lifetime is correlated with the amount of time spent in flight, and amounts at most to two days. The males do not eat, as their mouthparts are completely regressed. Most of the females, in contrast, are wormlike creatures without eyes or body appendages. They stay in the caterpillar's bag and in some cases do not even leave the pupal case. There are fully developed winged females in only a few species of bagworm moths; only in certain other species the females, though wingless, do leave the bag and await the male while clinging to it on the outside. The males are attracted by sexually attractive odoriferous substances produced by the females; the scent glands of those remaining in the bag are located in the thorax, quite in contrast to the situation in other lepidopterans, where the scent glands are in the abdomen.

Once a male bagworm moth has found a female, he pushes his abdomen, which can be extended to three times its ordinary length, into the case to inseminate her. Then she lays all her eggs within the case, collapses like an empty sack, and falls out. The caterpillars which hatch leave the case built by their mother and set to work immediately to make their own.

There are species of bagworm moths which reproduce without males, by parthenogenesis. In this case the embryo obtains the full complement of genes by the fusion of two nuclei during the maturation divisions of the egg; from then on it develops in the ordinary way. This process is particularly remarkable, and has been most carefully investigated, in the European species *Solenobia triquetrella*. (The related North American species, *S. walshella*, has both males and females.) There are several subspecies of this moth, in some of which there are males, and hence females whose eggs must be fertilized, while other species usually reproduce parthenogenetically but can occasionally be inseminated by males. Another species, the European *Apterona crenulella*, is distinguished by its snailshell-type case. Here the subspecies have a particular geographic distribution: the purely parthenogenetic *Apterona crenulella helix* lives in central Europe, whereas in southern Europe there are only subspecies which reproduce bisexually; the two forms overlap at the southern edge of the Alps. Another well-known European species is *Psyche viciella* (see Color plate, p. 341), whose bag is not uncommonly found spun onto plants in sedge

fields. The EVERGREEN BAGWORM (*Thyridopteryx ephemeral formis*) is frequently a pest of cedar and arborvitae in the warmer parts of the U.S.A.

The CLEARWING MOTHS (family Aegeriidae, formly called Sesiidae) are very easily recognizable by their narrow wings, which bear scales only along the margins and otherwise are as clear as glass and thus resemble those of some wasps. The brightly colored body enhances the resemblance. Some species have distinctive long hairs on the hindlegs, so that they look like bees with pollen baskets. Most of these small to medium-sized moths fly on days when the sun is shining. The more than 800 species are distributed worldwide.

The HORNET MOTH (*Aegeria apiformis*; see Color plates, pp. 327 and 347) of Europe and North America earns its name from its appearance; such a striking similarity of a defenseless creature to an insect like a wasp or hornet, protected by defensive weaponry, is an example of mimicry (see Chapter 1) and is not uncommon among the Lepidoptera. Much has been written about whether the mimic, the defenseless insect, really is protected by this device and if so, why. Probably predators learn to avoid the stinging wasps and, as a consequence, avoid the very similar, harmless mimics as well, since they cannot distinguish them from their models.

The caterpillars of the clearwing moths are pale, naked larvae living within plant stalks, tree trunks, or roots, where they often bore long galleries. Some cause galls in their food plants, while others live in the galls produced by gall wasps. Certain species can be pests if there is a mass outbreak; one of these is the hornet moth, whose caterpillar lives in the trunks of old poplars and destroys the wood with its galleries, and another is the caterpillar of *Bembecia marginata*, which often does great damage to raspberry plants. Before pupation, the caterpillar builds a cocoon of bits of wood just below the surface of the bark, separated from the outside by only a thin wall. There it pupates, and when the moth is ready to emerge the pupa breaks through the thin wall and pushes itself halfway out, using the backward-pointing spines arranged in a ring around the abdomen. One can often see the empty pupal cases sticking out of the stems of plants.

The CARPENTER MOTHS (family Cossidae) are medium-sized to large moths, usually dark in color and patterned to look like bark, and distinguished by the sturdy structure of the body. The mouthparts are largely regressed, so that they cannot eat. They fly primarily at night. With about 800 species, they are found in all parts of the world.

The naked, weakly colored caterpillars live in the stems and roots of perennial plants, often in the trunks and branches of large trees, where they can do appreciable damage. Since their food is usually of rather low nutritive value, the larger species require two or more years for development. The caterpillar of the common European GOAT MOTH (*Cossus cossus*; see Color plate, p. 347) and the North American *Acossus centerensis* spend two

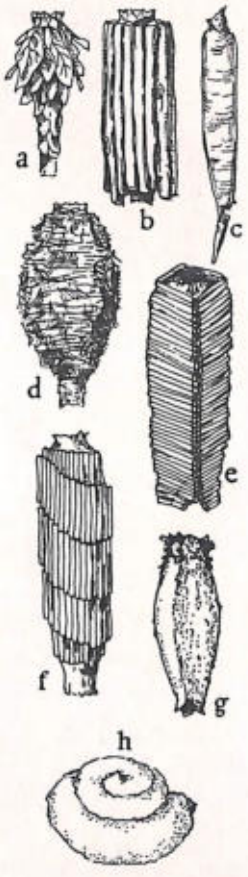


Fig. 15-22. Various cases built by the bagworm:
(a) *Canephora* sp., with bits of leaves and grass;
(b) *Eumeta* sp., with longitudinally arranged twigs;
(c) *Euketicus* sp., made entirely of silk;
(d) *Phalacropteryx* sp., with little sticks arranged crossways and bound together with silk;
(e) *Amicta* sp., with sticks arranged in a square tower;
(f) a tropical species, with sticks arranged in a helix;
(g) *Solenobia* sp., covered with bits of lichen;
(h) "snailshell" of an *Apterona* species, covered with sand.



Fig. 15-23. Many leaf rollers spin, or roll, leaves together and live inside.

years in the trunks of poplars and willows or other deciduous trees, betraying their presence by the frass (sawdustlike excrement which falls out of the holes) and by the strong smell of wood vinegar (a mixture of acetic acid, methanol, and other volatile compounds) it sends out. Another species just as annoying to mankind is the widely distributed LEOPARD MOTH (*Zeuzera pyrina*), whose caterpillars live in fruit trees. The wings of the moths have numerous steel-blue spots on a white ground. Another, an Australian wood-boring species, is one of the largest lepidopterans, with a wingspan of 25 cm.

An economically much more important family is that of the LEAF ROLLERS (Tortricidae), with 1500 species; many species of this ubiquitous little moth are severe pests throughout the world. As moths, the leaf rollers are sometimes gaily colored and characterized by the angular outline of the wings. The caterpillars of many species live in rolled-up leaves which they have pulled together by means of their strands of silk. Other species live singly or in groups in nests of plant materials fastened together with silk; in so doing they do damage to the plants beyond that caused by their eating.



Fig. 15-24. The caterpillars of the small ermines (*Yponomeuta* sp.) construct extensive webs in which the pupae are fastened.

For example, outbreaks of caterpillars of the PEA-GREEN OAK TWIST (*Tortrix viridana*; see Color plate, p. 341) in certain years have defoliated entire oak groves in Europe. Another notorious pest is the GEMMET SHOOT (*Evetria buoliana*), distinctive because of its pretty chestnut-red-patterned forewings. Its caterpillars spin together the tips of young pine shoots and then eat them, sometimes slowing the growth of the plant to a considerable degree. There is a whole group of fruit-tree leaf rollers which is unpopular with gardeners; the best-known of these is the apple tree pest called the CODLING MOTH (*Laspeyresia pomonella*), which from its original home in Europe has been inadvertently transported all over the world. The females lay eggs in the blossoms of the apple tree, and the small caterpillars burrow into the young fruit, later feeding in its core. Fully grown, the "worms" (as they are erroneously called) leave the apple through a hole they bore and pupate in the ground. They spoil a great number of apples every year; a serious attempt to control them with sprays is very expensive, since the long flying period of the moths demands repeated spraying.

In European wine-producing areas *Cochylis ambiguella* is much feared, for the caterpillars of the first generation spin the blossoms together and eat them. The second generation appears in summer, when the caterpillars develop in and on the grapes. This species is one of the worst pests in vineyards, second only to the grape phylloxera (see Chapter 11). With the widespread modern use of air transport, leaf-roller species are often carried accidentally from one part of the world to another, where they find a new home. Therefore it has become customary to inspect very carefully all imported plants; shipments infested by leaf rollers are destroyed.



Fig. 15-25. The plume moths rest with wings outstretched but rolled up.

The five families mentioned so far all belong to the superfamily

TINEOIDEA. This group also includes a number of other families, of which we shall mention only the DIAMOND-BACK MOTHS (family Plutellidae). The most important of these is the DIAMOND-BACKED MOTH (*Plutella xylostella*); its caterpillars, in almost every part of the world, feed primarily on cabbage and related plants as well as on wild cruciferous plants.

Family: Yponomeutidae

Any observant student of nature in summer can see thick webs on the spindle tree (*Euonymus*), often covering whole bushes. These contain large numbers of small caterpillars, which may completely defoliate the plants. These are caterpillars of the ERMINE MOTH (family Yponomeutidae), in the abovementioned case the European species *Yponomeuta evonymella* (see Color plate, p. 341) and the American species *Y. padella*. Caterpillars of these species always live in such large associations and thus make extensive webs, where they also pupate. The small moths have narrow wings, the forewing being white with many small black spots. There are many very similar species in this family, some of which are injurious to cultivated plants, particularly fruit trees, because they eat the leaves and their webs hinder setting of the fruit.

Caterpillar communities of this sort are found in a number of different lepidopteran families. In comparison with the associations made by other insects, however, they can hardly be considered as an initial stage in the formation of a real society. In relative terms this association is a very loose one, and it lasts only during the caterpillar stage; the adult moths scatter as soon as they hatch. Living in a common web, the caterpillars are protected to a certain extent from enemies, for not many animals are able to force their way into the tough tissue.

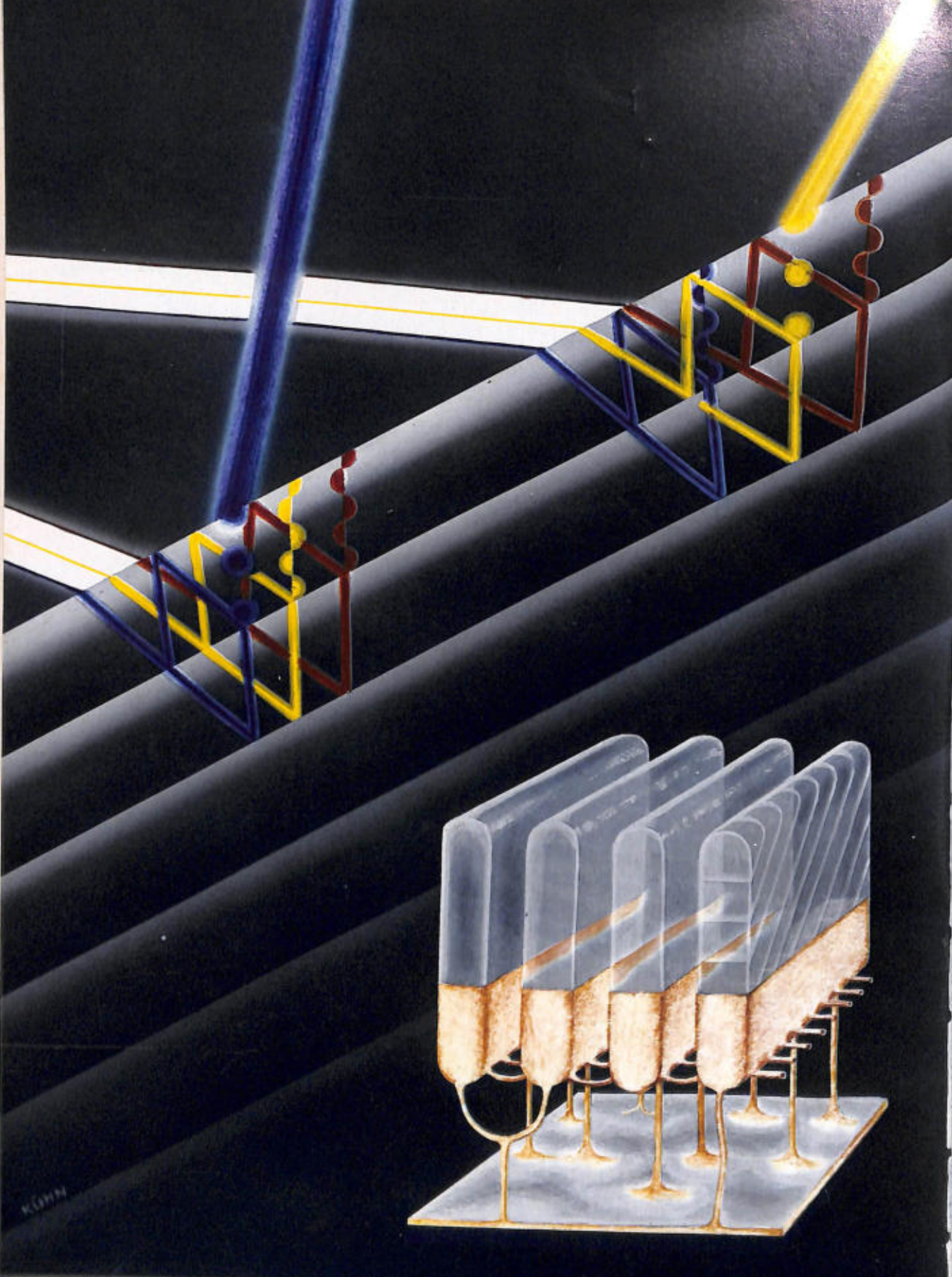
Despite their names, the PLUME MOTHS (Pterophoridae) and the MANY-PLUMED MOTHS (Orneodidae) are not particularly closely related; the plume moths are closer to the Pyralididae. But in the structure of their wings (see Color plate, p. 341) they are strikingly similar. Members of both of these very widely distributed families have wings divided into several lobes by deep indentations between the veins; the ends of the lobes are bordered with a long, hairy fringe which enlarges the area of the wing. In the many-plumed moths, each wing is split down to its base into six narrow lobes. In the plume moths, the indentations reach only as far as the middle of the wing, dividing the forewing into two lobes and the hindwing into three. These small, fragile animals, with wingspans at most 2 cm, are not capable of remarkable performance in flight. Their flight is more like a gentle drifting through the air, and they are easily carried away by the wind.

Families: Orneodidae and Pterophoridae

Moths of both these families usually fly by night and rest in plants during the day, the plume moths in a most unusual position: unlike other moths, they do not lay their wings back against the body, but rather stretch them out to the side, rolling them up to form a rod. Thus the moth presents a T-shaped appearance, and in its natural surroundings it is hard to recognize as a moth; the observer at first supposes himself to be looking at

▷ Examples of Batesian and Mullerian mimicry: above the gray lines in each column are the inedible models and below them, the mimics. 1-7. An African series, consisting of inedible species of the family Acraeidae (1-3) and their mimics of the families Nymphalidae (4-6) and Papilionidae (7). 8-11. Underside of the wings of four African pierid species. 12-17. A South American series, consisting of inedible species of the family Ithomiidae (12, 15), Danaidae (13), and Heliconiidae (14) and their mimics, two species of the family Pieridae (16-17).


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Iridescent colors of a lepidopteran wing. (Explanation of the picture opposite.) Iridescent colors are widespread among insects, and are often admired. They are produced not by absorption due to pigments, as are many colors, but by the phenomenon of optical interference.

The course of events is represented schematically in the illustration. A requirement for the production of iridescent colors is that the surface of the reflecting body—the wing scales, in the case of the Lepidoptera—consist of very thin transparent lamellae. At the bottom right of the picture is a piece of a wing scale, greatly enlarged; the element at the far right includes the diagonal lamellae found in the Morphidae. The main part of the picture shows these lamellae even further enlarged.

If white light (containing all colors of the spectrum) strikes the surface at a certain angle, the individual colors are refracted to a different extent as the light enters the transparent layer; a rainbow is produced in the same way as with a prism. Just one beam of light, at two different angles of incidence, is shown in the plate. For simplicity only the colors blue, yellow, and red (displaced from one another for clarity) are drawn in. When the rays reach the interfaces between the deeper lamellae, they are partially reflected and partially transmitted to the next interface, where the process is repeated.

Because of these multiple reflections, the light which reemerges from the wing scales (the light we see) has contributions from different rays of light which have traveled different paths, some reflected immediately, others from the second interface, and so on. Now the way that light propagates and combines can best be treated in terms of electromagnetic wave theory; that is, light behaves as though it were an undulating wave, with a spatial wave length corresponding to its color, in a sense going through maxima and minima as it proceeds along its direction of propagation. When two rays combine (or "interfere") such that the maxima of one fall on the mimina of the other (as suggested by the alternating semicircles in the diagram), they cancel so that no energy is propagated; if the maxima coincide, however, (as suggested by the full circles) they reinforce one another.

Several factors determine whether the differently reflected rays will have path lengths giving cancellation or reinforcement. These include the thickness and indices of refraction of the lamellae, the wave length of the light, the angle of incidence, and the fact that each reflection can produce a reversal (maximum for minimum) of the waves.

The situation is far more complex than that shown in the plate, but it can happen that all these factors combine to allow primarily one color and not the others to reemerge. On the left, the interference is indicated diagrammatically for the reinforcement (of blue) and cancellation (of yellow and red) at the first interface below the surface. On the right, at a different angle of incidence, the geometry has changed so that now it is yellow for which reinforcement applies. It is therefore understandable that the colors can change, or shimmer. In certain situations, the incident light may not be reflected at all, and then the surface appears black. In the morpho butterflies the lamellae of the scales are set at an angle; it turns out that only blue wavelengths can be reflected, so that the butterflies appear blue or black, depending on the angle of incidence. In the Uraniidae, on the other hand, the lamellae are parallel to the surface and can—again, depending on the angle of incidence—reflect many of the colors of the rainbow.

a part of the plant. This kind of conformity in the appearance of an animal with objects in its surroundings is an effective protective device, and one which frequently occurs among the Lepidoptera. Creatures so disguised actually seem to seek out resting places which correspond to their coloration, patterning, and posture.

Family: Coleophoridae

The CASE BEARERS (family Coleophoridae) are noteworthy because of their ability to build shelters for themselves as caterpillars, as do the bagworms. But in contrast to the bagworms, the case bearers only rarely use extrinsic materials for their structures; they make them entirely of their own silk, spun and glued into parchmentlike tubes. The tubes are small, at most 2 cm in length; frequently they are curved or even rolled up in a spiral at the back end. There is only one opening, at the front, through which the caterpillar puts out its head and thorax when walking. These caterpillars are very much restricted to specific food plants and would starve rather than eat a plant of another sort. This property is called monophagy, and is widespread among lepidopteran caterpillars; it presents great difficulties to anyone wishing to raise them, since the proper plants are often quite hard to find. The moths in this family are small, even minute; ordinarily the coloration is simple and dull, but sometimes they have a lovely metallic sheen. Their wings are narrow, and they are not especially good flyers. So far several hundred species are known, but the total number may well be much larger.

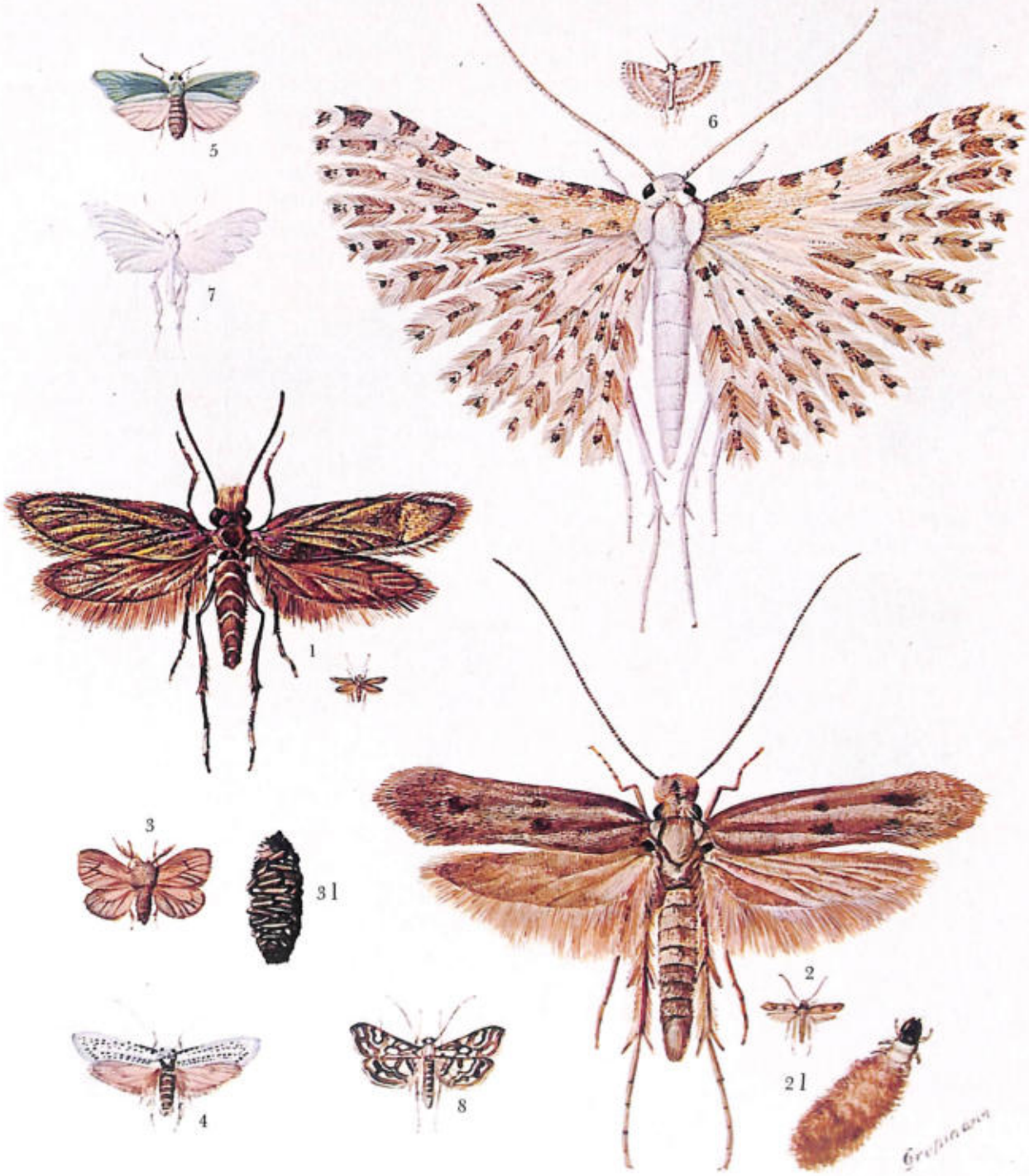
Family: Pyralididae

The usually brightly colored, shiny SNOUT MOTHS (family Pyralididae) are of small to medium size; some of the roughly 12,000 species are found in all parts of the world. Most of them, however, live in the tropics, where a great variety of forms has evolved. And their habits are just as varied; some of the remarkable characteristics of snout moths are unique among the Lepidoptera. All snout moths share one characteristic, the tympanal organ on the anterior part of the abdomen; this auditory organ detects the ultrasonic "sonar signals" of bats, and by giving an early warning, often enables the moths to escape these predators. Furthermore, snout moths of some species are able to produce sounds themselves, rattling or cracking noises generated by windowlike membranes at the bases of the forewings. We distinguish a number of subfamilies, quite different in appearance and way of life.

The subfamily Galleriinae includes the GREATER WAX MOTH (*Galleria mellonella*), a dusky insect with a wingspan of about 4 cm. The caterpillars can do great damage to beehives, since they feed on the wax and thus destroy the comb. In addition, they cover large areas inside the hive with their dense, irregular webs, making life impossible for the bees. Beekeepers loathe wax moths and fight them with every means at their disposal. People who maintain aquarium and other pets, though, put the caterpillars to good use as an accessory food for their animals.

Caterpillars of the subfamilies Schoenobiinae and Nymphulinae have become adapted to life in or on aquatic plants; in many cases they have

▻
Primitive moth: 1. *Micropteryx calthella*, enlarged and actual size.
Tineid moth: 2. The case-making clothes moth (*Tinea pellionella*), enlarged and actual size; 2*l*, caterpillar in its case.
Bagmoth: 3. *Psyche viciella*; 3*l*, caterpillar case.
Ermine moth: 4. *Yponomeuta evonymella*. Leaf roller: 5. The pea-green oak twist (*Tortrix viridana*).
Many-plumed moth: 6. *Orneodes grammodactyla*, enlarged and actual size.
Plume moth: 7. *Alucita pentadactyla*. Pyralidid moth: 8. *Hydrocampa nymphaeata*.


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European moths. Lymantridae: 1. One of the black arches (*Lymantria monacha*), sitting; 2. The scarce vapourer (*Orgyia recens*), wingless female on her cocoon, mounted male with wings spread out. Arctiidae: 3. The garden tiger moth (*Arctia caja*). Saturniidae: 4. The emperor moth (*Saturnia pavonia*), mounted moths; 4*l*, caterpillar; 4p, pupa in opened cocoon. Lasiocampidae: 5. The common lackey (*Malacosoma neustria*), mounted moths; 5e, eggs; 5*l*, caterpillar; 6. The oak eggar (*Lasiocampa quercus*), mounted moths.

even become true aquatic animals, an achievement found nowhere else in the order. These caterpillars obtain oxygen in various ways. Some of them spin bits of plants together to form air-filled underwater chambers in which they live. Others extract oxygen directly from the water by means of tracheal gills, small protrusions of the body wall which are richly supplied with fine tracheae. Caterpillars of the genera *Nymphula* and *Cataclysta* are found almost everywhere in fresh water; they live in small cases constructed of plant materials. Species of the genus *Elophila* spin netlike webs in which they catch not only particles of food, but also air bubbles which they breathe; these caterpillars usually live in rapidly flowing brooks.

The subfamily Schoenobiinae includes the European moth *Acentropus niveus*, whose females can have either of two types of wings, a stumpy-winged form and a form with normal wings, which can fly. The appearance of these different forms is determined in part by variations in the cycle of development from one generation to the next; normal wings are formed primarily in autumnal generations. The moths emerge from the pupal case under water and thus must be provided with a way of getting to dry land. They are covered with a dense layer of wax which repels the water and makes them so buoyant that they rise to the surface. Once at the surface of the water, the moths run over it to the shore or to plants rising above the surface; they climb these and spread their wings.

The many species of GRASS MOTHS (subfamily Crambinae) are found throughout the world; the moths are distinguished by their long palps which extend forward like a snout. One serious pest in this group is the SUGARCANE BORER (*Diatraea saccharalis*), which attacks sugarcane plants in the tropics. At rest, the moths fold back their narrow wings and roll them around the body.



Fig. 15-26. The case containing the caterpillar of a coleophorid moth (*Coleophora* sp.) The caterpillar produces open mines on leaves.

Moths of the subfamily Phycitinae have similarly narrow wings, usually with a characteristic patterning of transverse stripes in various shades of gray. Among these is the MEDITERRANEAN FLOUR MOTH (*Anagasta kuehniella*), a popular laboratory animal for all sorts of zoological experiments. It is not popular with anyone else, however, because of the damage it does to stored dry foods, particularly flour. The South American snout moth *Bradypodicola hahneli* occupies a peculiar habitat: it lives in the fur of sloths, the caterpillars feeding either on the hair itself or on the algae which grow there (see Vol. XI). This epibiotic way of life is highly unusual among the Lepidoptera.

Family: Uraniidae

There are only 100 species of URANIIDS (family Uraniidae), found exclusively in the tropics. The majority are small, dark moths which fly only at night. But there are also some large species active during the day; with their glowing colors, these are among the most beautiful lepidopterans of all. Their magnificence equals that of the brightest butterflies, and a further source of confusion is the presence in some species of "tails" at the back of the hindwings, reminiscent of the swallowtail butterfly.

In the Indo-Australian region, one finds the genera *Alcides* and *Nyctalemon*, in which the blue color at the wing margins changes to green or yellow, depending on the direction from which the light comes. Species of the South American genus *Urania* glow in shades of blue, green, red, and gold, and have long tail extensions on the hindwings. But the largest and most beautiful species is the Madagascan uraniid *Chrysiridia madagascariensis*, with several wing tails and particularly brilliant and varied coloration. It has green and blue stripes on a black background, with purple spots on the hindwings, and a gleaming white fringe around the edge of the wing. As the light strikes it differently, the shimmering colors change in an indescribably magnificent display. Iridescent colors (see Color plates, pp. 312/313 and 338) are no rarity among insects, but they are seldom so striking as in the uraniids and certain butterflies.



Fig. 15-27. Tympanal organ on the abdomen of a moth; the opening (O) is protected by an earlike cover.

Family: Geometridae

The GEOMETERS (family Geometridae) are rather amusingly named, for geometer means one who measures the earth. The name refers to a very characteristic behavior of this family. The caterpillars have only two pairs of limbs on the abdomen, the last pair of abdominal feet and an extra pair of appendages at the end of the body, and for this reason they move as though measuring the path by the length of their bodies (hence the alternative names, measuring worm and inchworm): the caterpillar first stretches the front end of its body far forward and takes hold with the thoracic legs, then it pulls up the hind feet, making a loop in the air with the body (they are also called loopers), and sets them down just behind the thoracic feet. Now the anterior end can be extended again, and so on.

With about 4000 species, the geometers form one of the largest lepidopteran families. They are distributed throughout the world. The delicate moths have broad wings with a spread of 5 mm to 10 cm; most of them are of small to moderate size. They are not skilled flyers, but rather flutter through the air, and the great majority are active only at night. During the day they rest with outspread wings, whose coloration is usually matched to the surroundings they select. This type of protective coloration provides an excellent camouflage, and the resting moths can be discerned only with difficulty. Here, again, one receives the impression that the animals actively seek out a resting place corresponding to their coloration. Green species usually sit on the underside of green leaves, whereas gray and brown moths choose tree trunks, rocks, and the like. There are only a few really brightly colored geometer species, and even those are not easy to detect in their natural surroundings, for the alternation of spots and stripes with which they are decorated has the effect of "dissolving" the outline of the body into the surroundings. This is sometimes referred to as somatolytic patterning.

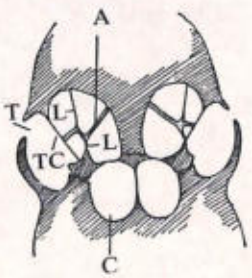


Fig. 15-28. Section through the tympanal organs in the thorax: the auditory nerve (A) is attached to the tympanum (T) and held in place by two ligaments (L); outside the tympanum lies the tympanal cavity (TC) and medial to it is another cavity (C) for pressure equalization.

An example of the importance in the life of the geometers of coloration matched to the background is found in the PEPPERED MOTH (*Biston betularia*). Only 100 years ago these European geometers were always white with only a sparse sprinkling of black spots, so that they were well camou-

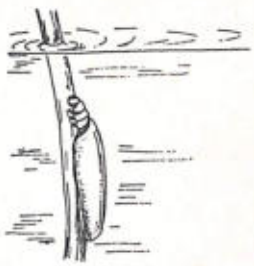


Fig. 15-29. Caterpillar of a pyralidid moth (*Nymphula* sp.) with its case under water.



Fig. 15-30. The Mediterranean flour moth (*Anagasta kuehniella*, family Pyralidae).

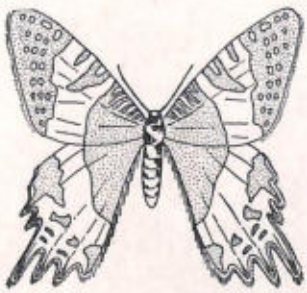


Fig. 15-31. The uraniid moth *Chrysiridia madagascariensis* displays its striking wings.

flaged on the light trunks of birch trees. Then suddenly, probably as a result of a mutation, there appeared in the industrial regions of England the completely black form, carbonaria. Since these moths could hide much better on the soot-blackened trunks, their numbers increased rapidly and they began to expand their range, presumably by a process of natural selection involving their avian predators; the birds ate the white moths, which were no longer camouflaged, and overlooked the black ones. This process of selection extended even into central Europe, though in remote areas the white moths could still survive, for there the black form was more vulnerable to the birds. A similar phenomenon occurs in the related North American species, the PEPPER-AND-SALT MOTH (*B. cognataria*).

Most of the geometer caterpillars are also excellently camouflaged; the long thin body is appropriately colored and frequently even has knobby thickenings and projections which give it the appearance of a short twig. This effect is enhanced by the caterpillar's resting posture. It holds onto a branch with only the abdominal feet, keeping the body outstretched at an angle similar to that expected of a real twig. But this attachment to the substrate by only two pairs of legs is rather insecure. The caterpillars reinforce it by another means: a thin, almost invisible thread of silk runs from the spinneret on the head to the tree branch, where it is firmly glued down. Should the caterpillar fall, it remains hanging from this thread and can climb back up along it. Sometimes, like caterpillars of other families, they fall intentionally as a way to escape from an enemy; a caterpillar suddenly falling through the air usually ends up beyond the reach of its attacker. Young caterpillars also use this technique to change their territory; by dangling from a long thread, they can move to neighboring trees.

Only a few of the many geometrid species, chosen for their familiarity or economic importance, will be mentioned here. The conspicuous green of the medium-sized European geometer *Geometra papilionaris*, oddly enough, is not a fast color; dampness changes it to a dull yellow. The caterpillars of the FALL CANKERWORM (*Alsophila pometaria*) can sometimes destroy whole deciduous forests. Other trees are often injured by geometers of the genera *Erannis* and *Operophtera*. Since the females are almost wingless, they can be controlled by simple measures. After emerging from the pupae, which lie in the ground, they climb up the trunks of trees; if one encircles the tree with a band of glue, the moths become stuck there, and any eggs laid below the glue are easy to collect. One of the best-known European species is the MAGPIE MOTH (*Abraxas grossulariata*), which used to be noticeable by its effect on currant and gooseberry bushes but today has become rather uncommon. In the U.S.A., the CURRANT SPANWORM (*Itame ribearia*) takes its place. The magpie moth's bright patterning is a good example of somatolytic coloration (see Color plate, p. 348). Actually, the pests are only a very small fraction of the geometrid species, most of which have no economic significance for humans (cf. Color plate, pp. 363/364).

A number of lepidopteran families were once grouped as "spinners," because the caterpillars spin elaborate and capacious structures. Many of these, however, are not closely related to one another. Of the numerous families characterized by this behavior, only a few can be described here.

Family: Limacodidae

The SLUG-CATERPILLAR MOTHS (family Limacodidae) are of small to moderate size, look very woolly because of their covering of hairs, and are often brightly colored. There are green species, some with red or brown transverse stripes, and others with a metallic sheen. The European *Cochlidion limacodes* is brown with darker cross stripes. One of the most common species in the U.S.A. is the SADDLEBACK CATERPILLAR (*Sibine stimulae*), which as a larva, has stinging hairs on its body. These are extremely irritating to the skin. Most members of this family, which includes about 500 species, are tropical.

The limacodids can be easily identified by their caterpillars, they have an arched dorsal surface, a flat ventral surface, and no legs at all. Hence, these slug-caterpillars crawl forward slowly, rather like their namesakes, on paired suction ridges. The very small head can be withdrawn far into the thorax. Many species have strong sharp spurs on the back which can cause appreciable wounds in human skin. Others bear fleshy outgrowths, and still others have a thick, transparent skin that looks like hard gelatin. The caterpillars pupate in rounded, hard-shelled cocoons with a specially made cover which the moth pushes off when it is ready to emerge.

A South American species, *Phobetroh hipparchia*, pupates in an unusual manner. It does not strip off the outer layer of the body, as most caterpillars do, but rather detaches itself from it and remains inside. Here it spins a cocoon, and the old skin, armed with urticating hairs, lies over the cocoon like a shield.

▻
European moths.
Hawkmoths: 1. The death's head hawkmoth (*Acherontia atropos*) in flight; 2. The broad-bordered bee hawkmoth (*Hemaris fuciformis*), mounted.
Owlet moths: 3. The common yellow underwing (*Triphaena pronuba*), mounted; 4. The red underwing (*Catocala nupta*), mounted. Carpenter moth: 5. The goat moth (*Cossus cossus*), resting; 5*l*, caterpillar in the wood of a willow.
Clearwing: 6. The hornet moth (*Aegeria apiformis*), mounted.

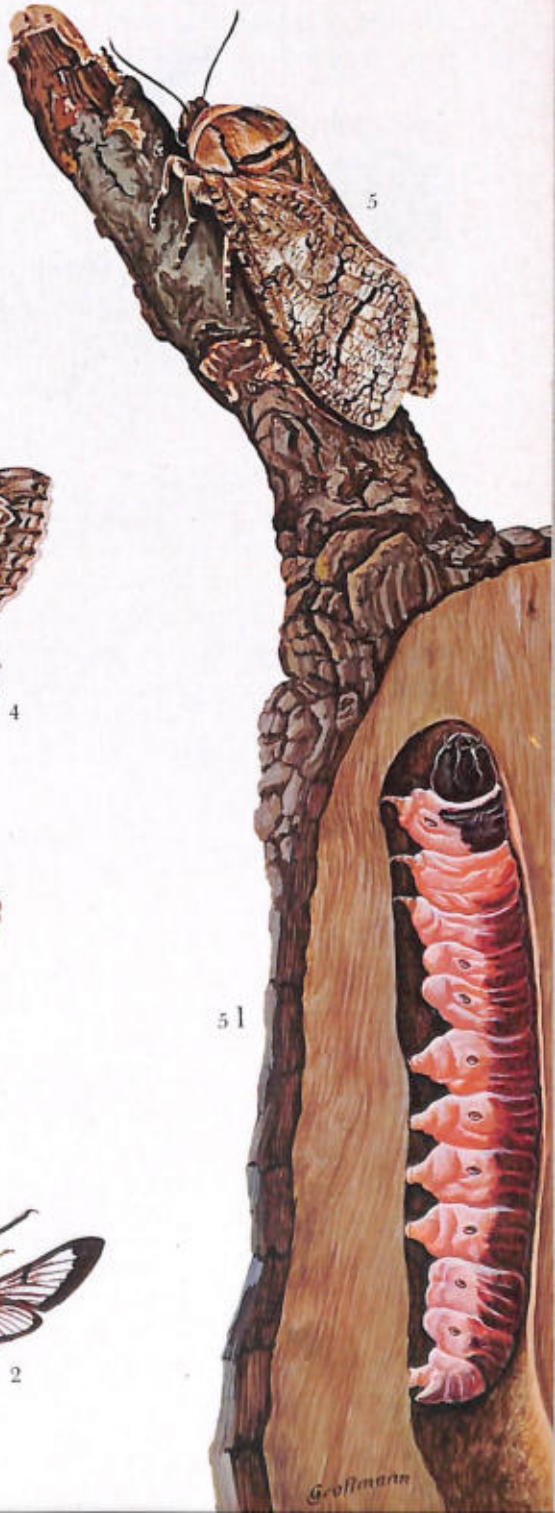
Family: Saturniidae

The GIANT SILKWORM MOTHS (family Saturniidae) are medium-sized to large; some of the very largest lepidopteran species, especially with respect to wing area, belong to this family. The wingspan of these moths can reach 25 cm. The broad wings are densely covered with scales and usually have round or angular transparent eyespots. The tip of the forewing is often drawn forward into a sickle shape. Some species have extraordinarily long, narrow tail extensions on the hindwings. As a rule the saturniids are very brightly colored, with red, brown, yellow, and green areas separated by dark bands. The body is sturdy. The males in particular, active by day in many species, can fly rapidly and with agility. The more sluggish females fly only at night and exclusively for the purpose of laying their eggs. In both sexes the mouthparts are regressed, so that the moths cannot eat. Male saturniids probably have the largest antennae of all the Lepidoptera; there are two pairs of branchlets on each segment. The antennae of the females are much smaller and simpler.

The caterpillars are large, corresponding to the size of the moths, but vary in shape. There are some quite simple forms without any outgrowths, while others bear rows of round or rodlike papillae on the back, often with



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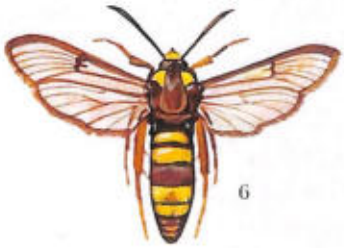
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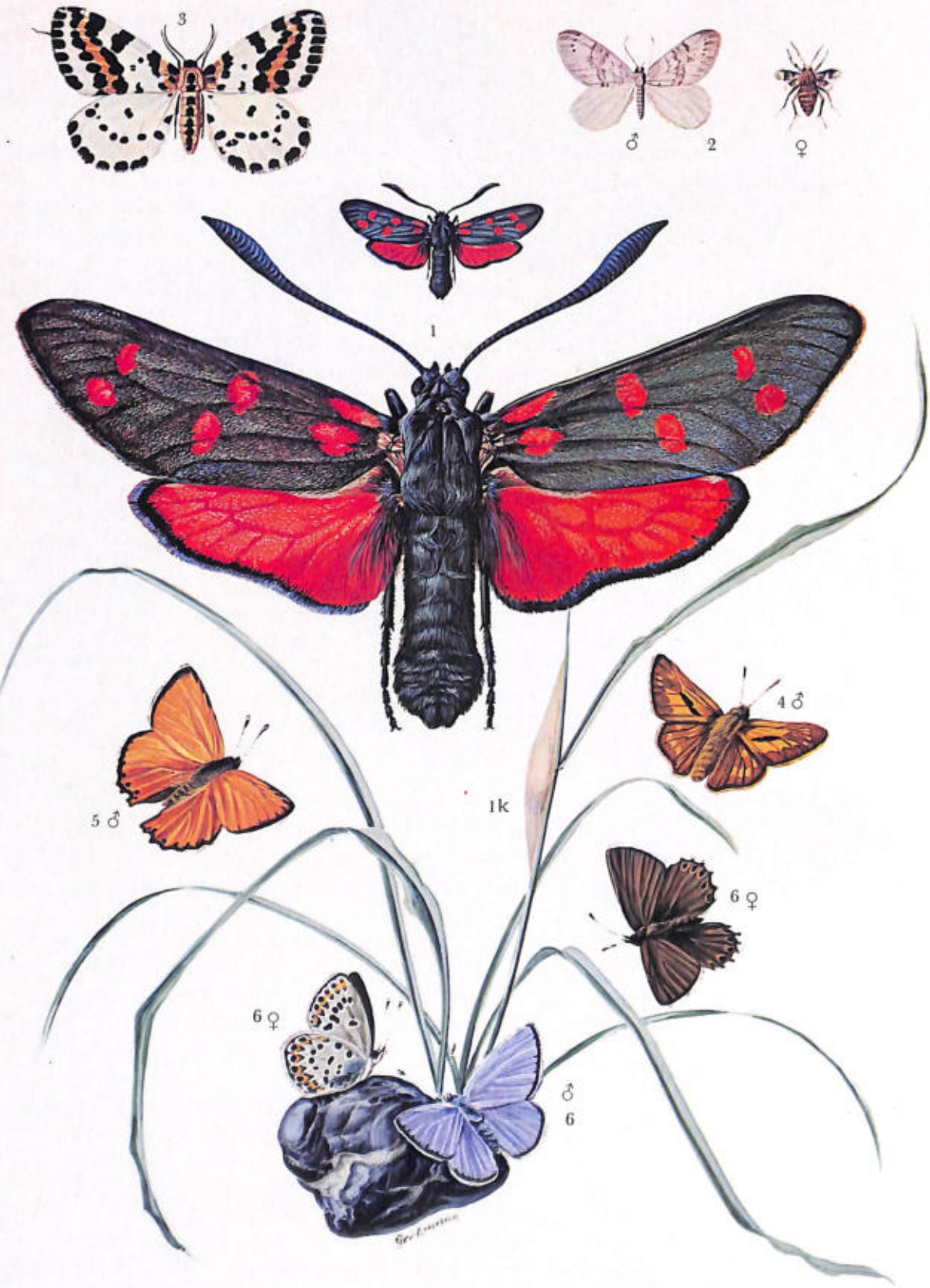


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European moths and butterflies. Burnet: 1. The six-spot burnet (*Zygaena filipendulae*), mounted, enlarged and actual size: 1k, cocoon.
Geometers: 2. *Cheimatobia brumata*, mounted; 3. The common magpie moth (*Abraxas grossulariata*), mounted.
Skipper: 4. *Hesperia comma*, in flight.
Blues: 5. *Heodes virgaureae*, in flight; 6. The common blue (*Polyommatus icarus*), resting and in flight.

glowing colors, and still others are densely covered with hairs or bristles. The American species of the genus *Automeris* have sharply pointed spurs, feared because of their extremely irritant effect. Usually the caterpillars pupate in solid cocoons, sometimes elaborately constructed, with a special opening through which the future moth can emerge. This entranceway is made of elastic threads rather like an oyster basket, arranged so that the moth can pass through to the outside without difficulty, but an enemy cannot get through in the other direction.

The threads spun by some species of this family are used as silk. They are not, however, of the same quality as the true silk produced by *Bombyx mori*. These secondary suppliers of silk include the eastern Asian CYNTHIA MOTH (*Samea cynthia*), which, together with its food plant, the tree of heaven (*Ailathus glandulosa*), has been introduced into the warmer regions of Europe and the U.S.A. This is a large olive-green moth with wingspan up to 15 cm; the wings are decorated with reddish cross stripes and glassy crescents. The large species of the Asian genus *Antheraea* also supply silk; the so-called Tussah silk comes from *Antheraea yamamai* in Japan, *Antheraea pernyi* in China, and *Antheraea paphia* in India.

Compared with the other Lepidoptera, the saturniids *Coscinocera hercules* and *Attacus atlas* are true giants. The first of these, a native of New Guinea, has the greatest wing area; on the hindwings there are tail extensions. The forewings of the reddish *A. atlas* are drawn out into a sickle shape and have three large. triangular glassy windows; the wingspan can be 25 cm. When these two moths fly, one can mistake them for medium sized birds. The gigantic caterpillars of these species pupate between the leaves of their food plants, in a spindle-shaped cocoon fastened to twigs for security with a strong thread; it looks more like a fruit of the tree than a structure made by an insect.

The North American fauna includes about eighty saturniids. In central Europe there are only five species, of which the SMALL EMPEROR MOTH (*Saturnia pavonia*; see Color plate, p. 342) is the best known and most widely distributed. In the U.S.A. there are three species closely related to *S. pavonia*. In the spring, yellowish to reddish males fly all day in irregular dashes, searching for the larger females, which sit hidden among plants. The females fly only after copulation, looking for suitable food plants on which to deposit their eggs. The caterpillars are grass-green, with knobby projections; they pupate in the "oyster-basket" cocoons mentioned above. One of the largest European lepidopterans is *Saturnia pyri* ∅, which occurs in the southern part of central Europe and in the Mediterranean region. The large caterpillars are light green. decorated with sky-blue papillae. They live on fruit trees as well as in other places. It was this species that the great French entomologist Jean-Henri Fabre chose in the last century for his famous experiments on the means by which the two sexes of moths find each other. He determined that the females secrete odoriferous substances which can be detected by the males over long distances. Even an

empty box which a few days previously had contained a female was sought out by the males. At the same time, Fabre showed that the sense of vision does not suffice to bring the pairs together. He placed female saturniids under a thick glass cover where they were clearly visible, but the males ignored them because the scent could not penetrate the cover.

Hemileuca tau is another well-known European saturniid species. The red-brown wings of the males are decorated with blue-black eyespots within which there is a white pattern in the form of a T (hence the specific epithet). In the spring, the males fly into beech woods when the sun is shining and young leaves are beginning to sprout. The larger, paler females, on the other hand, are active only at night. The same group includes the LUNA MOTH (*Actias luna*) of North America and its Asian relative *Actias selene* (see Color plate, p. 327). These are large moths of a delicate green color, with red eyespots and long tail extensions of the hindwings. One of the most remarkable apparitions in the insect fauna of Madagascar is *Argema mittrei* (see Color plate, p. 359). Its glowing yellow wings bear a pattern of red-brown as well as eyespots colored red, blue, and black; the wingspan amounts to 15 cm. The narrow "tails" on the hindwings, broadened at the end, are themselves about 15 cm long; those of the females are somewhat shorter.

Among the American saturniids, the species of the genus *Rothschildia* (see Color plate, p. 327) resemble *Attacus atlas*. The genus *Automeris* (see Color plate, p. 359) is represented by numerous species in the New World. The forewings of these small moths are inconspicuously colored, rather like wilted leaves, but the hindwings have bright eyespots on a glowing background. When the moth is at rest these are invisible, since the hindwings are covered by the forewings. If a resting moth is disturbed, it spreads the forewings away from the body, exposing the eyespots on the hindwings. The attacker then either draws back in fright and leaves the moth alone, or it hesitates long enough that the moth can take flight. Such patterns are referred to as warning coloration and are of frequent occurrence among Lepidoptera. Of course, they offer no absolute protection; once an attacker has had several such experiences it may learn that it is in no real danger from this apparition, with disastrous consequences for the moth. The caterpillars of the *Automeris* species, as mentioned above, are equipped with sharp spurs which can cause painful wounds.

The family Lasiocampidae includes moths of quite different sizes, all with sturdy bodies and a thick coat of hair. Most of them are not very brightly colored, brown and gray being predominant. But the hairy caterpillars often have very striking colors, and some even have a "mirror" of metallically gleaming hairs, broadened like scales, on the back. All of them pupate in solid cocoons which may have openings with lids for the moths to emerge. This family, like so many in the order, occurs all over the world.

Some of the lasiocampids are notorious and severe pests. Among these

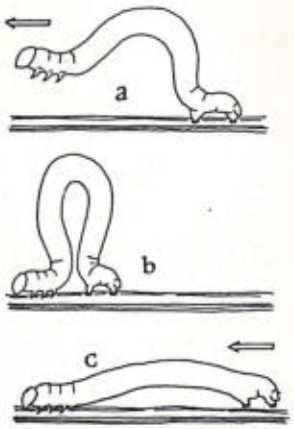


Fig. 15-32. a-c, three steps in the process of locomotion of a measuring worm; the caterpillar is moving in the direction of the arrow.



Fig. 15-33. A geometrid caterpillar in resting position, camouflaged as a twig. It is secured by a thread running from the spinneret to an attachment point on the tree.

Family: Lasiocampidae

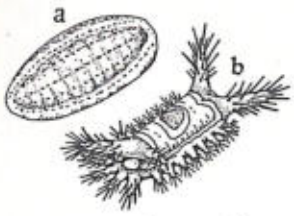


Fig. 15-34. a-b, caterpillars of tropical Limacodidae, with thick, transparent cuticle and numerous sharp spines.

are the TENT CATERPILLARS, for example the European *Malacosoma neustria* (see Color plate, p. 342), and six North American species. The moth has a wingspan of up to 3 cm. The caterpillars feed on fruit trees, to whose thin twigs the female fastens a remarkable arrangement of eggs. The eggs are glued close together in a continuous helix as the female gradually progresses around the twig. The caterpillars are very brightly colored, patterned in longitudinal lines of blue, red, yellow, and black. They live in communities in nests which they spin, leaving them only to forage for food. On such excursions they spin a thread all the way to the feeding place, and when they return to the nest they follow exactly the same path back. Since there are so many of them, this results in the formation of "streets" of silk along the twigs, which the caterpillars travel continually. The caterpillars separate only when they have reached full growth; then they pupate in fissures in the bark or between leaves, in a soft silken case.

All the moths in this family have regressed mouthparts and do not eat; as a consequence, they live only a few days. But if one takes into account the period of development from the egg to emergence of the imago, some of the lasiocampids are among the longest-lived of all the Lepidoptera. The alpine *Eriogaster arbusculae*, for example, often lies in the pupal case for seven years, so that its total life span is up to eight years (during most of which, of course, it is dormant). Widespread and often commonly encountered central European lasiocampids are the OAK EGGAR (*Lasiocampa quercus*; see Color plate, p. 342), with chocolate-colored wings and yellow cross bands, and the PINE LAPPET (*Dendrolimus pini*), whose coloration and patterning are superbly matched to pine bark.

Family: Bombycidae

The few hundred species of BOMBYCIDS (family Bombycidae) live primarily in tropical regions. The moths, ordinarily small and inconspicuously colored, would hardly arouse any interest if it were not that they include the only "domestic animal" among the Lepidoptera. This is *Bombyx mori*, the animal to which the terms SILKWORM or SILK MOTH, without qualification, refer. Its caterpillars produce the silk prized by mankind for thousands of years; even the modern proliferation of artificial fibers has not ousted pure silk from its position of economic importance. In those countries where the climate is suitable for silkworm culture, the production of silk is still a main industry and source of income.



Fig. 15-35. The cocoon of a tropical saturniid, hanging like a fruit; the opening from which the moth emerges can be seen.

The culture of silkworms began in China, about 4000 years ago. Later it spread to Korea and then to Japan and southern Asia. At the time of the Romans, silk fabrics were carried to Europe along the famous trade route that passed through the interior of Asia; these imported goods were among the most costly treasures of rich citizens. In the 6th Century A.D., certain monks, defying strict prohibitions and the threat of severe punishment, succeeded in bringing eggs of the silkworm and seeds of the mulberry tree, on whose leaves the worms feed, to Byzantium by way of India. The silk industry spread from there throughout the Mediterranean region and even further. On several occasions attempts have been made

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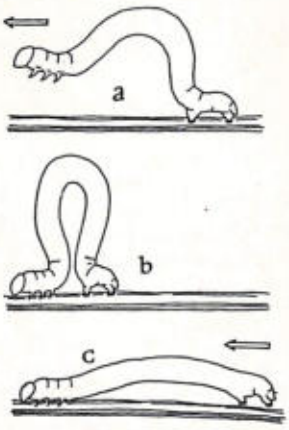


Fig. 15-32. a-c, three steps in the process of locomotion of a measuring worm; the caterpillar is moving in the direction of the arrow.



Fig. 15-33. A geometrid caterpillar in resting position, camouflaged as a twig. It is secured by a thread running from the spinneret to an attachment point on the tree.

Family: Lasiocampidae

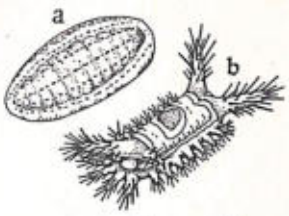


Fig. 15-34. a-b, caterpillars of tropical Limacodidae, with thick, transparent cuticle and numerous sharp spines.

are the TENT CATERPILLARS, for example the European *Malacosoma neustria* (see Color plate, p. 342), and six North American species. The moth has a wingspan of up to 3 cm. The caterpillars feed on fruit trees, to whose thin twigs the female fastens a remarkable arrangement of eggs. The eggs are glued close together in a continuous helix as the female gradually progresses around the twig. The caterpillars are very brightly colored, patterned in longitudinal lines of blue, red, yellow, and black. They live in communities in nests which they spin, leaving them only to forage for food. On such excursions they spin a thread all the way to the feeding place, and when they return to the nest they follow exactly the same path back. Since there are so many of them, this results in the formation of "streets" of silk along the twigs, which the caterpillars travel continually. The caterpillars separate only when they have reached full growth; then they pupate in fissures in the bark or between leaves, in a soft silken case.

All the moths in this family have regressed mouthparts and do not eat; as a consequence, they live only a few days. But if one takes into account the period of development from the egg to emergence of the imago, some of the lasiocampids are among the longest-lived of all the Lepidoptera. The alpine *Eriogaster arbusculae*, for example, often lies in the pupal case for seven years, so that its total life span is up to eight years (during most of which, of course, it is dormant). Widespread and often commonly encountered central European lasiocampids are the OAK EGGAR (*Lasiocampa quercus*; see Color plate, p. 342), with chocolate-colored wings and yellow cross bands, and the PINE LAPPET (*Dendrolimus pini*), whose coloration and patterning are superbly matched to pine bark.

Family: Bombycidae

The few hundred species of BOMBYCIDS (family Bombycidae) live primarily in tropical regions. The moths, ordinarily small and inconspicuously colored, would hardly arouse any interest if it were not that they include the only "domestic animal" among the Lepidoptera. This is *Bombyx mori*, the animal to which the terms SILKWORM or SILK MOTH, without qualification, refer. Its caterpillars produce the silk prized by mankind for thousands of years; even the modern proliferation of artificial fibers has not ousted pure silk from its position of economic importance. In those countries where the climate is suitable for silkworm culture, the production of silk is still a main industry and source of income.



Fig. 15-35. The cocoon of a tropical saturniid, hanging like a fruit; the opening from which the moth emerges can be seen.

The culture of silkworms began in China, about 4000 years ago. Later it spread to Korea and then to Japan and southern Asia. At the time of the Romans, silk fabrics were carried to Europe along the famous trade route that passed through the interior of Asia; these imported goods were among the most costly treasures of rich citizens. In the 6th Century A.D., certain monks, defying strict prohibitions and the threat of severe punishment, succeeded in bringing eggs of the silkworm and seeds of the mulberry tree, on whose leaves the worms feed, to Byzantium by way of India. The silk industry spread from there throughout the Mediterranean region and even further. On several occasions attempts have been made

to introduce the industry to the U.S.A., but these always failed because of the unfavorable climatic conditions there.

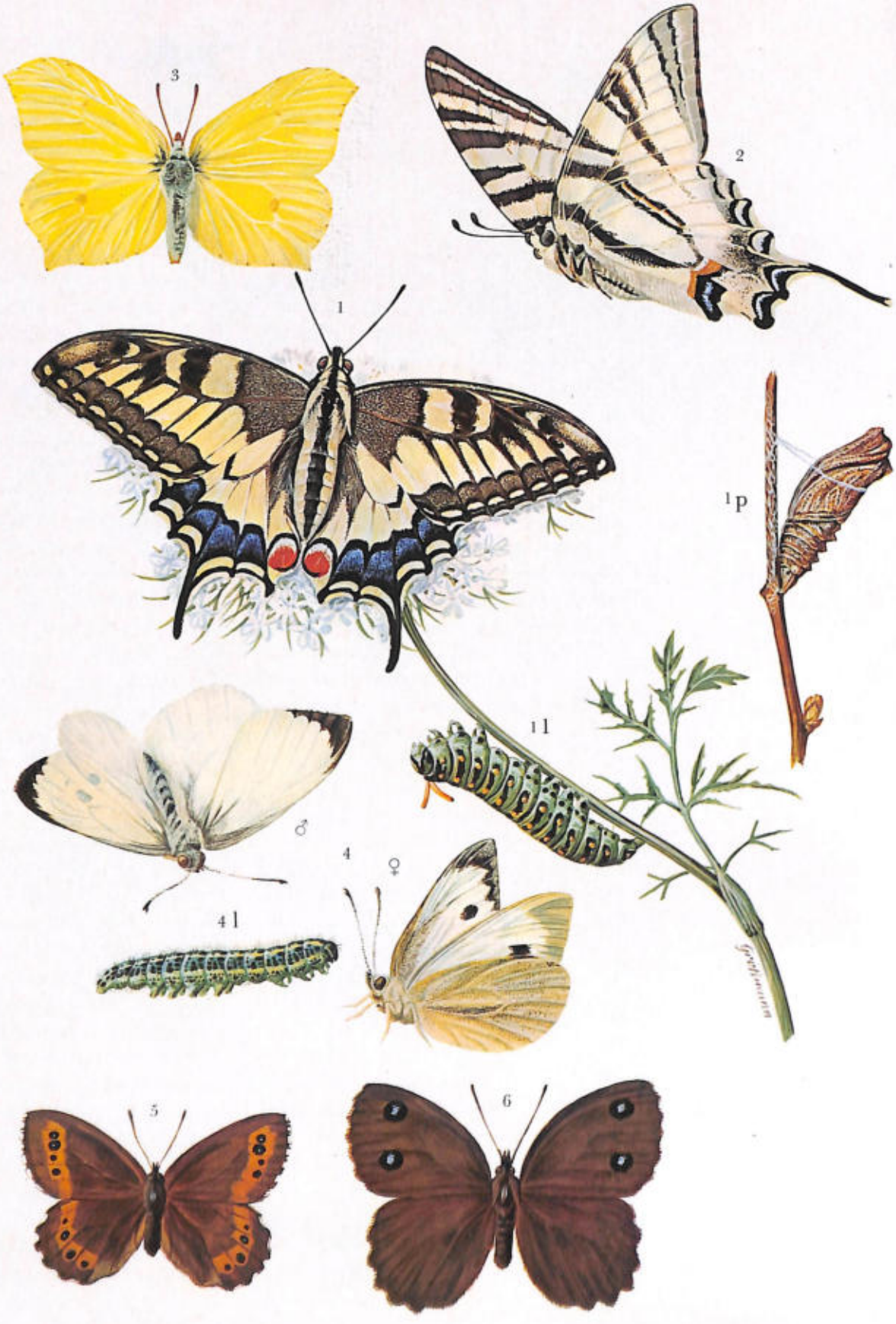
In the last century the European silk industry was faced with a grave danger in the form of pébrine, a disease produced by a species of Sporozoa (see Vol. I) of the genus *Nosema* which infect the silkworms. The famous French scientist Louis Pasteur succeeded in discovering the pathogen and thus in distinguishing healthy batches of eggs from infected ones; this can be done because the infection occurs by way of the eggshell. Moreover, healthy varieties of silkworm were imported from Japan to revive the European silk industry. The silkworm has been so thoroughly domesticated that it can no longer survive independently in nature; among other things, the moth has lost its ability to fly. For a long time it was in doubt whether there was still a wild race of silkworm moths. Today it is generally assumed that the species *Theophila mandarina*, which is widespread in Asia, was the origin of the silkworm strain. If that is true, the rules of zoological nomenclature require that the scientific name of the silkworm moth be changed. The two forms differ considerably in external appearance; the wild form is dark brown with distinct markings, whereas the domestic form is usually white with very faint darker cross stripes.

The silkworm is known not only for its silk; it has also played an important role in research on sexual attractant substances (pheromones; see Chapter 1). The German Nobel Prize winner Adolf Butenandt succeeded in isolating small quantities of the odoriferous substance from the scent glands of a great number of female pupae, and he was able to determine its chemical composition. Eventually it proved possible to manufacture the substance synthetically so that it is now used in several different laboratories. Among other things, it has been shown that the males detect these substances with the olfactory hairs on their antennae, whereas the females are unable to smell their own scent. Since the odoriferous substances are usually present in the open air in only very small concentrations, and the males must detect them at great distances, the surface of the antennae is much enlarged to make room for as many olfactory hairs as possible. This is accomplished by the branchlets, lateral outgrowths which give the antenna the appearance of a feather. The threshold for detection of such odoriferous substances, is extraordinarily low; in theory, a single molecule of the substance would be sufficient to excite one of the appropriate sensory cells and thus inform the moth of the odor. But the moths smell only the substances of their own species; it has been shown that the slightest alteration in the molecule reduces the animal's ability to detect it. Other odors are not detected at all. Nevertheless, within its limits, the sense of smell of the Lepidoptera is one of the outstanding sensory performances in the animal kingdom.

Research in lepidopteran olfaction is carried on intensively, since the results are of great practical significance. If it were possible to determine the species-specific odoriferous substances of those lepidopterans which

▷
European butterflies Nymphalidae: 1. The fritillary *Argynnis niobe*, at rest; 2. The painted lady (*Vanessa cardui*), at rest; 3. The red admiral (*Vanessa atalanta*), at rest; 4. The small tortoise shell (*Aglais urticae*), in flight; 4l, caterpillar on a stinging nettle (*Urtica*); 4p, pupa; 5. *Araschnia levana*, summer form: (a) upper side, (b) underside; (c) spring form; 6. The purple emperor (*Apatura iris*), in flight.


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are pests, one could bait traps with the substances and catch all the males within a considerable area. Then the eggs of the females could not be fertilized, and reproduction would be prevented. This would be the best possible kind of pest control; only the pest itself would be affected; none of the animals which share its habitat would be hurt, as they almost invariably are with traditional methods.

Family: Liparidae

The TUSSOCK MOTHS (family Liparidae) are small to medium-sized moths with many species, occurring in all parts of the earth—often as pests. Their brightly colored, hairy caterpillars not infrequently have brushlike tufts of hair on the back, sides, and posterior end; often they live in associations within large silken nests. They leave these to forage for food but return regularly, and some species even pupate together in loose cocoons.

◁ European butterflies. Papilionidae: 1. Swallowtail (*Papilio machaon*), at rest; 1*l*, caterpillar with osmeterium behind the head protruded; 1p, chrysalis attached by a girdle of silk; 2. *Iphiclides podalirus*, in flight. Pieridae: 3. The brimstone (*Gonepteryx rhamni*), mounted; 4. The large cabbage white (*Pieris brassicae*), in flight and at rest; 4*l*, caterpillar. Satyridae: 5. The alpine *Erebia ligea*, mounted; 6. *Minois dryas*, mounted.

The BLACK ARCHES (*Lymantria monacha*; see Color plate, p. 342) are among the best-known lymantriids—one might even say that they have achieved notoriety. They are pretty moths, with forewings patterned in black zig-zag lines on a white ground. The caterpillars live on conifers, and their occasional mass outbreaks have caused devastation in the European evergreen forests. The caterpillars of a close relative, the GYPSY MOTH (*Porthetria dispar*; see Color plate, p. 325) lead a similar life on deciduous trees, fruit trees in particular. Gypsy moths originated in Europe; when they were introduced to North America they were able to do considerably more damage, since their natural enemies were absent. Fruit trees are also attacked by the caterpillars of the BROWN-TAIL MOTH (*Nygmia phaeorrhoea*); the moth is snow-white, with golden hairs at the end of the abdomen. In some species of lymantriids the females have become wingless or have retained only short stumps of wings. The best-known of these is the SCARCE VAPOURER (*Orgyia recens*; see Color plate, p. 342). After hatching, its females stay on the cocoons; there they are fertilized and then lay their eggs, which are stuck like little pearls to the cocoon.

Family: Sphingidae

Some of the best-known moths are the HAWKMOTHS (family Sphingidae); the appearance and behavior of both caterpillars and moths make them easy to distinguish from all the other lepidopterans. Both moths and caterpillars are large, sturdy creatures, which seldom pass unnoticed. The moths are among the best lepidopteran flyers. Their strong, streamlined body is powerful enough to make the narrow wings beat rapidly, so that in flight they are only a blur and often make a faint buzzing sound. Moreover, the hawkmoths are able to hover in the air, sucking nectar from a flower with the long proboscis, which in tropical species may be as much as 28 cm long.

These frequent visitors of flowers play an important role in pollination. In fact, many long, tubular flowers depend upon hawkmoths, since no other insect can reach the deep base of the blossom. The realization of this fact put the great natural scientist Charles Darwin on the track of a new species of hawkmoth. In 1862, as he was summarizing his research on orchids in a book, he noted that on Madagascar there was an orchid of the

genus *Angraecum*, whose nectar-secreting glands were hidden so deep in the flower that they could be reached only by a hawkmoth with an equivalently long proboscis. No such species of hawkmoth was known at the time, but Darwin thought that one must exist on Madagascar. A few years later such a hawkmoth was actually found and received the name *Macrosilia morgani praedicta*—the third name in honor of Darwin's astuteness.

The great majority of hawkmoths fly at dusk or at night. But a few species are active only in the sunshine, among them the BROAD-BORDERED BEE HAWKMOTH (*Hemaris fuciformis*; see Color plates, pp. 347 and 363/364) and *Hemaris scabiosae*. Their wings largely lack scales and are as transparent as glass, which gives these hawkmoths a resemblance to bumblebees, particularly since the sturdy body has a furry covering of hair like that of the bumblebees, and there is a bright pattern of stripes across it. They differ from bumblebees, of course, in their behavior when sucking nectar; they hover in front of the flower like true hawkmoths. It is likely that their similarity to the well-armed bumblebees protects them to some extent.

One of the most remarkable hawkmoth species is the DEATH'S HEAD HAWKMOTH (*Acherontia atropos*; see Color plate, p. 347), a striking animal because of its size and the skull-like marking on the back of the thorax. But it is equally unusual in its manner of feeding. Whereas the proboscis of most other hawkmoths is long and thin, the death's head has a short but massive one. With this the hawkmoth pierces the combs of bees and sucks the honey; on one of its nocturnal visits to a beehive it can take in as much as a teaspoonful of honey. To prevent the bees from rushing to the attack, it makes chirping noises by sucking air into the head. These noises have the same effect as certain tones produced by the bees themselves for mutual inhibition of aggressiveness. By its chirping, the death's head hawkmoth turns these inhibitory bee sounds to its own advantage. But it is not always successful in finding the way back out of the hive, and then the bees eventually do sting the intruder to death; later the beekeeper finds its body embalmed in wax.

In a number of hawkmoth species, the moths do not take food. Two of these are the POPLAR HAWKMOTH (*Laothoe populi*) and the European EYED HAWKMOTH (*Smerinthus ocellata*; see Color plate, p. 327) or the North American *S. jamaicensis*. The brownish forewings with their notched edges make the resting moths look like dead leaves, since the hindwings are hidden. But when a moth is disturbed it spreads out the forewings and the hindwings come into view. These, like those of the previously mentioned species of the saturniid genus *Automeris*, have a brightly colored eyespot which startles an attacker when it appears suddenly. Experiments with chickens have confirmed this; when they peck at an eyed hawkmoth and it displays its "eyes," they always draw back at first. But if this procedure is repeated several times, they eventually learn that there is no danger and eat the moth. This example shows, once again, that all protective devices in nature are of only limited value; if this were not the case,



Fig. 15-36. The lappet moth *Gastropacha quercifolia* at rest resembles dead leaves in both color and shape.



Fig. 15-37. In position to attract a mate, the female silkworm moth (*Bombyx mori*) extends the scent glands at the end of her abdomen.

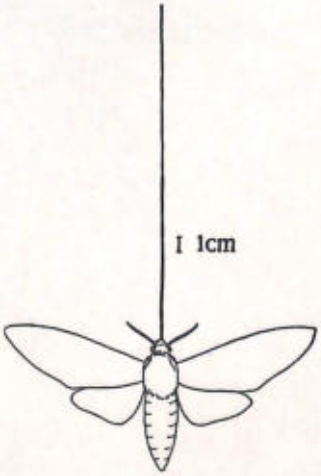


Fig. 15-38. The extra-long proboscis of a tropical hawkmoth.

there would be a boundless multiplication of the invulnerable animals.

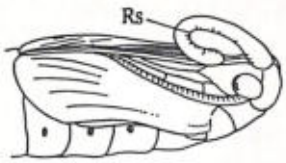


Fig. 15-39. In the chrysalis, the long proboscis of the convolvulus hawk is formed as a loop inside the proboscis sheath.

In view of the considerable flight performance of hawkmoths it is not surprising that many of them are migratory. For example, every year death's head moths, CONVOLVULUS HAWKMOTHS (*Sphinx convolvuli*), HUMMING-BIRD HAWKMOTHS (*Macroglossum stellatarum*; see Color plate, pp. 363/364), and other species fly from the Mediterranean region to central and northern Europe, sometimes going as far as the Arctic Ocean.

During this flight they deposit eggs; their offspring appear in late summer and autumn but live only until the first frosts, for these tropical animals are unable to withstand the weather prevailing at such latitudes. Moreover, most of the hawkmoths which develop in these northern regions have proved infertile. Despite the (to us) obviously poor outlook for this undertaking, the moths take off every year on a new migration, sometimes only in small numbers but at other times in millions. They are obeying an instinct, and the factors which release this behavior are not yet understood.

Family: Notodontidae

The PROMINENTS (family Notodontidae) are particularly distinguished by the unusual form of their caterpillars. The moths are usually inconspicuously colored; only a few species are colorful, sometimes with metallically shining spots and in other cases green, brown, yellow, or almost pure white. Many of these colors have a protective effect, camouflaging the resting moths to look like parts of plants. This effect is enhanced by the body posture: some species roll the wings around the body, raising the abdomen away from the substrate, so that they resemble a short twig. The prominents live in all parts of the world; there are many species.



Fig. 15-40. The caterpillar of the lobster moth has elongated forelegs and the last abdominal feet are modified into clubs (see also Color plate, p. 325).

The caterpillars of the PUSS MOTHS (*Cerura* spp. see Color plates, pp. 324 and 363/364/ and *Harpyia* spp.), some species of which are found in central Europe, are particularly striking. They are green with a reddish "saddle" on the back; the last pair of abdominal legs has been modified into two long projecting rods, which together form a fork. If the caterpillar is disturbed, it extends the fork forward over the back, pushing out of the tips red filamentous tubules which carry a sharp-smelling secretion. At the same time, it can spray acrid fluid from a gland in the thorax below the head, with a range of up to 10 cm. This fluid has a marked effect when it gets into the human eye, and no doubt frightens away attacking birds. But these weapons are not entirely effective against the worst enemy of these caterpillars, the parasitic wasps (see Chapter 17); one often finds puss moth caterpillars which are condemned to death by the wasp larvae inside them.



Fig. 15-41. The common silver Y moth (*Autographa gamma*).

Another unusual caterpillar is that of the PEBBLE PROMINENT (*Notodonta*; see Color plate, p. 325). It has a row of humps on its back and is colored violet and yellow, rather like dying leaves. But the caterpillar of the LOBSTER MOTH (*Stauropus fagi*; see Color plate, p. 325) is even more remarkable; its thoracic legs are long and thin like a spider's, the end of the abdomen is thickened, and the last pair of legs has been transformed into short clubs. At rest, the caterpillar raises the abdomen in the air, with the thoracic legs stretched forward close together.

Family: Thaumetopoeidae

The PROCESSIONARY CATERPILLARS (family Thaumetopoeidae), whose moths are an inconspicuous gray color, are closely related to the prominents; there are only a few species, all from the Old World. They have become generally known because of the behavior of the caterpillars. Large numbers of these live communally in spacious silken nests, going out together to look for food and then returning together. These excursions are made strictly in marching order, with one caterpillar crawling just behind another and keeping track of the one in front by its sense of touch. If one forces such a marching column of caterpillars—for example, *Thaumetopoea processionea*—to form a ring, they will go on for hours walking in a circle until finally one of them breaks out. Jean-Henri Fabre noted that one such "caterpillar ring" made no less than 335 circuits. These caterpillars are also notorious for their glandular hairs. These fine but sharp hairs, associated with glands which produce an irritating secretion, easily penetrate the skin and then break off, causing violent inflammations. If they are carried about by the wind in large numbers, they can make whole areas of woods impossible to enter and even injure grazing cattle. There is an authenticated case of the death of a boy who climbed a tree, encountered a caterpillar nest, and came into contact with many of the caterpillars. In the last few centuries the processionary caterpillars have become rare in central Europe. On the other hand, the related *Thaumetopoea pityocampa* frequently appears at the southern edge of the Alps; its white webs, the size of a basketball, can be seen in pine woods there, and the caterpillars do no little damage to the trees.

Family: Noctuidae

With no less than 20,000 species, the OWLET MOTHS (family Noctuidae) are numerically the leading lepidopteran family. There are owlet moths with a wingspan of only 5 mm, but the largest of all lepidopterans, the South American *Thysania agrippina*, also belongs to this family. Owlet moths are found in all possible habitats, from the tropics to the edge of high mountain glaciers and far into the polar regions. Most of them are a plain gray or brown color with indistinct patterning, but there are also brilliantly colored owlet moths which need not fear comparison with the beautiful butterflies. Some of these owlets fly by day, while most of the others are nocturnal. Their proboscises are well developed for sucking flowers; some prefer fruits or the juices of damaged trees.

All the owlet moths are distinguished by one common characteristic: they have paired auditory organs (tympanal organs) which, in contrast to those of other lepidopteran families, lie at the posterior edge of the thorax. With these pits, over which there is a chitinous cover, the owlet moths detect the echolocating calls of the bats and often manage to escape them by adept flight maneuvers. Some species even produce tones resembling those of the bats; this confuses the bats, which then give up the attack. These tones encompass not only a range of ultrasonic frequencies, inaudible to humans, but also include audible frequencies which we hear as a distinct rustling.

▷
Tropical moths.
Saturniidae: 1. *Argema mittrei*, in flight; 2. The io moth (*Automeris io*), mounted.
Limacodidae: 3. *Parasa pastoralis*, in flight.
Zygaenidae: 4. *Semioptila flavidiscata*.
Hepialidae: 5. *Charagia ramsayi*, in flight.


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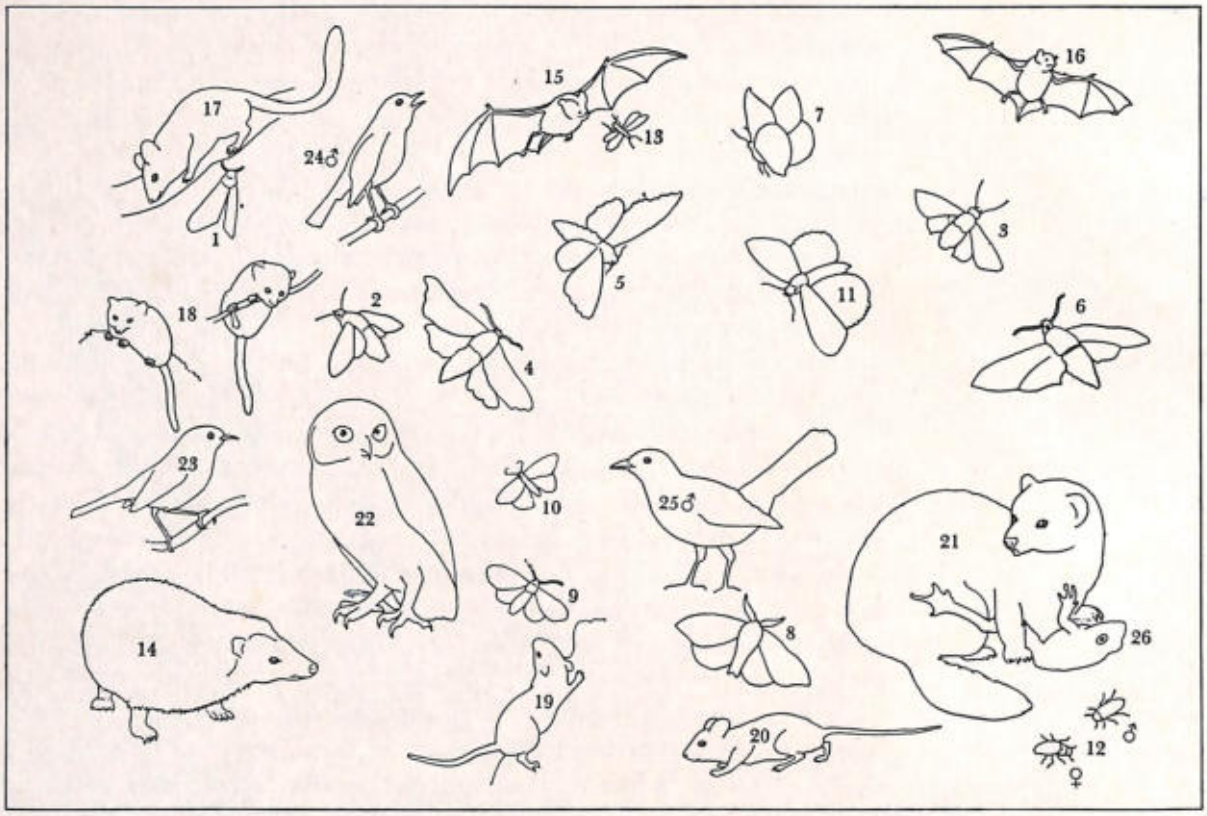
There are great differences among the owlet caterpillars. Those of species which forage for food at night are usually inconspicuous and not very hairy; so are the caterpillars living within parts of plants. In species active by day the caterpillars often have a lively coloration, and some bear long hairs or tufts of hairs like the caterpillars of the Lymantriidae. They feed primarily on plants, though some, for example, the DUN-BAR (*Cosmia trapezina*) also attack and eat other caterpillars. For pupation, most species prepare a subterranean chamber of particles glued together; others, however, construct cocoons of silk, sometimes mixed with caterpillar hairs or wood shavings.

Among the best-known owlet moths are the UNDERWINGS (*Catocala* spp.; see Color plates, pp. 347 and 363/364). These large moths have red, blue, or yellow hindwings, while the forewings are patterned like bark in gray or brown. This moth, like others previously mentioned, is thus effectively camouflaged, for it rests on objects which resemble the forewings, with the hindwings hidden. When disturbed, the underwings suddenly display their garish hindwings; the attacker is taken aback and hesitates, and the moth has time to flee. Conversely, when an underwing settles on a tree trunk after flight and hides the hindwings, it looks as though the moth has suddenly disappeared.

The underwings belong to the subfamily Catocalinae and have numerous similarly patterned tropical relatives, with forewings often colored like dead leaves. Some of these tropical species pierce fruits with the proboscis to suck out the juice, thus making themselves unpopular in orchards.

The subfamily Plusiinae includes many species distinguished by the metallic shine of their wings; the markings on the wings can look like letters of the alphabet. One of the best-known is the COMMON SILVER Y MOTH (*Autographa gamma*); its wing marking looks like a Y (or the Greek letter γ). Every year this migratory moth flies into central Europe from the south, covering great distances. It is active both by day and by night, and in some years it appears in enormous swarms. Among the many inconspicuous owlet moths are the numerous species of *Agrotis* and *Euxoa*, whose caterpillars (often called CUTWORMS, along with those of some other genera) live hidden in the earth. They stay underground in tubes except at night, when they climb up onto their food plants or drag parts of plants back into the tubes. This activity not infrequently does considerable damage; for example, the TURNIP DART (*Agrotis segetum*) makes its presence felt in meadows and fields of grain. Another well-known moth with ground-dwelling caterpillars is the COMMON YELLOW UNDERWING (*Triphaena pronuba*; see Color plate, p. 347); its hindwings are a glowing yellow with a marginal border of black. It is frequently encountered in gardens, and the moths occasionally find their way into houses. Caterpillars of owlet moth species of the genus *Leucania* also live on grasses, sometimes appearing in such great numbers that they gather and march off to find a

◁
Tropical butterflies. Riodinidae: 1. *Ancyluris arcius*, mounted. Nymphalidae: 2. Indian leaf butterfly (*Kallima inachus*), with wings open (a) and closed (b); 3. *Agrias sardanapalus*, mounted. Morphidae: 4. *Morpho cypris*, in flight. Pieridae: 5. *Delias hierta*, at rest, showing the underside of the wing. Papilionidae: 6. *Armandia lidderdalei*, mounted; 7. *Troides superbus*, a southeastern Asian birdwing, in flight.



Twilight in a central
European park.
Insects: Lepidoptera: 1. The hawkmoth *Hyloicus pinastri*, with eggs; 2. The hummingbird hawkmoth (*Macroglossum stellatarum*); 3. The bee hawkmoth (*Hemaris fuciformis*); 4. The hawkmoth *Mimas tiliae*; 5. The hawkmoth *Marumba quercus*; 6. The hawkmoth *Celerio galii*; 7. The arctiid *Callimorpha quadripunctaria*; 8. The saturniid *Hemileuca tau*; 9. The notodontid *Cerura bicuspis*; 10. *Abraxas marginata* (a geometrid species); 11. The red underwing (*Catocala nupta*).

Coleoptera: 12. The large firefly *Lampyris noctiluca*. Mecoptera: 13. The scorpionfly *Panorpa* sp.
Mammals: Insectivora: 14. Hedgehog (*Erinaceus europaeus*; see Vol. X). Chiroptera (see Vol. XI): 15. The bat *Barbastella barbastellus*; 16. The bat *Pipistrellus pipistrellus*. Rodentia (see Vol. XI): 17. *Eliomys quercinus*; 18. The dormouse (*Muscardinus avellanarius*) with nest; 19. *Apodemus agrarius*; 20. The wood mouse (*Apodemus silvaticus*). Carnivora: 21. The weasel *Mustela putorius* (see Vol. XII).
Birds: Owls: 22. The little owl (*Athene noctua*; see Vol. VIII). Passeriform birds (see Vol. IX): 23. The robin *Erithacus rubecula*; 24. The nightingale (*Luscinia megarhyncha*); 25. The blackbird (*Turdus merula*).
Amphibian: 26. The grassfrog (*Rana temporaria*; see Vol. V), a favorite prey of the weasel.





new feeding place; this behavior has earned the moth the name army worm.

Some owlet moths injure forests; of these, the best-known is probably the PINE BEAUTY (*Panolis flammea*), because of its occasional mass outbreaks. The caterpillar bears various stripes of green along its body, and is thus excellently camouflaged among the needles of its food plant. Some species of the genus *Mamestra* can make themselves unpleasantly noticeable in the garden, among them the EUROPEAN CABBAGE MOTH and the BERTHA ARMYWORM (*M. configurata*), of the western U.S.A.; their caterpillars often penetrate deep into the heart of the cabbage.

Families: Arctiidae and Zygaenidae

The TIGER MOTHS (family Arctiidae) are among the best-known lepidopterans; their many species are distributed throughout the world. The caterpillars, with such a long, dense coat of hairs that it looks like a bear's fur, feed on many kinds of herbaceous plants and move about very nimbly. Not uncommonly, especially in late summer, they can be seen crossing streets. For pupation, they make a loose web of silk in the ground, weaving their long hairs into it.

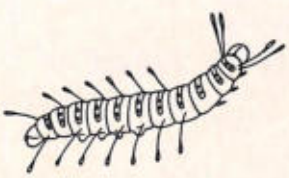


Fig. 15-42. The caterpillar of the alder dagger (*Acronycta alni*) bears long spatulate hairs.

The glaring colors on the wings of the tiger moths, especially the hindwings, offer still another example of warning coloration. In this case the warning is effective because the blood of the moths contains evil-tasting substances, so that after a few attempts to eat them a bird or other predator learns that animals with such striking colors are unsuitable for food. In some species the deterrent effect is increased when the moths exude a yellow blood fluid from behind the head. The color of these droplets, and presumably their scent as well, repel the attacker and afford vital protection to the moth.

The best-known and most common tiger moth in Europe is the GARDEN TIGER (*Arctia caja*; see Color plate, p. 342). The largest and rarest central European species is *Pericallia matronula*, whose forewings are brown flecked with yellow, while the hindwings are yellow flecked with black. Its development requires an unusually long time, two years, for the caterpillar twice enters a period of winter dormancy. This may be the reason this species is so rare. These dormancy periods are a critical phase in the caterpillar's life; many of them die then of diseases produced by fungi, bacteria, or viruses. This also makes it difficult to raise these moths.



Fig. 15-43. A tropical owlet moth with leaflike forewings. The hindwings, hidden when the moth is at rest, are brilliantly colored and are displayed when the moth is startled (see p. 361).

The SMOKY MOTHS or BURNETS (family Zygaenidae), like the members of the following family (Syntomidae), include species of nocturnal moths as well as diurnal species, the bright colors of which equal those of the butterflies. Most of the burnets are distributed in the Old World; they do not occur in North America. In Europe there are several species of the genus *Zygaena*. These SIX-SPOT BURNETS (see Color plate, p. 348) have narrow, steel-colored forewings with red spots, and red hindwings with a black border. In summer they are often found sitting on blooming thistles and the plants called mourning bride, sucking the nectar; they are so sluggish that one can easily capture them with one's hand. They feel no

need to flee, since the repugnant taste of their body fluids makes them inedible, and their glowing colors give warning of this situation.

Shiny green forewings are the hallmark of the FORESTERS (*Procris* spp.) These burnets belong to the subfamily Chalcosiinae, many butterflylike species of which are common in the tropics. The similarity between some burnets and butterflies is so great that they are difficult to tell apart. The butterflies find this to their advantage, since their enemies confuse them with the inedible burnets and thus avoid them. This sort of imitation of warning coloration by species which are actually edible is called Batesian mimicry. Another sort of mimicry, Mullerian mimicry is found among the WASP MOTHS (family Syntomiidae), the many species of which occur in all parts of the world, but predominantly in South America. The small, narrow-winged moths resemble wasps in color and in the presence of glassy "windows" on the wings; there are even some species with the abdomen sharply constricted like the "waist" of a wasp and with a thin appendage at the end of the abdomen, consisting of long hairs, which looks deceptively like a sting. That such similar patterns of color and structure should arise in two such different insect groups as wasps and moths is difficult to explain, and there is some disagreement as to whether this mimicry should be interpreted as imitation for the sake of protection.



Fig. 15-44. South American syntomid, illustrating mimicry of a wasp.

Family: Hesperiidae

The SKIPPERS (family Hesperidae) are usually considered as butterflies, since they have clubbed antennae and fly only by day. But intensive investigations have shown that they are a separate group, not closely related to the other butterflies. This distinction is demonstrated by a species from Australia which has wings connected by a frenulum, a characteristic of the moths which never occurs among the true butterflies.

The naked caterpillars of the skippers spin together leaves of their food plants to make silken tubes in which they live; they also pupate there, inside small cocoons. The moths are usually small but thick-bodied and distinguished by particularly broad heads. Their narrow, sharp-tipped wings can be set in rapid, whirring motion by the powerful thoracic muscles; these agile flyers flit about, quick as an arrow, in a peculiar hopping trajectory. The wings are not very strikingly colored; in the subfamily Pyrginae they are gray or brown with white spots, and in the subfamily Hesperiinae they are brown or reddish. On the forewings, males of the Hesperiinae bear a conspicuous dark stripe consisting of especially large scales. These are associated with glands, whose secretions very probably act as a pheromone, assisting the sexes in finding one another by attracting the females. Other skippers have well-developed proboscises, indicating that they are specialists in sucking nectar from flowers.



Fig. 15-45. At rest, hesperiid butterflies lay the forewings together far back over the body.

In Europe there are only a few species of skippers, but the group is well represented in the U.S.A. These belong to several genera, *Pyrgus* and *Hesperia* (see Color plate, p. 348), small, inconspicuous animals which are easily overlooked, and the attractive LONG-TAILED SKIPPER (*Urbanus proteus*).

Family: Papilionidae

Some of the most beautiful butterflies belong to the family Papilionidae;



Fig. 15-46. Head and thorax of a papilionid caterpillar, with osmeterium protruded.

these are familiar to most people, although only a few species are represented in Europe. Even in the tropics there are not a great number of species. These tropical forms, with their extraordinarily brilliant coloration, are among the most decorative objects in nature. Most of the SWALLOWTAIL species belong to the genus *Papilio*; their hindwings are usually elaborated to form tails. The common European swallowtail is *Papilio machaon* (see Color plates, pp. 327 and 354). In the U.S.A. the TIGER SWALLOWTAIL (*P. glaucus*) is best known. There are also species in which the females have no tails, and others, like the African *P. dardanus*, in which the females may take either of the two forms.

Even longer tails distinguish species of the genera *Iphiclides* and *Graphium* (see Color plate, p. 328), most of which are light yellow or green. The long tails enable them to glide through the air for long distances. This maneuver can be readily observed in the European species *Iphiclides podalirus* (see Color plates, pp. 25 and 354), which is found only in warm areas. In Germany, this butterfly has been classified as a protected animal, since its numbers were steadily declining. Its caterpillar feeds on sloe bushes; as the sloe hedges disappear, the moth gradually loses a factor vital to its existence.

Papilionid species of the genus *Battus* are found mainly in the tropics, where their caterpillars live on syringia bushes. These butterflies are inedible, since they contain poisonous substances obtained from their food; they bear brilliant red and black warning colors which are often imitated by edible species. One can classify these with other inedible species into series of animals whose coloration is mimicked by that of edible ones.

The largest and most beautiful butterflies are the southeastern Asian BIRDWINGS (*Troides* spp.; see Color plate, p. 360). These are noteworthy because the sexes are differently colored; the males are yellow, green, or blue, while the somewhat larger females are brown with lighter spots. The wingspan can be up to 25 cm, so that these are the largest butterflies of all, though a few moths exceed them in size. Because of their size and beauty they are among the most prized collectors' items; they cost a great deal to buy, since they can be captured only with difficulty. They have the rather unusual habit of flying to the tops of giant jungle trees, and are seldom found near the ground.



Fig. 15-47. *Teinopalpus imperialis.*

The caterpillars of the swallowtails and their relatives are usually very compactly built, and gaily patterned and colored in a great variety of ways. They have one common characteristic: behind the head they can extend a fleshy forked osmeterium colored a brilliant yellow or violet, which diffuses strong aromatic odors. This seems to serve two functions: first, that of repelling enemies, and second, that of removing from the body the essential oils the caterpillar consumes with its food. The pupa, or chrysalis, is fastened loosely by a girdle to a twig or stone; the end of the abdomen is anchored in a cushion of silk by fine hooks, and the girdle passes around the middle of the body.

The widespread species of the genus *Parnassius*, the APOLLOS, include

only "tailless" species, occurring in the mountains of the northern hemisphere. Most of these butterflies are whitish in color, with black spots, and eyespots on the hindwings with red or blue centers. The three species living in Germany are protected: ♂ *Parnassius apollo*, the alpine ♂ *Parnassius phoebus* (see Color plate, p. 463 in Vol. XIII, where it is erroneously called *Parnassius delius*), and the black form ♂ *Parnassius mnemosyne*. The most beautiful species are also the rarest, living in the high mountain regions of Asia, often only in restricted areas and at heights up to 6000 m, the upper limit for insect life of any kind. Their hairy caterpillars pupate in a loose silken cocoon on the ground, quite in contrast to the other papilionids. They are therefore considered a more primitive group, retaining some characteristics from earlier stages of evolution. Three species live in the mountains of the western U.S.A.



A few other genera, each with only a few species, deserve mention; these occupy a systematic position between the Apollos and the swallowtails. *Zerynthia hypsipyle* (formerly called *Thais polyxena*) is a small butterfly which flies at the southern boundary of the Alps; its wings have no tails, but it is very brightly colored. In contrast, the magnificent green *Teinopalpus imperialis* and the members of the Asian genus *Armandia* have three tails on each wing.

Family: Pieridae

The WHITES (family Pieridae) include many of the best-known butterflies, not only white but also yellow or yellow-orange. Their caterpillars, naked or only sparsely clothed with hairs, pupate to form chrysalides attached by girdles to the substrate; at the head of these chrysalides there are sometimes humps or projections so long that they can be mistaken for thorns or the tips of twigs. Many species of whites display sexual dimorphism—that is, the males and females are colored and patterned differently. The best-known example of this phenomenon is the BRIMSTONE (*Gonepteryx rhamni*; see Color plate, p. 354), the males of which are lemon-yellow, while the females are almost white. The brimstone also has some remarkable features in its life cycle. It passes through two dormant periods, the first soon after emerging as an imago in summer. In fall the butterfly becomes active again before entering the second, winter diapause. During this period it often sits out in the open on a twig, but not even the sharpest frost injures it. In spring the butterfly bestirs itself again, flying until summer; in this period it mates and lays its eggs. Thus the brimstone reaches the greatest age possible for a lepidopteran imago, nine to ten months. Ordinarily the life span of species which take food amounts to three to four weeks, while those with regressed mouthparts live for some days or even only a few hours.

The CLOUDED YELLOWS (the many species of the genus *Colias*) are yellow or orange in color; they live in temperate regions. Two species are pests in the U.S.A., the ALFALFA CATERPILLAR (*Colias eurytheme*) and the CLOUDED SULPHUR (*C. philodice*). In central Europe, one frequently encounters the PALE CLOUDED YELLOW (*C. hyalae*), called in Germany the "gol-



Fig. 15-48. The chrysalis of *Anthocaris cardamines* looks like a thorn.



Fig. 15-49. The black-veined white (*Aporia crataegi*).



Fig. 15-50. A lycaenid caterpillar with ant-attractant glands.

den eight" because of the figure-8 marking on the underside of the hindwing. Another common species there is *C. croceus* (see Color plate, p. 311). This is a migratory butterfly, unable to survive the winter north of the Alps; every year, in various numbers, it crosses the Alps from the Mediterranean. In certain years the migration involves millions of individuals. It is still not clearly understood what sets off these migrations; though it is assumed that their function is to extend the range of the species, nothing is known about the actual causative factors. It may be that there is a population explosion in the original home of the butterflies, or perhaps food shortages or unusual weather conditions play a role. Clouded yellows are among those Lepidoptera which penetrate even the most extreme habitats, barely compatible with insect life, such as the highest mountains and the edge of the arctic ice-cap; some species are permanent inhabitants of these regions. Even the tiniest plants suffice to provide the caterpillars with the necessary food.

In the subfamily Pierinae are some well-known species unwelcome in gardens; such as the CABBAGE WHITE (*Pieris brassicae*; see Color plate, p. 354), whose caterpillars are often found on cabbages, Brussels sprouts, and the like. The cabbage white is also a migratory butterfly, although it travels for shorter distances and not only in one direction, in contrast to the long-distance migrants, which usually fly north. The IMPORTED CABBAGEWORM (*Pieris rapae*) and the GRAY-VEINED WHITE (*Pieris napi*) feed on both wild and domesticated cruciferous plants. The caterpillars of the Old World BLACK-VEINED WHITE (*Aporia crataegi*) used to be notorious fruit-tree pests, but today this butterfly has become quite rare as a result of the chemical control methods used in orchards.

In the tropics there live many unusually brightly colored pierid species belonging to the genera *Catopsilia* and *Delias* (see Color plate, p. 360); these deserve special mention. The members of the genus *Catopsilia* are powerful flyers of great endurance; they are real migratory butterflies, flying for days in giant swarms along a straight path; if this course takes them over the open sea, they are doomed. They fall exhausted into the water and drown. Then they are washed to shore, and their bodies pile up in long rows on the beach.

Family: Lycaenidae

Although the BLUES (family Lycaenidae) are usually of small size, they are among the best known of butterflies, since the many species are widespread and include great numbers of individuals conspicuous by their glowing blue or shiny red colors. They are especially numerous in the tropics, where the most beautiful species are found.

The lycaenid caterpillars are of distinctive appearance, shaped like pillbugs with highly arched back, flat ventral surface, and short legs. The small head is usually hidden beneath the thorax. On the abdomen most species have a gland which secretes a substance highly prized by ants; for this reason they are often visited by ants and thus enjoy a certain degree of protection from their enemies. The caterpillars of some species are even

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carried by the ants into their nests, where they eat the brood of their hosts, and other species invade the nests of the ants independently. In general, these caterpillars prefer animal food; some of them feed on aphids all their lives.

In the subfamily Plebeiinae the males are often blue while the females are brown. The underside of the wings bears a regular pattern of small dots. Of this group of small butterflies, one of the most common European species is the SILVER-STUDDED BLUE (*Plebeius argus*), which is at home in many different habitats. Several southern species represent the genus in the U.S.A. The butterflies form typical "sleeping associations"; many of them assemble in a small area and sit, head down, among plants. Many generations of the COMMON BLUE (*Polyommatus icarus*; see Color plate, p. 348) are found in Germany all summer long. The caterpillar of the European LARGE BLUE (*Maculinea arion*) lives on thyme for a short while; then the red ant, *Formica rufa*, takes the caterpillar to its nest, where it remains until the next spring. Only after emerging as an imago does it leave the ant nest to lay its eggs on a thyme plant once again.

Males of the COPPERS (a group of genera together called the Lycaenini) are usually brilliant red or coppery colored, while the females are more brownish and not so shiny. Like the other Plebeiinae, the caterpillars secrete a sugary fluid, but it comes from many small glands in the body wall rather than from one abdominal gland. The most common European species are *Lycaena phlaeas* and *Heodes virgaureae* (see Color plate, p. 348); the latter is found most often in damp meadows.

The predominantly tropical HAIRSTREAKS (subfamily Theclinae) are distinguished by thin appendages on the hindwings. Since these butterflies fly among foliage and around the crowns of the large jungle trees, they are hard to observe and even harder to catch. Many species display glowing colors and spots with a metallic sheen, and some have iridescent wings like those of the magnificent large morphid butterflies (discussed below; see Color plate, p. 360). The compact pupae are fastened to the upper sides of the leaves of the food plants; colored black and white, they resemble the bird droppings also frequently encountered in such places.

Family: Riodinidae

The closest relatives of the blues are the METAL-MARKS (family Riodinidae, formerly Erycinidae), which in some respects represent a transition to the following butterfly families. The small metal-marks are distributed over the whole world, but are particularly common in the New World tropics. In Europe there is only one species, the DUKE OF BURGUNDY (*Nemeobius lucina*), which flies in the spring. The tropical species resemble moths and butterflies of many other groups, so that one would not at first think they all belong to one family. Another closely related family is that of the SNOUT BUTTERFLIES (family Libytheidae), with only seventeen species. The palps of these butterflies are elongated like a snout, and the wing margins bear angular projections. The species *Libythea celtis* is sometimes encountered along the southern edge of the Alps. The migratory

Libytheana bachmanii lives in the eastern U.S.A. and frequently is abundant in the south.

Family: Morphidae

Butterflies in the family Morphidae (see Color plates, pp. 327 and 360) are without doubt among the most beautiful of all. Not only are they very large, with wingspans up to 20 cm; they are most strikingly distinguished by the wonderful shimmering blue of the wings of the males. The females, on the other hand, are a plain brownish color. About fifty species are known; they live in South America, where they circle around the tall jungle trees and only rarely descend to earth. Sometimes, though, one can see them on the ground, drinking from puddles of water or licking fallen fruit. Their magnificent blue color is produced not by pigments, but rather by optical interference (see Color plate, p. 338) as with the other iridescent Lepidoptera. To watch these butterflies flashing in the sunlight at the treetops, from an airplane flying slowly above the jungle, is an unforgettable experience.

Unfortunately, because of their impressive coloration, the wings of the morphos are made into all sorts of "artistic" objects and sold as souvenirs. Kitsch of this sort, to be found in all the South American port cities, is not a pleasant sight to the student of insects. The caterpillars of these butterflies live in large associations and pupate there as well. They are very hairy, and have poison hairs which can cause considerable inflammations in human skin. Morphos are often raised by humans in order to meet the requirements of the souvenir industry; it is very difficult to catch large numbers of these high-flying butterflies in an undamaged state.

Family: Nymphalidae

The BRUSH-FOOTED or FOUR-FOOTED BUTTERFLIES (family Nymphalidae) are an extremely large group including some of the favorite butterflies, for example, the European TORTOISE SHELL (*Aglais urticae*; see Color plate, p. 353), the European PEACOCK (*Nymphalis io*; see Color plate, p. 312), and the North American COMPTON TORTOISE SHELL (*N. j-album*). Both of the European species can be seen flying in early spring, since they spend the winter as adults and are coaxed out from their hiding places by the first warm rays of sunshine. The caterpillars of these butterflies are often quite gaily colored, with long spurs on the back which sometimes may be branched. They pupate to form a strangely shaped object with all sorts of protuberances, hanging head down with only the end of the abdomen anchored in a small mass of silk. The chrysalis is decorated with golden or silvery spots, but these disappear after the imago has emerged.



Fig. 15-51. Distribution and migration of the painted lady (*Vanessa cardui*).

The wing margins of nymphalid butterflies are often notched and bear projections; together with the dusky coloration of the underside, this effectively camouflages the butterflies when they sit with their wings held together above the back, for then they look like dead leaves. The forelegs are reduced, forming cleaning tools which are no longer useful for holding onto a substrate. In the Indian LEAF BUTTERFLY (*Kallima* spp.; see Color plate, p. 360) this sort of camouflage is brought to perfection. The outline of the wing, when the butterfly is at rest, is identical to that of a pointed

leaf, with the stem represented by a narrow projection from the hindwing. Not only are there markings in the form of stripes, which correspond to the midrib and some side ribs of the leaf, but there are even small spots which resemble holes or rotting spots in the leaf. In my own experience, this disguise is so effective that the butterfly cannot be detected by the human eye, whether it is sitting on the ground under old leaves or even on a tree trunk. One is the more surprised to see it fly away since then the blue and yellow colors of the upper side of the wing suddenly become visible.



Fig. 15-52. The comma butterfly looks like an old leaf when its wings are raised.

The FRITILLARIES (*Argynnis* spp.; see Color plate, p. 353) are nymphalid moths, most of which have distinctive shiny silvery spots on the undersides of the hindwings, while the upper sides show reddish-brown areas and black spots. One of the best-known species is the SILVER-WASHED FRITILLARY (*Argynnis paphia*). The fritillary caterpillars usually live on violets, but the females never lay their eggs directly on these plants. Rather, they lay them somewhere nearby, a very reasonable behavior since the eggs must remain over the winter, whereas the violets die back during the winter and only come up again in the spring. The eggs are safer on stones or tree trunks. Other nymphalids frequently seen in the U.S.A. are the MOURNING CLOAK (*Nymphalis antiopa*), the COMMA BUTTERFLY (*Polygonia comma*), which has earned its name by the silvery C-shaped marking on the underside of the hindwing, and in Europe, *Araschnia levana* (see Color plate, p. 353), which has two quite different patterns of color, depending on the season of the year. In the spring generation these butterflies are red-brown, whereas the summer generation is black and white (an example of seasonal dimorphism).



Fig. 15-53. Male (above) and female (below) of *Hypolimnas mysippus*. The female resembles an inedible danaid.

Well-known migratory butterflies in this family are the cosmopolitan PAINTED LADY (*Vanessa cardui*; see Color plate, p. 353) and the RED ADMIRAL (*Vanessa atalanta*; see Color plates, pp. 327 and 353) of Europe and North America. Every year these butterflies fly from northern Africa across the Mediterranean, sometimes traveling as far north as Scandinavia. Occasionally they appear in enormous numbers. In large, loosely structured groups they proceed directly toward their goal, and there they reproduce. Some of the progeny try to fly back in the autumn, but it has not yet been established whether they are able to cross the Alps at this time of year, when it has already grown quite cold. Its migratory urge has made the painted lady one of the most widespread of all lepidopterans; it is found everywhere in the world except South America.

The Nymphalidae, like some of the previously mentioned families, include certain species which imitate inedible members of other groups. Among these are the American VICEROY (*Limenitis archippus*), which is difficult to distinguish from one of the Danaidae, the MONARCH butterfly (*Danaus plexippus*). Experiments with birds have demonstrated that they avoid the mimic once they have learned that the model, the monarch butterfly, has an unpleasant taste. In the African species *Hypolimnas*

mysippus only the female resembles the inedible butterfly *Danaus chrysippus*; the male is quite differently colored, so that anyone who does not know all about them could easily mistake the two sexes for two different species

One group of nymphalids, of a wonderful iridescent blue color, is found predominantly in the tropics but is represented in central Europe by two species. These are the PURPLE EMPERORS (*Apatura iris* and *Apatura ilia*; see Color plates, pp. 312/313 and 353). Only the males are iridescent; the females are a dull brownish color. The purple emperors quite often fly together with the GREAT VICEROY (*Limenitis populi*), the largest European butterfly. They hover around the tops of trees and seldom come to earth. But one can easily lure them down with cheese and other strong-smelling materials, since they never visit flowers but rather suck fermenting and decaying juices. Species of the South American genera *Prepona* and *Agrias* (see Color plate, p. 360) are particularly colorful, and therefore much prized as collectors' items; they not only display yellow, blue, and red spots, but often glorious iridescent colors as well.

Family: Satyridae

The most striking characteristic of the WOOD NYMPHS (family Satyridae) is the round eyespots, which may be on the upper as well as the lower sides of both pairs of wings. These butterflies, distributed worldwide, are represented by about fifty species in North America. Apart from the eyespots, they are not usually strikingly colored; most of them are brown, in many different shades. The wing veins, swollen into bubbles at the base, contain sense organs which probably are auditory in function. The antennae are also characteristic in form; their very narrow, clublike ends are set off only slightly from the shafts.

The caterpillars of most wood nymphs live on grasses. They have hardly any hairs, but often are decorated with stripes along the body which camouflage them well among the narrow blades of grass; the hind end terminates in two narrow points. They either form a hanging chrysalis (see Fig. 15-17) or prepare loose cocoons on the ground and under stones, in which the pupae lie.

Among the European wood nymphs, the most conspicuous are the MARBLED WHITE (*Agapetes galathea*), with its checkerboard patterning, and *Brintesia circe*, with striking black-and-white coloration. The males of the GRAYLING (*Hipparchia semele*) carry out real courtship behavior before mating, performing dancing movements in the air and on the ground. A similar type of courtship has been observed in a number of other butterflies.



Fig. 15-54. Caterpillar and chrysalis of a satyrid.

In the Alps, there are numerous species of ALPINES (*Erebia* spp.; see Color plate, p. 354), dark brown animals with red-brown spots and yellow eye masks. Some of these live in mountain areas so high and cold that they barely support life, while others inhabit arctic regions, flying over the inhospitable tundra. In correspondence with the climate of their environment, their development proceeds very slowly; it usually lasts two years,

with two winters spent as a caterpillar. Thus it can happen that within a limited area a species appears only every other year, unless there is another strain with the life cycle shifted by a year to fly in the intervening period.

In European meadows one frequently encounters the small RINGLETS (*Coenonympha* spp.), recognizable by their light brown wings, as well as *Maniola jurtina*. The dark brown color of the latter species is changed if they becoem wet; after these butterflies have been out in the rain, they often display light spots.

Family: Danaidae

Only a few species belong to the family of the MILKWEED BUTTERFLIES (Danaidae); they live primarily in the warmer regions of the world, where the caterpillars feed mainly on poisonous plants of the family Asclepiadaceae (milkweeds, etc.) and are thus inedible. The caterpillars bear warning colors, brilliant cross stripes, and in addition usually have two pairs of long, filamentous appendages. The hanging chrysalides are compact, barrel-shaped, and often decorated with golden spots; they, too, can be very brightly colored.

The coloration of the danaid butterflies, despite its variability, is always a warning color which marks their inedibility. For this reason danaids are hardly ever attacked and do not appear shy—as though they knew how safe they are. The body is remarkably tough; they can withstand pressure on the thorax that would kill any other butterfly.

One of the best-known danaid species is the American MONARCH BUTTERFLY (*Danaus plexippus*; see Color plate, p. 314). It stands out not only because of its size, but also because of the migrations the butterflies make regularly every year in North America. In the spring they fly north to Canada, and in fall they return to the south, always following certain routes and usually even seeking out the same places to spend the night. They spend the winter in certain locations in Florida and California, thousands of them sitting crowded close together in trees or on houses. Single monarch butterflies have even been observed far away, over the ocean, and it is possible that they are able to cross an ocean.



Fig. 15-55. Routes followed by migrating monarch butterflies (*Danaus plexippus*).

In Africa and Asia there live similar species, which, like the monarch, are imitated by butterflies of other families (in particular, swallowtails and nymphalids) according to the principle of Batesian mimicry (see Color plate, p. 337) discussed above with the example of *Danaus chrysippus*. Species of the genus *Euploea* are quite differently colored, with magnificent iridescent blue and violet colors on a dark brown ground. Some South American danaids have narrow wings, resembling the members of the two families described below; they fly together with butterflies of these families, forming a Mullerian series of mimicry, since all of them are inedible.

Families: Heliconiidae and Ithomiidae

These families associated with the danaids are the HELICONIIDS (Heliconiidae) and ITHOMIIDS (Ithomiidae), found only in North America. They are widely known for their inedibility. Their smell alone is repellent enough, and the body fluids actually seem to have a poisonous effect. Thus

there are many cases of mimicry in which these butterflies serve as models for others, particularly since they usually appear in great numbers; in fact, they are among the most numerous of all tropical butterflies. The similarity between model and mimic is usually so great that one cannot tell the species or even the family of a flying butterfly; identification is possible only with captured animals (see Color plate, p. 337).

In some of these delicate butterflies the narrow wings are orange, with black stripes and spots and additional yellow and white dots. Others have large, glassy windows in the wings, which make the butterflies almost invisible in the half-light of the jungle, as they fly about with a whirring sound. This kind of wing coloration, too, is imitated by several butterflies of other families. Probably the most impressive mimicry series are those which include geographical modification. According to the range of distribution of the species, the appearance changes; thus differently colored races are formed. The astonishing thing about these series is that all the participating species (that is, not only the protected models but the mimics as well) change their patterning in the same way according to the region they inhabit, thus maintaining the principle of identical warning colors throughout their range of distribution.

Because of their inedibility, the heliconiid and ithomiid butterflies are bold in their behavior. They congregate in great swarms quite openly at certain sleeping places, using the same locations every night. Any other butterfly would be doomed by such a prominent gathering of conspecifics. But these thoroughly protected creatures need not be concerned at all.

16 The Scorpionflies

Order: Mecoptera, by H. Wundt

The common and scientific names of many animals provide a concise identification, but say nothing about their systematic relationships. This is certainly the case for the SCORPIONFLIES (order Mecoptera); the name refers entirely to their appearance. They are closely related neither to scorpions nor to flies, but constitute an independent order of insects. This order has played such a fundamental role in the evolution of the orders Trichoptera (caddis flies), Lepidoptera (butterflies and moths), Diptera (flies), and Siphonaptera (fleas) that all five orders are grouped in the superorder Mecopteroidea.

We shall discuss only the most important mecopteran families: the common or true scorpionflies (Panorpidae), the hanging scorpionflies (Bittacidae), and the snow scorpionflies (Boreidae).

The mecopterans most frequently encountered in Europe are of the family Panorpidae. These are the COMMON SCORPIONFLIES (see Color page, p. 302, and Fig. 16-1). The wings, usually spotted brown, are stretched out horizontally when the insect is at rest, not held rooflike over the abdomen as are those of the Neuroptera. These scorpionflies are much more common in areas of moderate climate than in the tropics. On the upward-pointing end of the abdomen the males have a thickened appendage similar to the abdominal sting of the scorpion. But it contains no poison gland; rather, it is a pincer apparatus with which the male clasps the female and draws her to him for copulation. In these insects, as in some others, "the way to the heart is through the stomach," for the male offers his partner a protein-rich droplike mass formed in his salivary glands. This offering is greedily consumed by the female.

Both larva and imago of the panorpids eat almost everything imaginable in the way of animal and vegetable material, usually at some stage of putrefaction. Digestion takes place in part outside the mouth. The insect vomits out the digestive juices of the midgut so that the enzymes liquefy the food to a certain extent. This liquid food is then lapped up with the elongated, beaklike head.



Fig. 16-1. Pupa of a scorpionfly (*Panorpa* sp.) in the ground.

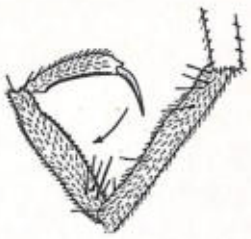


Fig. 16-2. Prehensile leg of a hanging scorpionfly (*Bittacus* sp.)

In contrast, the HANGING SCORPIONFLIES (family Bittacidae; see Color plate, p. 302) are definitely hunters. These animals, found in Europe in the summer, particularly in the woods around water-meadows, are in appearance reminiscent of the crane fly genus *Tipula* (a member of the Diptera; see Chapter 19), with their long legs and four long wings. In the twilight they hunt their prey while flying, or cling with the forelegs to a stem, letting the body hang freely with outstretched middle and hind legs, and wait for small insects to pass. Whereas hunting spiders extend their range by building a net, the scorpionflies accomplish much the same thing with their very long prehensile legs. The last tarsal segment can be snapped back against the preceding one, catching prey as in a mousetrap. The long, daggerlike mouthparts on the beak of the markedly elongated head then bore a hole in the prey and suck out its body contents. Most species of hanging scorpionflies live in Africa and North America. In the U.S.A. there is a wingless species, *Bittacus apterus*, of which it is said that while hunting insects it swings from one grass blade to another as nimbly as a monkey.

The SNOW SCORPIONFLIES (family Boreidae; see Color plate, p. 302), easily recognizable as mecopterans by the greatly elongated head, have become remarkably adapted to life in the winter. In autumn, when other insects are dying or entering a period of dormancy, the snow scorpionflies appear in moss and pass the whole winter feeding on dying and dead insects. On days when there is no wind one can usually see them running about on the snow; they are conspicuous in spite of their small size (only a few millimeters in length) because of their dark, shiny, bronze-green color. The larvae develop in the spring and summer, pupating in September, and in October the adults emerge. With their greatly regressed wings, they are no longer capable of flight; in compensation, the elongated hindlegs allow them to make jumps of as long as 15 cm, at least during the cold season.

17 The Hymenoptera: Sawflies, Ichneumons, and Their Relatives

Superorder: Mecopteroidea

Order: Hymenoptera, by F. Bachmaier

The order HYMENOPTERA (superorder Mecopteroidea) includes such generally familiar insects as the sawflies, horntails, gall wasps, bumblebees, wasps, bees, and ants. The countryside, especially in spring and summer, is hardly imaginable without the buzzing of the flower-seeking bees and the indefatigable busyness of the ants. From the human viewpoint, some Hymenoptera are considered pests, for there are those among them that destroy plants, and others, "useful" animals, some even regarded as friends, since they pollinate flowers, produce wax, and supply us with honey. But there is also an indirect kind of beneficial activity that should be valued even more highly. This is offered by the countless wasps which parasitize animals injurious to forests and crops; their activities limit the numbers of these pests.

Distinguishing characteristics

The Hymenoptera, as a rule, are at most medium-sized insects, and some are minute (L 0.2 mm–5 cm). Among the largest forms are the horntails, hornets, and bumblebees. But many parasitic wasps and gall wasps are really tiny, and some fairy flies, only 0.2 mm long, are the smallest of all insects.

The imago has two pairs of membranous wings, usually as transparent as glass. The wings are similar, except that the forewings are considerably larger than the hindwings. The base of the forewing is covered with horny scales called tegulae. There is a fold at the posterior margin of the forewing which, in flight, engages in a row of hooks under the anterior margin of the hindwing, locking the two wings of each side together to form a single, firm aerodynamic surface. At rest, the wings lie flat and unfolded (except in the yellowjackets) over the abdomen. The wing venation is fully developed, especially in the forewings; only in the modified families of parasitic wasps, with predominantly small to very small animals, is the venation regressed, in some cases only a single branch of a vein remaining in the forewing. Even this may have disappeared in some genera, so that the wings appear entirely without veins. (The names of the individual veins and the cells they enclose are given in Fig. 17-1.) The stinging wasps, in

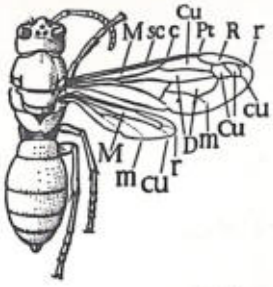


Fig. 17-1. Diagram of the wing venation in a hymenopteran (the giant hornet): c, Costal vein; cu, Cubital vein; Cu, 1st, 2nd, and 3rd cubital cells; D, 1st and 2nd discoidal cells; m, Median vein; M, Median cell; Pt, Pterostigma; r, Radial vein; R, Radial cell; sc, Subcostal vein.

particular, fly well and rapidly. Some forms are only temporarily winged (for example, the ant queens) or lack wings altogether (for example, some parasitic wasps and the worker ants).

The head is flexibly attached to the thorax by a small neck. On either side of the head there is a compound eye, and in the front are three ocelli, though the latter are occasionally absent. The antennae are usually filiform with an elongated shaft; in some groups they are geniculate or have a thickened, clublike ending. The number of antennal segments is extremely variable, ranging from three to about seventy-five. The mouthparts are adapted for chewing and licking, though in the bees they have been modified into a sucking proboscis (but even bees have well-developed mandibles, which they use in building the nest). The walking legs are normal, differing only slightly from one another. The forelegs are usually equipped with a toilet apparatus for cleaning parts of the body, primarily the antennae. Occasionally the legs are modified for digging or carrying collected pollen. The thorax and abdomen may be either broad and rigidly connected, or separated by a "wasp waist"; the abdomen is sometimes even constricted to form a sort of stalk. But this constriction is not between the thorax and the first abdominal segment, but rather between the first two abdominal segments, with the first abdominal segment included as the terminating element in the structure of the thorax. The females have a hollow spinelike structure at the end of the body, which in the Symphyta and some wasps (the Terebrantes) is used for egg deposition, while in the other wasps and bees (the Aculeata) it is a poison-bearing, defensive weapon.

Development

The development of the Hymenoptera involves complete metamorphosis preceded by several larval stages and a dormant pupal stage. In the primitive families of Symphyta the larvae usually resemble lepidopteran caterpillars, but these so-called pseudocaterpillars have more abdominal legs (six to eight pairs) than do the lepidopterans. On the other hand, the larvae of the remaining families, in general, have the appearance of maggots. With occasional exceptions, the pupae belong to the free, or exarate, type.

Life history

There is such great variability in ways of life of the various groups of Hymenoptera that it is hardly possible to make general introductory statements. For example, a female may produce only a few eggs, as does the thread-waisted wasp *Bembex rostrata*, or she may produce several million, like the queens of some ants and bees. Some larvae are free-living, in which case they may be vegetarians, miners, gall-producers, or parasites. On the other hand, they may develop in brood cells provisioned with pollen, honey, or paralyzed or killed arthropods (particularly insect larvae and spiders); they may even grow up in a nest in which they are fed by the parents. Some species lay their eggs in the nests of other Hymenoptera (brood parasitism). The last larval stage usually spins a cocoon in which the insect pupates.

As imagos, the Hymenoptera are terrestrial; only a few species enter

water at all, and then only to lay eggs. The majority feed on flower pollen, nectar, and the honeydew produced by aphids, though some species are predators. In three separate groups, the ants, bees, and yellowjackets, most members of which are solitary, the instinct to form colonies has developed independently. The social species display the most advanced form of brood care in the whole insect kingdom.

Number of species

So far, well over 103,000 species of Hymenoptera are known; there must be many more, especially in the tropics, which have not yet been described. In the U.S.A. there are about 1500 species of Hymenoptera, of which a good four-fifths are parasites. It is the third largest insect order.

Systematic classification

The order Hymenoptera is divided into two suborders: A. the Symphyta, animals with a broad junction between the thorax and the abdomen; and B. the Apocrita, animals with a "wasp waist." The Apocrita are further subdivided into two groups: 1. the Terebrantes; and 2. the Aculeata (see Chapter 18). Formerly, and by some researchers even now, these two groups were regarded as suborders along with the Symphyta.

Suborder: Symphyta, by F. Bachmaier

The sawflies, horntails, and their relatives belong to the suborder Symphyta; the ichneumons and related parasitic and gall-forming wasps, which belong to the suborder Apocrita, are discussed below. The members of the Symphyta are a well-defined group, with respect to the appearance of both larva and imago. Phylogenetically, they are the most primitive Hymenoptera of all; the first true hymenopteran, *Pseudosirex*, in the Solnhofen shale (Upper Jurassic, 150 to 135 million years ago), looked like the present horntails.

Distinguishing characteristics

Most of the Symphyta are of medium to large size (L up to 40 mm). They are reluctant and awkward flyers. It is easy to recognize them by the connection between the abdomen and the thorax, which extends over the full width and height of the body, with no suggestion of a "wasp waist." The mouthparts are of the chewing type. The antennae vary greatly in form, being bristle-shaped or knobbed, or bearing sawteeth or combs. The wing venation is quite complete, more so than in any other hymenopteran group, and is especially distinctive because of the presence of the so-called lanceolate cell in the forewing. The ovipositor apparatus of the females is characteristically designed for placing the eggs within plant tissue; it consists of two blades (the first valvulae) with rows of sawteeth. The form of these teeth is often the only clue to the identification of otherwise very similar species. In wood-boring forms the ovipositor has sturdy drills in place of the flat saw blades. The saw blades, which move with respect to one another during egg-laying, are guided by a sheath formed from the second valvulae, closed at the top. These three parts together form a canal through which the egg is pushed into the plant tissue. The sheath is not involved in the operation of sawing or drilling. The ovipositor can either be hidden in the abdomen or, as in the horntails, can permanently extend for some distance.



Fig. 17-2. *Pseudosirex* (female) fossil from the Solnhofen shale (Upper Jurassic).

The larvae are all vegetarian, with the exception of the Orussidae,

which occupy a special position as parasites. Most of the symphytan larvae are at first glance very like caterpillars of the Lepidoptera (see Chapter 15 and Fig. 17-4), so that they are sometimes called pseudocaterpillars. But this similarity does not justify the conclusion that the two insect groups are closely related. Rather, this is a clear case of convergent adaptation: similar ways of life find expression in the similar external appearance of the animals. Whereas the larvae of certain Symphyta (the leaf rollers, the stem sawflies, and the horntails) have only thoracic legs—and even those can be regressed—most symphytan larvae have six to eight pairs of abdominal feet. The lepidopteran caterpillars, on the other hand, have only five pairs of abdominal feet. The two larval forms may be most readily distinguished by the fact that in the pseudocaterpillars of the Symphyta only the first abdominal segment lacks feet, whereas there are no feet on either the first or the second abdominal segment of lepidopteran caterpillars. But among both the Symphyta and the Lepidoptera there are exceptions, especially in the case of larvae which burrow within stems, trunks, and roots, or mine in leaves.

Development

The shape of the pseudocaterpillar body is usually approximately cylindrical but may be flattened, as in some larvae which seek food on the surface of a leaf (see Fig. 17-5) rather than at its edge. An even-more-marked flattening is found in the mining species. The larva of the European sawfly *Platycampus luridiventris*, which lives on alders, is quite flattened, like a sowbug. Many symphytan larvae, especially those living on the exposed surfaces of plants, are relatively brightly colored, with green, yellow, brown, and blackish hues which in most cases provide a definite camouflage. Some cover themselves with threads of silk or with white secretions in the form of mucus or blobs of wax; these have also been interpreted as offering protection against enemies. Other species, which live in associations as larvae, produce large communal webs—a behavior shared with the caterpillars of various lepidopteran species. A limited number pass through the developmental stages in leaf mines or in galls on leaves nad stems.

Once the larva is full-grown, it ordinarily spins a cocoon, in some cases above ground on plants and in others, in the soil. To get into the ground, the larvae, even those living on high trees, usually simply let themselves fall and move hardly any distance from the place where they happen to land, so that under a heavily infested tree one can often find a great number of cocoons within a few square meters. The cocoons are generally thick and tough. The larvae of cimbicid sawflies make latticework cocoons. Forms which do not make cocoons are able to harden the walls of their burrows in the soil with glandular secretions so that they can withstand considerable pressure. The horntails, which burrow in wood, make chambers there for pupation.

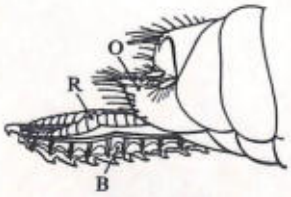


Fig. 17-3. End of the abdomen of a female sawfly seen from the side: O, Ovipositor sheath; R, Ridge along sawblade which interlocks with a groove in the sheath; B, Blade of the saw.

The spinning of a cocoon, or the successful search for a burrow, is not directly followed by pupation of the Symphytan larvae. They lie in a con-

tracted, slightly curled position (as prepupae or semi-pupae), often for a long time—months or even as long as four years—before they enter the relatively brief pupal stage and undergo metamorphosis. This resting phase seems to occur in many symphytans, but is not characteristic of particular species; rather, it depends on the individual. The pupa itself is thin-skinned, with the limbs standing free from the body, not fused to it within a common case like the pupae of the Lepidoptera. This type of pupa is referred to as exarate.

After the imago has burst the pupal case, it usually remains in the cocoon or burrow for some time, waiting for the wings to harden. In the most favorable cases it can emerge simply by biting a hole in the surrounding cocoon, but in general it must also break through a layer of soil, or a stem or gall. The achievements of the horntails in this respect are particularly remarkable, for they must gnaw with their mandibles through a layer of wood that can be several centimeters thick.

Food plants

The food plants favored by symphytans are certain deciduous trees and bushes, among which the willow occupies first place in Europe; there are about eighty species living on willows. Next come the birch, alder, rose, and poplar. About twenty species are to be found on pines, spruces, and oaks. Many species have a wide range of acceptable food plants; they are polyphagous (from the Greek *πολύς* = many, and *φαγεῖν* = to eat). Others have a more limited food selection, choosing from only a few plants, usually closely related; they are oligophagous (from the Greek *ολίγος* = few); and still others are restricted to a single species of plant; they are monophagous (from the Greek *μόνος* = single).

From an economic point of view, the Symphyta can be injurious or at least annoying, as, for example, with certain voracious leaf and needle eaters. In woods composed of only one kind of tree, where the balance of nature is disturbed, some leaf-eating sawflies tend to multiply enormously, and are then among the most severe pests known to foresters. The horntails, too, can cause damage, because their larvae make passages throughout the wood, reducing its value.



Fig. 17-4. Pseudocaterpillar of the currant sawfly (*Nematus ribesii*). In contrast to lepidopteran caterpillars, only the first abdominal segment lacks feet.

The Symphyta are exposed to numerous enemies during the course of their development; these include not only birds and mammals, but in particular parasitic insects. There is hardly another group of insects which is attacked by so many parasites as, for example, the conifer sawflies. Even the horntail larvae living deep in wood are not safe. The large ichneumons (Terebrantes, see below) of the genera *Rhyssa* and *Megarhyssa* can drill through to them with their several-centimeter-long ovipositors, having first detected the larvae with their astonishingly sensitive sense organs. Bacterial, fungus, and viral diseases also frequently bring about the collapse of a symphytan population outbreak.



Fig. 17-5. The flattened, sluglike larvae of the sawfly *Caliroa cerasi*, reducing a cherry leaf to a skeleton.

The greatest numbers of both species and individuals are found in the northern temperate zones of both the Old World and the New. In contrast, there is a conspicuous paucity of species in the tropics. On the earth

as a whole there are something like 7000 species of Symphyta; 1000 are known to inhabit the U.S.A.

The suborder Symphyta is now divided into six superfamilies with a total of fourteen families: 1. Xyeloidea (one family), 2. Megalodontoidea (two families), 3. Siricoidea (three families), 4. Orussoidea (one family), 5. Cephoidea (one family), and 6. Tenthredinoidea (six families).

Family: Xyelidae

The XYELIDS (superfamily Xyeloidea, with the single family Xyelidae and few species) are small insects, at most 5 mm long, which differ greatly from the other Symphyta in appearance. The females are characterized by a long, projecting ovipositor. Large numbers of *Xyela baheri* can often be found on pines in the western U.S.A. in the spring; the larvae, which have feet on all abdominal segments, live there in the staminate pinecones.

Families: Pamphilidae and Megalodontidae

The MEGALODONTOIDS (superfamily Megalodontoidea) include the two families Pamphilidae and Megalodontidae. The larvae of the latter family live in groups, in webs on herbaceous plants, particularly Umbelliferae; for example, the European *Megalodontes spissicornis* is found on the sulfurwort (*Peucedanum* sp.) This family is of little significance. On the other hand, the Pamphilidae, sometimes called LEAF-ROLLERS, deserve more attention, for among them are a number of pests in forests and orchards. The leaf-rollers may be immediately identified by the many-segment antennae, almost as long as the body, by the broad head, and above all by the flattened, sharp-edged abdomen. The larvae have no abdominal feet, and are conspicuous due both to their relatively long antennae and to an appendage consisting of several segments at the end of the body. They live in tubes which they make by rolling up leaves, or in sacklike webs. Since such webs are often sticky, in some species the excrement adheres to them and remains in the sack, sometimes almost filling it. Pupation occurs in the ground, and no cocoon is made.



Fig. 17-6. *Xyela julii* (female), a symphytan wasp often found on blooming pine trees in the spring.

The species important to forestry belong to the genera *Acantholyda* and *Cephalcia*; they attack pine and spruce trees almost exclusively. A great deal of damage can be done by the large European *Acantholyda posticalis* (L 11–15 mm). The head is decorated with various yellow dots and spots; the brown-black back of the abdomen has a reddish color on the broad lateral margins. With a definite preference for pines, this insect appears predominantly in stands of trees 40–100 years old, in northern and central Europe, Siberia, northern Mongolia, and Japan. The adults fly on warm May and June days from nine in the morning until one in the afternoon. The female lays her boat-shaped eggs singly on older needles, first sawing a short slit, then coating it with a glue and depositing the egg on it. Immediately after hatching, the young larvae begin their spinning activity. When full-grown they are olive-green, with red-brown stripes along the sides; at this stage they live singly in transparent, loose tubes of silk containing few feces, for they clear their excrement from the tubes. The larva bites off the pine needles, leaving the sheath part behind; the pieces are pulled into the tube and eaten. The larva proceeds upward while feeding,



Fig. 17-7. Leaf rolls of the rose web-spinning sawfly (*Pamphilius inanitus*), in which the larvae live.

so that the ends of branches and the crowns of the trees often remain undamaged. In August, the larvae let themselves fall to the ground and enter the soil. There they make a bean-shaped hole, usually 8–12 cm deep in an area shaded by the tree, and rest for one to three winters before pupating. Ordinarily the wasp has a generation period of three years. The significance of this leaf-roller to forestry is considerable, for if their numbers are large a stand of trees becomes defoliated and generally dies, especially in places where the pines have already been weakened by other insects.

Females of the magnificent steel-blue *Acantholyda erythrocephala* may be distinguished by their tile-red heads. This species occurs primarily in young plantations of pines, nine to fifteen years old. The female lays the cylindrical eggs in close-packed rows of three to thirteen, on the upper side of the previous year's needles. The larvae live in communities, in large webs which are smooth on the outside and contain only a little excrement, each larva in its own tube. In 1925 this species was introduced into North America; since then it has become dispersed throughout the eastern U.S.A. The species *Acantholyda hieroglyphica* is of less significance to forestry in Germany, where it prefers two- to six-year-old pine plantations.

One pest on spruce trees in Europe is *Cephalcia abietis*. The length of the imago is 11 to 14 mm, the head and thorax are a shiny black with yellow spots, and the abdomen is black anteriorly and otherwise red-yellow. The larvae, initially a dirty gray-green but becoming lighter after the last molt, live in associations in large webs; here the brownish excrement accumulates in large quantities, so that gradually very conspicuous sacks of feces are formed. This species, too, has a tendency to population outbreaks. It primarly endangers stands of spruce 60–120 years old, in hilly and mountainous regions. More than 2000 larvae per square meter of soil have been counted, and the trees, bearing web-sacks as large as a child's head, are a horrifying sight. Nevertheless, the usual consequence of such an infestation is simply a reduction of new growth. The closely related *Cephalcia alpina* occurs mainly on larches in the Alps.

Among the pests on fruit trees is the COMMON WEB-SPINNING SAWFLY (*Neurotoma saltuum*; L 11–24 mm, coloration variable). It flies in May and June, and prefers pear trees or, less commonly, plum trees, hawthorns, or medlars. The female lays about 200 eggs, in groups of thirty to sixty, on the leaves of these plants. The larvae spin a communal nest, loose but still rather firm, which soon becomes dirty brown, soiled by balls of feces. The leaves spun into the web are eaten from the edge inward. Once the enclosed leaves have been consumed, the larvae move on and spin a new, larger nest in the vicinity; proceeding in this way, a colony of larvae can make as many as six nests. In the summer the larvae are full-grown; they let themselves down on a silk thread and spend the winter 6–12 cm deep in the ground. Pupation occurs the next spring or the one after that. An American member of the genus *Neurotoma* is the PLUM WEB-SPINNING SAWFLY (*N. inconspicua*), which feeds on sand cherry and plum trees.

▻
Above: Female mosquito (*Culex* sp.) on human skin, drinking blood. Below: Male malaria mosquito (*Anopheles* sp.); only the females bite.

▻▻
Above: Female hover fly laying an egg in an aphid colony (see Chapter 20). Below left: Robber fly (see Chapter 20) with its prey. Below right: Female of *Ctenophora flaveolata*.

▻▻▻
Above: The eyes of horseflies (see Chapter 20) produce a magnificent display of color. Below left: Fruit flies mating (see Chapter 20). Below right: The large horsefly *Tabanus bovinus* (see Chapter 20).







In central Europe the genus *Pamphilius* is represented by sixteen species. Among them is the ROSE WEB-SPINNING SAWFLY (*P. inanitus*), which leads an especially remarkable life: the larvae make leaf rolls up to 5 cm long, in which they live alone. A leaf-house of this sort is a little work of art; it is composed of many individual strips of leaf, overlapping like shingles, which the larva has cut off from the margins of a rose leaf and joined with silken treads.

Family: Siricidae

There are three families in the superfamily Siricoidea; the horntails (Siricidae), the wood wasps (Xiphydriidae), and the syntexids (Syntexidae). By far the best-known of these are the HORNTAILS, for their size alone (L up to 40 mm) makes them one of the most striking hymenopteran families. They are elongated, powerfully built wasps with an almost perfectly cylindrical body; the females have a strong, protruding ovipositor, and the terminal segment is reinforced for drilling. In both shape and color, the two sexes differ distinctly (sexual dimorphism), and body size can vary greatly within a single species. The whitish, eyeless larvae have three pairs of stumpy thoracic legs and no abdominal feet; the body terminates posteriorly in a horny spine. They burrow in wood. We distinguish seventy species of horntails, classified into eight genera and two subfamilies. In Europe there are four genera and fifteen species (or subspecies). The subfamily TREMECINES (Tremecinae) breeds in dead or weakened deciduous trees; in the U.S.A. it is represented by the genus *Tremex*, with one species, the PIGEON TREMEX (*T. columba*). The subfamily SIRICINAE is confined to conifers.

The LARGE HORNTAIL (*Urocerus gigas*; L, ♂♂ 12–30 mm, ♀♀ 15–40 mm; see Color plate, p. 437) is a large European species. The head is black with touches of yellow at the sides behind the eyes; the thorax is black, and the abdomen of the male is red with black-brown base and tip, while that of the female is light yellow with the middle segments black-violet. Two species of the genus occur in North America.

The primary flight period of the large horntail is during the summer months. Usually one sees only the females, since the males evidently keep more to the crowns of the trees where mating occurs. After copulation, the females come down to lay their eggs. In hot weather, particularly, they whirr about actively and noisily, preferring sunny clearings where cut wood is lying. Despite the rather dangerous impression they make, they are quite harmless to man; one can grasp them without fear. The females lay their eggs for the most part on wood which is still covered with bark. They select only weakened trees, or those with damaged bark. and are particularly attracted by freshly felled tree trunks and stumps. While laying her eggs, the female stands on the wood with legs extended and drives the ovipositor 6–10 mm straight down, through the bark and into the sap-wood; then she lays one to eight eggs in the hole she has drilled. The act of egg-laying lasts ten to fifteen minutes as a rule, but may go on for almost two hours. Often six to ten such drillings follow in succession. In

◁ The male dance fly (see Chapter 20) inseminates the female, which meanwhile is sucking on her "wedding gift," a golden-eye (see Chapter 12).

a month a female can deposit up to 1000 eggs. The larvae chew out cylindrical, curved passages in the wood; as the animal grows, their diameter increases rapidly where the larvae have moved away from the hole drilled by the mother. At first the larval passage runs in the soft summer wood of one annual growth ring, but as it progresses it turns inward toward the center of the trunk. With the terminal spine at the end of its body, the larva presses the bore dust so firmly together behind it that even when one cuts through such a passage one can hardly tell it from the wood. The passages end in pupal chambers which are free of bore dust and usually lie a few centimeters under the surface of the wood. The terminal spine of the larva also assists it in moving forward. The adults which emerge leave the wood through circular flight holes after a period of development which ordinarily lasts three years but may extend to four or six.

The large horntail is relatively unimportant to the forester, for the damage it causes is slight. Even with a heavy infestation, the mechanical properties of the wood suffer hardly at all from the presence of larval passages. But the situation can be unpleasant if the adult insects, because of the long time they require to develop, appear only after the wood has been cut, finished, and used for construction. They can find their way out through obstructions like linoleum, roofing paper, plaster, and even lead plates. For example in a certain sulfuric-acid factory considerable damage was caused when horntails gnawed through lead-sheathed wooden boxes. The large horntail is found in western, southern, and central Europe, as well as in northern Africa; its preferred food trees are the silver fir and spruce, but it eats pines and larches as well. Related European species which live in the same way are *Urocerus augur* and *U. tardigradus*. They differ from one another in the patterning of the abdomen.

The POLISHED HORNTAILS (*Sirex juvencus*), the blue-black female with a glorious metallic sheen and the male with a broad yellow-red band on the abdomen, are the most beautiful horntails in Europe. One often finds their larvae when splitting firewood. The species is distributed throughout the northern part of the Old World. A closely related species, *S. cyaneus* occurs throughout Canada and the U.S.A. In the horntail *Xeris spectrum*, which occurs both in Europe and in North America, the female has an ovipositor almost as long as the body. The larvae prefer to live in pine stumps but will also feed on the wood of silver fir and spruce. This species is also widespread, and is frequently seen in all the northern regions of the earth.

Families: Xiphydriidae and Syntexidae

The WOOD WASPS (Xiphydriidae) are represented in Europe by two genera and six species, and in the U.S.A. by one genus, with six species. They develop in deciduous trees and in general are rather rare. The most common European species is *Xiphydria camelus*, living on alders and birches; in the U.S.A. the most common species is *X. maculata*, living on maple and apple trees.

The SYNTEXIDS (Syntexidae) comprise only a single North American species, *Syntexis libocedrii*, whose larva lives in California, in the wood of the incense cedar.

Family: Orussidae

The PARASITIC WOOD WASPS (superfamily Orussoidea, with the single family Orussidae) comprise a very small group which nevertheless is distributed throughout the world; it occupies a special position among the Symphyta because of its parasitic way of life: the larvae are said to be ectoparasites of wood-dwelling beetle larvae. Probably the Orussidae represent a very specialized phylogenetic offshoot, which has undergone extensive modification, particularly in the structure of the ovipositor. There is thought to be only one species in Germany, the 7–15-mm-long *Orussus abietinus*; seven species live in the U.S.A.

Family: Cephidae

The superfamily Cephoidea is represented by the single family of the STEM SAWFLIES (Cephidae), with about 100 species, forty of which live in Europe. They are slender animals with abdomens which may be either cylindrical or laterally compressed so that they have a knifelike appearance. The larvae are a creamy white; their thoracic legs are reduced in size and there are no abdominal feet. They bore cylindrical tunnels in grass stalks or in the pith of shrubs; occasionally they burrow in woody twigs.



Fig. 17-8. Female of *Orussus abietinus*, a species occupying a special position in the Symphyta because of its parasitic habit.

The most important agricultural pest among the Cephidae is the slender EUROPEAN WHEAT-STEM SAWFLY (*Cephus pygmaeus*; L 6–8 mm; see Color plate, p. 437). The female flies in May and June, laying eggs on the uppermost parts of rye, wheat, barley stalks, and various wild grasses, one egg to each stalk. The larva gnaws its tunnel downward in the stalk, making a pupal chamber in the base of the stalk under a plug of bore dust; above this plug it bites an annular furrow in the stem wall, so that the stalk breaks off easily. Moreover, the heads of the attacked plants often bear no grains, or only small ones. When the grain is mown the larvae are generally in no danger, since they are so low in the stalk that they remain behind in the stubble. This wheat-stem sawfly is widespread in Europe, northern Africa, and the Near East, and has even been introduced to North America, east of the Mississippi, where it has been known since 1887 and has done increasing damage. The AMERICAN WHEAT-STEM SAWFLY (*Cephus cinctus*) is a severe pest, particularly in the extensive grain-growing areas of Canada. There it has been combatted by importing a European parasitic wasp which is the main parasite of the European wheat-stem sawfly.



Fig. 17-9. *Cimbex lutea* (female), a cimbicid sawfly recognizable by the buttonlike or clublike thickening at the end of the antenna.

Another stem sawfly, *Janus compressus*, makes itself troublesome in tree nurseries and espaliered orchards in the warmer regions of Europe, since the activity of the larvae in the pith of the plants causes the tips of the young shoots to break off. Two species are minor pests in the U.S.A.

The superfamily Tenthredinoidea (to which the term SAWFLY is restricted by some entomologists) contains the great majority of the sawflies. We distinguish six families: 1. the Argidae, 2. the Blasticotomidae, 3. the Cimbicidae, 4. the Pergidae, 5. the Diprionidae, and 6. the Tenthredinidae.

The ARGIDS (family Argidae) are small sawflies (L 7–12 mm), usually

Families: Argidae and Blasticotomidae

dark in color and often with a metallic sheen. They are distinguished by the antennae, which consist of only three segments, the last of which is strikingly long. They are distributed worldwide, with 400–500 species described, of which most live in the tropics; there are about forty species in Europe and thirty-two species in the U.S.A.

This group includes the ROSE SAWFLY (*Arge ochropus*), one of the most important pests of both wild roses and garden varieties. The female lays sixteen to eighteen eggs in a row along young, juicy rose shoots. A shoot so "processed" looks as though a top-stitched seam had been made in it, so that this insect is known to some gardeners as the sewing fly. Infested shoots curl up, wither, and are unable to develop their buds. The greenish-gray, often S-shaped larvae, colored yellowish on the dorsal surface, feed on the leaves in groups, beginning at the edges. They have an extraordinarily large food requirement, so that on occasion the plant becomes entirely defoliated. The larvae pupate in a double-walled cocoon, lying near the surface in the ground. Usually there are two generations per year.

The rather primitive family Blasticotomidae is represented by only one species, *Blasticotoma filiceti*, in Europe. The larvae, which lack abdominal legs, burrow in the stalks of various ferns.

Family: Cimbicidae

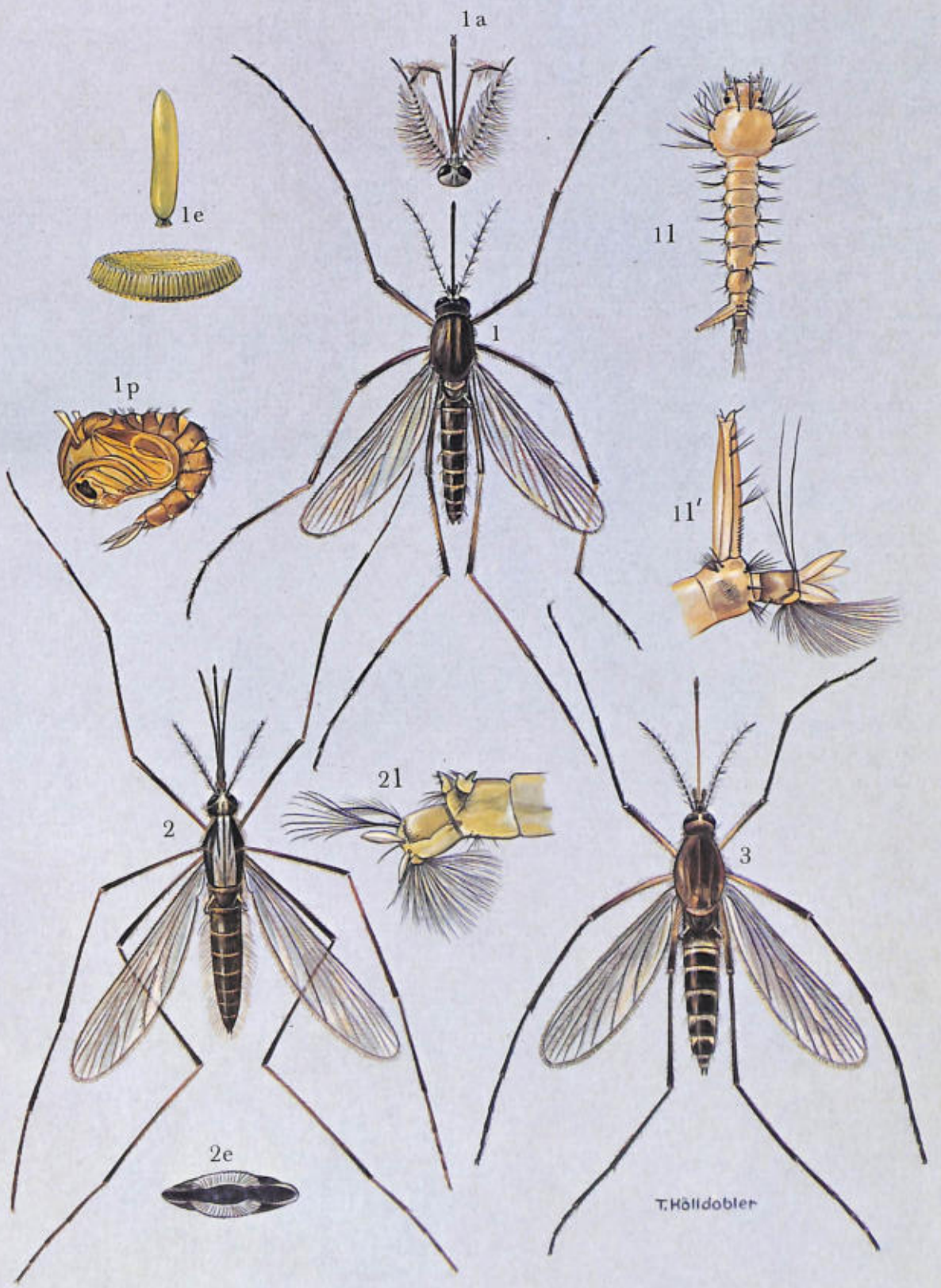
By far the largest of the sawflies (L up to 28 mm) are the CIMBICIDS (family Cimbicidae); they are easy to distinguish from all the other families by the end of the antenna, shaped like a club or knob. The larvae, too, are quite striking; they are usually green, strongly built, with six to sixteen feet. The imagoes sometimes ring young shoots in order to lick up the juice which oozes out. Around 130 species have been described, forty-five of which are European. Only twelve occur in the U.S.A.

In Europe and northern Asia the GREAT BIRCH SAWFLY (*Cimbex femoratus*), colored black and brown, is not uncommon. The large, ponderous larvae (L up to 45 mm) feed on the leaves of various deciduous trees, but prefer birches. In feeding, which they do mainly in the evening twilight and at night, they take up a peculiar position as though riding astride the edge of the leaf. When in danger they roll themselves up in a spiral and squirt blood at the attacker with considerable force, from openings lying above the spiracles on the sides of the body (reflex bleeding). In the fall the fullgrown larva spins a solid dark-brown cocoon, in the shape of a long egg, which is glued along a twig and serves as winter quarters for the larva. It pupates in the spring; the imago emerges by chewing out a circular lid from the upper end of the cocoon. The ELM SAWFLY (*C. americana*) feeds on a variety of trees in the U.S.A. The matte black, long-haired BIRCH SAWFLY (*Trichiosoma lucorum*) occasionally undergoes population explosions, and then the bluish-green to yellowish larvae can defoliate miles of birch-bordered avenues.

▷
Mosquitoes: 1. Northern house mosquito (*Culex pipiens*; L 7 mm); a, head of the male; e, egg and egg mass; *l*, larva and hind end enlarged to show the respiratory siphon; p, pupa; 2. Malaria mosquito (*Anopheles bifurcatus*, L 8 mm); e, egg; *l*, hind end of the larva with respiratory siphon, 3. *Aedes communis* (L 9 mm).

Family: Pergidae

The PERGIDS (family Pergidae) resemble the cimbicid sawflies in the shape of the antennae. The pergids are characteristic of the Australian fauna, but also have some representatives in South America. The larvae


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1p
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2e
T. Hölldobler


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ERICH DITTMANN
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of the species in the genus *Perga* have no abdominal feet; they live in communities on the leaves of species of eucalyptus.

Family: Diprionidae

The CONIFER SAWFLIES (family Diprionidae) are smallish insects (L under 10 mm) with broad, compact bodies. The antennae of the males either have dense combs of long hairs in one or two rows, or appear as bushy plumes; those of the females have sawteeth on the underside. The larvae often live in associations. They have six to sixteen legs; the antennae are very small and indistinctly segmented. Pupation occurs within a double cocoon. Ten genera are known, with sixty species, all in the northern hemisphere. There are some noteworthy pests in the genera *Diprion* and *Neodiprion*. Seven genera, with sixteen species, live in Europe, and thirty-five species live in the U.S.A.

The best-known of the European species is the PINE SAWFLY *Diprion pini* (L, ♂♂ 7–8 mm, ♀♀ 8–10 mm; see Color plate, p. 437). Since there are frequent population outbreaks of this species, it is the pest most feared by foresters. The coloration of the two sexes is different: the males are deep black, but the females are pale yellow with the head and the middle of the abdomen black. The species is found in Europe and northern Africa. The main food plant is the pine, among others the jack pine, Austrian pine, and white pine; it attacks trees of all ages, but prefers underdeveloped trees with thin trunks which have been growing on poor soil for twenty to thirty years.

In warmer regions these sawflies swarm in April and May and again in July and August, but in areas with a less favorable climate they do so only once, in June and July. In either case, it is only the males that fly, while the females usually creep sluggishly about on branches. The female deposits her eggs by slitting a groove along a pine needle with the saw of the ovipositor. In this narrow crevice she lays ten to fifteen eggs in a row, and then she covers them with a foamy, sticky mass. One female can produce as many as 150 eggs. It may occur that eggs are laid without having been fertilized and nevertheless develop (parthenogenesis). The yellowish-green larvae have a black marking like a semicolon over each abdominal leg. They live on the pines in large associations. At first they eat only the fleshy parts of the needles, leaving the midribs, but older larvae consume the whole needle right down to the stalk. When the larvae are disturbed or in danger, they raise the front part of the body and, from the mouth, squirt a fluid smelling strongly of resin. They pupate at the end of June in a brownish-gray, barrel-shaped, tough cocoon fastened to the needles or twigs. At the end of July and in August the adult sawflies, the second generation of the year, leave the cocoons by chewing a circular lid in the end of the cocoon. Their larvae feed through the first part of the autumn, then descend to the ground and spin themselves into a cocoon in the litter there, where they spend the winter. They pupate in the spring, but often only after lying in the cocoons for one or more years. The number of enemies of this sawfly is surprisingly large. Among the parasitic insects

◁ Nematocera: 1. The garden March fly (*Bibio hortulana*; L 11 mm); 2. A moth fly (*Psychoda* sp.); 3. A black fly (*Simulium* sp.); 4. A crane fly (*Tipula oleracea*; L 25 mm); 5. A crane fly (*Ctenophora atrata*; L 25–32 mm). Brachycera: 6. An erinnid fly (*Erinna atra*; L 13 mm); 7. A large horsefly (*Tabanus bovinus*; L 18–20 mm); 8. The horsefly *Chrysops caecutiens* (L 10 mm); 9. The horsefly *Haematopota pluvialis* (L 5.7–11 mm); 10. A soldier fly (*Stratiomyia* sp.); 11. A robber fly (*Asilus crabroniformis*; L 25 mm); 12. The robber fly *Laphria marginata* (L 15 mm); 13. The bee fly *Bombylius discolor* (L 13 mm); 14. The bee fly *Hemipenthes morio* (L 13 mm); 15. A hump-backed fly (family Phoridae); 16. The hover fly *Volucella bombylans* (L 16 mm); 17. The drone fly (*Eristalis tenax*; L 14 mm).

alone, there are sixty different species which attack the eggs, larvae, and pupae. Furthermore, mice, birds, and the larvae of predatory beetles dispose of many of these pine sawflies.

Of the nineteen species of the subgenus *Gilpinia*, two are especially worth mentioning; they both live on spruce trees and are frequently confused with one another: *Neodiprion polytoma* and *N. hercyniae*. Although in the Old World neither species is of significance to forestry, in the 19th Century the EUROPEAN SPRUCE SAWFLY (*N. hercyniae*) was accidentally brought to North America, and since 1930 it has become a forest pest of the first rank in Canada and the northeastern U.S.A. It has destroyed vast regions of forest, and an extensive and expensive effort was needed to control it. Hundreds of millions of parasites were turned loose, most of which originated in Europe and had been cultured in laboratories. Some of them became established and, together with a virus disease, contributed significantly to checking the plague. The last member of this group deserving mention is the EUROPEAN PINE SAWFLY (*N. sertifer*), next to *Diprion pini* the most important forest pest of all the conifer sawflies in Europe and northern Asia.

Family: Tenthredinidae

The great majority of all sawflies belongs to the large family of the TRUE SAWFLIES (Tenthredinidae); this includes forms which differ greatly in appearance and way of life. The length of the imago ranges from 2.5 to 14 mm, and the coloration is often conspicuously bright. They are frequently found on flowers, though some live by preying on other insects. The larvae live either singly or in associations, and often become active only at dusk or at night. Most of them are leaf-eating pseudocaterpillars, with six to eight pairs of abdominal feet; some produce leaf mines or form galls. They inhabit all parts of the world except Australia, where their place is taken by the Pergidae already described. So far 250 genera with around 4000 species are known, 800–900 of them in Europe, and 750–800 in the U.S.A.

The emerald-green color of the GREEN SAWFLY (*Rhogogaster viridis*; see Color plate, p. 437), common everywhere in central Europe, makes it especially conspicuous. It usually stays among bushes and shrubs, where it hunts other insects, chewing up and swallowing those it catches.

The BIRCH SAWFLY (*Croesus septentrionalis*, see Color plate, p. 437) has peculiar shovellike broadenings of the hindlegs, at the end of the tibia and in the first tarsal segment. The green larvae are yellowish with black dots both on the first and on the two to three last segments. They live in associations, preferring birch trees, where they straddle the edges of the leaves, one behind another. When such a group is disturbed, the larvae adopt a position presumably meant to frighten off the attacker: suddenly they all bend the hind end of the body into an S shape, raised in the air, so that they look like a row of question marks. They may remain for a while in this posture, or they may move the raised part of the body back and forth, keeping time with one another.



Fig. 17-10. Leaf of the almond-leafed willow (*Salix triandra*) with bean-shaped galls made by the willow sawfly *Pontania proxima*.

Quite a few of the true sawflies are pests in fruit trees. For example, the IMPORTED CURRANT WORM (*Nematus ribesii*; L 6–7 mm; see Color plate, p. 437) infests gooseberries and sometimes currants in Europe and the U.S.A. Depending on climatic conditions, there may be two to four generations annually. The larvae are a bluish green, the first and eleventh segments orange-yellow with black dots. At first they chew insignificant holes in the leaves in a characteristic manner, starting at the edge and eating all but the ribs. This happens so rapidly that gooseberry bushes which appear to have all their leaves on one day are suddenly bare on the next. The larvae pupate in or on the ground, in a black-brown parchmentlike cocoon. This species originated in northern and central Europe, but since 1857 has been carried to North America.

Two species of the genus *Hoplocampa*, *H. minuta* and *H. flava*, are among the worst enemies in Europe of plum trees. Sawflies of both species are 4–5 mm long and resemble one another in their behavior, but they can be readily distinguished by their colors, the former being black and the latter, yellow-brown. The females lay, on the average, seventy glass-clear eggs in pockets in the calices of closed or opened blossoms. As soon as the larva hatches, it burrows into the young fruit and hollows it out. An easily recognizable sign of infestation is the little lumps of feces that are thrown out and remain stuck around the entrance hole. The young plum is filled with feces having a buglike smell; it turns blueish prematurely and finally falls off after the larva has moved to a new plum. In this way, each larva destroys four to six plums before it spins itself into a silky cocoon as much as 10 cm deep in the soil. Close relatives of these species are the EUROPEAN APPLE SAWFLY (*Hoplocampa testudinea*) and *H. brevis*, which infests pears. Before burrowing into the fruit, they make a gallery that is visible from the outside, which gives warning of the infestation. Economically they are of less significance than *H. minuta* and *H. flava*.

The agriculture of southeastern Europe, especially, has suffered from *Athalia rosae*. The larvae are black-gray, turning gray-green after the last molt; in the regions where they occur they are called black caterpillars. They feed almost exclusively on cruciferous plants (mustard, rape, rarely turnips). Although an individual larva gnaws only small holes in the vanes of the leaves, when there is a mass outbreak of larvae only the ribs of the leaves remain. Since the young larvae are easily overlooked, one is repeatedly surprised by the suddenness with which they can strip a field bare, sometimes almost overnight.

In forestry, sawfly species of the genus *Pristiphora* are particularly dreaded. The FIR SAWFLY (*Pristiphora abietina*) is one of the most important pests in the fir trees of central Europe. The imago, 4.5–6 mm long, is pale brown in color, the dorsal surface largely black-brown. Its flying period lasts from the end of April to the beginning of June. The female slits open the needles on the highest shoots which have sprouted in May, on trees twenty to sixty years old, and deposits eggs in them singly. Firs which

sprout late, and those standing in the open, are preferred. The light-green larvae consume only needles sprouted in the same year. They pass the winter in a cocoon in the ground and pupate there in the spring. Infestations by these sawflies cause not only a diminution of new growth but also, especially in young trees, malformations of the tops of the trees, such as excessive branching.

Another notorious despoiler of the forests is the LARCH SAWFLY (*Pristiphora erichsonii*; L 8.5–9 mm), distributed throughout the northern temperate zone of both hemispheres. The head and thorax are largely black, while the abdomen is red with black first, sixth, seventh, and eighth segments. These sawflies fly from May to July, during the period when the long shoots are sprouting.

The larch sawfly reproduces almost exclusively by parthenogenesis. The gray-green larvae at first feed in groups, later separately, on the needles of the short shoots. Whereas it is destructive only in certain areas of central Europe, in Great Britain and North America the species has been known for unusually severe outbreaks since the end of the 19th Century; in many areas there the larch woods were 80–100 percent destroyed. Even the smaller larch sawfly *Pristiphora laricis*, the sawfly most commonly found on larches in central and northern Europe, can cause serious damage, especially in nurseries.

Among the many species of the genus *Pontania* are the gall-producing sawflies. The larvae of the WILLOW RED-GALL SAWFLY (*Pontania proxima*) are found in fleshy, bean-shaped galls on willow leaves, usually with red discolorations on the upper surface. They occur in both Europe and the U.S.A. The *Fenusa* spp. larvae make mines in the leaves of trees and shrubs. Whereas the latter genus is of hardly any significance to the economy of Europe, the species *F. ulmi* and *F. dohrni*, carried to North America, became destructive leafminers of elms and alders, respectively, there.

Suborder: Apocrita

The suborder Apocrita comprises those Hymenoptera in which, in contrast to the sawflies, the first abdominal segment has become an intermediary structure (the propodeum) fused to the thorax. The abdomen is attached to the thorax by a stalk or pedicel formed by reduction or constriction of the second segment. The increased flexibility thus achieved facilitates the placing of the ovipositor or sting. The larvae have neither legs nor eyes; they are maggotlike or secondarily modified. The suborder is divided into two parts: A. the Terebrantes, which includes the parasitic and gall-forming wasps, and B. the Aculeata, including the other wasps, bees, and ants.

The Terebrantes, by F. Bachmaier

Distinguishing characteristics

Neither the Symphyta nor the Aculeata (to be treated in this and the next chapter) include the variety of forms encountered in the large group Terebrantes (formerly often called Parasitica). The latter are tiny to medium-sized; the group includes the fairy flies, only 0.2 mm long and thus the smallest of all known insects. Despite the bewildering diversity in body structure, they all (except for a few cynipoids, chalcidoids, and

proctotrupoids) possess an extra leg segment, the trochantellus, between the coxa and the trochanter. The wing venation is not nearly as complete as in the Symphyta, and is often regressed so as to leave only a few rudiments of veins. In some cases the wings are reduced or entirely absent. The females have an ovipositor, which serves for egg-laying and sometimes also for paralyzing the host; it is composed of three parts, and can either be withdrawn somewhat into the abdomen or extend far out from it.

Life of the imago

Most of the Terebrantes, especially the males, are decidedly short-lived; others live for some weeks or even, if they pass the winter as imagoes, several months. In order to remain active, they seem to require carbohydrate; for this reason many species feed from flowers. Honeydew, the sugar-containing excretions of aphids and scale insects, is particularly appreciated. Usually the eggs in the females become ripe only after the females have left the pupal cases, so that they also must eat food rich in protein for the final development of the eggs in the ovaries. Protein is obtained from the body juices of a host. The female pierces such a host with her ovipositor and licks or sucks the resulting wound, and may even expand it with her mandibles. If the food donor happens to be lying in a cocoon, however, there is a space between the pierced body of the host and the wall of the cocoon, which prevents such licking. But evolution has found a way round this difficulty; there emerges from the ovipositor a secretion which hardens instantly and, once the drill apparatus has been removed, forms a narrow, closed tube through which the body fluid either rises by capillary action or is sucked up by the wasp.

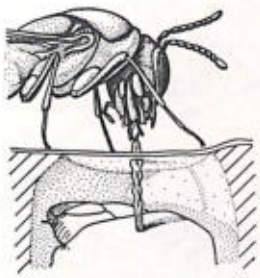


Fig. 17-11. Female of a chalcidoid wasp (*Habrocytus cerealellae*) taking in the body fluid of her host, the caterpillar of the moth *Sitotroga cerealella*, through the tube she has constructed.

The imagoes prefer places which offer the best living conditions for their offspring, for their lives are devoted entirely to reproductive activities. These instincts and the associated sensory performances are extremely well adapted to their purposes. Some female Terebrantes are able not only to distinguish their own host species from closely related species, but even to tell the difference between individuals in which eggs have already been deposited and those which have not been attacked. In the latter case, the sense organs located at the end of the ovipositor, often in great numbers, are probably critical. In the search for and recognition of hosts suitable for egg deposition, it is likely that the sense of smell ordinarily plays the main role, though vision is certainly also involved. In some cases it is not the host animal itself that acts as the releaser for host-selection. That is, some species respond to the scent of certain plants or to certain life forms of the hosts; for example, they may select mine- or gall-dwelling insects belonging to quite different orders. In these cases the searching behavior of the female ready to lay eggs is guided primarily by the plant on which the host lives, or by its life form, and only secondarily by the host itself; in other words, there is an ecological association with the host. Nevertheless, errors of such instinctive behavior are not uncommon (as, for example, in the cases of superparasitism and multiparasitism to be discussed below).

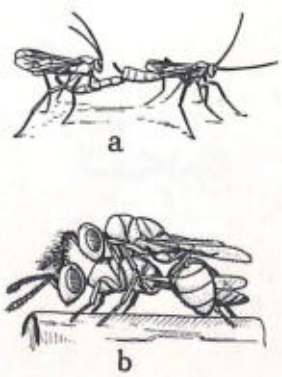
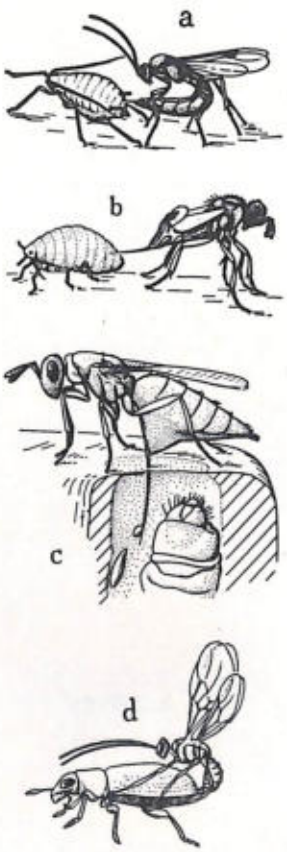


Fig. 17-12. Copulatory positions of two parasitic wasps; (a) the ichneumon *Heteropelma calcator*, and (b) the chalcidoid *Eurytoma masii*; see also the fig wasp in Fig. 17-34.

These wasps spend much time in cleaning activities, bouts of which occur between all other actions. Although mouthparts, legs, wings, and abdomen are continually cleaned, the greatest attention is devoted to the antennae, where the most important sense organs are located; the antennae are drawn through an identation in the first tarsal segment of the foreleg, equipped with a comb and closed off by a spur on the tibia.

Reproduction and egg-laying

In the present state of our knowledge of the Terebrantes, we distinguish five possible modes of reproduction: 1. Sexual reproduction or zygogenesis, by parents of two sexes; 2. Zygogenesis as a rule, but with occasional parthenogenesis (development of an unfertilized egg); 3. Parthenogenesis as a rule, with males infrequent or only in special areas of the range of distribution; 4. Obligatory parthenogenesis, with males entirely lacking; 5. A regular alternation between a sexual generation and one consisting entirely of females (heterogony). The last of these, alternation of zygogenetic and parthenogenetic generations, occurs among the gall wasps and in isolated cases among the parasitic wasps. The offspring produced parthenogenetically may be: (a) males only (the most common case in the Hymenoptera), (b) females only, or (c) both males and females, in which case the two sexes may be represented in approximately equal numbers, or one of the other may predominate.



Copulation, as a rule, is preceded by courtship of the partners, in which the female plays a relatively passive role, while the male makes his state of excitation known by whirring or trembling of the wings and strokes of the antennae. Rhythmic striking of the female's antennae by those of the male is an important element. The mating instinct of the male is usually very strong, whereas the females do relatively little and often even try to drive away the importunate partner. For example, the male of species of the chalcidoid genus *Trichogramma*, which is parasitic in insect eggs, is already sitting on the host eggs in an excited condition when the female emerges; as soon as she appears he hurls himself upon her, even though her wings may not yet have unfolded. Copulation itself takes only a very short time. Two of the possible copulatory positions are shown in Fig. 17-12.

In the vegetarian species of the Terebrantes, the egg is usually pushed into the plant tissue with the ovipositor; less commonly, the plant is not pierced. In the species that eat insects, the following forms of egg deposition are known: 1. Piercing the host and burying the egg in its body, either in the body cavity or in certain organs such as the brain, salivary gland, or midgut; 2. Attaching the eggs to the host externally; 3. Depositing the eggs in the immediate vicinity of the host; 4. Depositing the eggs in the open, with no host present (in this case a great number of eggs are usually laid). Forms (2) and (3) are realized predominantly where the host animals live in secluded places like webs, mines, galls, or within wood. The posture adopted by the female during egg-laying is by no means uniform. Wasps with short ovipositors tend to curve the abdomen

or push it forward between the legs, often so far that the tip of the drill apparatus is in front of the head. Other species deposit their eggs behind them, with the head pointing away from the site of the operation, and still others brace themselves firmly on their legs and hold the abdomen out straight while positioning the drill vertically, at right angles to the abdomen. The process of egg-laying can be almost instantaneous or it may take hours. The latter applies when the eggs must be laid on or near hosts living deep in wood.

The number of eggs a female produces also varies considerably, and is unknown for most species. In females of the parasitic genus *Ephialtes*, for example, only about fifteen eggs ripen, whereas in the chalcidoid family Eucharitidae there can be up to 5000; in the latter family, the larvae do not find a host directly at hand when they hatch, so there is a high mortality at this stage. The more or less elliptical, sometimes curved eggs contain differing amounts of yolk. Tiny yolkless eggs can easily pass through the narrow canal of the ovipositor and swell up quickly by absorbing fluid within the host; in eggs of the braconid *Perilitus rutilus* a twelve-hundred-fold increase in size has been observed. Larger, yolk-containing eggs either have a short stalklike appendage, which is the only part guided by the channel within the ovipositor, or they slide along in a glandular secretion outside the ovipositor. Eggs rich in yolk are usually equipped with a very long stalk. They may be laid with either the body of the egg or the stalk forward; in either case passage through the channel within the ovipositor is accompanied by stretching of the elastic membrane of the egg (the chorion) and displacement of some of the contents into the stalk, forming a long, thin cylinder which readily moves through the channel to the host. The chorion is delicate and usually smooth, though occasionally, particularly in some chalcidoid families, it is covered with very fine spines.

◁ Fig. 17-13. Positions of various female parasitic wasps during egg deposition: (a) the aphidiid *Lysiphlebus testaceipes* laying eggs in an aphid, (b) the chalcidoid *Aphelinus mali* piercing a woolly apple aphid (*Eriosoma cornigerum*) while facing away from it, (c) the chalcidoid *Habrocytus cerealellae* laying eggs on a caterpillar of the moth *Sitotroga cerealella*, (d) *Pygostolus falcatus* piercing a weevil of the genus *Sitona* by pushing her ovipositor under the elytra of the host.

Polyembryony

Development of the eggs of certain braconids, chalcidoids of the family Encyrtidae, and proctotrupoids of the family Platygasteridae involves the curious phenomenon called polyembryony (see Fig. 17-15). Such pronounced polyembryony is unique in the animal kingdom, and suggests a special relationship of these wasps to their environment. The essential feature of this phenomenon is that from a single egg, by asexual divisions, a number of offspring (up to 2000) can be produced. This process is the same as that which produces identical twins in humans. The eggs of most parasitic wasps which reproduce in this way are laid in the eggs of the host animals, but it appears that only those wasp eggs develop which happen to be in the embryo; those which are laid in the yolk perish.

Larvae and pupation

The larvae are colorless and appear either transparent or white. The head capsule is only poorly developed; the antennae, if present, are very short. Of the mouthparts, the mandibles are usually distinctly regressed and the other parts, even more so, often to the extent of being unrecognizable. The midgut is closed off from the hindgut, the connection between the two being formed only a short time before pupation. The full-grown

larvae are very uniform in structure; the body has the shape of a bulky cylinder, often curved ventrally, and is divided into more or less similar segments (typical maggots).

In many cases, however, the first larval stage has a thoroughly deviant, and often quite astonishing, appearance. Frequently there are caudal appendages in the shape of pointed processes, as long as the body, or rounded vesicles. The caudal vesicles of the cabbage-white parasite *Apanteles glomeratus* of both Europe and North America are known to serve for the uptake of oxygen. The larvae of some proctotrupoid wasps are fantastic creatures, with the anterior part of the body massively developed and with powerful mandibles (see Fig. 17-16). Their appearance is more reminiscent of the Lower Crustacea than insect larvae, so that they have acquired the name cyclopoid larvae (*Cyclops* is the generic name of a small crustacean; see Vol. I). The first-stage larva of the chalcidoid family Perilampidae is termed the planidium type; it bears relatively strong dorsal chitinous plates, extending around to the ventral side, and processes which resemble limbs.

When the larva is ready to pupate, the cavities of the midgut and hindgut become continuous, so that the feces which have been retained during the whole larval period can be discharged. Some parasites undergo metamorphosis inside the host, and others, outside; the gall wasps always metamorphose within the gall. Often a cocoon is spun. The cocoons of different species vary greatly in shape, size, color, and construction and are thus of use in identification. The species which do not spin cocoons are primarily those which enjoy the protection of the host pupa or cocoon, and of course those hidden in galleries within wood or in galls. In the Cynipoidea and Chalcidoidea there are actually no true cocoons at all; in the chalcidoid family Eulophidae the pupae may even lie in the open on leaves. The pupae themselves are in general soft-skinned and in the majority the limbs are free (they are exarate; see Fig. 17-17) as in the other Hymenoptera, although among the chalcidoid wasps there are some with so-called obtect pupae, having wing and leg cases fused to the body wall.

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Flies: 1. The fruit fly *Rhagoletis cerasi* (L 3.5 mm ; 2. The frit fly *Oscinella frit* (L 3 mm); 3. The beelouse (*Braula coeca*; L 1–1.5 mm); 4. The pomace fly *Drosophila melanogaster* (L 2 mm); 5. The dung fly *Scatophaga stercoraria* (L 9 mm); 6. The housefly (*Musca domestica*; L 7.5 mm); 7. The little housefly (*Fannia canicularis*; L 5.5 mm); 8. The stable fly (*Stomoxys calcitrans*; L 6.5 mm); 9. A tsetse fly (*Glossina* sp.); a, dorsal aspect; b, lateral aspect, starved; c, the same, after feeding; d, the same, giving birth to a full-grown larva; 10. The louse fly *Lipoptena cervi* (L 5–6 mm); 11. A bat fly (family Nycteribiidae); 12. The blowfly *Calliphora vomitoria* (L 14 mm); 13. The gray flesh fly (*Sarcophaga carnaria*; L 17 mm); 14. The blowfly *Lucilia caesar* (L 11 mm); 15. A horse bot fly (*Gastrophilus* sp.; L 16 mm).

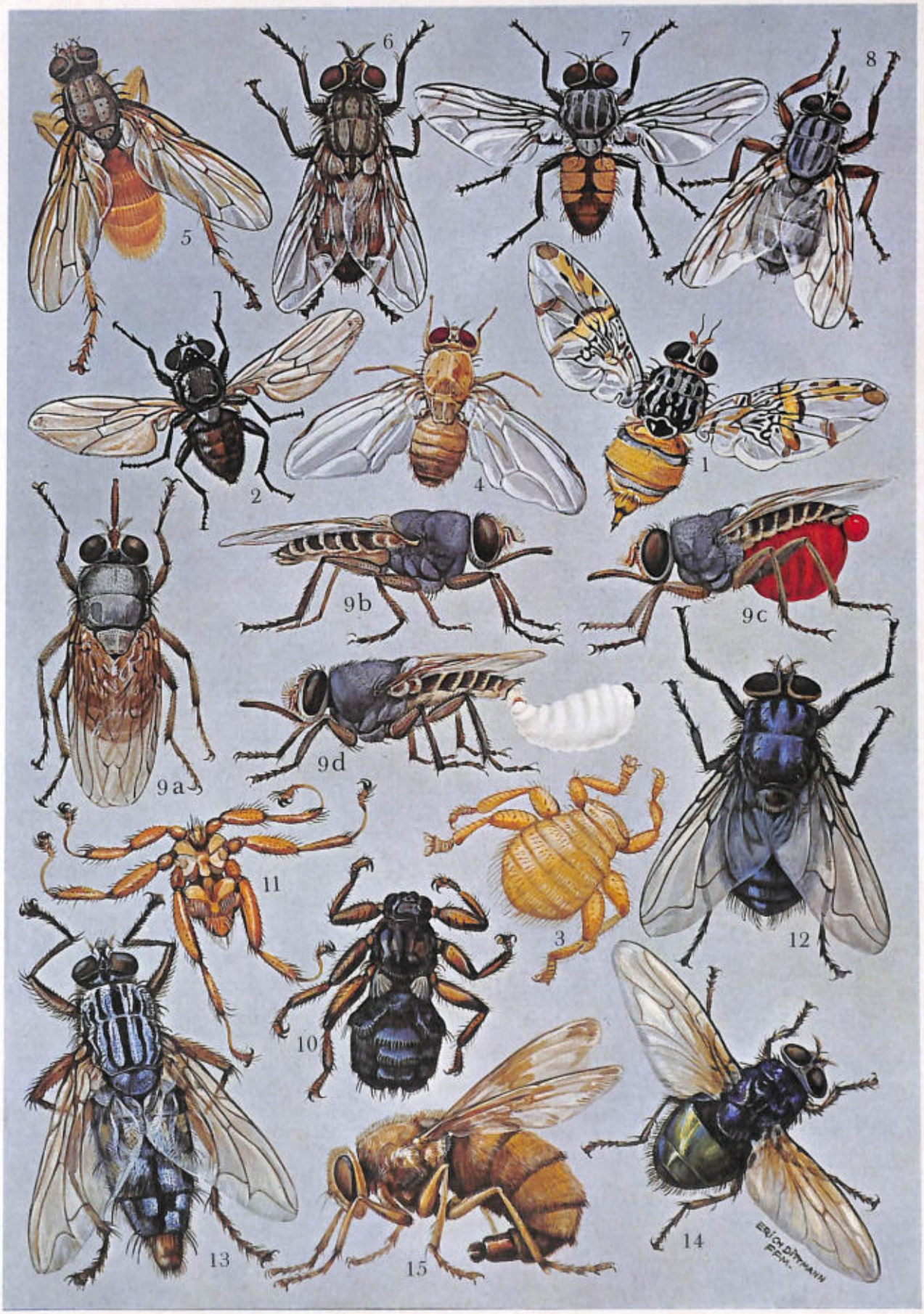
Emergence

As they emerge, the wasps often must overcome formidable obstacles—for example, the larval skin or pupal case of the host, its own cocoon or that of the host, the walls of the galls, and so on. They penetrate these coverings by biting through them, often in a quite distinctive, species-specific manner. Ordinarily the males emerge before the females.

The entire course of development spans very different periods of time, depending on the species and on climatic conditions. Species are known which develop in about a week, and can therefore have many generations per year, but on the other hand there are species with only one or two generations per year. In gall-forming cynipoid wasps the development of one generation can, under certain circumstances, extend for as long as two years.

Parasitism

The relationships between the parasitic Hymenoptera and their hosts


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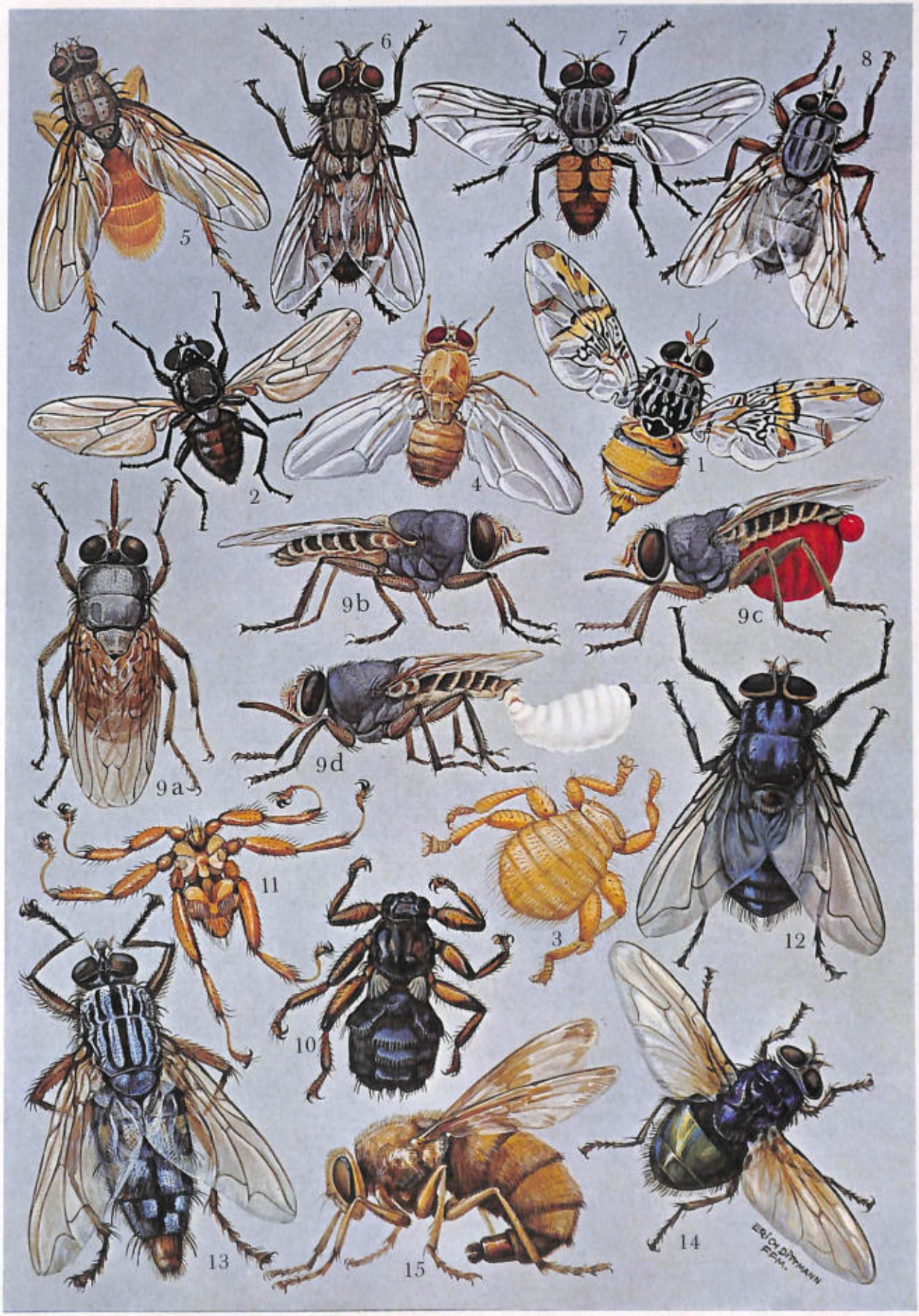
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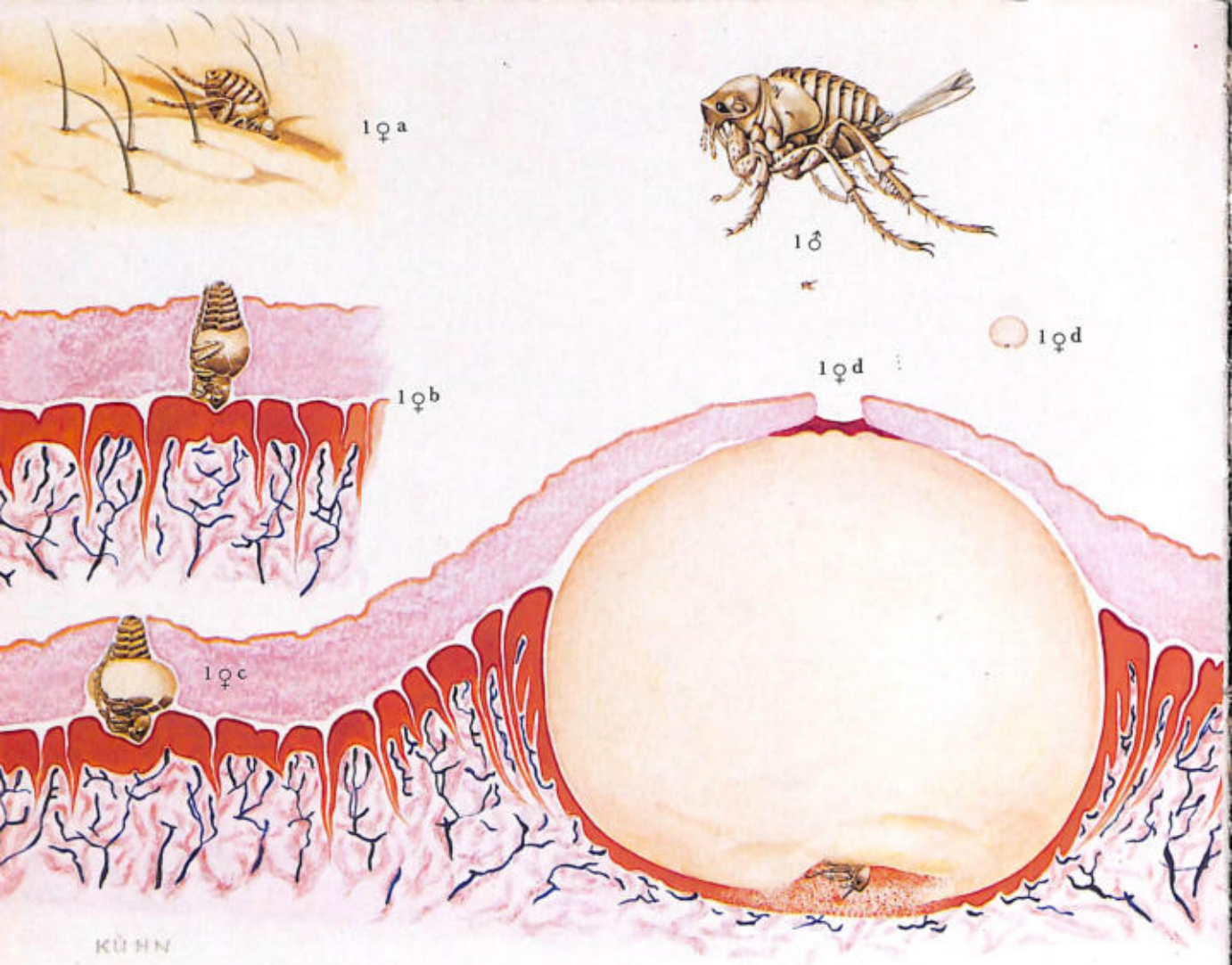
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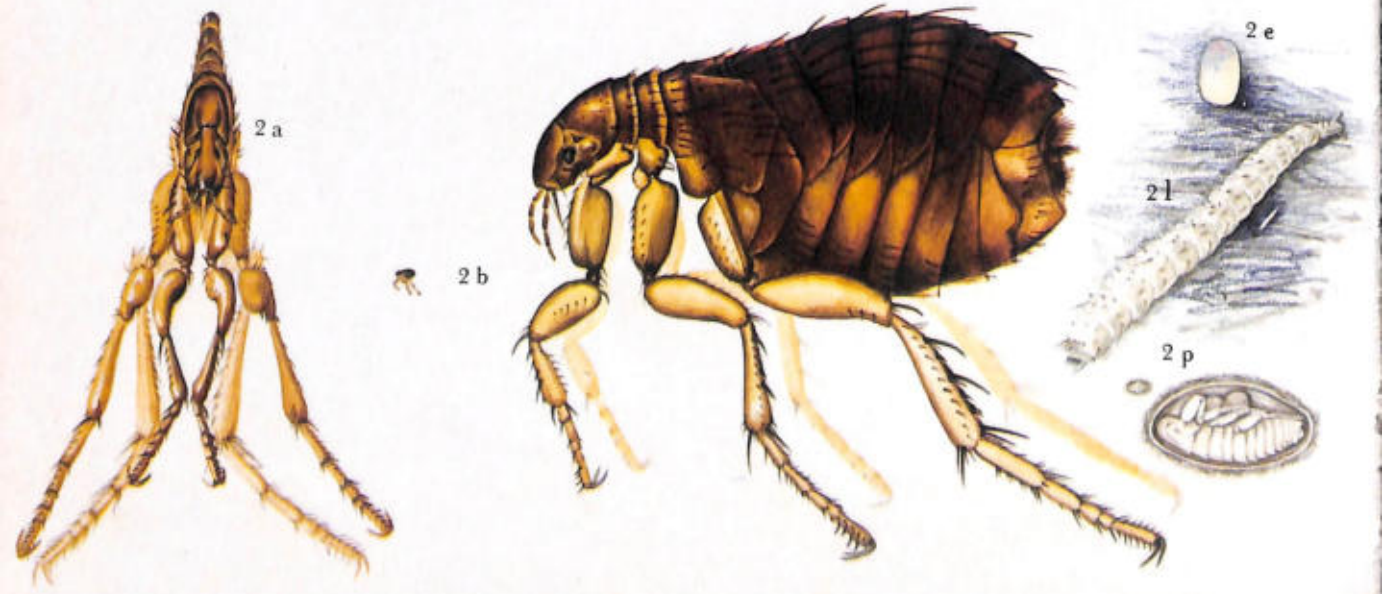
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Parasitism

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Fleas (see Chapter 21): 1. The jigger (*Tunga penetrans*); ♂ male with copulatory organs extended, enlarged and actual size; ♀ female, (a) penetrating a fold of the human skin, (b) shortly after penetration, with the body beginning to swell, (c) after further penetration, with increased swelling, (d) maximally swollen and releasing the eggs through the opening in the epidermis; ♀ a–d enlarged, ♀ d′ actual size. 2. The human flea (*Pulex irritans*); (a) from the front, (b) from the side, enlarged and actual size; (3) egg, enlarged, (l) larva, enlarged and actual size, (p) pupa in opened cocoon, enlarged and actual size.

can also take an extraordinary number of forms. Zoologists classify these according to the following headings: 1. In ectoparasitism, the parasitic larva eats the host from outside; the host may remain active for a limited time or—and this is the rule—may have been paralyzed initially by the sting of the mother animal. 2. In the case of endoparasitism, the parasite larva lives within its host, while the latter may stay alive and continue to eat for a considerable time. 3. Primary parasitism describes the situation in which the host is not itself a parasite. 4. Hyperparasitism is any form of parasitism of one animal upon another parasite, including secondary parasitism (in which a parasite attacks a primary parasite) and tertiary parasitism (in which a secondary parasite is attacked by a parasite). 5. In solitary parasitism, the female parasite lays only one egg on or in each host. 6. In gregarious parasitism it is always the case (a normal element in the behavior) that several eggs are laid in the same host animal. 7. In connection with the last two forms, the previously described polyembryonal parasitism should be mentioned. 8. Superparasitism denotes the fact that a host animal is by chance infested by a greater than usual number of larvae of the same parasite species, either because the female accidentally lays eggs for the second time in an animal visited previously, or because several females have deposited eggs in the same host. Whereas in gregarious parasitism the parasite larvae share an adequate food supply, in superparasitism their competition is abnormally severe. 9. In multiparasitism, a single host animal is by chance infested by two or more larvae of different parasite species; either both species survive (a rarity), one species develops while the other perishes, or neither species is able to develop. Superparasitism and multiparasitism both represent a greater than ordinary infestation of the host with parasites. It is assumed in such cases that the sensory ability of the parasite female is inadequate, in that she is unable to tell an already-infested host from one in which no eggs have been laid.

Parasites which are strictly monophagous (can reproduce on only one species of host) are probably fairly rare. By far the greatest proportion of the parasitic wasps use several (oligophagy) or many (polyphagy) species within a systematic group (genus, family, or order) as hosts. Primarily it is other insects which serve as hosts, but spiders, pseudoscorpions, ticks, and myriapods are also parasitized by wasps. They most often infest eggs, larvae, and pupae, and only rarely are they found in adults. It is not surprising that adult aphids are infested, since here the imago is hardly different from the larva. But even beetle imagoes may be attacked, for example, by braconid wasps.

Plant-eaters and gall-producers

Only a very small number of parasitic wasps, all of them belonging to the Chalcidoidea, have adopted a vegetarian way of life and become gall-producers or seed-dwellers. The main gall-producers are in the superfamily Cynipoidea, and those of the subfamily Cynipinae will be mentioned here as examples. The galls they form have always attracted the attention of natural scientists, because they are so conspicuous; in the course of cen-

turies many proposals about the causes of these galls have been debated. The beliefs that the galls begin to form under the influence of the undeveloped egg, or even of glandular secretions given off when the eggs are laid, have been refuted. In many species, to be sure, the actual development of the gall is induced by the fully developed embryo while still in the egg, but in most cases the larva must hatch first. And for the further development of the gall, the presence of the larva is essential. If the larva dies, the gall ceases to grow. It is certain that gall formation depends upon a species-specific influence of the embryo and the larva. For example, an oak leaf is capable of producing quite different gall forms, depending on the species of gall wasp which has attacked it. It is probable that the larval secretions or excretions act as a growth hormone which interferes with the metabolic processes of the plant.

Only a few of the Terebrantes are noteworthy plant pests; here we shall mention only a few genera of chalcidoid wasps of the families Eurytomidae and Torymidae, which damage grain and seeds. The role of the Terebrantes as regulators of the balance of nature is incomparably important; the maintenance of equilibrium in the biocenosis is more valuable to all of us. One hundred species of parasitic wasps have so far been successfully employed in biological pest control, and the intention is to greatly increase this effort in the future. Perhaps such biological control will make it possible to limit even more strictly the chemical eradication of destructive insects, with its many disadvantages.

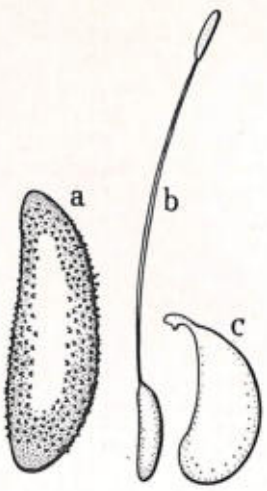


Fig. 17-14. Various egg forms of the Terebrantes: (a) that of the chalcidoid *Dibrachys cavus*, chorion covered with fine spines, (b) that of the gall wasp *Biorhiza pallida*, with a long stalk, (c) that of the parasitic wasp *Polyblastus cothurnatus*, with a short, hooklike appendage.

Classification of the many species

The group Terebrantes includes an enormous number of species. So far roughly 70,000 species have been described, and this number will surely be considerably increased by research yet to be done. Even among the native forms, new discoveries can be expected. The group is sub-divided into seven superfamilies, with forty-seven families: 1. Trigonaloidea (one family), 2. Ichneumonoidea (six families), 3. Evanoidea (three families), 4. Cynipoidea (five families), 5. Chalcidoidea (twenty-two families), 6. Pelecinoidea (one family), 7. Proctotrupoidea (nine families).

Family: Trigonalidae

The superfamily Trigonaloidea consists of only one family with few species, the TRIGONALIDS (Trigonalidae). With respect to the form of the regressed ovipositor and the wing venation they have a certain resemblance to the Aculeata. Here we have a group that is ancient yet highly specialized in a particular direction. In central Europe it is represented by a rare species, *Pseudogonalos hahni* (L–910 mm). This animal is distinguished by a dark cross band in the forewing, and by an unusual life history. The larvae develop as hyperparasites within either the caterpillars of the Lepidoptera or the pseudocaterpillars of the Symphyta, where the larvae of other parasitic wasps or larvivorid flies are their real hosts. The female lays her eggs neither on nor in the hosts, but rather on leaves. She sits on the upper surface of a leaf with her abdomen pointed toward the edge, then bends the abdomen around to the underside of the leaf and attaches the eggs there, either one by one a short distance apart, or together

in little groups. In order to develop further, these very small eggs (hardly over 0.1 mm long) must be taken in along with their food by caterpillars which happen to be eating there. As a further condition, development can proceed only if this chance caterpillar is infested by parasites. These two requirements understandably coincide only in rare fortunate instances. Nevertheless, the continuation of the species is ensured by the unusually large number of eggs laid; for example, a single female is said to be able to lay more than 10,000 eggs. From the first stage to the third, the larva lives inside its host without injuring any of its vital functions. At the appropriate time, the host larva leaves the primary caterpillar host, by then moribund, and spins its species-specific type of cocoon. After molting to the fourth stage the trigonid larva in turn leaves its host, itself now on the point of death, but remains within the cocoon, continuing to eat the host from the outside. Pupation also occurs in the cocoon of the host. In June or July the imago emerges. It is thought that this species has just one generation per year. Five species in four genera live in the U.S.A.

Superfamily: Ichneumonoidea

The superfamily Ichneumonoidea is divided into six families: 1. Aphidiidae, 2. Braconidae, 3. Ichneumonidae, 4. Agriotypidae, 5. Stephanidae, 6. Megalyridae.

Family: Aphidiidae

The APHIDIIDS (Aphidiidae), with thirty-five genera and about 300 species, are uniform in both appearance and way of life. They are all parasitic on aphids (family Aphidae in the order Homoptera) and are thus highly useful. The adult aphidiids, about 2 mm long, are inconspicuous and difficult to find. But in aphid colonies one can often see individual aphids which are rigid and swollen into a ball; upon opening them carefully, one finds the larva or pupa of an aphidiid wasp, perhaps a species of the genus *Aphidius* or *Trioxys*, which has consumed the entire contents of the aphid's body. Moreover, the skin of the aphid has been lined with silk and evidently drenched with secretion which stiffens it, turning it into a sort of "mummy"; using silk, the larva attaches this case firmly to the substrate, through a slit bitten in the ventral wall. One exception is the genus *Praon*, members of which leave the hollow aphid and, between its legs, construct the cocoon in which they pupate. The dead aphid thus sits on a pedestal spun by the larva, a quite peculiar sight.

The aphidiid imagoes emerge by gnawing an almost circular lid in the mummy's dorsal wall; the lid may be left attached at one point, so that after the wasp has emerged the lid falls back into place. To lay their eggs, the females force their abdomens forward between their legs, so that the tip of the drill apparatus is far in front of the head. In a matter of seconds the victim is pierced and an egg is deposited within it.

Family: Braconidae

The BRACONIDS (family Braconidae), with over 5000 described species, are closely related to the following family, the ichneumons, but usually may be distinguished from them by the slower, more sluggish movements of the braconids. Moreover, the braconids lack the second recurrent vein in the forewing, and their abdomens are differently constructed. Usually

they are rather small wasps, inconspicuously colored, though in the tropics there are some large, magnificently glowing forms with brightly spotted wings and strikingly long ovipositors. One species of the genus *Iphiaulax* (cf. Color plate, p. 447) in Columbia, for example, has a body 14 mm long, but an ovipositor 175 mm in length. The braconids are predominantly parasites in lepidopteran caterpillars and the larvae of beetles and flies; they are of considerable economic importance and, since they have very little tendency toward hyperparasitism, are probably even more useful than the ichneumons. Several species have already been used for the biological control of destructive insects. For example, species of the genus *Opius* were employed very successfully in the battle against fruit flies in Hawaii.

The widespread and well-known black braconid wasp *Apanteles glomeratus* (L about 2.5–3 mm) lays numerous eggs in newly hatched caterpillars (gregarious parasitism), especially those of the cabbage white. In a single caterpillar one can find between thirty and fifty larvae, and in isolated cases there may be as many as 150. The total number of eggs a female of this braconid species can lay in the course of her life is estimated to be near 2000. Once the larvae are fully grown, they leave the body of the host almost simultaneously (see Color plate, p. 466) and immediately spin themselves into small, sulfur-yellow cocoons for pupation. The surfaces of the dying and desiccating caterpillars are then densely covered by the mass of cocoons. It is easy to misinterpret the situation and regard these little cocoons as "caterpillar eggs," as they are colloquially called in some places.

Another European species, *Apanteles congestus*, parasitizes a number of lepidopteran caterpillars. After leaving the host the larvae, in contrast to those of *A. glomeratus*, make loose communal webs rather than separate cocoons; each web, usually attached to a grass stalk, contains many small, elongated individual cocoons. The webs look like little balls of cotton hanging on the grass, and also resemble certain cocoons spun by spiders for their eggs; in fact, the two are often confused. The best-known species of the genus *Meteorus* is *M. versicolor*, a parasite in caterpillars of black arches and the moths *Leucoma salicis* and *Panolis griseovariegata* in Europe and the U.S.A. The *M. versicolor* larvae make rather long, light-brown cocoons; these are curious in that each hangs on a thread, the length of which depends on the species and may be more than 15 cm. In the cocoons, which swing back and forth like little pendulums at the slightest breath of wind, the pupa rests head down.

The genus *Habrobracon* is closely related to *Bracon* and is now combined with it; it represents a group of braconids distinguished by the way in which the edge of the clypeus is cut back, forming a circular mouth opening between it and the mandibles (hence the group name Cyclostomi, meaning round-mouthed). The genus includes species parasitic on destructive insects and thus of economic importance, such as *Habrobracon gelechiae* and *H. hebetor*; these are among the chief enemies of moths which



Fig. 17-15. Polyembryony: a caterpillar of the common silver Y moth (*Autographa gamma*) infested by the encyrtid *Litomastix truncatellus*. Up to 2000 offspring from one egg of the parasite can emerge from a single host caterpillar.

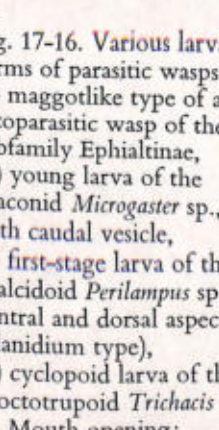


Fig. 17-16. Various larval forms of parasitic wasps: (a) maggotlike type of an ectoparasitic wasp of the subfamily Ephialtinae, (b) young larva of the braconid *Microgaster* sp., with caudal vesicle, (c) first-stage larva of the chalcidoid *Perilampus* sp., ventral and dorsal aspects (planidium type), (d) cyclopoid larva of the proctotrupoid *Trichacis* sp.; m, Mouth opening; 1. Antenna; o, Mandible; b, Leglike appendages; g, Genital appendages; d, Gut.

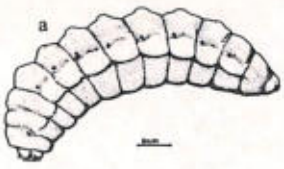
damage potatoes and flour, respectively. *H. hebetor* is easy to culture, and thus has become widely used in zoological institutes, particularly for research in genetics. Another group of braconid wasps is distinguished by an unusual development of the mandibles, which are bent outward so that they do not touch, even when in use. Two genera with many species are *Dacnusa* and *Alysia*, parasites of dipterans. The shiny black *Alysia manducator* (L 3–5 mm) of Europe and Greenland develops in the larvae of *Lucilia* spp. and other carrion flies.

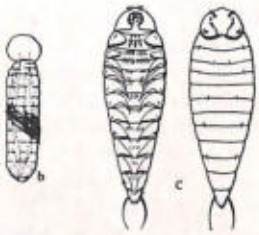
Polyembryony occurs in species of the genus *Macrocentrus*; as many as fifty progeny can develop from a single egg. Remarkably, some braconids —*Perilitus* and related genera—lay their eggs and undergo larval development in the imagoes of lady beetles, weevils, and some chrysomelid beetles.

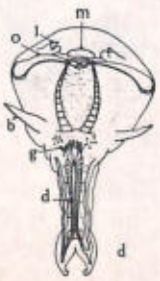
Family: Ichneumonidae

The ICHNEUMONS (family Ichneumonidae), with well over 30,000 species, of which several thousand inhabit central Europe, are the most extensive family of the Terebrantes; for this reason, subdivision of the group is particularly difficult. In the northern temperate zone there are a great many species; toward the south the number decreases considerably, but those found in the tropics are especially beautifully colored.

Medium-sized to large animals, most of the ichneumons are slender with fully developed wings, but in other respects they are extremely variable. The forewings, in contrast to those of the braconids, have two recurrent veins. The length of the ovipositor varies depending on the hosts of each species; it can be entirely hidden, so that it is somewhat difficult to tell the sexes apart, whereas in other cases (for example, in species which must pierce hosts hidden deep in wood) it may reach several, times the length of the body. Wasps with short ovipositors, in particular can also use them as defensive stings with a very noticeable effect (as, for example, in *Ophion luteus* of Europe or *O. slossonae* of the eastern U.S.A.).







Ichneumons are parasitic in insects of all holometabolous groups, but they prefer Lepidoptera; in addition, they occasionally attack spiders (for example, the tribe Polysphinctini, members of which are external parasites on the bodies of spiders) and their egg cocoons as well as pseudoscorpions (see Vol. I). Primary parasitism is the rule, though there are a number of species which are obligatory (i.e., always) or facultative (i.e., sometimes) secondary parasites. The imagoes are extremely lively, nimble animals, especially on sunny days. Some species, for example, the pale brown Ophioninae, are also active at twilight and at night, and fly to artificial light sources; in these species, the ocelli are conspicuously large. The average life span of the imago is very short. The males die soon after copulation, while the females tend to live rather longer, some of them (the larger species of the subfamily Ichneumoninae) even surviving the winter in protected places, usually under bark and moss at the bases of old trees.

Among the largest European representatives of the Ichneumonidae are the genera *Rhyssa*, *Megarhyssa*, and *Ephialtes*, all of which are characterized

by an exceptionally long ovipositor. In forests of conifers in the northern hemisphere one occasionally encounters *Rhyssa persuasoria* (see Color plates, pp. 447 and 465); in Europe this wasp is called the "pipe cleaner," since with her wings laid back and her ovipositor, longer than the body, the female resembles such an instrument. These are strikingly dark animals, almost 40 mm long, with yellowish-white patterning and long legs of a light rusty color. They parasitize horntail larvae. To deposit the eggs in the larvae, the female must drive her ovipositor into solid wood, often as deep as 6 cm. The task requires twenty to forty minutes. It is astonishing not only that the female can drill so deep, but also that she drills in the right spot and strikes a larva.

The *Ephialtes* species, too, lay their eggs in this way. The hosts they prefer are the larvae of long-horned beetles, but the larvae of other wood-dwellers of similar habits (aegeriid and cossid moths, see Chapter 15) are also selected. The interesting process of drilling down to the host has been observed closely in this genus: the female, using her antennae, checks the wood for signs of the presence of a host; once she has found a promising spot, she raises her abdomen with the ovipositor gradually into a vertical position. Then the ovipositor is pivoted so that it too is vertical with its tip on the substrate. In view of the difference in length of the body (34 mm) and the ovipositor (45 mm), this position can be attained only by drawing the legs close together and extending them; the difference between the lengths of the first and third pairs of legs (15 mm and 30 mm, respectively) is critical. At this stage, the drilling apparatus is still accompanied by the two sheath elements, but as soon as the drilling procedure begins these elements are raised vertically, parallel to the body axis. As the ovipositor sinks deeper into the wood, the female brings the front end of her body gradually forward, by small movements of the forelegs, so as to compensate for the decreased length of ovipositor still outside the wood. When the ovipositor has been driven about 10 mm deep into the wood, the ichneumon begins to make small rapid movements of the legs which turn the body around the ovipositor, slowly at first and then with increasing speed; at this stage one is indeed reminded of the operation of a rotating drill. At first the ovipositor seems hardly to make perceptible progress, but as soon as the turning of the ichneumon reaches a quick tempo it goes in more rapidly; in much less time than was required for the first 10 mm, it is completely buried.

The *Megarhyssa* species, such as the European *M. leucographa* and *M. superba*, and *M. atrata* and *M. macrurus* of the U.S.A., parasitize primarily the species of the horntail genus *Tremex* and, in accordance with the food-plant association of the host, are to be encountered on deciduous trees. The black and yellow *Protichneumon pisorius* (L 22–28 mm; see Color plate, p. 447) reaches an impressive size. It is found predominantly in coniferous woods, where it finds large hawk-moth caterpillars and places one egg in each of them. The caterpillars can continue to develop to the pupal



Fig. 17-17. Exarate pupa of the parasitic *Gelis* sp., whose females are wingless.



Fig. 17-18. *Pseudogonalos hahni* (female). The larvae live as hyperparasites in lepidopteran caterpillars and pseudocaterpillars, where they attack the larvae of parasitic wasps or flies.



Fig. 17-19. Pupal cocoon of an aphidiid wasp of the *Praon* sp., spun below the body of the hollowed-out, dead aphid.

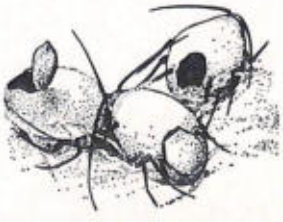


Fig. 17-20. The "mummy" of the aphid *Brevicoryne brassicae* after the aphidiid wasp *Diaeretus rapae* has left it by chewing out a round lid.

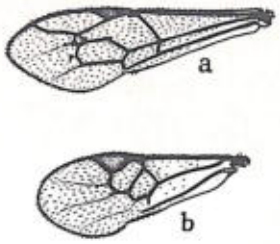


Fig. 17-21. Forewing of an ichneumon (a) and a braconid wasp. (b) The braconid wing lacks the second recurrent vein of the ichneumon wing.



Fig. 17-22. The pupal cocoons of the braconid *Meteorus* sp., hanging on threads; the wasps have already left the cocoons.

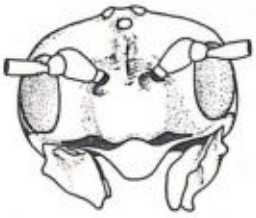


Fig. 17-23. Head of a braconid wasp of *Alysia* sp. The mandibles gape and are bent outward, so that they never touch or overlap.

Family: Agriotypidae

stage; then, instead of the expected moth, there emerges an ichneumon!

Among the most common ichneumons in all Europe is *Pimpla instigator* (see Color plate, p. 447). Its ovipositor is only half as long as the abdomen. The female runs about with its wings slightly raised, looking for lepidopteran pupae to pierce. The species has been cultured upon numerous hosts, including almost all of the lepidopterans harmful to forests (gypsy moths, black arches, common lackeys, pine beauties, and many others); it is thus one of the most useful of the European parasitic wasps.

In the biotic community of the forest there are still other ichneumons that are effective enemies of economically undesirable American insects; *Cratichneumon unifaciatorius*, a parasite in pupae of the white marked tussock moth; the European *Pleolophus basizonius*, a parasite in the larvae within the cocoons of the conifer sawflies; the American *Banchus inermis*, a parasite in the striped garden caterpillar (*Polia legitima*), and *Therion circumflexum* (see Color plate, p. 447), a parasite common in pine woods of both Europe and North America, which enters the caterpillars of the pine beauty and pine lappet and stays on into the pupal stage. *Therion circumflexum* is a predominantly reddish-yellow insect with smoky brownish areas on the wings, easy to recognize by its flight even in the open; it stretches its long hindlegs far out and the antennae upward, with the laterally compressed abdomen pointing downward. The fully grown larva pupates in a loose web, where the feces of the larvae form a sort of container for the pupa; it lies there with only the front end of the body exposed (see Fig. 17-25).

Along with these primary parasites, so welcome to us, there are other species which, in turn, secondarily parasitize the primary braconids and ichneumons, decreasing the effectiveness of the primary parasitism. This hyperparasitism characterizes almost all species of the genus *Gelis* of Europe and North America (see Color plate, p. 447), which superficially resemble ants because of the wingless females, as well as many species of the European and American genera *Mesochorus* and *Hemiteles*. Members of the subfamily Diplazontinae are also destructive from the human point of view, even though they are exclusively primary parasites; they infest the eggs or young larvae of hover flies, interfering with the contribution of the latter to the eradication of aphids.

The family of the AGRIOTYPIDS (Agriotypidae), with only one European species, *Agriotypus armatus*, represents an offshoot of the Ichneumonoidea specialized for life in the water. The imago is 5–8 mm long, shiny black with three brownish bands on the wings, and immediately identifiable by a sharp spine on the scutellum, pointing up and back. The second and third abdominal segments are fused dorsally.

The females climb down into the water on plants and stones, to a depth of 15–30 cm, the body remaining enclosed in a shiny, silvery layer of air. Underwater they seek out the cases of caddis flies and lay eggs in the prepupae and pupae within them. Before it actually pupates, the *A. armatus*

larva spins a cocoon to which is attached a thin band, on the average 25 mm long and 0.7–1 mm wide, which may have a respiratory function; its presence on a caddis case is a clear indication that the parasite is inside.

The STEPHANIDS (Stephanidae) are a small family with 100 species, of which only one, *Stephanus serrator*, is found in Germany, and even it is rare. Seven species are known in the U.S.A. The main area of distribution is in Africa. These ichneumonoids seem to be parasites in wood-boring beetle larvae, as the long ovipositor indicates. The same way of life characterizes the MEGALYRIDS (family Megalyridae), whose few species occur predominantly in Australia.



Fig. 17-24. *Daschia brevitarsis* (female), of the ichneumonoid subfamily Diplazontinae, parasitic in hover fly larvae.

Superfamily: Evanoidea

The superfamily Evanoidea comprises three families, whose common characteristic is the junction of the abdomen with the thorax: it is high up on the mesothoracic segment. In other aspects of body shape they differ greatly from one other. The ENSIGN WASPS (family Evaniidae) can be recognized by the short, stalked, laterally compressed abdomen and the ovipositor, which always is short; the abdomen appears to be carried like a flag on the powerfully built thorax, and has given the family its English name. The larvae live in the egg capsules of cockroaches. The best-known is *Evania appendigaster*, which is distributed worldwide along with its host, the Oriental cockroach. The European species *Brachygaster minuta* parasitizes the native wood cockroaches. In the U.S.A., species of the genus *Hyptia* have a similar role. The GASTERUPTIIDS (family Gasteruptiidae) have a strikingly slender abdomen and an elongated (in some cases very long) ovipositor; the prothorax is drawn out like a neck, and the hind tibiae are swollen at the ends (so that they are called gout wasps in Germany; see Fig. 17-30). They are parasitic mainly on solitary bees, less commonly on thread-waisted wasps and yellowjackets. The species of the genus *Gasteruption* are natives of the south, though the genus is represented in central Europe by several uncommon species. The AULACIDS (Aulacidae) are always equipped with a long ovipositor and are characterized by the clublike abdomen. They are parasites of the larvae of horntails and beetles (metallic wood-borers and long-horned beetles) which burrow in wood; in Australia and America they are more numerous, in both species and individuals, than in Europe.

▻

Fig. 17-25. (a) Pupa of *Therion circumflexum* in its fecal case. (b) Schematic longitudinal section through cocoon and case. W, Loose webbing between outer and inner walls of the parasite's cocoon; F, Fecal case; L, Last larval skin.

Superfamily: Cynipoidea

The superfamily containing the GALL WASPS (Cynipoidea) consists of small animals (L 1–5 mm, rarely more), most of which are colored inconspicuously in black and brown. They are easily recognizable by the wing venation (no pterostigma) and the more or less laterally compressed abdomen, which in the female houses an ovipositor which can be of astonishing length. The antennae usually have thirteen segments, never more than nineteen, and are not geniculate. The scutellum often has pits or cuplike indentations. There are around 1600 species, divided into five families: 1. Ibaliidae, 2. Liopteridae, 3. Eucoilidae, 4. Figitidae, and 5. Cynipidae.

The cynipoid wasps can be divided into two main groups on the basis

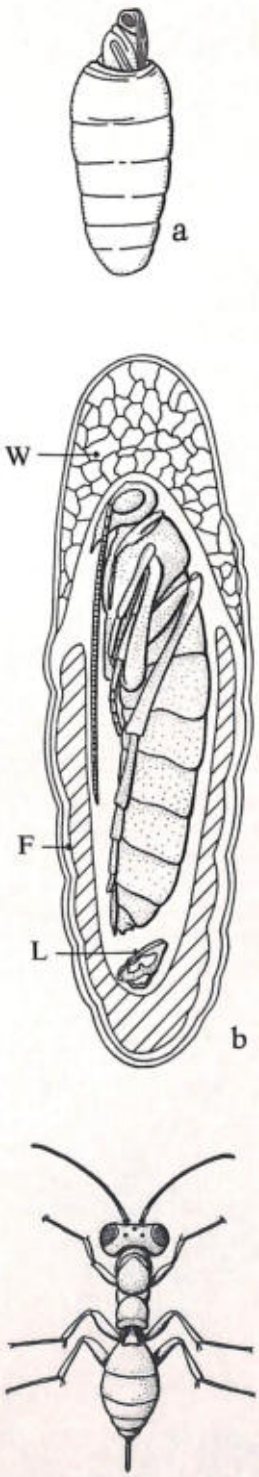


Fig. 17-26. *Gelis* sp. (female); an example of a wingless parasitic wasp.

of the way they obtain food; some feed on plants, whereas others live as parasites of other insects. Among the vegetarians are both gall-formers, which produce galls themselves and feed on this mass of tissue, and inquilines which live in galls not formed by themselves (for example, the species of the genus *Synergus* in oak galls). The inquilines and the gall-formers both belong to the GALL WASPS (subfamily Cynipinae). All the other cynipoids are parasites; they are considered as phylogenetically earlier wasps, and they exceed the gall wasps in both number of species and economic significance.

The host plants preferred by the gall-forming wasps are oaks. About ninety percent of the known species live on this genus of plants, while the rest are distributed on rose, maple, and various perennial plants such as knapweed, hawkweed, poppy, and others. On the oak species native to Germany there occur about 100 different wasp galls, most of which are so distinctive that it is actually easier to distinguish them than the insects which produced them. In the U.S.A. there are well over 800 species. The color plate on page 438 gives an impression of the variety of possible forms, though only small sample is shown there.

As already mentioned, the reproduction of gall wasps is quite remarkable, if only for the fact that in most species there is a regular alternation of generations, a bisexual generation being followed by an all-female parthenogenetic generation. The galls produced by the two generations frequently bear no resemblance to one another, and even the imagoes can differ greatly in size and shape. For this reason animals of the two generations were formerly mistaken for different species, and in some cases even given different generic names.

A widely known European example is the COMMON OAK GALL WASP (*Cynips quercusfolii*, see Color plate, p. 438). This species causes the round, sappy galls, yellow at first and with a reddish tinge in the fall, several of which are often found on the underside of an oak leaf. They may be up to 3 cm in diameter. From these large galls there emerge, in late fall or winter, the females of the parthenogenetic generation, which lay their unfertilized eggs in still-undeveloped oak buds on mild winter days. The larvae which hatch produce small (only 2–3 mm) egg-shaped bud galls, covered with velvety reddish or violet hairs, from which the two sexes of the bisexual generation hatch in the early summer. After copulation, the female deposits her eggs in a rib on the underside of a young oak leaf. The larvae from these eggs produce the large galls, and the cycle is complete. In the U.S.A., many species of the genus *Amphibolips* cause oak galls.

The European OAK-APPLE GALL WASPS (*Biorhiza pallida*; see Color plate, p. 438) emerge in July from bud galls (called oak apples) which are often the size of a human fist. They contain many chambers, so that a few galls can produce a great number of wasps, some male and some female. The females are polymorphic (of different forms) with respect to wing structure. There are females with long wings, others with short wings which

cannot fly, and even some with no wings at all. This tendency toward regression of the wings is thought to be associated with the fact that the females creep into the ground to lay their eggs, where the wings are more a hindrance than an advantage (see Fig. 17-31). The galls of the subsequent, parthenogenetic generation are then found on the roots of the oak; these may have either one or several chambers. In December at the earliest, there emerge from these the female wasps, considerably larger than those of the bisexual generation and always without wings. They creep up the trunk of the tree, laying eggs in buds even at temperatures near freezing; from these develop the large oak apples with which the cycle began. In the U.S.A., various species of the genus *Philonix* cause oak apples.

With the MOSSY ROSE GALL WASP (*Diplolepis rosae*; L 3–4 mm; see Color plate, p. 438), one usually finds only females; there is likely to be but one male for every 600 females. Thus reproduction occurs almost exclusively by parthenogenesis. The eggs are laid in the leaf buds of wild roses, and around them develop roundish galls up to 5 cm thick with a mossy surface, entirely covered with filamentous outgrowths. These are very prominent gall formations, and most of them contain several larval chambers. In Germany they are colloquially called "sleep apples" because of the old belief that if laid under one's pillow at night they will bring sleep. The species *Periclistus brandtii* lives as an inquiline in these galls; its larvae live in the smaller, thick-walled chambers, often continuous with one another, between the chambers enclosing the rose gall wasp larvae. Thus they have very little effect on the development of the latter. There are quite a number of wasps of other families parasitic on both the gall-former and the inquiline; in fact, almost all gall-inhabitants are subject to severe infestation by parasites. Sometimes only the parasites emerge from the galls, and not a single gall wasp. The species has been introduced into the U.S.A.

Among other gall wasps, *Diastrophus rubi* (see Color plate, p. 438) and related American species cause spindle-shaped swellings on the twigs of blackberries. Species of the genus *Aylax* (with two species in the U.S.A.) produce galls on various herbaceous plants; the genus includes *Aylax papaveris* (on the seed capsules of poppies) and *Aylax lini* (on flax stalks).

Among the Cynipoidea which live as parasites, the IBALIIDS (family Ibaliidae) are particularly remarkable for both their structure and their behavior. This group includes the largest cynipoids (8–18 mm), so striking in form and color that they cannot be mistaken for any other insect. The most common species in central Europe is *Ibalia leucospoides*; its abdomen is laterally compressed to such an extent (see Fig. 17-32) that when seen from above it looks like the blade of a knife. It somehow houses an especially long ovipositor—22 mm long in an abdomen which is only 8 mm long. The surprising length of this device is associated with the fact that the ibaliids parasitize horntails, piercing their eggs or young larvae. To do this, they introduce the ovipositor into the opening of the channel drilled in the wood by the horntail, for the ovipositor is hair-thin and so flexible



Fig. 17-27. *Agriotypus armatus* (female), a parasite of the prepupae and pupae of caddis flies.



Fig. 17-28. Pupal case of the caddis fly *Silo* sp., showing the bandlike "respiratory" structure of its parasite, the ichneumonoid wasp *Agriotypus armatus*.



Fig. 17-29. *Evania* sp., an ensign wasp, distinguished by the short, stalked, laterally compressed abdomen.



Fig. 17-30. *Gasteruption assectator* (female), a gasteruptiid wasp, with bulbous swellings of the hind tibiae.

that it cannot drill through hard wood as can that of *Rhyssa persuasoria*, discussed above. The larva develops within the host for a period of at least two and usually three years. A similar species, *I. maculipennis*, is a parasite of *Tremex columba* in the U.S.A.

The few species of the rather large LIOPTERIDS (family Liopteridae) are inhabitants of the tropics. We know essentially nothing of their life cycle. The EUCOILIDS (family Eucoilidae) are parasites in Diptera, laying their eggs in the young larvae of the host; the imagoes emerge from the host pupa. *Eucoila eucera* is an important parasite of the large frit fly (see Chapter 20 and Fig. 17-33). There are also some species of FIGITIDS (family Figitidae) that develop in fly larvae—for example, the European *Figites scutellaris*, or the American *F. floridensis*, the many hosts of which, including species of the genera *Lucilia* and *Sarcophaga*, live in maggoty flesh. The species of the figitid genus *Anacharis* are an exception, because of their association with neuropterian hosts. Finally, secondary parasitism occurs in the CHARIPINES (subfamily Charipinae of the family Cynipidae); the wasps in this group can easily be raised from infested aphids, in which their hosts are the primary parasites, the larvae of the Aphidiidae.

Superfamily: Chalcidoidea

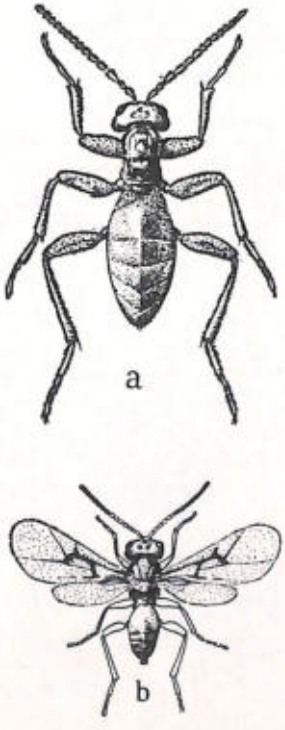


Fig. 17-31. The oak-apple gall wasp (*Biorhiza pallida*): (a) the parthenogenetic female, always wingless, and (b) the winged female of the bisexual generation.

The CHALCIDOIDS (superfamily Chalcidoidea) include primarily small to minute Hymenoptera, most of which are 1–2 mm in length. There are forms which measure only a few tenths of a millimeter. With its 0.2-mm-long body, one chalcidoid of the family Mymaridae is probably the smallest of all insects; in comparison, other chalcidoids are real giants, up to 16 mm long. Their coloration is frequently bright, with a metallic sheen, but in some groups black predominates, and yellow patterning and pale brown tones also occur. The sculpturing of the body surface and the amount of hair are extremely variable. The group is distinguished by the short, geniculate antennae which almost always have one to three ring segments (anelli) between the pedicel and the base of the flagellum. The wing venation is much regressed, and neither pterostigma nor closed wing cells are present. The prothorax does not extend as far laterally as the bases of the wings. The ovipositor arises on the ventral surface a little way forward from the tip of the abdomen; it may either be hidden in the body or extend for a great distance. There is an unimaginable variety of forms among the chalcidoids. The great majority live as parasites of other insects, though certain species parasitize spiders and mites. The life histories, too, are extremely varied. Only about 200 species have secondarily adopted a vegetarian habit, developing in seeds and grasses; some of these even form galls. Thus far 25,000–30,000 species of chalcidoid wasps have been described, but this number may well increase by severalfold as more research is done. In Europe there are around 5000 species in 450 genera. The Chalcidoidea are divided into twenty-two families, of which we will select only those most important and most remarkable for their way of life. In the Systematic Classification section at the end of this volume, however, all the families are listed in a sequence reflecting their relationships.

The family containing the FIG WASPS (Agaonidae) is distributed throughout the warmer regions of the world. Its members develop in fig blossoms, where they produce galls. In the U.S.A. and the Mediterranean region, a common fig wasp is *Blastophaga psenes*. The trees which bear edible figs have only female flowers. The male flowers grow on other trees, the so-called caprifigs, inside receptacles (synconia) which also contain female flowers, some with short pistils. The fig wasps develop in the latter, turning the flowers into galls. Before the females emerge, the males, with their abdomens folded under the body and sometimes extended far forward, gnaw open the galls and proceed to copulate. The appearance of these flightless males makes them hard to recognize as Hymenoptera. The males never leave the synconia, but the females, after they have been inseminated, find their way into the open. Since the exit from the synconium is narrow and surrounded by the male flowers, the females become covered with pollen as they leave. The flowers of the edible figs have long pistils; no wasps develop there, and the flowers can be fertilized only if pollen-laden female wasps fly to them from the caprifigs. Though they cannot lay eggs which will develop in these flowers, wasp females spend considerable time among them in the vain search for suitable flowers, thus pollinating many of the blossoms.



Fig. 17-32. *Ibalia leucospoides* (female), a parasitic cynipoid wasp of striking shape which infests the larvae of horntails.

Even in antiquity, therefore, caprifig branches were hung in orchards of edible figs. This is still done today, and the procedure is called caprification. Ordinarily there is no need for it, since most varieties of fig ripen their seedless fruits even without fertilization. But there are certain types (for example, the Smyrna fig) in which fruits set only after the flowers are pollinated, and in this case the fig wasps (caprifiers) are indispensable.



Fig. 17-33. *Eucoila eucera* (female), a cynipoid wasp which lives as a parasite of the large frit fly.

The LEUCOSPIDIDS (family Leucospididae), up to 16 mm in length, are the largest chalcidoid wasps. Black and yellow, they are somewhat reminiscent of yellowjackets (family Vespidae, see Chapter 18), and like them they fold their forewings longitudinally when at rest. The enlarged, toothed hind femora indicate a close relationship to the Chalcididae. But their most striking characteristic is the position of the ovipositor, which is bent forward over the back so that in some species its end reaches the posterior margin of the thorax. *Leucospis gigas* (see Color plate, p. 448), a species more common in southern Europe, lives in the nests of mason bees. The North American species *L. affinis* lives in the nests of many leafcutting bees.

Another family, whose members are relatively large, is that of the CHALCIDIDS (Chalcididae); like the leucospidids, they may be recognized by the greatly thickened hind femora. Here only the European *Chalcis sispes* (see Color plate, p. 448) will be mentioned, a species which develops in the larvae of the chameleon fly.



Fig. 17-34. The flightless male of the fig wasp (*Blastophaga psenes*) copulates with the female, still shut in her fig-blossom gall.

The TORYMIDS (family Torymidae) are slender animals, a lively metallic green, blue, or gold. They are considered the most beautiful of the chalcidoid wasps. The females, usually equipped with an ovipositor which

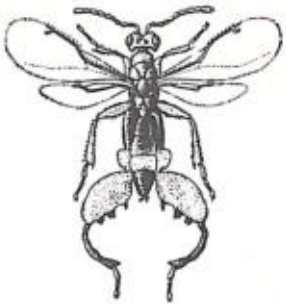


Fig. 17-35. The torymid *Podagrion bellator* (male), distinguished by its greatly thickened, toothed hind tibiae, lives as a parasite in the eggs of the praying mantis (*Mantis religiosa*; see Chapter 6).

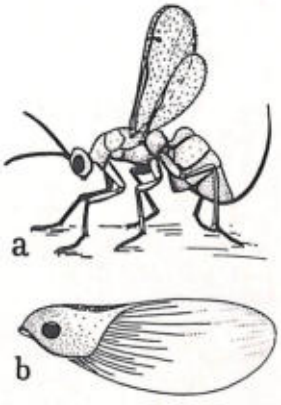


Fig. 17-36. (a) Female of the torymid *Megastigmus spermotrophus*, a pest in seeds of the Douglas fir; (b) a Douglas fir seed with a hole through which the wasp has emerged.



Fig. 17-37. The eurytomid *Harmolita fulvicollis* forms galls on species of grasses of the genus *Brachypodium*.

projects far from the body, pierce primarily the larvae of gall-producing wasps and Diptera. For example the, European and North American *Torymus bedeguaris*, shown in the color plate on page 448, attacks the larvae of the mossy rose gall wasp in its galls. The European species *Podagrion bellator* is exceptional in that it parasitizes the egg packets of the praying mantis (see Chapter 6). Within the genera *Megastigmus* and *Syntomaspis* are a number of pests such as *Megastigmus spermotrophus* in the U.S.A., in the seeds of spruce trees, the North American *Torymus druparum* in those of apple and pear trees; the apples and pears attacked by the latter remain small and fall off prematurely.

The EURYTOMIDS (family Eurytomidae) are generally black, and usually parasitize gall-forming insects. But even in this family we find vegetarian species which do agricultural damage in both the field and the greenhouse. For example, larvae of the North American WHEATSTRAWWORM (*Harmolita grandis*) and WHEATJOINTWORM (*H. trictii*) develop in wheat stalks: the ORCHIDFLY (*Eurytoma orchidearum*), which originated in South and Central America, was accidentally introduced to European greenhouses; and the CLOVERSEED CHALCID (*Bruchophagus phatyptera*) lives in clover seed and is distributed throughout the world.

The small family of the PERILAMPIDS (Perilampidae) is distinguished not only by the highly arched thorax and the spotted pattern on the body, but in particular by the remarkable way in which its members reproduce. These wasps lay their eggs neither in nor on the host; their first-stage larvae are of the planidium type described earlier in the chapter. An example is the Canadian *Perilampus tristis* (see Color plate, p. 448), which develops as a hyperparasite in the gemmet shoot caterpillar. Females of this species lay their eggs in the open on pine needles. After hatching, the planidium larva waits there until a caterpillar comes by, and then very quickly attaches itself and burrows inside. Within the caterpillar's body it waits for its real host, the primary parasite of the caterpillar, and attacks it. The development of *Perilampus tristis* is thus dependent on two improbable events, first on the appearance of a caterpillar and then on its being infested by a primary parasite. The numbers of eggs laid is correspondingly large, amounting to several hundred.

Planidium larvae are also found among the EUCHARITIDS (family Eucharitidae), which shine in metallic colors. On the scutellum there is often a long, backward-pointing projection. All species of this family develop as parasites of ant larvae or pupae; in order to reach their hosts, the planidia allow themselves to be carried by ant workers into the nest. The females of certain species may lay as many as 15,000 eggs.

The PTEROMALIDS (family Pteromalidae) comprise a very great number of species, and because of their uniformity a systematic subclassification is very difficult. Among them is the 3-mm-long metallic green *Pteromalus puparum*, found throughout North America. Each female of this species lays about fifty eggs in soft-skinned pupae, particularly those of the pierid

butterflies. After the larvae have eaten the entire contents of the pupa, they themselves pupate. Each imago which results gnaws a round hole through the pupal case as it emerges, so that the empty pupal case looks like a sieve.

The many species of ENCYRTIDS (family Encyrtidae) are parasitic primarily in scale insects, and some species have proved to be extremely effective in the biological control of these pests. However, other orders of insects and even ticks, including the common European species *Ixodes ricinus* (see Vol. I), also serve as their hosts. In some genera (*Litomastix*, *Copidosoma*, *Ageniaspis*) which are parasites of Lepidoptera, polyembryony occurs; as a result a rather large caterpillar may be host to as many as 2000 encyrtids. The numerous and very similar species of *Ooencyrtus* live in the eggs of lepidopterans and bugs.

Another family including a great many species is that of the EULOPHIDS (family Eulophidae). Most of these wasps are small, and their cuticle is usually only weakly sclerotized. Their habits are quite variable; the eggs, larvae, and pupae of a variety of insect groups are attacked, and many species live in leaf-mining insects. The species of the genus *Eulophus*, the most common of which is *Eulophus larvarum*, pierce free-living lepidopteran caterpillars, and the larvae, which develop there communally, pupate on the surface of a leaf around the dead body of the host. The *Eulophus* pupae are obtect (with limb cases fused to the body), not exarate as are most Hymenoptera.

The tiny TRICHOGRAMMATIDS (family Trichogrammatidae) develop exclusively as parasites in eggs. *Trichogramma* species are among the most valuable animals for experiments on biological pest control (see Fig. 17-40). *Trichogramma minutum* is easy to culture in eggs of the Mediterranean flour moth; in the U.S.A. a daily production of almost one million wasps has been achieved. This species is now a commercially available product, which can be purchased whenever needed to combat mass outbreaks of the appropriate destructive insects. *Prestwichia aquatica*, a European species, deposits its eggs in the eggs of aquatic bugs and beetles; for this purpose it dives underwater, swimming with its legs (see Fig. 17-41).

The last chalcidoid family, the FAIRYFLIES (Mymaridae), are recognizable by the wings, narrow bands set on stalks and bordered with a long fringe (see Fig. 17-42). They, too, parasitize exclusively insect eggs. This group includes one of the smallest known insects, the 0.2-mm-long *Alaptus magnanimus*.

The superfamily Pelecinoidea, with the single family of the PELECINIDS (Pelecinidae), is restricted to North and South America. The females are among the most striking hymenopterans, with their unusually long, tubular abdomens; they can be 50–60 mm in overall length. The New World species *Pelecinus polyturator* (see Color plate, p. 448) lives as an endoparasite of soil-dwelling lamellicorn beetle larvae.

Wasps of the superfamily Proctotrupoidea are small to very small (L 0.4–11 mm), predominantly black, and not metallic in appearance.

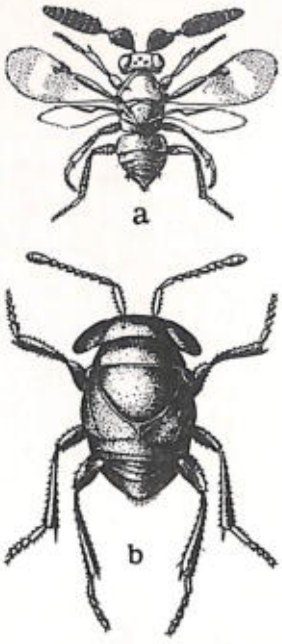


Fig. 17-38. The chalcidoids of the family Encytridae are distinguished by unusual structure of their antennae and body. (a) *Mira macrocera* (female), with conspicuously broadened antennae; (b) *Semen apterum* (female), with compact body and greatly shortened wings.

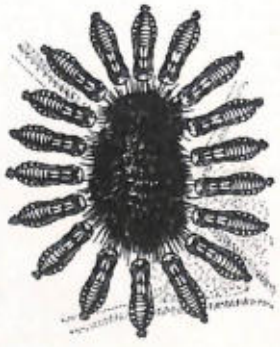


Fig. 17-39. Pupae of the communally parasitic chalcidoid wasp *Eulophus larvarum* on a leaf, regularly arranged around the dead host caterpillar (diagrammatic). The *Eulophus* species form obtect pupae.

The antennae are usually not geniculate; the rings so characteristic of the chalcidoids are lacking. The wing venation is extremely variable, more or less regressed and sometimes entirely lacking. The sides of the prothorax extend back to the bases of the wings. The ovipositor originates at the tip of the abdomen and in proportion to the size of the abdomen, within which it must find room, it can be surprisingly long. The proctotrupoids are without exception parasitic in other insects; hyperparasitism is rare. Thus far, about 4000 species are known, in nine families, of which the following six will be mentioned: 1. Heloridae, 2. Proctotrupidae, 3. Ceraphronidae, 4. Diapriidae, 5. Scelionidae, 6. Platygasteridae.

The few species of HELORIDS (family Heloridae) are distinguished by their prominent wing venation and stalked abdomen; they are parasites of neuropterian larvae. The imago emerges from the cocoon of its host animal. The European species *Helorus anomalipes* and the North American *H. paradoxus* undergo their development in the larvae of green lacewings (see Chapter 12 and Fig. 17-43).



Fig. 17-40. *Trichogramma semblidis* (female), a tiny chalcidoid wasp which pierces preferentially the eggs of drone flies (see Chapter 20).

The PROCTOTRUPIDS (family Proctotrupidae) may be recognized by the fact that the sheath of the sting protrudes somewhat; since the two halves of the sheath lie close together, the tip of the abdomen appears to be extended. Most of these wasps parasitize the larvae of beetles and dipterans. The larvae feed singly or in groups within their victim, but break out of it to pupate. *Phaenoserphus viator* has been cultured from the larvae of ground beetles and click beetles.

A subdivision of the scutellum characterizes the CERAPHRONIDS (family Ceraphronidae). Many species—in contrast to the other proctotrupoids—develop as hyperparasites in aphids and scale insects, their actual hosts being aphidiid and chalcidoid wasps. The larvae of hover flies are often attacked as well. The ceraphronid larvae are usually ectoparasites of their own hosts, but they undergo their development within the host's host, in its cocoon or puparium.



Fig. 17-41. *Prestwichia aquatica*. Above: female; below: male with greatly shortened wings. The female dives under water to lay eggs in the eggs of aquatic insects.

The DIAPRIIDS (family Diapriidae) comprise more species than the first three proctotrupoid families considered. In the main, they are parasitic in Diptera, laying eggs in their larvae or pupae. Females of the North American species *Diapria conica* (see Color plate, p. 448), of common occurrence in Europe as well, prefer to pierce the young puparia of the drone fly, depositing all their eggs—thirty-five on the average—in a single puparium.

There are very many species of SCELIONIDS (family Scelionidae); these wasps are parasitic in insect eggs, especially those of lepidopterans and bugs, but occasionally also in those of mantids and spiders. *Telenomus dalmani*, which lives in Europe and North America, is one of the parasites of a moth living on blackthorns, while other *Telenomus* species develop in the eggs of tree-injuring lepidopterans and are therefore considered useful. In the biological control of grain pests of the heteropteran genera *Eurygaster* and *Aelia*, several closely related *Aholcus* species, for example, *A.*

rufiventris (see Color plate, p. 448) and *A. semistriatus*, play a critical role. *Mantibaria manticida*, a European wasp parasitic in the eggs of the praying mantis, reproduces in an interesting way. The females climb onto the imagoes of the host mantis and sometimes let themselves be carried around for weeks. In so doing they discard their wings, usually holding on with the mandibles to the bases of the host's wings. Should one of the wasps accidentally mount a male mantis, she must die with him. But those which succeed in attaching to a female mantis creep to the genital region when she lays her eggs and deposit their own eggs in the still-foamy, soft mass.

The last proctotrupoid family to be described is that of the uniformly constructed PLATYGASTERIDS (Platygasteridae), most of which are parasitic in gall midges. They pierce the developing eggs, and their larvae develop in the larvae and pupae of the host. The ovipositor can often be long, even though it does not protrude like those of other Terebrantes.

The special problem of finding room to house the long ovipositor has been solved in a unique way by species of the genus *Inostemma*. These wasps have a long, horny projection running out from the first abdominal segment, curving forward over the thorax and, in some species, even extending out over the head. This horn has no other function than to enclose the ovipositor, which is greatly elongated in these animals. The first-stage larvae of the platygasterids are of the odd-looking cyclopoid type mentioned previously. *Platygaster herrickii* is a very effective enemy of the Hessian fly, which does millions of dollars worth of damage in North America each year.

The group Terebrantes, including a varied assortment of vegetarians as well as primary, secondary, and tertiary parasites, all in bitter competition with one another, gives us a particularly clear illustration of how questionable are the concepts "useful" and "destructive," terms often based only on transient human economic values. In this chapter and in others of this volume we have occasionally simplified by speaking of "pests" and "beneficial insects"; but we must not forget that these pests contribute fundamentally to the balance of nature, and that excessive populations of them are often the fault of man himself. The factors determining equilibrium in biotic communities are sufficiently complex that human interference can often have unsuspected and detrimental results.



Fig. 17-42. Female of a fairyfly species, distinguished by stalked forewings with long marginal hairs.



Fig. 17-43. *Helorus anomalipes* (female), with its stalked abdomen and striking wing venation, is a parasite in the larvae of green lacewings (see Chapter 12).



Fig. 17-44. *Inostemma* sp. (female). The much elongated ovipositor is housed within the "horn" which arises on the first abdominal segment and bends forward over the thorax.

18 Hymenoptera: The Aculeate Wasps, Ants, and Bees

The Aculeata, by W. Rathmayer

The subgroup Aculeata within the order Hymenoptera has been named for the highly developed weapon its members use for hunting and defense (the Latin *aculeatus* means "equipped with a sting"). These sting-bearers include the bees and ants, as well as a number of other families usually called wasps. Whereas bees and ants form clearly defined groups, readily classifiable as families or superfamilies, the term "wasp" is too generally applied for it to be equivalent to a single systematic entity. It is used for quite a number of different families, some of them large, which vary widely with respect to form and habits. We must thus rely heavily on scientific names in our discussion of the different kinds of stinging wasp, as we did for the parasitic and gall-forming wasps in the previous chapter.

The Aculeata share with the Terebrantes (Chapter 17) the characteristic constriction between the thorax and the abdomen; they differ from the Terebrantes in several respects, apart from their sting. All members of the Aculeata lack the trochantellus (the extra leg segment of the Terebrantes). The females usually have thirteen antennal segments, while the males have twelve. The wings, especially in the female, may be temporarily or permanently lacking. Body length ranges from less than 1 mm to over 70 mm.

Two important characteristics of the Aculeata deserve more detailed discussion: the sting, and the complex patterns of behavior in which the females provide for their offspring.

The sting was developed in the course of evolution from the ovipositor apparatus. This modification involved a change of function, for it no longer serves for egg-laying; rather it is employed as an effective weapon of defense or as an injection cannula for the paralysis of prey. In view of the origin of the device, it is obvious that only female Hymenoptera can sting. The sting consists of several reciprocally movable chitinous elements. Into it there open the ducts of two glands, one of which produces poison. In the stinging Hymenoptera the eggs are ejected from the opening of the genital chamber at the base of the ovipositor.

Behavior associated with provision for the young has reached a peak of development in these wasps. As a rule, the mother not only prepares a place for her offspring to live, but provides them with all the food which will be required for their development from egg to pupa. Often the females dig multi-chambered nests in the ground or in wood. Free-standing nests made of clay or a paperlike material are not uncommon. Each chamber is eventually closed, becoming a nursery for one larva. The mother supplies each cell with sufficient food, whether pollen or flesh in the form of paralyzed animals, before laying the egg. It is only in the more highly evolved social forms that the larva is fed by the adults until it pupates. In any case, the larvae of the Aculeata never have to forage for their own food. Unlike other insect larvae, they would be incapable of doing so, for they lack any sort of locomotor organ. Being restricted to one place, moreover, they are faced with a major difficulty: their chambers and the food stored there must not become contaminated with feces. How is this problem solved? The gut actually remains closed during the entire larval period, until the beginning of the dormant period which precedes pupation. Only then, at a time when the animal has ceased to eat, is the barrier broken through so that all the accumulated feces are discharged.

The stores of food prepared by the females offer a natural opportunity for parasites. In almost all families of aculeate wasps, there are species which make no such maternal preparations for their progeny; rather, they take advantage of both the building and the foraging skills of other wasps, smuggling their eggs into the brood cells of the latter. Some of these uninvited guests have developed quite wily methods. But an aculeate wasp of a parasitic species never breaks into the cell of a stranger just for its own nourishment; such behavior is always connected with reproduction. That is, they confine themselves to brood parasitism. The adults themselves feed, almost without exception, on plant products obtained from flowers. Only in the larval stage do they consume animal tissue; in the case of the bees, not even the larvae are carnivorous.

Classification of the Aculeata

Systematists divide the Aculeata into seven superfamilies with over twenty-five families. The great majority of species lead solitary lives, but in three families (the Vespidae and the bee families Apidae and Halictidae) there are both solitary and social species. The first stages of transition to a social way of life are demonstrated by certain sphecid wasps. The ants (Formicidae), finally, are all social insects. The social forms, in particular, have achieved a development of behavior unique in the animal kingdom ang awe-inspiring to any biologist.

Family: Bethylidae

The BETHYLIDS (family Bethylidae), all small, black wasps, are a primitive family which has only recently been reassigned to the Aculeata. The females frequently have reduced wings or none at all; they walk about, looking for beetle larvae or lepidopteran caterpillars. Having found suitable prey, the attacker stings it several times at random, injecting a paralytic poison; then she licks up the body fluid oozing out of the wounds,

a welcome addition of protein to her usual vegetarian diet. She prepares no nest into which to bring the victim, but does sometimes take it to a protected niche, where she deposits on it one or several eggs. Other females may approach and add their eggs to hers. In fact, some species regularly live in associations, sharing prey animals.

Soon the larvae hatch, bore through the body wall of the victim, and suck it out. After two to five days, shortly before pupation, they leave the remains and spin cocoons. Ten to twenty days after that, the new generation emerges, to live from one to three months. Since bethylids frequently attack destructive insect larvae (the North American *Laelius trogodermatis*, for example, prefers the larvae of dermestid beetles), they have a certain economic importance.

Family: Cleptidae

The CLEPTIDS (family Cleptidae) form a small family, whose members are slender wasps with a metallic sheen, resembling the cuckoo wasps. In thick grass, the females search for cocoons containing the larvae of sawflies; because of their secluded way of life, they can be observed only with difficulty. Species of the genus *Cleptes* chew a hole in a sawfly cocoon and introduce a flexible egg-laying device, depositing an egg on the inhabitant. Then the hole is closed with saliva. After four days the larva hatches and begins to eat its host. After ten days it pupates, and in a few weeks it is an adult.

Family: Chrysididae

The CUCKOO WASPS (family Chrysididae), with their magnificent metallic coloration, are among the most beautiful Hymenoptera. The numerous European species are shining ruby-red, green, or blue; the tropical species, in which a deep violet predominates, are even more striking. There are more than 2000 species, all parasites of other Hymenoptera, particularly of bees, thread-waisted wasps, and yellowjackets. Therefore one is most likely to find them near the breeding places of their hosts —clay walls, wooden posts, and sand pits—but also on leaves, where they are looking for their favorite food, honeydew. It is of course dangerous to live as a parasite of such well-armed hosts, since a single sting can mean death. How do the cuckoo wasps avoid this risk? The underside of the abdomen, which consists of only three segments, is concave. If the legitimate owner of a nest comes home and surprises the uninvited guest, the intruder immediately rolls up into a ball and "plays dead." Head and legs fit so well into the depression in the abdomen that the whole vulnerable underside is protected. The exposed surfaces are heavily armored, and the bee's sting cannot pierce them. Eventually the nest-owner pushes the "lifeless" little ball outside, and the cuckoo wasp has survived the episode.



Fig. 18-1. The cuckoo wasp *Chrysis* sp. defends itself by rolling into a ball and playing dead.

The genus *Chrysis* alone comprises more than 1000 species. The males emerge before the females, early in the summer. After copulation, the females seek out the nests of their hosts; the golden-red and blue *Chrysis dichroa*, for example, looks for nests of species of bees of the genus *Osmia*. Having found one, she crawls in while the owner is away and examines the cells. If she finds host larvae there, she pushes her ovipositor—a struc-

ture formed from the last abdominal segments, which can be collapsed like a telescope—into the chamber and smuggles in one, or sometimes several, eggs. When the bee returns home, it does not notice the deception. But only one *Chrysis* sp. larva can develop in each host cell. If several eggs have been deposited there, there is a battle to the death between the parasite larvae. Since the younger larvae are weaker, they are siezed in the jaws of the oldest one, lifted up, and sucked out. When only one victorious larva remains, it turns finally to the host larva and sucks it out as well. In a few days the larva pupates, and, after spending the winter as a pupa, emerges in the spring as an adult.

The females of the species most common in Germany, the FIRE CUCKOO WASP (*Chrysis ignita*; see Color plate, p. 475), parasitize the potter wasp (*Eumenes coarctata*). In North America, a related species, *C. coerulans*, parasitizes the common North American potter wasp, *E. fraternus*. The larva hatches and addresses itself immediately to the consumption of the host egg and the paralyzed caterpillars which had originally been carried in to feed the host. The largest German species, *Parnopes grandior* (L up to 12 mm), lives with *Bembex* wasp species. Since the nests of the latter are closed in with sand, the parasite must dig through it to get to the larval chambers.



Fig. 18-2. The prehensile feet of dryinid wasps: one of the two claws on the first leg is curved like a sickle (1) and is much longer than the other (2); the fifth tarsal segment is also elongated (3), forming the lower jaw of the pincers.

Family: Dryinidae

The DRYINIDS (family Dryinidae) have an intriguing life history. There are more than 300 species of these small insects, all of which are parasitic in cicadas and their relatives. The antennae consist of only ten segments. In many females the first pair of legs is equipped with conspicuously large, movable pincers. The effectiveness of these pincers in overpowering the victim is very graphically described by Kiefer in H. Bischoff's book on Hymenoptera: "To overcome the jumping cicada, the dryinids use their prehensile legs; with one pair of pincers the prey is siezed by the neck and pushed down, while the other immobilizes its hindlegs. Then the wasp begins to lay eggs with her ovipositor, boring into the defenceless victim lying in front of her. This process takes several minutes. When it is finished, the animal is set free. The cicada soon recovers from its minor injuries, hopping about and eating as though nothing had happened." After a few days, though, the larva hatches. The front end of its body remains in the body of the host, which it slowly begins to suck out. The chorion of the egg and the exuvia which accumulate after each molt bulge outward, forming a large, many-layered bubble. Cicadas infested by dryinid wasps can easily be recognized by this structure. Before pupation, the larva finally leaves the body of the host. The life cycle lasts about one and one-half to two months.



Fig. 18-3. The wingless female of *Gonatopus pilosus* shows the typical dryinid form, the first pair of legs bearing movable pincers.

Family: Scoliidae

DIGGER WASPS of the family Scoliidae, of which there are over 1000 species, are predominantly tropical insects. They are densely covered with hair, and usually are very large and brightly colored. Since they much prefer warm conditions, there are only about a dozen species in Europe; among them is the largest European member of the Hymenoptera, the

YELLOW-FRONTED DIGGER WASP (*Scolia flavifrons*; L up to 50 mm; see Color plate, p. 475). It is most common in the Mediterranean region, especially in places inhabited by its hosts, the larvae of the rhinoceros beetle *Oryctes nasicornis* (see Chapter 13) and, less often, those of the stag beetle *Lucanus cervus* (see Chapter 13). Despite their size and their possession of a sting, they are not dangerous to humans.

The adult digger wasps of the Scoliidae feed on plant materials and are often to be found on umbelliferous plants. All of them parasitize beetle larvae, especially those of lamellicorn beetles (see Chapter 13). The females dig into soil or fallen leaves with their powerful forelegs, finding their way with their highly developed tactile sense to the passages of their subterranean victims. After it has been stung several times, the beetle larva is completely paralyzed and is drawn into the deepest part of its tunnel. There an egg is attached to the victim, and the larva which hatches finds itself provided with food which has been preserved alive. Once this is eaten up, pupation soon follows. In the following year the adult emerges.

Family: Tiphiidae

The ROLLING WASPS (Tiphiidae) are a very old family. In body structure and habits they are so similar to the scoliids that they have frequently been assigned to that family. In Germany there are only a few species of the genus *Tiphia*, all medium-sized animals. Like the scoliids, the tiphiid females lay their eggs on beetle larvae of the family Scarabaeidae. Often the injected poison produces only a temporary paralysis; it lasts just long enough for the egg to be attached.

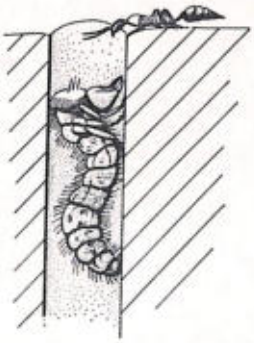


Fig. 18-4. A female *Methoca* sp. has discovered a tiger-beetle larva waiting in its sand tube for insect prey; to overcome the larva, she must first let herself be seized in its mighty jaws.

Recently a new species, which formerly constituted a family of its own, has been assigned to the Tiphiidae. This is *Methoca ichneumonides*, and its life history is particularly interesting. The wingless female (L 5–8 mm) closely resembles an ant; one finds her on sand in sunny spots. Reuter's excellent description is most graphic: "*Methoca* has distinguished itself by choosing a very dangerous sort of insect, the rapacious larva of the tiger beetle *Cicindela*, as its prey. This larva lies in wait for its own prey in a vertical tube it has made in the ground, closing up the entrance with its head and prothorax. While the larva snaps at her, the female *Methoca* circles about looking for a chance to climb onto its head. When this has been accomplished, the *Cicindela* larva throws back its sickle-shaped mandibles and seizes her by the head or thorax; but the body of the female wasp is so slender that it is simply held between the mandibles without being injured. Now when she is lifted up by the larva, she is in a position to make the first paralyzing sting—in its throat or between the anterior coxae. Playing the role of prey, she has turned the tables on her predator." The paralyzed beetle larva slips to the bottom of its tube and is soon eaten by the wasp.

Family: Mutillidae

There are several thousand species of VELVET-ANTS (family Mutillidae; see Color plate, p. 475), a family rather misleadingly named after the wingless females, which are very like ants except for the downy hairs covering the body. In the tropics, especially, a great number of species are

very brightly colored. The natives are aware of their painful sting. In many species, the winged male clasps a female, holds her with his legs, and flies with her into the air, where they copulate.

The female velvet-ants build no nests of their own; they are without exception parasites, mostly of other Aculeata. They run nimbly along the ground from one nest to another, until they find one belonging to their host. If the cells already contain eggs and food stores, the velvet-ant quickly adds her own egg to the chamber. The larva of the parasitic wasp hatches earlier than that of the host and proceeds directly to consume the nest owner and the stored provisions.

The EUROPEAN VELVET-ANT (*Mutilla europaea*) spends its youth in the nests of bumblebees. The female wasps are brown-red except for the abdomen, which is an iridescent black-blue with white, hairy bands. They are so thickly armored that the powerful jaws and sting of the bumblebee have no effect. The female lays her eggs with those of the bee, on which the parasite larva later feed.

Family: Pompilidae

The SPIDER WASPS (family Pompilidae, formerly called Psammocharidae) are a uniform family, named in this case not for their appearance but for their preferred prey. Several thousand species are known, in all parts of the world, and there are probably many undiscovered species still awaiting description, especially in the tropics. In comparison with the tropical species, most of which display a magnificent metallic iridescence, the European forms are disappointing; the basic coloration, only slightly varied, is black, with only the first abdominal segments colored red-brown or sometimes decorated by yellow or white spots. The wings are opaque and smoky in many cases, and when the wasp walks they are held up at an angle. The spider wasps are characterized by strikingly long legs, often bearing spines; the tarsal claws have combs of bristles. These modifications are apparently useful in the burial of prey.

Spider wasps are encountered particularly in sunny, sandy places or on paths in woods, where they hunt their prey, walking in a characteristic way with twitching wings and antennae. Ninety-nine percent of the Pompilidae hunt spiders. Among them are remarkable specialists: for example, some species hunt only jumping spiders or wolf spiders, whereas others seek out victims living in webs. The wasp *Episyron* spp. even manages, by a clever trick, to move about without danger in the webs of the spider *Araneus* sp. (see Vol. I). The wasp plucks at the web, startling the spider so that it leaves its lair and glides to the ground on a thread. The wasp runs down the thread after it, finds it on the ground, and gives it a paralyzing sting. Another genus, the gigantic (wingspan up to 10 cm) *Pepsis* of the U.S.A., Mexico, and Central America, even overpowers the well-armed bird spiders, which can be as big as the palm of one's hand. But the fight does not always end in favor of the wasp. Should the spider succeed in driving its poison-filled jaws into the wasp's body, *Pepsis* is doomed.

The victims of these wasps are paralyzed by a swift penetration of the

sting through the soft membranes connecting the thorax and abdomen, or into the joints at the bases of the legs. The way the injected poison produces such a rapid loss of the ability to move is still entirely a mystery. Once it was thought that the wasp had to strike the nerve centers of the spider with its sting. But even fifty years ago this view was refuted; it was shown that a spider is paralyzed even if one injects wasp poison at any arbitrary point in the abdomen. It is probably important that the poison get into the blood stream. The mechanism of paralysis will be discussed further in connection with the thread-waisted wasps, later in this chapter. A spider paralyzed by a spider wasp usually goes on living for many weeks, if one prevents the wasp larva from eating it as soon as it hatches. The record is held by a spider stung by a *Cryptochilus affinis* (see Color plate, p. 475), which still showed signs of life after being paralyzed for four months. For humans, the sting of a spider wasp is extremely unpleasant, for the poison causes a burning pain, but there is no swelling such as is produced by the stings of hornets or bees.

The characteristic behavior of the spider wasps is well illustrated by a species common in Germany, *Pompilus rufus*. Once a female has captured a spider, she seizes it by one leg with her mandibles and drags it away, walking backward and pulling it after her. She never transports it in flight, as the thread-waisted wasps do. In order to drag this cumbersome burden more easily, many spider wasps simply bite off the long legs of the spider. Only a few, for example, *Pompilus plumbeus*, carry the spider while walking forward, like a retriever carrying a pheasant. In contrast to the thread-waisted wasps, most of the spider wasps begin to build a nest only after a successful hunt. While she builds, the wasp keeps the paralyzed victim hidden in the grass, between the needles of a pine branch or in a fallen cone. Somewhere in the vicinity of this hiding place, the wasp finds a suitable spot and digs out a nest chamber, moving her forelegs rapidly in alternation to scrape away the sand. From time to time she checks the spider. When the nest is finished, the wasp carries the spider to it; at the edge of the nest she changes her grip and pulls the spider in by its spinnerets. An egg is laid on the motionless victim, and then the spider is buried alive as the wasp pulls down the walls of the tunnel. Finally, with hammering movements of the abdomen, she closes the nest entrance tightly with sand. The larva, which hatches within a few days, pupates after it has consumed the spider; it spends the winter in the pupal cocoon and in the following year emerges as an imago.

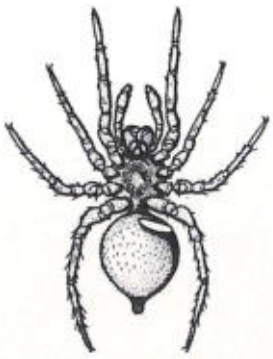


Fig. 18-5. A pompilid wasp, a species of the genus *Cryptochilus*, has fastened her egg on the ventral surface of a paralyzed wolf spider.

Not all spider-wasps go to the trouble of catching a spider for each of their offspring. This is the rule, but there are very interesting exceptions. For example, *Anoplius infuscatus* (see Color plate, p. 475) operates as a regular "burglar." Oldberg has several times observed females of this species breaking into the nests of other wasps, in order to steal the spider stored there; the thief then buries the prey somewhere else, after depositing an egg of her own on it. Even more interesting behavior is shown by the

parasitic spider wasps. The white-spotted *Ceropales maculatus* (see Color plate, p. 475) may often be encountered in sandy regions. The females neither make their own nest chambers nor capture their own prey. Rather, they lie in wait until they see another spider wasp transporting her spider to a future nest place. What happens then has been described by Bouwman in Olberg's book (listed in the references at the end of this volume): "Among the wonders of wasp life, I have encountered none as surprising as this. I saw a *Pompilus plumbeus* coming along with her paralyzed spider, when a *Ceropales* dropped out of the air next to her. The *Pompilius* was taken aback and let go her prey. *Ceropales* immediately threw herself upon the spider . . . , curved her abdomen, and flew away. The whole performance had lasted less than five seconds. Even with a lens nothing was to be seen on the spider, on either the thorax or abdomen. I examined the abdomen once more in a systematic way, and finally discovered, on the right side of the ventral surface near the attachment to the thorax, a little gray-white dot. At last the situation became clear. The spider's respiratory apparatus, two lung books covered by porous chitinous plates, is just at this position in its body. The little dot was the end of the *Ceropales* egg, which did not fit completely into the lung chamber because the spider was so small, and thus by chance the secret was betrayed. Earlier observers had apparently been unable to find the egg, because it was in the lung chamber! But it is still incomprehensible that *Ceropales* can operate with such speed and accuracy." Placement of an egg, though, is not always achieved so directly. Often there are battles between the two wasps. But the parasite usually does manage to take advantage of a favorable moment and to smuggle her egg into the spider. Then she leaves the scene of the attack, and the *Pompilus* spp. wasp which was originally in possession of the spider carries it, with the invisible egg of the stranger, to the intended nest site, lays her own egg on it, and buries it. The parasite larva hatches first, devours the *Pompilus* sp. egg, and then has a fat spider all to itself.

The THREAD-WAISTED WASPS (family Sphecidae), many of which are also called DIGGER WASPS, comprise a very great number of species, and are distributed throughout the world. Most species are black with yellow markings on the body, but reddish and—particularly in the tropics—metallic iridescent colors are not uncommon. The shape of the body is as varied as the coloration.

Family: Sphecidae

All thread-waisted wasps have a similar life history. Every species, apart from a single known exception, is solitary. The females hunt the most diverse sorts of insects. Each kind of wasp specializes in a particular victim, and is adept at hunting it out and overcoming it. Other insects of the same size are ignored, even though there may be hordes of them in the vicinity. Representatives of almost all insect orders appear on the list of possible prey of this family. Among the species native to Germany, some hunt only flies, others only aphids or ants, and still others only bugs, cicadas, or thrips. Certain species are adapted to preying on cockroaches, grass-

hoppers, crickets, caterpillars, small butterflies and moths, bees, weevils, or even spiders. Specialization can be carried to the point that a wasp species concerns itself with only a single prey species; for example, the bee-killer wasp hunts only the honeybee. The restriction in the behavior of the adults is the more astonishing, since it seems to be a matter of indifference to the larvae what insect they are given to eat. They even thrive on an artificial diet. The inflexibility of the wasps' behavior with respect to prey is illustrated by the North American species *Aphilanthops frigidus*: the females hunt only during the nuptial flight of species of the ant genus *Formica*, attacking winged female ants. The countless *Formica* sp. females running about on the ground after discarding their wings are untouched. This rigid behavior seems even more surprising when one learns that the wasps later bite the wings off the captured ants before placing them in their nests.

The weapon used in the hunt, as a rule, is the sting. Only *Diodontus* sp. overpowers the small aphids she captures for her progeny by crushing the neck region with her jaws. The majority of the other species hunt in another way; having caught sight of the prey animal, the wasp flings herself upon her victim, clasps it in her legs, and stings it one or more times in the underside. In well-armored species there are only a few places, such as the throat or the basal leg joints, where they are vulnerable. To find these "Achilles' heels," many wasp species have sensitive tactile organs at the end of the sting sheath. The fact that the sting always enters through the ventral surface of the prey has led to certain misinterpretations. This habit has been thought to be related to the ventral position of the nerve centers, and the conclusion was drawn that the hunter knew as precisely as a surgeon how the nervous system of its victim was arranged; with an accurately aimed sting, she was said to put out of action the precise center of the system.

In the case of the bee-killer wasp, at least, this is not true. This wasp always drives her sting in through the thin membrane behind the first pair of legs of the bee. Although there is a nerve center, or ganglion, in the immediate vicinity of this spot, dissection of stung bees demonstrated that in most cases the ganglion was uninjured. The channel made by the sting passed beside it and entered the muscles. Moreover, if one injected the poison from one of these wasps anywhere into a bee, a profound paralysis always resulted. But the bee became motionless sooner, the closer the injection point was to the leg muscles. This might therefore be the reason that the wasps usually sting the ventral side of their victims, near the limbs. It is certain that bee-killer poison does not directly affect the nervous system of the bees, but rather first puts the muscles out of action. It is most probable that the mechanism is like that of curare, the arrow poison of some South American Indians, which paralyzes vertebrates: the nervous commands arriving at the nerve endings can no longer be converted to contractile responses of the muscle cells. In many cases the victims recover

from this paralysis, taking up their normal activities as though nothing had happened.

After stinging their victims, the wasps frequently knead them with their mandibles, presumably to hasten the distribution of poison through the body. But at the same time they lick up the blood that comes out of the sting-wounds, the protein it contains being a useful supplement to their vegetarian diet. Then they bring the prey to the nest hole they have made in advance. Some species grasp the victim with their mandibles and drag it to the nest, often over considerable stretches of rough ground. But most hold the prey with their legs and fly home. Species of the genus *Oxybelus* transport captured flies by spearing them on their stings and whizzing away in a flight which ends with a perfect landing at the entrance to the nest.

The passages leading into the nests of the thread-waisted wasps are found in sandy ground, rotten wood, or the pith of plant stalks. Very frequently the nests are built on a branching plan, with a number of chambers. But linear structures divided into cells, and even free-standing clay structures, are common. Each cell is provisioned with several prey animals, but serves as a nursery for only one larva. For example, a completed nest of *Trypoxylon* sp. consists of up to thirty chambers. Since every cell is provided with about ten spiders, a single female in one nest alone creates a "mausoleum" for 300 spiders.



Fig. 18-6. Male sand wasps spend the night in this characteristic sleeping posture; they cling to a stalk of grass with their forelegs and mandibles.

The life span of these wasps ordinarily amounts to just one summer. Rarely, there appear two generations per year. The winter is passed in the pupal stage, and in early summer it is the males which first emerge searching for females ready to mate. This arrangement tends to separate brothers and sisters, so that incest is largely avoided. After copulation, the males wander about idly, spending the greater part of their lives looking for food in flowers and leaving the females to provide for the next generation. In the evenings they gather, sometimes in groups of several hundred, on particular branches or blades of grass; they return consistently to these night after night during the whole season, to spend the night in a thick clump, all in a characteristic sleeping position.

The sand wasp

In Germany the SAND WASP *Ammophila adriaansei* (formerly called *Ammophila campestris*; L about 20 mm; see Color plate, p. 476) is particularly common in regions of sandy heath where pines are growing. This species is conspicuous because of the abdomen, colored red at the base and attached by a long stalk. Their fascinating brood-care behavior has found a place in all textbooks on behavioral science. Their prey are caterpillars, which they often drag long distances on foot to the nest, a hole in the sandy soil. It is known that the wasp orients herself by landmarks such as bunches of grass, pine cones, or little trees, the exact location of which she has noted during the outward flight; thus she can find her way home again. After pulling the captured caterpillar into the nest, the sand wasp lays an egg on it and temporarily closes the nest entrance with little stones. Later

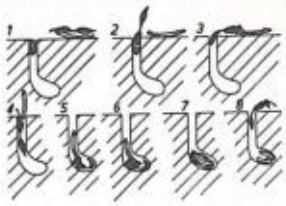


Fig. 18-7. The sand wasp *Ammophila adriaanse* pulls a paralyzed caterpillar into the nest (schematic): 1, laying the caterpillar down; 2, opening the temporary nest closure; 3, turning around; 4, 5, 6, pulling it in; 7, laying the egg; 8, crawling out.

she opens the nest to check the development of the egg and, if necessary, to bring in fresh food for the larva after it has hatched. Usually one female takes care of several nests at once. But how can she keep track of just what task needs to be done in which nest at any given time? Her brood care proceeds in what can be thought of as a chain of individual actions. When one has been completed, the new state of affairs itself releases the next step in the sequence. There are five basic states, each of which is the prerequisite for a new action to occur which leads to the next state; only when this state is achieved can the subsequent behavior be begun, and so on. The five states are: 1. "Nest empty"; this releases the behavior of carrying in a caterpillar, laying an egg, and temporarily closing the nest. 2. "Nest with caterpillar and egg"; this releases temporary closing of the nest. 3. "Nest with caterpillar and freshly hatched larva"; this releases the provision of additional caterpillars. 4. "Nest with older larva"; this releases the provision of additional caterpillars and the final closing of the nest. 5. "Nest with larva which is already beginning pupation"; this releases only the final closing of the nest. It is the specific stimulus situation in each of the different nests, therefore, that automatically releases an appropriate instinctive behavior. No insight on the part of the sand wasp, such as was postulated by earlier investigators, is necessary. A very similar behavior is displayed by the wasp *Bembex rostrata*. Here, too, the females take care of several nests at once, and after examination of the temporarily closed cells they supply the larvae as necessary with flies.

The bee-killer wasp

At one time, one of the most common sphecid wasps was the BEE-KILLER WASP (*Philanthus triangulum*), but today it has become quite rare. Ignoring more innocuous prey, these wasps hunt the well-armed honeybees. But how can they tell a honeybee from a fly or a bumblebee? At first they are guided only by vision. All objects of about the size of a honeybee are at least approached. The decisive stage of discrimination is left to the antennae, with their sensitive organs of smell. The wasp hovers like a helicopter in the air downwind of the interesting object, testing whether it smells like a bee. If it does, the wasp waits for a favorable opportunity to hurl herself down onto the victim while it is peacefully gathering nectar or pollen, and seizes it with her legs. Then both animals fall to earth in a tangle of limbs and wings. Even as they fall, the wasp paralyzes the bee with her sting. The subsequent events were described by Karl von Frisch as follows: "Then she embraces the part of the bee's abdomen where the honey stomach is located and presses the nectar out of the bee's mouth, refreshing herself with a drink the bee has gathered from the flowers for quite another purpose. Now, holding the bee beneath her, she flies to the hole she has already dug in sandy soil, a deep tunnel leading to the brood chamber. Having arrayed three or four such bees side by side in the chamber, she lays an egg on one of them and continues her activities in another chamber of the nest, or begins to dig a new hole. From the egg hatches a larva like the maggot of a fly, which proceeds without delay to



Fig. 18-8. The female bee-killer wasp has attacked a honeybee and is injecting her with paralyzing poison through the soft membrane behind the first pair of legs.

eat up the bees provided for it, one after another. Since they have been paralyzed by the wasp's sting, but not killed, they stay fresh like a well-preserved supply of meat; but they are defenseless, even against the sluggish maggot. Fully grown, the larva pupates in the brood chamber, to emerge in the following summer and continue the work of the mother."



Fig. 18-9. A brood chamber of the bee-killer wasp; three paralyzed bees have been brought as a food store for the larva, soon to hatch from the egg (E).

Formation of social systems by sphecid wasps was first discovered in the small (L 2 mm) Puerto Rican species *Microstigmus comes*.The nest is constructed of waxy plant materials; hanging on the undersides of palm leaves, it measures about 1 cm and consists of a dozen cells. Up to eighteen wasps inhabit one nest. This little community is further distinguished by a division of labor, for it is likely that only one of the females is completely mature and lays all the eggs. The others watch over the nest and cooperate in providing the larvae with food.

In many hymenopteran species, the sexes are assisted in finding one another for mating by attractant odor substances. The females of the thread-waisted wasp *Gorytes mystaceus*, for example, secrete from glands on the abdominal wall a substance smelling of fern and lemon, which acts to attract the males. A certain plant, the orchid *Ophrys insectifera*, has turned this scent to its advantage. It smells like a wasp female in mating condition, and the lip of the flower even resembles a wasp in shape and hairy texture. The male is taken in by this double deception; he tries to copulate with the flower and, in the process, pollinates it. But the actual ejaculation of seminal fluid can be brought about only if additional stimuli are present. The female wasp can provide these, but the flower cannot, so that a waste of sperm—disadvantageous to both wasp and flower—is avoided.

Family: Vespidae

The family Vespidae is particularly interesting, since it includes all stages in the sequence leading from the solitary life to the highly developed society with a division of labor. As a rule, two characteristics distinguish the vespid wasps from other wasps of similar appearance. The first is that the forewings are longitudinally folded at rest. This arrangement results from the fact that the connection between forewing and hindwing, which guarantees continuity of the wing surface during flight, is not released when the animal is at rest. When the wings are closed, the hindwing is pushed under the forewing, so that the latter is folded over. The second difference is in the form of the eyes: there is an indentation of the front edge of the compound eye which gives it a kidney shape.

Subfamily: Eumeninae

Systematists divide the Vespidae into eleven subfamilies. The POTTER WASPS (Eumeninae) are in large part still solitary animals; some, however, especially species native to Africa, display the first stages of social development. In Europe and North America two genera are quite common: *Eumenes* (see Color plate, p. 476) and *Odynerus*. The first of these is characterized by the shape of the abdomen; the first abdominal segment is narrow and stalklike, and is followed by a broad, bell-shaped second segment. Their coloration is usually black and yellow. The females build

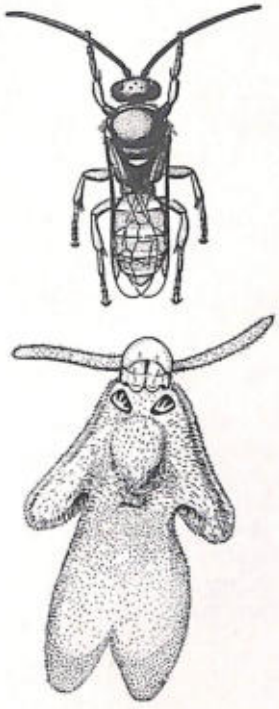


Fig. 18-10. The lip of the orchid *Ophrys insectifera* (below) mimics, in both form and odor, a female of the sphecid species *Gorytes mystaceus* in mating condition (above).



Fig. 18-11. Three urns constructed by a potter wasp; the left one is cut open to show its contents, food for the larva and an egg hanging from the top by a thread.

elaborate urns of clay, attached to plants either singly or in groups of two or three. The moist clay is collected by the wasps in the form of small balls, and is flown to the nest site clasped between the head and forelegs. The mandibles are used to spread the clay into a thin wall. A finished cell, round in shape and with a neck at the top, is just like a tiny jug. It has been reported that wasp structures of this sort once served as models for the Indians as they made their own clay vessels. Each jug is meant as a nursery for a single larva. The mother wasp first fastens the egg inside the top of the urn by a thread, so that it swings free. Then she loads the chamber with a number of paralyzed weevil larvae, and finally closes the neck with a last little lump of clay. The young larva soon hatches and turns its attention to the living food.

Another species also common in Germany is *Odynerus spinipes*, patterned in black and yellow. The females dig passages which end in chambers in vertical walls of sand. The debris thus produced is mixed with saliva and used by the wasp to build a sort of tubular vestibule outside the nest entrance, about 15 mm long and curved downward. Perhaps its function is to disguise the nest entrance from any parasites which might fly past. In some clay walls one can find several thousand of these curious tubes in close proximity. This species, too, fills the nest chamber with paralyzed caterpillars only after the eggs are laid. In North America the common potter wasp is *Eumenes fraternus*.

A few of the African potter wasps are known for their remarkable transitional behavior, which represents a stage between the laying in of provisions for the future young and the more advanced true brood care. These wasps show us the path toward the higher social forms. The prerequisite for such development is that the mothers must maintain the association with the larvae after they have hatched. In *Synagris spiniventris* this happens only in rare instances; if there is an abundance of prey, the nest chamber is filled all at once with food for the larva, and then closed permanently. In this case, the mother takes no further interest in the larva. But when the hunting is bad only a few caterpillars are collected at first, and as the larva grows, more are brought from time to time. The nest is not permanently closed until shortly before pupation. *Synagris cornuta* goes a step further along the path of social development: the females first chew up the prey, and then feed the larvae from mouth to mouth.

Subfamily: Stenogastrinae

Another important preliminary stage which helps us to understand the evolution of insect societies is found among representatives of the Indo-Australian STENOGASTRINES (subfamily Stenogastrinae). The females of *Stenogaster depressigaster* build multi-celled nests of paper. They feed their larvae with a thick soup of chewed-up prey insects mixed with their own glandular secretions. The mother lives through the hatching of several generations. She and a few of her daughters, which look exactly like her, together form a little community in the same nest. The daughters build their own cells in the maternal nest and lay eggs of their own. But each

female is concerned only with her own offspring. A division of labor is unknown, all members of the group having the same "rights and duties."

The POLYBIINES (Polybiinae) comprise more species than any other vespid subfamily. Almost all are native to the tropics, especially South America. Even in simple forms, such as some African species of *Belonogaster*, several females together care for the larvae in the fifty to sixty cells of a nest. Here, too, all the females perform the same tasks, are fertilized, and lay eggs. But here the formation of a society has progressed somewhat, for the females feed not only their own offspring, but all the larvae indiscriminately. The exchange of food between larvae and adults (trophallaxis) is common. Thus the community of families becomes a cooperative.

In species of the genus *Polybia* we meet, for the first time in the Vespidae, a division of labor. Here only some of the females in a nest lay eggs, while the others have regressed ovaries and concern themselves only with nest building, care of the larvae and other tasks. Externally, the latter appear to be complete females. Their infertility is probably due to poor nutrition during their larval period.

The *Polybia* species must be considered social wasps. Unfortunately, we know essentially nothing about the way most of them live. There are some observations which indicate that certain species have even developed a language, not unlike the dancing of the bees, so that they can communicate with one another about the location of a rich source of food. Future investigation may show that their social development is at the highest level within the Vespidae.



Fig. 18-12. Nest of the eumenine wasp *Odynerus spinipes* in a vertical clay wall, consisting of entrance tube (T) and six cells supplied with caterpillars; the eggs (E, colored black) hang free in the space.

Subfamily: Polistinae

Turning to the POLISTINES (subfamily Polistinae), we once again find species native to Europe and North America. *Polistes gallicus* is actually quite common in Europe, as is *P. canadensis* in North America. All members of the subfamily are social wasps. Early in the spring the female *P. gallicus* goes in search of a suitable site for a nest. In cooler regions this may be a niche in a wall, an abandoned birdhouse, or a protected place under a roof, whereas in warmer areas the nest is fastened to the stems of plants in the open. With a rapidly hardening pulpy mass of chewed-up dry plant materials mixed with saliva, the female builds an open comb consisting of a single layer of hexagonal cells. This is attached to the substrate by a strong stalk. Most of the cell openings point down at an angle, so that no rain water can collect in them.

While one female is building, others of the same species join her. The founder of the nest does not drive them away, and all of them collaborate in the construction. The community is called polygynous, since it consists of several females of equal status. But this equality is of short duration; very soon the colony becomes monogynous, for the first female demotes the later arrivals to the status of assistants. By way of a behavioral ceremony as yet almost completely unknown to us, a rank order evolves among the nestmates like that in a dovecote or chicken yard. The first, highest-ranking female soon becomes the main egg-layer. She eats the eggs which were

laid by the accessory females. The duty of these lower-ranking females is now restricted to care of the first larval generation. When these larvae have become adults, the queen drives the accessory females away for good.

The first group of wasps to be raised in the colony is composed entirely of females, but because their ovaries are nonfunctional they can act only as workers. They care for the other young their mother has meanwhile produced, foraging for food and feeding the queen and their young sisters. In autumn, finally, no new workers emerge; rather, the larvae become complete females or, in the case of those from unfertilized egg cells, males. In the same autumn the females are inseminated, and they spend the winter in a protected place under bark or moss, emerging in spring as young queens to found new colonies. But their eventual fate, whether to become queens or to be turned into workers, is decided by the situation in their future nest. The old colony from which they emerged has died out in late fall, as the old queen laid fewer and fewer eggs.

The life history of some parasitic Polistinae species of the genus *Polistes* is especially intriguing. *Polistes atrimandibularis* actually takes over the nest of *Polistes biglumis*. Before it can occupy the nest there is a battle, which the more powerful wasp, the parasite, usually wins. The highest-ranking *P. biglumis* female, the queen, is banished from her throne but not from her kingdom; by a ritualized demonstration of superiority involving chewing of antennae, riding, and twitching of the sting, the new queen demotes the old one to a worker. Now the former queen, like her daughters in the nest, lays no more eggs. The parasitic wasp takes over this privilege, and the host wasps are servants, caring for the offspring of their conqueror. In such a nest, the host species dies out without descendants.

Subfamily: Vespinae

The last vespid subfamily, the HORNETS (Vespinae), includes most of the species immediately recognized as wasps by the layman. Among them, for example, are the black-and-yellow visitors of fruit and cakes which we see in our dwellings in the fall, looking for sweet things to eat. Although all the species occurring in Europe and America were formerly assigned to the genus *Vespa*, nowadays this name refers only to the GIANT HORNET (*Vespa crabro*; see Color plate, p. 476). The other species have been assigned to the genera *Dolichovespula*, *Paravespula*, or *Vespula*, depending on whether or not there is a "cheek" between the mandible and the lower edge of the eye, and on other features. In general, they are characterized by yellow or brownish markings on a black ground. The hornets differ from the Polistinae in that their abdomens do not broaden gradually behind the junction with the thorax, but rather expand immediately, as though the waist had been cut in with a knife. All the species are social, building a permanent nest of paper enclosed in an outer shell.

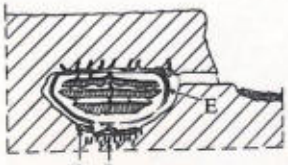


Fig. 18-13. Section through a subterranean nest of the wasp *Paravespula rufa*; the three comb-plates are covered by an envelope (E) of paper; rubbish (R) produced by the colony is often the home of certain fly larvae (L).

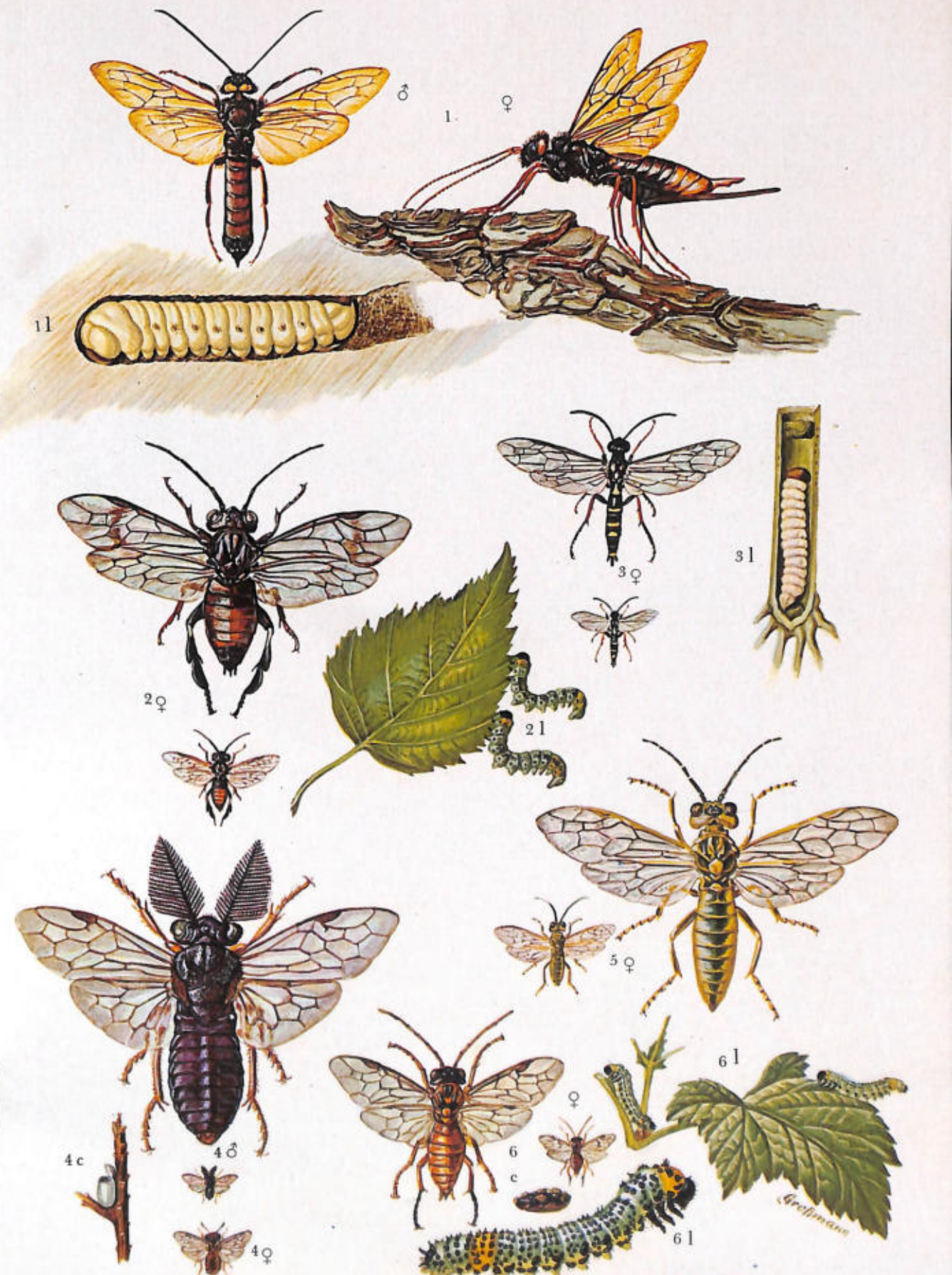
Even people who are not interested in wasps are familiar, perhaps from personal experience, with at least one of their characteristics, the painful sting. But the popular belief that three hornet stings can kill a man and seven can kill a horse is certainly mistaken. The decisive factors are where,

and whom, the hornet stings. A sting on the tongue or in a large blood vessel is always dangerous. In the first case the swelling can interfere with breathing, and in the second there can be internal bleeding, because one component of the poison makes the walls of the capillaries permeable. Moreover, there are people who are hypersensitive to the poison and react by going into shock. Usually, though, hornet poison causes only severe pain. The basis of this effect has recently been discovered by biochemists: the poison contains, among other things, considerable quantities of serotonin, acetylcholine, and histamine. A chemist once declared that if presented with the task of composing a mixture with a very painful effect out of the reagents in his laboratory, he would have chosen just these substances, in similar proportions.

The female hornets spend the winter in a characteristic posture, quite rigid in a hiding place under bark or moss, in rotten wood, or in cracks in masonry. The first warm sunny days in the spring awaken them to new life. Their first act is to look for the sweet nectar of flowers. Soon thereafter, each female begins to keep an independent watch for a suitable nesting place. A distinction is made, on the basis of nest location, between wasps which make exposed nests and those with nests enclosed in a shelter; among the enclosed-nest builders there is a further distinction between those which work above ground and those which make subterranean structures. One of the builders of exposed nests is *Dolichovespula media*, which attaches its nest to branches in shrubbery. Enclosed nest sites are chosen with regard to the prevailing temperature and light, as well as the humidity and the surroundings of the site. The wasp *Dolichovespula saxonica* and the giant hornet build in hollow trees or under the frameworks of houses. Subterranean nest sites include mouse nests, mole tunnels, and any sorth of hollow under plant roots. The common species in North America is the COMMON YELLOWJACKET (*Vespula maculifrons*).

Most wasps obtain their building material from weathered wood. They chew off fine splinters from boarding, telephone poles, etc. and mix them with saliva, which serves as glue. At the nest site, the wasps stroke these little balls of paper with their mandibles, spreading them out into fine strips, and glue them together. First one hexagonal cell is attached to the ceiling by a little stalk, with the opening down. After a week a small plate of five to ten cells has been created; this is the work of a single female, the nest founder and future queen, who has already mated the previous year. Later, when the numerous workers join in the construction, the nest grows to an impressive size. In subterranean nests, the hole must be considerably enlarged to permit expansion. New levels of the comb are added progressively from the top down, with pillars connecting the different tiers. Then the combs are completely covered by a balloonlike envelope which may be either elastic or brittle (as is that of the giant hornet). The single opening, for entrance and exit, is located at the bottom; it also serves as the ventilation hole. The multilayered envelope both protects

▻
Symphyta: 1. The large horntail *Urocerus gigas* (male, and female laying eggs); 1l, full-grown larva in feeding gallery (all actual size); 2. The birch sawfly *Croesus septentrionalis* enlarged and actual size; 2l, larvae in defense posture on a birch leaf; 3. The European wheat-stem sawfly (*Cephus pygmaeus*), enlarged and actual size; 3l, larva in wheat stalk, ready to pupate, enlarged; 4. The pine sawfly *Diprion pini*, enlarged and actual size; 4k, pupal cocoon after the imago has emerged; 5. The green sawfly (*Rhogogaster viridis*), enlarged and actual size; 6. The currant sawfly (*Nematus ribesii*), enlarged and actual size; 6*l*, larvae, enlarged and (eating a gooseberry leaf) actual size; 6k, pupal cocoon.


♂
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the hive and assists in temperature regulation, since the layers act like those in a storm window. Wasps are also capable of regulating the temperature themselves; even on autumn nights when the outside temperature falls to 10°C, the interior of the nest stays within a half degree of 30°C. How is this possible? The females can move their flight muscles while leaving the wings uncoupled, like an automobile with the clutch in. The associated metabolic activity generates heat and warms up the wasp. Like a little stove, it radiates this heat. If, on hot summer days, the outside temperature rises above the 30° optimum for the wasps and their brood, the workers bring in water rather than food, spread it over the cells, and cause it to evaporate by beating their wings. This cools the nest very effectively.

Social organization of hornets

The queen begins to lay eggs as soon as seven to ten cells have been built. After five or six days the larvae hatch, and the mother must feed them herself. In about twenty more days they begin to spin their pupal cocoons, closing each cell with a lid of silk. When another twenty days have passed, the adult wasps emerge, chewing their way to freedom through the lid of the cell without the help of the mother. All of them are female, but they are incomplete females: conspicuously smaller than their mother, they have underdeveloped ovaries, and they all belong to the worker caste. Should anything happen to the queen, however, the ovaries of some of the workers will develop, and they will lay eggs. Since such eggs are unfertilized, males hatch from them. The production of this caste is probably associated with the fact that the mother was the only nurse for the larvae of this generation and could not provide them with enough nutrient-rich food. It is also possible that the queen feeds them certain substances which inhibit development of the ovaries. In the course of the summer, many such broods of workers are born. In warm regions of northern Africa, where the best possible food situation prevails, families with more than 100,000 members have been known, living in gigantic nests measuring over 1 m.

◁
Gall wasps and the plant galls they produce: Oak galls: 1. The common oak gall wasp (*Cynips quercusfolii*), (a) leaf galls, (b) leaf gall cut open, with larva, (c) bud gall; 2. The oak-apple gall wasp (*Biorhiza pallida*), bud gall; 3. *Andricus quercuscalicis*, acorn gall; 4. *Cynips longiventris*, leaf gall; 5. *Neuroterus quercusbaccarum*, leaf gall; 6. *Trigonaspis megaptera*, leaf gall; 7. *Neuroterus numismalis*, leaf galls. Other gall wasps: 8. The mossy rose gall wasp (*Diplolepis rosae*), male and female, enlarged and actual size; (a) gall; 9. *Diastrophus rubi* gall on a blackberry stem.

Within the colony there is a strict division of labor: the queen alone lays the eggs, while some of the workers act as nurses and construction laborers, others fly out of the nest in search of food, and still others guard and defend the nest. Since the forager wasps are primarily looking for sweet plant juices, one finds them on fruit of all kinds. In the fall, when the population of the colonies is largest, they are often found there in masses. They bite only through the surface of the fruit, in order to lick up the sugary juices that come out, but in some fruits like grapes or plums these wounds cause premature rotting, so that the wasps can do considerable damage. They also hunt insects, which serve as protein for the larvae. In seconds, they cut up the prey with their mandibles and chew it into watery pulp.

On its return, the successful forager is met by nestmates and freed of its burden. It keeps for itself only as much as is essential, letting it pass through a valve from the crop into the stomach as needed. In response to

the begging of the nest workers, the collector lets the rest of the food in the crop out through the mouth; it is licked up by the begging workers and passed on by them to other hungry workers when they beg in turn. In this way food flows from crop to crop, eventually becoming distributed to all members of the society. The term "social stomach" is therefore a pertinent description of the crop. Finally, the workers feed the queen and the larvae with the contents of their crops. In some cases (for example, with the giant hornets), if a larva is hungry and there is no nurse nearby, it can make very distinct noises by scratching with the jaws on the walls of the cell. This signal induces the nurses to feed it.

During feeding—in fact, even at the slightest touch—the larvae themselves bring forth from the mouth a drop of fluid, as clear as water, which is immediately licked up by the nurses. It has been observed that the nurses often touch the larvae with their mandibles without feeding them, and that they may even pull on the larvae and massage them in order to obtain this droplet. For a long time the possible significance of this procedure remained a mystery. One suggestion was that the glandular secretions of the larvae are regarded by their nurses as a prized delicacy, serving as a reward or stimulus for feeding the larvae. But this is probably no more correct than the alternative supposition that the workers in this way get the excess water of the larvae out of the nest. Rather, the secretion of the larval salivary glands is of high nutritive value to the adult wasps because of its sugar content. Since most hornets do not lay up stores of food (as do the ants and the social bees), the adults give all the food they cannot eat themselves to the larvae. Periods of bad weather can thus be times of crisis, when the flying wasps cannot go out to bring new supplies. Then, especially in large colonies, there is soon a food shortage which can be a serious threat to the whole community. Thus the wasp larvae are a living food store, from which all the other members of the society can obtain a vital, nourishing drink at any time by simple mechanical stimulation.

In fall, the workers begin to build larger cells in the lower levels of the nest. Within these, a bisexual generation of males and fertile females grow. After emerging, these wasps remain in the nest for some time, but take no part in the work of the community; they allow themselves to be fed by their sisters. Mating frequently takes place in the mother's nest. Then the reproductive animals begin to leave the nest, and the first flight of each is a permanent departure. In the open, the males copulate again, with females from other nests, and then soon die. But the inseminated females survive the winter and found new colonies in the following spring. The old nest colony eventually perishes, late in the fall.

Among the Vespidae, like the Polistinae, there are species lacking the instinct to care for the young; these have no worker caste of their own, and therefore let their offspring be cared for by workers of other species; they are social parasites. Species of the genus *Pseudovespula* are among these, represented in Germany by two species: *P. adulterina* lives with

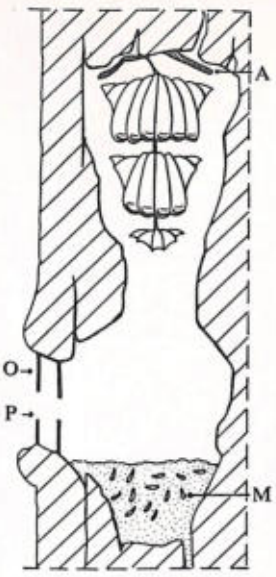


Fig. 18-14. Diagram of a hornet nest in a hollow tree (the envelope surrounding the three combs is shown only at its attachment point (A); the opening of the hollow (O) is narrowed to a small passage (P) by lamellae built by the hornets; in the decaying rubbish accumulated below the nest there are fly maggots (M).

Dolichovespula saxonica, and *P. omissa* lives with *D. sylvestris*. Another species parasitic in this way is *Vespula austriaca*. The female of this species, externally very like the host species, invades the nest of *Paravespula rufa* after some workers have been born, kills the legitimate queen, and from then on takes her place. The workers take no notice of this change of specific leadership. The larvae of the parasite produce sexually mature, complete females and males, which are nursed by the host workers as though they were their own siblings.

Ants are the most successful social insects, if by success we mean holding one's own under the most diverse circumstances. Almost 10,000 ant species have spread out from their original home, the tropics, as far as the polar circles, the peaks of the highest mountains, and desert regions almost devoid of plant life. The variety of life histories displayed by the ants is unequalled by any other invertebrate.

Superfamily: Formicoidea, Family: Formicidae, by H. Markl

Within the hymenopteran group Aculeata the ants (superfamily Formicoidea, with the single family Formicidae) occupy a place close to the tiphiid wasps, in that they arose from solitary wasps related to wasps like the Tiphiidae. The oldest fossil ants come from the Cretaceous; they are about 100 millions year old.

Distinguishing characteristics

These various ants range from small to quite large (L from less than 1 mm to 4 cm). One or two anterior segments of the abdomen are constricted, forming a knobby stalk or pedicel (as is characteristic of the suborder Apocrita). In primitive forms there is a poisonous sting, but in the more highly evolved examples this is often regressed and replaced by even more effective chemical defense mechanisms. The mandibles are all-purpose tools, used even as weapons; their structure is quite variable, corresponding to the way of life (see Fig. 18-15). There are nine or ten subfamilies.

Social organization: workers

All the ants live in communities. A fully developed colony can comprise over a million members in some species, whereas in others it may include barely a dozen. The more highly developed social systems involve remarkably effective collaboration of the nestmates. A particularly striking behavior is the lively exchange of food; the older workers, which leave the nest to forage for food, give what they have collected to the younger workers remaining in the nests, and these in turn provide for the larvae and the reproductive animals. Often a special section of the gut is developed as a "social stomach"; the food taken in is stored there and can either be fed to other ants or used for the nutrition of the ant carrying it. The great majority of nest inhabitants are workers, always infertile, wingless females. These do all the work of the colony except the laying of eggs. It is not uncommon for the worker caste to be subdivided; in addition to miniature animals and medium-sized types, there can be giants with huge heads. The latter are called soldiers by analogy with the termites, although they do not in every case distinguish themselves as defenders of the nest (Fig. 18-16).

Queens and the founding of nests

The queen, a fertilized, sexually mature female, is reponsible for egg-laying; some nests may have several queens. As juveniles the queens have wings, as a rule, for they come together with the males (also usually winged) in a nuptial flight, to be inseminated. Whereas the males die soon thereafter, copulation is just the beginning of the female's task, the founding of a colony. Each female discards her wings and—by herself, in the simplest case—digs a hole which she enters and closes behind her; there she lays eggs and waits in seclusion for a few weeks, or in cold regions for almost a year, until the first worker emerges. During this time she relies entirely on food stored in her body. The flight muscles, now useless, are consumed internally; usually the female eats some of her eggs, and also feeds other eggs to the growing larvae. One larva receives preferential treatment and therefore develops sooner into her first tiny assistant. Now matters progress more rapidly. The nest hole is opened, food is brought in, and more and larger ants join the work force. From this time on, the queen can restrict her activities to egg-laying, for everything else is handled by the workers.

In the course of founding such an independent colony, the solitary female is exposed to great danger. Therefore many ants, particularly in the cooler climatic zones, have adopted a different procedure which minimizes the risk; the inseminated female returns to the nest in which she was born, and the colonies increase in number by sending out offshoots made up from the outset of both queen and workers. In many cases the inseminated female goes back not to her own nest, but to another of the same species, where she is accepted. And she may even be accepted in a nest belonging to a different species, in which case "mixed colonies" are formed, for the host workers care for the offspring of both species of queen. Often this condition is only transient; if the host queen dies, the nest soon becomes a pure colony of the guest species. Sometimes these mixed colonies function only if two particular species are involved. For example, the European JET ANT (*Lasius fuliginosus*) can develop in nests of *Lasius umbratus*, and the latter can grow in those of the GARDEN ANT (*Lasius niger*). In North America the genus *Lasius* is best represented by the CORNFIELD ANT (*L. alienus*), considered by some to be a subspecies of *L. niger*. A permanent social parasitism can develop from such associations. For if the guest female manages to hasten the demise of the host queen—perhaps by biting her head off, as *Bothriomyrmex decapitans* does to its host, *Tapinoma nigerrimum*—then the workers in the host nest soon have only the guest offspring to care for. To make the most of this situation, some of the parasites have largely ceased to produce any workers of their own. The guest larvae grow rapidly into reproductive animals, and these can attack other colonies. To be sure, the host workers live only for a certain time. Some parasitic ant species alleviate this inevitable shortage by robbing other nests of the host species and letting the stolen pupae grow up as "slaves" in the nests of their kidnappers.

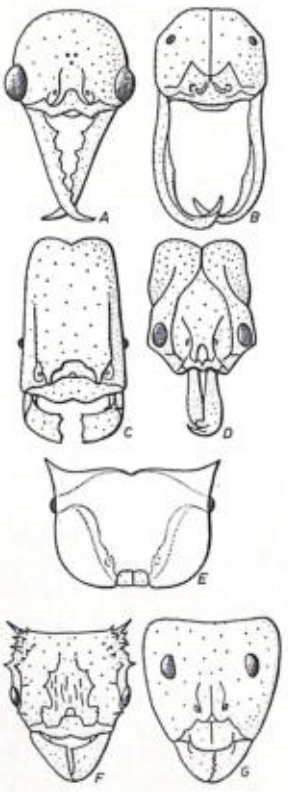


Fig. 18-15. Characteristic forms of mandibles in various ant genera: A, *Myrmecia*; B, *Eciton*; C, *Pheidole*; D, *Odontomachus*; E. *Cryptocercus*; F, *Acromyrmex*; G, *Camponotus*.

Social parasitism

Structure of the nests

The nests of ants are quite varied. In the most primitive case they consist of chambers and passages dug in the ground. The excavated soil is often piled around the entrance to form a crater. The wood ants in the cold zones construct gigantic piles of brush and the needles of conifers. The interior of the pile stays warm and the young in their chambers are protected from rain. Still other ants gnaw out nests in the wood of trees, seek out hollow branches, or arrange little nests in the soft wood of rotting trunks or even in fallen leaves. Finally, there are species which chew up plant materials; the resulting pulp is glued into elaborate nests of cardboard, located either in hollows or in the open on trees. Some tropical species make free-hanging "castles in the air" of leaves and silk.

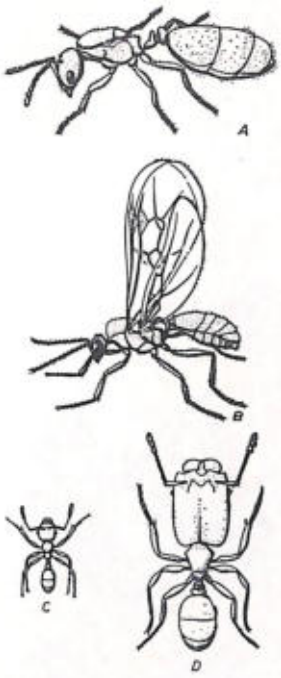


Fig. 18-16. The different castes of species of the ant genus *Pheidole*: A, queen; B, male; C, worker; D, soldier.

The ways in which the ants feed are equally varied. Primitive species are usually predators, hunting any kind of animal they can overpower. But many ants have become more versatile; they do not reject animal food, but in addition gather plant juices or fruits. Especially favorable food sources have become available to those species which collect the nutritious excrement of aphids and scale insects (honeydew; see Chapter 11 and Color plate, p. 502); they gain access to plant juices in this indirect way. The aphids sink their long proboscises directly into the vascular tissue of the plants, and the food which flows into their mouths is so rich that they cannot utilize it all; most is passed out again undigested as honeydew, which the ants and other insects drink. Still other ant species gather the seeds of plants, which can also be stored up for hard times. Finally, there are actually gardeners which eat fungi they have grown in specially prepared nutrient beds in their nests.

Orienting ability

Like all insects living in highly organized communities, the ants have special abilities to orient themselves—for they must be able to find their way back to the nest again and again—and to communicate with one another. Only by so doing can they cooperate to exploit food sources quickly. Orientation is accomplished primarily by vision and the sense of smell, but these are assisted by fine discrimination of the direction of gravity, which enables the ants to gauge the steepness of a path. Like the honeybees, ants orient themselves by the position of the sun, taking into account its apparent movement across the sky; they also use the direction of polarization of the indirect light from the sky to steer a course. Furthermore, they make good use of all sorts of landmarks, such as the outlines of trees.



Fig. 18-17. Two mites, *Antennophorus* sp., hanging on to the host ant.

In the dark, of course, such aids to orientation are of little use. Many of the ants therefore orient primarily by scent marks made by themselves. They smear the odoriferous secretions of special glands on the substrate, making a trail along which an ant need simply "follow its nose." Such a trail can be followed not only by its maker but by fellow ants as well. A trail leading to a source of food is thus an important means of communication. The lucky discoverer hurries home, marking the way as it goes, and there notifies its comrades of the find by rushing about and pushing

them impatiently; following the scent trail, the nestmates quickly locate the food.

Chemical communication

A chemical method of communication is also used in situations involving danger. The endangered ant gives off an alarm substance; smelling this, the workers become highly excited and, depending on temperament and the situation, either move to the attack or flee. Many ants can also make sound signals, by rubbing a sharp ridge on the second segment of the pedicel over a rippled surface on the next segment. Conspecifics can detect these noises only as vibrations picked up through the ground. Leafcutting ants which happen to become buried in their nest use this signal to make their location known and attract their colleagues, which dig them out.

Commensals and other guests

A number of other animals live in ant nests: isopods, mites, spiders, caterpillars, and—above all—beetles (see Chapter 13). Many of these are harmless tenants attracted by the warmth of the nest and the protection the ants can offer; at most, they eat the refuse of the nest-owners. Commensal animals also do little harm; for example, the bristletail *Lepismina* sp. (see Chapter 2) joins ants exchanging food and takes a drink for itself, and the mite *Antennophorus* sp. clings to the head of an ant and waits until a drop of food appears. Some beetles imitate the begging behavior of ants, thus diverting to themselves part of the flow of food in the colony.

But it can be a serious threat to the ants if the guests require a great deal of food, or if they go so far as to turn on the ant brood itself. This is done, for example, by the beetle *Lomechusa strumosa* (see Chapter 13), which lives with the BLOOD-RED ANT (*Formica sanguinea*). Its larvae smell like ant larvae and therefore are treated just as well—or even better, since they beg more eagerly. In addition, they suck out the ant larvae. The adult beetle also does this, but mainly it lets itself be fed, ensuring this care by producing in its own glands a substance which the ants lick up greedily. The related beetle *Atemeles pubicollis* goes even further: once a year, it changes its host. In summer it lives with *Formica polyctena* and in winter, with a species of *Myrmica*. In each case, it spends its time where the food is most abundant.

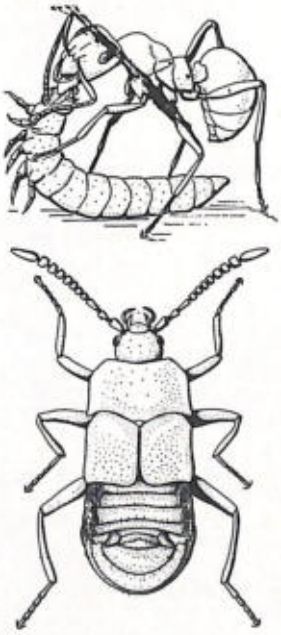


Fig. 18-18. The beetle *Lomechusa strumosa*: a larva being fed by an ant, and an adult beetle.

Only a few ants do real damage to humans, though they are an annoyance to us in our houses. On the contrary, wood ants can be of definite value in the eradication of plant pests.

Subfamily: Myrmeciinae

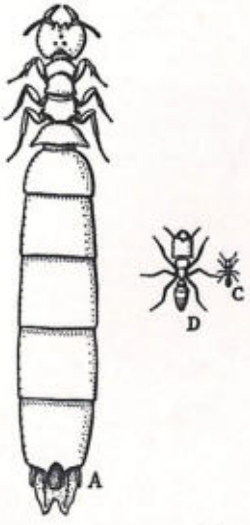
The BULLDOG ANTS (subfamily Myrmeciinae), with about 100 species, live in Australia. These animals are of impressive size, often 20 mm in length, and are feared because of their aggressiveness and the painfulness of their sting. In each nest in the ground there live at most a few hundred animals. Nimble hunters, they capture mainly insects and spiders, which they feed to their larvae. They themselves appear to prefer the sweet juices of plants. Social interactions between the inhabitants of the nest are not well developed in this subfamily.

Subfamily: Ponerinae

There are about 1000 species of PONERINES (subfamily Ponerinae; see Color plate, p. 523), distributed primarily in the tropics. These ants are usually slender, 3–30 mm in length, with a powerful sting, large, pointed



Fig. 18-19. A bulldog ant, *Myrmecia* sp.



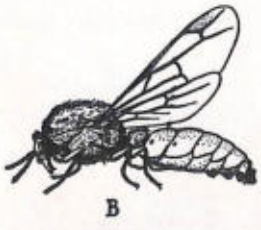


Fig. 18-20. The castes of the driver ant (*Dorylus*): A, female; B, male; C, worker; D, soldier.

Subfamily: Dorylinae

mandibles, and only one clearly demarcated segment in the pedicel of the abdomen. Most of them have a sound-producing organ. Their simple nests are often dug in the ground, but numerous species settle in rotting tree trunks or leaf litter. The latter are mostly small forms which pursue other small animals in the hidden crevices where they live. All the ponerines live as hunters. Sometimes they are exclusively associated with particular prey animals; species of *Termitopone* and *Megaponera*, for example, limit themselves to termites. *Odontomachus* sp. have long snapping jaws which they hold open and then let spring together on their victims at the slightest touch. Usually the workers hunt alone; occasionally even the queen, which differs little from the worker caste, joins the hunt. In fact, most aspects of ponerine social organization are rather simple. The larvae are presented with pieces of prey animals, which they consume. When inseminated, the females found new colonies, and they do so quite independently. A few divergent species of Ponerinae (for example, species of the genus *Leptogenys*) have developed into migratory ants. Their colonies, often very large, go on extensive hunting expeditions, during which they attack the nests of ants and termites.

This wandering habit is characteristic of the 200 species of ARMY ANTS (the Dorylinae; see Color plate, pp. 135/136). They, too, occur predominantly in the tropics. The best-known representatives in South America belong to the genus *Eciton* (see Color plate, p. 523) and in Africa, to the genus *Anomma*. The vast marching columns of these raiders have been described repeatedly by travelers. A colony of an *Anomma* sp., for example, can have more than 1.5 million members. Thousands upon thousands of army ants move forward in dense ranks at a speed of 20 m per hour. At the head of the column the ants fan out into a number of separate groups or a broad swarm, and the flood of ants pours over everything in its path. All living creatures flee before such an advancing horde. The unfortunate animal that moves too slowly is seized mercilessly in sharp mandibles and quickly torn to bits.

If such a swarm marches through a human settlement, the ants divest it of all undesirable vermin. Since the army ants can clean a whole house in a few hours, the inhabitants of such regions are not at all unwilling to turn it over to them for a while. Even such well-armed animals as bees and wasps must watch helplessly as their broods are torn from their cells. Only a few ant genera, such as the tree-dwelling species of *Azteca* or the leaf-cutter ant *Atta* sp., defend their nests successfully against the army ants, and therefore are usually left untouched. The predatory band is accompanied by antbirds (see Vol. IX), and many an animal escapes the ants only to fall victim to the birds.

The worker caste of the army ants includes diverse forms. In addition to workers of all sizes there are soldiers which, with their gigantic saberlike jaws, can easily bore through the human skin. These jaws are such an effective weapon that the sting—not always present—has relatively little

significance. In many army ants the eyes are reduced in size, or the animals are even blind. Some such species hunt in tunnels they dig through the loose layers covering the soil.

All the workers in a nest are descended from a single queen, which becomes huge (L up to 4 cm) in colonies with a large population. The abdomen of this wingless animal is swollen into a massive "egg factory." The winged males, too, are of impressive size. The migratory ants have no fixed, permanent nest; they simply make "bivouacs" for temporary use. In *Eciton* sp., the bivouac consists of a gigantic knot of ants clinging to one another; this clump hangs in a natural hollow and in the middle of it the queen and young find a protected resting place. The colony moves to a new site every month or so. These recurrent expeditions of species of *Eciton* have been quite carefully investigated by Schneirla. The pattern of movement is ascribable to the fact that the queen lays her eggs in batches rather than continually. After one batch of young enters pupation, there is suddenly much more highly nutritive food available to the queen than previously, and this again stimulates her production of eggs. When the larvae from these eggs hatch and begin to grow, the food requirements of the colony steadily increase. In the time interval between the pupation of one batch of young and the hatching of the next, the bivouac remains in one place; small excursions are adequate to supply the steady demand for food. But as the larvae grow, new hunting grounds must be found. The bivouac is moved by a few hundred meters each day, as great streams of hunters pour out in all directions. The migratory period comes to an end when the larvae are grown up and ready to pupate; then the colony once again makes a relatively permanent camp, for about twenty days.

Once a year, at the beginning of the dry season, reproductive animals are born. The females are wingless and must be hunted out by the winged males; they cannot found a colony by themselves. The colony of *Eciton* sp. divides into as many parts as there are inseminated young queens.

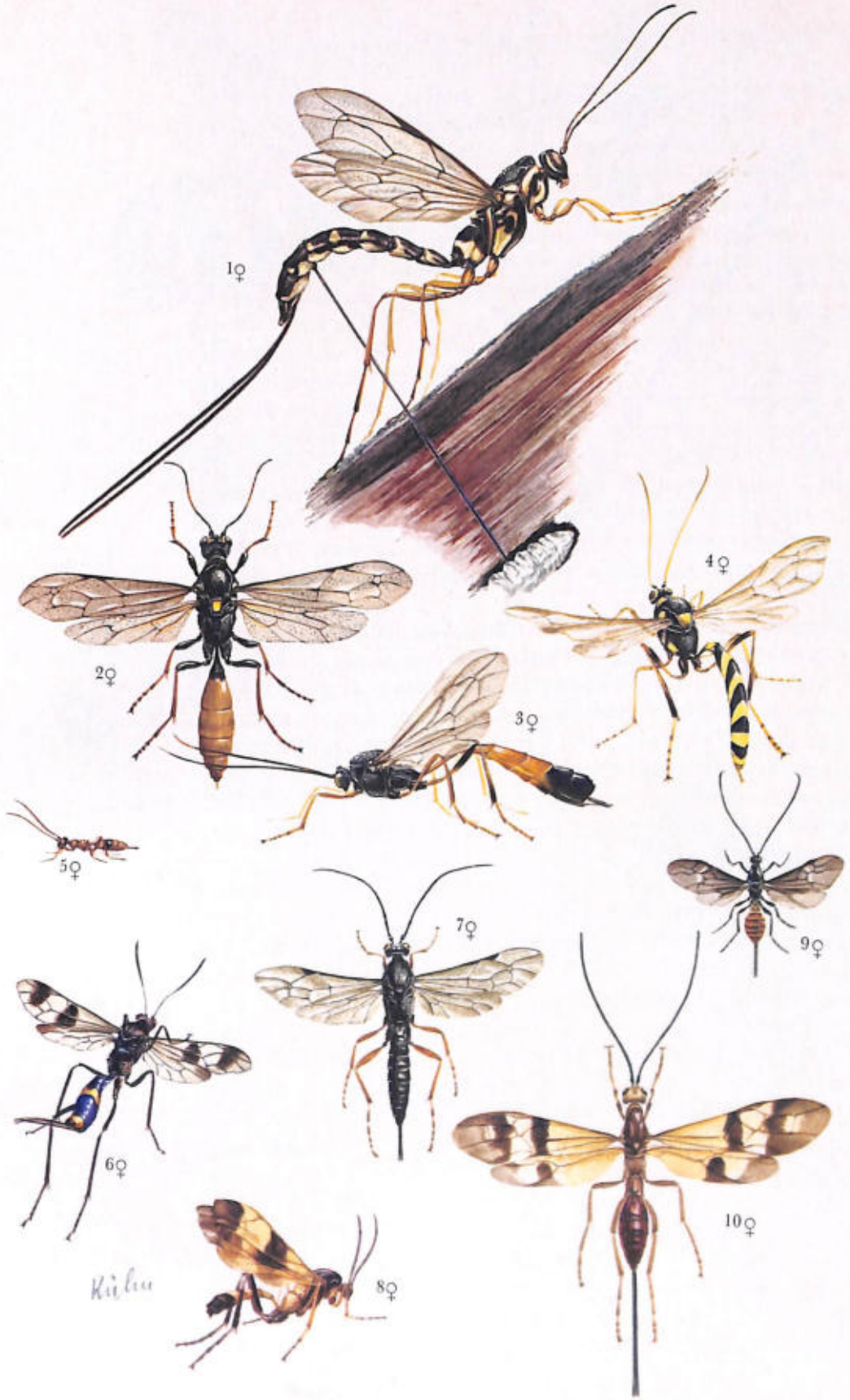
A migratory life of this sort has been invented several times by the ants. In addition to the army ants and the ponerine genus mentioned above, the ponerinelike, tropical CERAPACHYINES (subfamily Cerapachyinae), of which there are about 100 species, also lead a "gypsy" existence. So do the approximately twenty species of LEPTANILLINES (subfamily Leptanillinae), whose life history is unfortunately very little known. The migratory hunting habit is thought to arise as ants specialize in attacking the nests of social insects. This forces them to change their location continually, and to give up having a permament nest of their own.

Other migratory

The MYRMICINES (subfamily Myrmicinae), with more than 3000 known species, are the most extensive ant subfamily. In all of them the pedicel of the abdomen consists of two segments; most have retained the sting and also have a sound-producing organ. The workers are usually only a few millimeters long. The subfamily has spread nearly everywhere, though the greatest number of species is found in the warm latitudes.

Subfamily: Myrmicinae

▻
Ichneumons: 1. *Rh*
persuasoria, female,
cut to show her pie
the horntail larva w
2. *Protichneumon pis*
3. *Therion circumflex*
4. *Gravenhorstia pict*
5. *Gelis fasciatus*; 6.
species from the trib
Mesostenini, from I
7. *Pimpla instigator*;
8. *Areoscelis* sp., fro
Mexico. Braconid w
9. *Iphiaulax impostor*
10. A braconid from
Madagascar.


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Their life histories can be quite varied. Some groups form colonies which are among the most advanced in the animal kingdom.

In general, the social structure of the myrmicines is on a higher level than in the groups so far discussed. All the members of a colony are constantly engaged in a lively exchange of food. The larvae, too, are provided with specially prepared food to which glandular secretions have been added. The primitive species nest in the ground and take both vegetable and animal food; among them are species of the genus *Myrmica*. The evolutionary lines of descent from ancestors of this sort have led in quite different directions. One of these has led to the ants which are predominantly predatory and live either in rotting wood and fallen leaves, or in nests built in trees. Some of the tree-dwellers in the tropics build elaborate nests of cardboard; these include species of the genera *Crematogaster* (see Fig. 18-21) and *Myrmicaria*. Some have become true specialists with respect to their prey. For example, the BASICEROTINES (the group of genera called Basicerotini) and DACETINES (the group Dacetini) mainly go after the small springtails (Collembola; see Chapter 2). Often they have mandibles like a hinged trap, which spring shut on a prey animal the instant the hunter has crept close enough.

Another line of development has led to forms in which the workers are particularly slender and small. They build, within the nests of other ants or termites, their own nests with passages so narrow that only they can use them. Some species (for example, those of the genus *Solenopsis*) probably only steal from the nest owners. Others, on the other hand, overpower and eat their hosts. In parts of the southern U.S.A. several species are known as FIRE ANTS. They have become pests in agricultural areas because of their sting. Among the PHEIDOLOGETINES (Pheidologetini) one encounters many such termite hunters. Since these ants often form quite populous colonies, the females are usually very large. The extreme case is probably that of *Carebara vidua*, whose workers are so small that they can cling to the young queen during her nuptial flight, flying with her so that they are on hand to start work once the new colony is founded (see Fig. 18-22). Life as thieves or predators in the nests of other ants may well have led to the development of social parasitism in some forms; this way of life is not uncommon among the myrmicines. *Strongylognathus testaceus* (see Color plate, p. 523) has saberlike mandibles, so that it cannot feed its own larvae. This must be done by the workers of its host, the PAVEMENT ANT (*Tetramorium caespitum*); in this case, both queens can live together in the same nest. But the female *Epimyrma goesswaldi* is not so tolerant: she kills the queen of her host, *Leptothorax unifasciatus*. In the extreme case, the parasite produces no workers at all, but only reproductive individuals. For example, *Anergates atratulus*, which has been introduced into the U.S.A., has reached this level; it lives in nests of *Tetramorium* sp.

The most highly evolved forms of myrmicid ants feed on plants. They gather seeds or tend their own fungus gardens. The seed gatherers are

halcidoidea: 1. *Chalcis spes*; 2. *Leucospis gigas*; *Heydenia pretiosa*; *Torymus* sp.; 5. *Perimpus auratus*; 6. *Cerapcerus mirabilis*; 7. *Eucharis lscendens*; 8. *Phlebopenes ngicaudatus*, from Brazil. roctotrupoidea: 9. *Asolcus fiventris*; 10. *Proctotrupes adiator*; 11. *Diapria conica*. elecinidae: 12. *Pelecinus olyturator*.

found predominantly in subtropical regions. They lay in large stores of plant seeds in preparation for the long dry seasons, and chew them up as needed. Besides some species of the genus *Pheidole*, these include species of the Mediterranean genus *Messor* and the HARVESTER ANTS of the genus *Pogonomyrmex* in North America. Their nests often extend 1 m or more deep in the earth. The large nests of North African *Messor* species can cover an area 50 m in diameter and contain thousands of storerooms. A considerable part of the grain harvest never reaches the granaries of the people, but disappears into those of the ants. The large *Messor* soldiers are no more warlike than their fellows, but with their strong mandibles they can crack bigger kernels of grain.



Fig. 18-21. If a *Crematogaster* sp. ant is disturbed, it raises its abdomen.

Better than laying in stores is the growing of one's own food. This is accomplished by the LEAF-CUTTER ANTS (*Atta* and other genera) of tropical and subtropical America. Their nests are in the ground, and they bring all sorts of things into them; the primitive species, for example, gather insect excrement, while more highly evolved forms collect cut-up leaves and flowers from several kinds of plants. These materials are chewed up and processed to make a nutrient medium on which a certain species of fungus is grown. Under the care of the ants, the threads of fungus form knobby thickenings at their ends, which the ants pick and use for food for themselves and their brood. How they manage to make a pure culture of a single species of fungus in the moist, dark nest remains their secret. This compost gardening has been most perfectly worked out by species of the genus *Atta*; these animals are so successful that well over a million workers can live together in one nest. The worker caste includes several different kinds of ant. The smallest, only a few millimeters long, devote themselves primarily to work within the nest; they also accompany the larger workers, which often drag bits of leaf along paths over 100 m long, and defend them against parasites. The soldiers are up to 15 mm long, and in this genus their title is justified, for they hurl themselves upon every enemy. Their razor-sharp mandibles can tear bloody wounds even in human skin.



Fig. 18-22. The female of *Carebara vidua* flies with the tiny workers clinging to her legs.

The passages and chambers of such a gigantic colony can go down as much as 5 m. Each nest is founded by a single female. In a pocket of her foregut she has carried a little tangled mass of fungus threads along on the nuptial flight, and in the closed-off brood chamber she proceeds industriously to fertilize it with excrement. In this way she seeds the food supply of the future colony. It is clear that colonies which send out whole legions of workers to cut leaves can do considerable damage to cultivated plants. It has been known to happen that the foliage of an entire large orange tree is transported, cut into small pieces, into the depths of an *Atta* sp. nest in the course of one night. The sight of an endless line of little animals carrying their bits of leaves with them like green sails is highly amusing, however disappointing to the owner of the tree. There are chemicals available nowadays with which he can defend himself against these leaf-cutting ants.

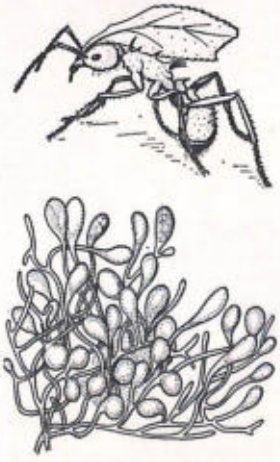


Fig. 18-23. A leaf-cutter ant and part of its fungus garden.

Subfamily: Pseudomyrmecinae

The PSEUDOMYRMECINES (subfamily Pseudomyrmecinae), with about 200 species, live mainly in the tropics. Their nests are found primarily in hollow branches. These ants, so long in body that they are almost snakelike, occupy themselves in hunting insects, no doubt considerably assisted by their conspicuously large eyes. They use their stings so effectively in defense that it has been thought that they afford protection to the plants on which they live. According to this view, some plants are supposed to provide special dwelling places for the ants. In fact, the hollow thorns of some acacia species and the hollow stems of the South American cecropias are almost always inhabited by ants; these include not only the pseudomyrmicines but also species of *Crematogaster* and *Azteca*. The ants bite small entrance holes for themselves, often at preformed break spots in the bark.

Subfamily: Dolichoderinae

The two remaining subfamilies, except for their very primitive members, have the sting regressed. The pedicel has only one segment, and there is never a sound-producing organ. The DOLICHODERINES (subfamily Dolichoderinae), of which about 300 species are distributed throughout the world, have developed a new defensive organ at the end of the abdomen in place of the sting. This is a gland which secretes a foul-smelling substance effective against attackers. But their main weapons are their sharp mandibles. The primitive members of the group live in trees; of these, *Azteca* spp. are some of the most widespread in the tropics of South America, and some of the most feared because of the ants' eagerness to bite. Only a few millimeters long, they throw themselves on any uninvited guest in such hordes that it hurriedly departs. Other dolichoderines have become ground-dwellers, some of them (such as *Leptomyrmex* spp.) penetrating even the dryest deserts. Most species feed on a mixed diet of captured animals and gathered plant materials; some also visit aphids. Not uncommonly (for example, among the Argentinian *Iridomyrmex* spp.), a colony has several queens. This makes it difficult to eradicate such a colony, for one queen is likely to escape. *Iridomyrmex* spp. can build a nest in practically any corner, and international trade has spread the genus to all the warm countries. In human dwellings it can be troublesome. But for the other ants in the regions it invades it can engender disaster, since it competes ruthlessly with them for living space.



Fig. 18-24. Hollow acacia thorns with the nest openings (O) of *Pseudomyrmex* sp.

Subfamily: Formicinae

The FORMICINES (subfamily Formicinae), with well over 2500 species, are found almost everywhere in the world. Many species have a large scale on the pedicel; the German species can thus be identified as members of this subfamily. The sting has regressed in all formicines, but the poison glands have been retained. The poison is either sprayed at an attacker or dripped into wounds made by the mandibles. The poison of wood ants consists of highly concentrated formic acid. The nutrition of formicines depends mainly on captured small animals and on the honeydew produced by aphids.

The genus *Formica*

Species of wood ants of the genus *Formica* (see Color plate, p. 523), to which the well-known RED ANT (∅ *Formica rufa*) belongs, have become

adapted to the temperate and cool latitudes throughout the Northern Hemisphere. They pile up the needles of firs, spruces, or pines, and dry brush over rotting tree trunks, forming hills which in shady hillside positions can grow several meters high. The piles of needles, in which the chambers are hidden, not only keep off the rain but permit regulation of the nest temperature. In sunny positions the hill is low and flat, so as not to be too strongly heated, whereas in shady sites it is large, capturing as much of the available sunshine as possible. The temperature of the innermost part of the nest is usually a quite steady 25°C. Wood ants are industrious destroyers of other insects. Since several hundred thousand animals live in a large colony, their food requirement is so large that wood ants can be extraordinarily useful in the control of insect pests.





Fig. 18-25. An aphid is "milked" by an ant.

The females, inseminated on a nuptial flight in early summer, are unable to found a colony by themselves. Often they are taken into a remote nest of the same species, and from these "mother nests" are formed "daughter colonies" which in time become independent.

But not uncommonly other species must "adopt" the pregnant female. Inseminated females of the BLOOD-RED ANT (*Formica sanguinea*) invade the nests of *Formica fusca* and hoard a collection of stolen pupae in a corner. The workers which emerge care for the strange queen as though she were their own, and for her progeny as well. Once the colony of the blood-red ant has grown larger, it makes repeated expeditions to other nests of the host ant species, bringing back new pupae so that there is always an adequate supply of "slaves." This sort of behavior has become an essential for survival of the Amazonian SLAVE-MAKING ANT (*Polyergus rufescens*); these ants are entirely unable to feed themselves or their brood, since their mandibles have been modified into long saber blades, useful only for battle and predation. In summer they go out daily in search of colonies of *Formica* spp., attacking those they find and carrying off their pupae. Any ant which defends its young is stabbed to death. But the attacked ants tend to seek safety in flight, taking with them as many of their own brood as possible. After her nuptial flight the female slave-making ant invades a nest of the slave species, kills its queen, and takes her place.



Fig. 18-26. A *Colobopsis* worker plugs the nest entrance with its flattened head.

The genus *Lasius*

Species of the genus *Lasius*, only a few millimeters long, are distributed mainly in temperate zones. Their nests, either earthen hills or structures of cardboard like those of the European JET ANT (*Lasius fuliginosus*), are penetrated throughout by fine galleries. These ants specialize in the exploitation of aphids. There are many imaginative tales about their relationship to these "ant cows," but the simple facts are remarkable enough. The ants lay out paths, identified by odoriferous substances, to the aphid colonies, and there they regularly gather honeydew. The ants do the aphids no harm; in a sense, the aphids ransom themselves with their sweet excretions. Moreover, it is an advantage to the aphids that the ants remove their waste products. When an aphid is touched by the antennae of an ant, it lifts its abdomen and lets a droplet emerge, and the ant sucks it up. The

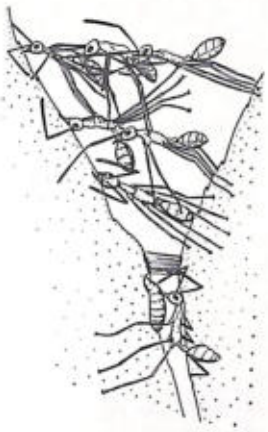


Fig. 18-27. Wielding their silk-spinning larvae like shuttles, weaver ants "sew" two leaves together.

ants take away with them other insects they meet in the aphid pasture, which have nothing to offer them, and thus protect their "herd" from predators.

Some species also make use of relatives of the aphids which feed on tree roots. They may actually live in the ant nest, where they are protected like domestic animals kept in a barn. Ants may surround or cover over any food source with walls of earth, and they sometimes do so with herds of aphids; this form of protection, too, is an advantage to the aphids. In some species of *Acropyga*, the ants' relationship to such animals is so close that each queen takes a few of "her" scale insects along with her on the nuptial flight.

The CARPENTER ANTS (*Camponotus* spp.) are also industrious collectors of honeydew. They are notorious destroyers of wood, preferring to chew out their nest—which can be quite extensive—in the wood of coniferous trees. The closely related *Colobopsis* spp. primarily infest walnut trees. The nest entrance is a narrow tube which can be plugged up by the workers, with their specially flattened heads. The great majority of ants related to the carpenter ant live as tree ants in the tropics. There they make nests not only in wood, but also on the surfaces of the trees, building them of their own form of cardboard or of leaves fastened together.

Ant weavers

The ultimate in this technique of nest construction has been evolved by the African and southern Asian members of the genus *Oecophylla*. These slender ants sew together leaves growing next to one another, by means of a thread of silk that only their larvae can produce. An ant holds a larva and uses it like a weaver's shuttle, pressing its mouth first onto the edge of one leaf and then, once the thread has stuck, to the edge of the other; going back and forth in this way, they spin a dense, firm tissue between the leaves. If the gap between the leaves is too large, several workers bridge it by holding onto one another, forming a chain. A colony of such weaver ants may have a number of leafy "cradles," in one or more trees, in which the brood grows up. Since the ants are eager insect hunters, some people have hung their nests in fruit trees as a method of pest control. The colonies are founded in an unusual way: the female ant simply glues her eggs to a leaf and waits until the brood emerges. Some workers are even able to lay eggs from which males, females, or workers can be produced. This situation is a rarity among social Hymenoptera.



Fig. 18-28. A replete of *Myrmecocystus* sp. storing food in its abdomen.

The desert ants

Of the ants which nest in the soil, the DESERT ANTS are the most remarkable. The species of *Myrmecocystus* living in the dry regions of North America have an ingenious method of storing up supplies. They feed a few workers so abundantly that their abdomens swell up, becoming as much as eight times the normal size. In cellar chambers, several meters under the surface of the ground, these repletes hang from the ceiling, waiting to regurgitate their contents to their fellows in the dry season. They can hardly move, and furthermore the exit from the cellar is usually much too narrow for their overstuffed bodies, so that they are imprisoned there.

In southern Europe, *Formica nasuta* makes use of this method of storing fluid reserves.

Superfamily: Apoidea, by J. Markl

The BEES (superfamily Apoidea) include, in addition to the universally known honeybee, more than 20,000 other species. They are distributed almost worldwide, and in the north their range extends well beyond the Arctic Circle. The smallest bees measure barely 2 mm, while the largest approach 4 cm in body length. They are among the most economically important animals, particularly since they play a critical role in the reproduction of numerous cultivated plants. Moreover, the study of their life history has charms all its own, for they have evolved fascinating forms of social interaction.

Distinguishing characteristics

Apart from the characteristics which distinguish all Hymenoptera, the following are peculiar to the bees. The first tarsal segment of the hindleg is, almost without exception, flattened and broadened. As a rule there is a dense coat of hair, in the female modified into brushlike pollen-collecting devices on certain parts of the body. In some bees these brushes are mainly on the hindlegs, while those of others are on the underside of the abdomen.

All bees feed on plants. They make provision for their offspring by laying the eggs in specially constructed brood cells stocked with a mixture of pollen and the nectar of flowers. Bees have evolved from thread-waisted wasps which fed exclusively on the products of flowers, not only as adults but even as larvae. Thus the poisonous sting became unnecessary for overpowering prey, but it has nevertheless been retained in most cases, as a defensive weapon. Anyone who has carelessly grasped a honeybee will have respect for this armament.

Life history of bees

Some bees are solitary, each female building her own nest and taking care of her own brood. In the social species, several females cooperate, and usually each has a specific set of tasks. The bees offer a detailed illustration of how insect societies may have developed in the course of evolution, for they include all transitional stages between a true solitary habit and the complex organization of large colonies. Moreover, numerous species of bees have independently evolved which do not care for ther own progeny, but rather smuggle their eggs into the prepared cells of other (usually related) species. More than one-third of the apoidean species are such parasitic or "cuckoo" bees. As adults, these bees have no pollen-collecting apparatus. On the other hand, their larvae often have enormous jaws, with which they kill the larvae of the host bees.

Since bees pollinate plants in the course of their foraging activities, there has gradually evolved—to the advantage of all concerned—a more and more extensive reciprocal adaptation of the structure of the flowers and the behavior of the bees. We are justified in the assertion that the glorious flowers which bring us such pleasure are due primarily to the influence of the bees, for which these displays are actually intended.

Classification

The bees are classified into six families, of which two, the Halictidae and the Apidae, have evolved social species.

Family: Colletidae

There are about 500 species of PLASTERER and YELLOW-FACED BEES (family Colletidae). These have retained quite primitive characteristics. The glossa (the main part of the proboscis) is short, and their collecting apparatus is often incomplete. They are distributed through all parts of the world, but are particularly prevalent in Australia. One peculiarity of these bees is that they line their brood cells—in the ground, in hollow branches, or in rotting wood—with a quickly hardening, watertight glandular secretion; hence the name PLASTERER BEES for the genus *Colletes*. The YELLOW-FACED BEES (*Hylaeus* spp.) have been named for the white-yellow markings on the face. Because they are so sparsely covered with hair, they look very much like wasps. In contrast to the other bees, they gather pollen in their crops.

Family: Andrenidae

More than 1000 species of MINING BEES (family Andrenidae) are distributed nearly everywhere. On the tibiae of the hindlegs, they have dense brushes for collecting pollen, and there are also long collecting hairs on other leg segments, on the thorax, and at the end of the body. The males, which lack all these devices, are also quite different from the females in structure and coloration. Since the glossa is usually not very long, the mining bees prefer to visit flat flowers like those of umbelliferous plants or roses. They dig their nests in the ground, as their name implies. As a rule these structures are quite simple; from a slanting passage 15–30 cm in length there branch off short side passages, each adjoined by a group of cells. Males and females survive the winter and mate in the spring, often very early.

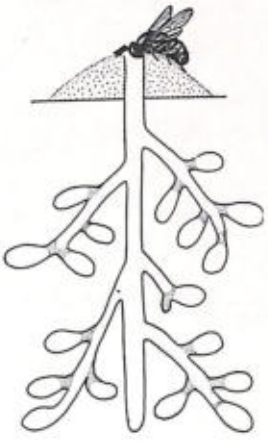


Fig. 18-29. The nest of *Evylaeus malachurus*.

Some mining bees have become adapted to feeding on quite specific flowers. For example, *Andrena florea* flies only to the flowers of *Bryonia alba*. The bee *Panurgus* sp. selects flowers of the composite plants, into which it can get its whole body; thus in collecting pollen the bee becomes dusted all over with it. The mining bees include numerous parasites, of which we shall mention species of the genus *Nomada* (see Color plate, p. 524). These are usually brightly colored, like wasps, and not very hairy. At the nests of their hosts, most of which are species of the bee genus *Andrena*, they lie in wait for a cell to become fully stocked. Then they slip into the nest and lay their eggs on the prepared food pellet. The fact that large numbers of *Andrena* sp. build their nests close together in suitable places makes this easy for the parasites.

Family: Halictidae

The several thousand species of BURROWING BEES (family Halictidae; also called MINING BEES like the Andrenidae) live in all parts of the world. They have collecting brushes, located on different parts of the legs in different groups. They are usually fairly small (L 3–11 mm), and they visit a number of different flowers. Although the life history is known for only a very few of them, what we do know deserves our closest attention; within this one family all the transitions from the solitary to the social habit have been found. We shall illustrate this sequence with examples from the subfamily Halictinae. The researchers who have contributed

most to our knowledge of these bees are the American Michener, the Japanese Sakagami, the French Plateaux-Quénu, and their collaborators.

The simplest burrowing bees, for example, the European *Halictus costulatus* and *H. nitidus*, are truly solitary; the females are inseminated in the fall, and in spring they build a nest in the ground from which, by the next fall, one generation of offspring has emerged. Two evolutionary paths can lead from such behavior to social life: either the progeny of a founder female may stay in the original nest and work together there, or several inseminated females may found a common nest. Both situations are found among the Halictidae. A common nest can be formed if sister bees spend the winter together and then stay together in the spring. Such a nest can also develop from colonies of individual nests located close together, and one finds this situation in certain species. The nests of communities of the European *Lasioglossum versatum* are sometimes connected by subterranean passages. It can easily happen that these networks become a single nest with a common entrance, within which each female takes care of her own cells. A nest of this kind can be much more readily defended against parasites, for one of the females can sit at the entrance to turn away uninvited guests. This in itself amounts to the beginning of a sort of division of labor. In *Lasioglossum inconspicuum* one female usually takes charge of egg-laying, although all are equally capable of doing so, while the others function as workers, gathering pollen and nectar. In *Augochloropsis sparsilis* some of the worker-females are not even inseminated; what they accomplish as workers is more valuable to the welfare of the community than their offspring would be.

Communal life is brought about in other halictid bees when a female produces several batches of young in the course of her life, and lives long enough to form a colony with her children. When this happens, at least some of the daughters become workers. If these workers are less well fed as larvae than those which are to become complete females, they are externally distinguishable; usually they are smaller. The more highly evolved the social structure, the fewer workers are inseminated and the later the males are produced. Among the colonies which last one year, that of *Evylaeus malachurus* (see Fig. 18-29) is the most advanced. The founder female at first cares for some cells herself, and from these come workers. The workers prepare the cells for the second batch of eggs laid by their mother. Once again workers are produced and they bring in food for their younger autumn siblings. The latter set of progeny consists of males and females, which mate in the same autumn. The situation is rather similar to that found in a society of bumblebees.

Social life has been further perfected by the southern European species *Evylaeus marginatus*, colonies of which become at least five years old. A female which has been inseminated in the fall digs a nest in the ground the following spring. She prepares cells until the middle of May; then she closes the nest and spends summer, autumn, and winter in it. In August

of this first year the first generation, all females, emerge; they stay with their mother in the nest. Not until the following spring do the daughters open the nest; they look like the mother, but function entirely as workers and are not inseminated. It is their task to extend the nest, bring in food, and in May to close the structure once again. Again the queen lays eggs, but now she does no other work. The second set of progeny also consists of only a dozen workers; the first set of workers has died during the summer. The third and fourth years are repeats of the second, the colony growing until it contains about 130 members. In the spring of the fifth year, the workers carry in more pollen than in earlier years. After the summer rest period the nest is opened, in September, and male bees fly out. They seek out and copulate with the females which have been produced at the same time in other nests, and the cycle is complete. The number of reproductive individuals in each nest can amount to 600. Since the first year, the queen has not left the nest, and in the fifth or sixth year she dies. The only other bee to reach such an advanced age is the queen honeybee.

The nest construction of the halictids can be extremely complicated. Only the simplest structures are like those of the andrenid mining bees. In contrast, the FOUR-BANDED MINING BEE (*Halictus quadricinctus*) puts together aggregations of cells of sand and waxy glandular secretions, forming a sort of comb which hangs from pillars of sand in a hollow underground (see Fig. 18-30). As one might expect, the Halictidae have also evolved numerous species of parasites.

Family: Melittidae

In structure, the MELITTIDS (family Melittidae), with about sixty species, mark a transition from the lower to the higher bees. With their long glossae they can suck even from deep flowers. The collecting brushes on the hindlegs can be very large (these have earned species of the genus *Dasypoda* the common name "trousered bee" in Germany; see Fig. 18-31). Though the nest is usually a simple hole in the ground, *Dasypoda* does not lay its pollen ball on the floor, but rather sets it neatly on three little pillars.

Family: Megachilidae

All the MASON BEES and LEAF-CUTTER BEES (family Megachilidae) gather pollen with a tuft of hairs on the underside of the abdomen, which they brush over the stamens of flowers. This extraordinarily widespread family, with its great number of species, is the most highly evolved group of solitary bees. Their elaborate nest structures are especially famed, but the life history is known for only a very few species. The most primitive forms use soil as a building material, but the more advanced use all sorts of plant materials—leaves, resin, plant hairs, and so on.

MASON BEES (*Osmia* spp.) create a very durable cement by mixing glandular secretions and soil; with it, they form cells which they hide in rock fissures, hollow branches, and the like. Other genera of the family mix dung and earth into a mortar. The places they make for housing their brood can be quite out of the ordinary; Karl von Frisch has described one of these most graphically: "The nest of a certain mason bee may well be

one of the most wonderful of all. This bee finds an empty snailshell for each egg; deep within it the food pellet for the larva is placed, and on this the egg is laid. A little distance away the bee builds a wall of chewed-up leaves, and then it stuffs all the rest of the shell with little stones and keeps them from falling out by making a second wall, of hardened leaf pulp, across the opening. Not satisfied with this protection for its child—which is in fact subject to the predations of many kinds of enemies—it collects one after another, in laborious flight, stalks and blades of dried grasses, light dry twigs, or pine needles; from these it builds a tent-shaped protective roof which eventually hides the snailshell entirely." *Osmia papaveris* builds many single-celled nests in the ground, lining them with poppy petals in which the food pellet for the larva is packed. Other species (for example, the WOOL-CARDER BEES, *Anthidium* spp.) prefer to build with resin.

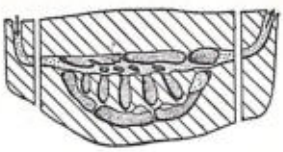


Fig. 18-30. Nest of the four-banded mining bee.

The LEAF-CUTTER BEES (*Megachile* spp.) are also rather remarkable. There are over 1000 species throughout the world. Karl von Frisch writes of them: "The leaf-cutter bee first prepares a tunnel—for example, in rotten wood. Then it flies to the green leaves of a bush (rose, lilac, raspberry or the like), and with the sharp scissors of its mandibles it cuts out a round or oval piece. This is rolled up and carried back to the tunnel. When enough bits of leaf have been gathered, the bee twists them into a sort of long thimble, to serve as a cradle for the young. In the thimble it places a food pellet of collected pollen and after laying an egg on that it proceeds to close the open end with more pieces of leaf, quite circular in shape." MASON BEE species of the closely related genus *Chalicodoma* (see Color plate, p. 524) build nests of sand and saliva and glue them to the outsides of walls or to stones. One female builds four to six such nests, each with six to ten cells side by side. Since it often happens that many females choose the same site for this activity, in the course of time quite extensive "apartment buildings" result.



Fig. 18-31. Hindleg of a bee species of the genus *Dasypoda*.

All these behavioral patterns are innate, and however sensible they seem to us, are nevertheless quite rigid and can be modified only very slightly. Once a mason bee has ceased its building and begun to carry in pollen, it does not concern itself in the least with a hole one makes in the cell, but simply lets its precious load fall through unnoticed.

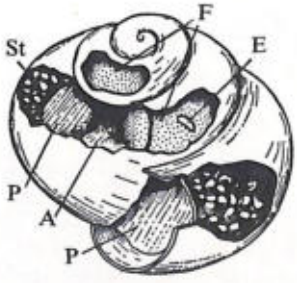


Fig. 18-32. The nest of a mason bee, in a snailshell. F, Food for the larva; E, egg; P, Partition made of chewed-up leaves; A, Air space; St, Little stones.

The bees with abdominal pollen baskets have given rise to many parasitic forms, which choose their closest relatives as hosts. Species of the genus *Coelioxys* prefer the nests of leaf-cutter bees. They must proceed rather cleverly if they are to succeed, for the host bee usually checks her work before laying her own egg, and throws out any undesirable occupant. But after the egg is laid, when she flies away to get the pieces of leaf for the lid to close the cell, if it is quick enough the parasite can get an egg in after all, for the host bee never checks the cell more than once.

The family Apidae includes both social species and truly solitary bees. All have a particularly long glossa, with which they can reach the nectar

Family: Apidae



Fig. 18-33. Leaf-cutter bees roll leaves into a thimble-shaped shelter for their brood.

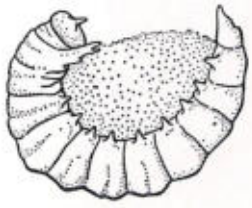


Fig. 18-34. A larva of the carpenter bee, *Allodape* sp., with its food pellet.

even of flowers of the Labiatae and Papilionaceae. The pollen baskets on the hindlegs reach a peak of perfection in this group. There are considered to be three subfamilies: Anthophorinae, Xylocopinae, and Apinae.

The subfamily Anthophorinae, to which the POTTER FLOWER BEES (*Anthophora* spp.) belong, is widely distributed and includes many species. Most of them are solitary, and a few are parasitic. The potter flower bees are the most adept flyers of all bees. They make their nests, often large numbers of them together, in the walls of clay and sand pits. Both the horizontal passage and the cells are carefully smoothed with claylike materials and mucus.

The CARPENTER BEES (subfamily Xylocopinae) include the impressively large (up to 3 cm) LARGE CARPENTER BEES (*Xylocopa* spp.), a metallic iridescent blue-black in color. The large carpenter bees are mainly encountered in warm regions but may also be found in central Europe. Males and females pass the winter in groups and copulate in the spring. The female then selects a hollow twig or a post of dry wood, often the very one in which she grew up, and chews out a vertical nest tube. Into this she places a large quantity of pollen, mostly from the flowers of leguminous plants, lays an egg on it, and erects a partition of wood debris and saliva; she makes ten to sixteen of these brood cells in a row.

Even among the large carpenter bees there are species which tend toward a communal way of life. This is true of the South African and Australian species which are relatives of the genus *Allodape*. Their nests are simple chambers in hollow branches, with the entrance kept very small and assiduously guarded by the female. There are no separate cells; all the larvae grow up in the same chamber. In contrast to all of the bees discussed so far, the larvae of these species are, as a rule, not even provided with food in advance; rather, the mother feeds them day by day. The larvae have peculiar projections on the ventral surface with which they hold on to the packets of food. The first females to emerge look like their mother, but initially remain uninseminated and work industriously to care for their siblings. Often the founder female dies after laying one or two batches of eggs; in this case, an inseminated daughter takes her place, lays more eggs, and together with her sisters raises her own children and those of her mother which remain. These small, short-lived communities thus display all the characteristics of a social system.

Subfamily: Apinae

The Euglossini

There are some solitary bees even in the subfamily Apinae; these comprise the group of genera called the Euglossini, which inhabits the tropical jungles of South America. These animals resemble bumblebees; they are brightly colored, often with a beautiful metallic sheen. They sometimes build large nests in hollows in the ground or in trees. Resin is used, not infrequently mixed with fragments of bark, dung, or soil. Occasionally several females work in the same structure, each on her own cells. An odd discovery was made by the botanist Vogel concerning the males in this group: one can see them on orchids, busily gathering something most

unusual. The flowers secrete an odor substance in fluid form, and the males use the tufts of hair on their forelegs to brush it off. Then they fly away, transporting the fluid in a container on the tibiae of the hindlegs. The males probably use this "perfume" to mark out courtship territories where they meet the females. These bees thus accomplish what the bumblebees and many others do with their own odor substances, by borrowing a scent. Two genera of Euglossini have adopted a parasitic way of life, raising their brood at the expense of their working relatives.

Social members of the Apinae

The social members of the Apinae are divided into three groups of genera, or tribes: the bumblebees (Bombini), the stingless bees (Meliponini), and the honeybees (Apini). All of them build their brood cells predominantly or even exclusively with wax, which is secreted by glands in the abdominal body wall. They always make both storage cells and brood cells. The way pollen is gathered by these most highly evolved bees has been described by Karl von Frisch, taking the honeybee as an example:

"The first tarsal segment of the hindleg is greatly enlarged and broadened, and on its inner side there is a thick fringe of stiff bristles. The tibia of the hindleg is also specialized, bearing on the outside a border of long hairs surrounding a smooth field, slightly indented in places, the corbiculum. The pollen clumps are carried home in the corbiculum, but the way they get into it is a story in itself: Each bee, as it prepares to fly out and gather pollen, takes along a bit of honey from the hive, in its honey stomach. When it arrives at the flowers, it lands on the stamens—as one can see especially well with large poppies or wild roses—rapidly scrapes down the loose pollen with its mandibles and forelegs, and simultaneously moistens the pollen with the honey it has brought along, making it sticky. If there is an abundance of pollen in the flower, it becomes caught among the hairs all over the body of the bee as it is working, so that the bee sometimes looks as though it had been dusted with flour. During the flight to the next flower, the legs under the body are in feverish activity; with the brushes on the hindlegs the bee sweeps the pollen out of its coat of hair and off the other legs, and then, with a stiff comb of bristles, the scopa, at the end of the tibia of each hindleg, it combs the pollen out of the brush on the other hindleg, alternating right and left. The pollen is thus caught in the comb, but only for a moment; for now it is sent over through the gap between tarsus and tibia by an adroit push with the tarsal spur, to the outside of the tibia and into the corbiculum. Bit by bit more pollen is added from below, each load pushing up the earlier accumulation, until the basket is full. The middle legs press and tamp it from time to time, so that the pollen remains compacted and none of it is lost."

In all the higher Apinae, the population is composed of three castes: 1. the inseminated queen, devoted predominantly or exclusively to the laying of eggs; 2. the workers, uninseminated females which differ from the queen in the structure of the body and are usually somewhat smaller; 3. the males, which usually do not appear until the mating season, having

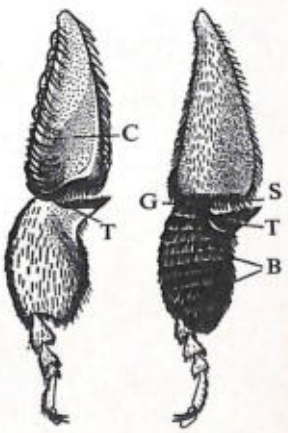


Fig. 18-35. Hindleg of a honeybee worker: left, outer surface; right, inner surface. B, Basitarsal brush; S, Scopa; T, Tarsal spur; G, Gap between tarsus and tibia; C, Corbiculum.

developed from unfertilized eggs. Both queen and workers arise from identical fertilized eggs. Their differentiation is brought about by the fact that the queen-larva receives an especially nutritious food, supplemented with the glandular secretions of the nurses, whereas larvae which must manage with simpler fare become workers.

The Bombini

BUMBLEBEES (Bombini; see Color plates, pp. 511 and 524), with about 200 species, primarily inhabit temperate and northern regions; in the south they are found mainly in mountainous areas. Their thick, often brightly colored coat of hair protects them from the cold. Usually their nests are in underground hollows; they are surrounded by a covering of moss and other materials, and the roof is often sealed with wax. With their long proboscises they penetrate the deepest blossoms. Some plants, for example, red clover, are almost entirely dependent upon bumblebees for fertilization. When the English brought clover to New Zealand the plants did not reproduce until, following the advice of Darwin, they imported bumblebees as well. The brood cells and storage cells of the nests, bulky and round like pots, are kneaded into shape from wax and resin. Large bumblebee nests can have several hundred members. In northern European latitudes the nests last for only one year.

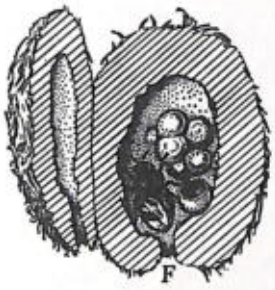


Fig. 18-36. Female bumblebee with brood cells and food receptacle, in the upholstered nest. F, Flight hole.

An inseminated female, having awakened from her winter dormancy, first builds a small nest within which she prepares a wax container for the first brood and a storage cell for honey. In the common brood cell about half a dozen progeny grow up, provided with food periodically by the mother. Since the food is in short supply, the larvae metamorphose into small workers, and these assist the mother in extending the nest and stocking it with food. In the course of the summer the food available to the young thus becomes more abundant, and they grow into larger and larger worker-females. Finally, reproductive females and males are produced, and they mate. The males mark out swarming territories, each species in its own particular type of surroundings, marking the routes over which they fly with odoriferous substances secreted by their glands. There they await their females. This sort of male behavior is not uncommon among bees. Adolf Haas found it in a number of solitary species as well. Except for the inseminated females, which go into hiding for the winter, all the inhabitants of the bumblebee nest die in late autumn. Bumblebees, too, have their parasites: the parasitic bumblebee *Psithyrus* leads an easy life at the expense of its more industrious relatives.

The Meliponini

When we speak of STINGLESS BEES, it may sound like a contradiction. Most people assume that all bees sting. Nevertheless, the several hundred tropical species of the tribe Meliponini, mostly small bees with regressed stings, are by no means defenseless. They bite rather than sting, and some pour a corrosive secretion onto the skin that burns like fire; still others spread glue on their opponents. The highly evolved social structure of these bees is hardly inferior to that of the honeybee. Some societies comprise up to 100,000 workers, which together can accumulate up to 45 kg

of honey. It is no wonder that South American Indians have taken certain species (in particular *Melipona beechii*) into their care in order to exploit them.

The inseminated queen need only lay eggs; her ovaries have swollen her abdomen to such an extent that she is incapable of flight. She obtains her food in the nest, feeding on the supplies stored in the brood cells before laying her eggs; sometimes she also eats eggs laid by the workers. The stingless bees, like the primitive bees, supply each larva in advance with all the food it will need. The workers often differ very little from the young females, but it is only the workers that collect food and defend the nest. They also bear most of the burden of construction, perhaps assisted by the males, which, remarkably, can produce wax like the workers. The nests of these jungle bees are usually located in hollow trees or underground spaces, though rarely they are found hanging free from branches. Only in the simplest case does the nest consist of a pile of brood cells, like that of the bumblebees. Usually horizontal combs are built of wax and resin, with brood cells on only the upper side. As many as forty such tiers of comb can be stacked up. An envelope of wax surrounds the brood nest, and the receptacles for stored pollen and honey are attached to the outside of this envelope; these receptacles can be as large a a chicken's egg. Finally, the whole nest cavity is surrounded by a second, multilayered envelope of wax, resin, and soil. There is an entrance tube leading to the nest entrance, so narrow at its end that one or a few workers can defend the entrance. Often ants and other thieves are prevented from entering by rings of glue placed outside the tubes. Only one species of the African stingless bees builds vertical combs like those of the honeybee.

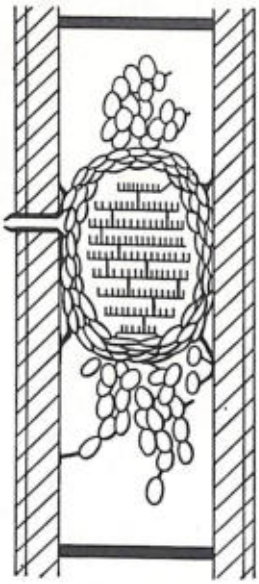


Fig. 18-37. The nest of a species of stingless bee in a hollow tree trunk.

The colonies multiply by swarming. One or several young females, together with some workers, move into a new nest site, usually at no great distance from the mother nest. Martin Lindauer has described this procedure: "The whole swarm does not move into the new home at once; rather, an advance party is first sent out to prepare the site for moving day. This party, consisting of 50–100 bees or more, clears out and cleans the future home; the bees also fly back and forth between the mother hive and the new location for days or weeks, bringing wax and resin and constructing the entrance to the hollow, providing it with a flight tube, and even making the first storage receptacles. As though this preparation were not enough, they even carry honey and pollen over from the parental hive, filling the storeroom. Only then does the queen, accompanied by another large group of workers and many males, move in." These colonies often live for several years.

The task of providing such large colonies with food presents problems of organization. Lindauer and Kerr discovered that the stingless bees, like honeybees, can direct the workers to particularly rich foraging grounds. We quote Karl von Frisch's description of this behavior, beginning with the more primitive species *Trigona iridipennis*:

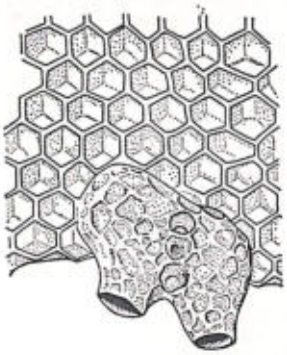


Fig. 18-38. Section of a honeybee comb: drone cells above, and two queen cells at the lower edge.

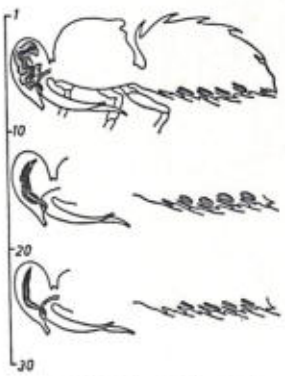


Fig. 18-39. Physiological changes having behavioral correlates (see text) in the life of a honeybee worker: the numbers signify days of life; on the right is shown the state of development of both the pharyngeal gland in the head and the wax glands in the abdomen.

"When these animals have discovered a good source of food they notify their comrades; they also let them know what it is that they are to seek, but they do this in the simplest way imaginable. After returning to the nest, a successful forager runs excitedly about on the comb, jostling its idle fellows and so gaining their attention. When three or four bees have turned toward it, the forager suddenly runs ahead of them to the flight hole, making marked shaking motions of the body. There it turns around and repeats the procedure, leading a new little group of bees to the entrance. These bees learn what odor to expect at the food source from the flower scent they detect on the forager. They fly out, and with no clue as to direction or distance of the food source they search about at random for a spot with the appropriate smell. It is understandable that with this strategy some of them, but only a few, are successful."

More highly evolved stingless bees like *Scaptotrigona postica*, again in the words of von Frisch, employ a more efficient technique: "Only an hour after they have found a spot with an abundant food supply, at some distance from their home, the area is teeming with busy collectors." How were they informed? "The foragers alert their comrades by running about excitedly on the comb and by bursts of buzzing which set the substrate into vibration. The hivemates note that there is something to be gathered, but they do not yet know where. They assemble in a swarm in front of the hive and wait. Now something very remarkable happens. The bee which has discovered the food, and which meanwhile has made several foraging flights, arrives at the food source in an especially excited state. It lands near the food place on the ground and works on a blade of grass, a stone, or another conspicuous object with its mouth, wiping onto it the secretion of its powerfully developed mandibular gland, the peculiar smell of which is discernible even to the human nose. That is, the bee marks the spot with scent, and then proceeds to do the same thing every 2–3 m along the way back to the nest, using stalks, leaves, or stones. It actually creates a scent trail leading from the colony to the goal, which makes it easier for the new bees to find their way. Having finally reached the colony, the marking bee throws itself into the swarm of waiting bees and then guides them, flying agitatedly back and forth, along the path to the feeding place."

Species of the genus *Lestrimelitta* are capable of building their own nests, but they also take by force those of other stingless bees. They have quite given up the laborious gathering of pollen and nectar from flowers. Instead, they attack other colonies, helping themselves from the full food containers.

The Apini

The honeybee

At present four species of TRUE HONEYBEES (tribe Apini) are known, all of them native to tropical southeastern Asia. But the domesticated HONEYBEE (*Apis mellifera*; see Color plates, pp. 512/513, 514, and 524) has been distributed by humans, who care for them for their own use, all over the world. In earlier times, before cane and beet sugar came into use, honey

was the only sweetener known to mankind. For that reason the bees were most highly prized for their honey and wax. Today, on the other hand, the beneficial activity of the bees in pollinating flowers has become more important. All honeybees build their combs of pure wax, which can be produced only by the workers. The combs are hung up vertically either in the open or in enclosed areas, and on both sides they have geometrically perfect hexagonal cells, a shape which minimizes the construction material required. The cells for the worker brood and those for the storage of honey and pollen are similar, while those for the males, the drones, are larger. The queens are raised in special vertically hanging chambers (see Fig. 18-38). Only the workers have the organs and instincts necessary for the activities of construction and foraging. The queen, somewhat larger than the workers, has as her only task the laying of eggs. Fertilized eggs give rise to workers or queens, depending on the food given to the larvae, while the drones come from unfertilized eggs. The time at which reproductive individuals are to be produced is determined by the workers, who then prepare the appropriate cells and food. All the larvae are fed and cared for continually during their development. A queen can lay as many as 2000 eggs in a single day. In her four to five years of life, she produces about 2 million eggs. More than 80,000 bees can live in a colony.

The tasks of the workers are manifold: they supply the colony with food, guard the nest, and build the combs. They also keep the combs clean, for these are used several times for the brood. By fanning with their wings the workers cool the nest, and by their muscular activity they warm it; thus they ensure that the temperature in the brood area stays close to 35°C. Although every worker bee is, should special circumstances demand it, capable of performing any of these tasks, ordinarily there is an orderly division of labor, corresponding to the age of the workers. In their first days of life they act as janitors, keeping the combs clean; next, after the pharyngeal gland in the head (see Fig. 18-39) has matured, they devote themselves to the larvae, feeding them first with the secretion of this gland and later with pollen and honey as well. At about the tenth day of life they fly out briefly for the first time and become acquainted with the surroundings of the hive. In the following days the pharyngeal gland becomes reduced and the wax glands begin to function. Now the worker bee becomes a construction worker, in addition having responsibility for the food stores and carrying away refuse. Finally, when it approaches the age of twenty days, the worker goes out into the open more and more often; at first it takes over guard duty at the flight hole, and then it forages with great industry for pollen and nectar until the end of its life, in summer, after four to five weeks of labor.

Bee colonies propagate by swarms. In the early summer, shortly before one or more queens emerge from the queen cells, the old queen leaves the hive with about half of its population. She first gathers her court into a

▷ The ichneumon *Rhyssa persuasoria* piercing a horntail larva. Note the characteristic position of the legs.

cluster near the hive and then follows the advance guard, which has found a new nest site. The young queens which have matured in the old hive fly out repeatedly until they have mated, each with several drones. This supply of sperm must last the queen a lifetime. They mate in flight, at assembly places where the drones often congregate in great numbers. There the drones fling themselves on every female which flies past and has the appropriate scent signal. The inseminated queen returns to the nest and stings to death any rivals which may still be present. The drones, too, meet with a pitiable fate in late summer; the workers drive them out of the nest with bites and stings, and let them starve.

Chemical signals are involved not only in mating; they play a role in many aspects of communication by bees. Each queen secretes a substance by which the workers are continually reassured that the colony is not without a mother. Scent signals spread the alarm when the bees are in danger, and also serve to identify food sources and the entrance to the hive.

Bees store up honey collected from various sources. Blossom honey is the thickened nectar of millions of flowers, which has passed through the stomachs of many bees and been altered by glandular secretions. Bees also collect the sweet excretions of aphids which stick to leaves; with this they form the leaf honey or pine honey which is considered such a delicacy. Since a good colony can store as much as 1 kg of honey per day, the number of foraging flights undertaken in a day is astronomical. This efficiency depends upon two special achievements: the bees can orient themselves, and they can communicate with one another. Let us first consider the orientation; each bee must cover the distance between hive and collecting place as quickly and accurately as possible. How it does this has been investigated in the greatest detail during the last fifty years by Karl von Frisch and his coworkers. The bee uses all its senses. Its sense of color leads it to the bright flowers, and its sense of smell enables it to distinguish the different flower species. On the flight out and back, it not only observes conspicuous landmarks, but also uses the sun as a compass by keeping the flight path at the proper angles to the direction of the sun. Even the fact that the sun seemingly moves across the sky does not confuse the bee. Its sense of time permits it to take the time of day into account in its flights, correctly altering the setting of the sun compass. This sense of time also makes it possible for the bee to go, at each time of the day, to the sort of flower that is producing nectar just then. Even if the sun is covered by clouds, the forager is not helpless. The direction of polarization of the light waves which come down to us from a patch of blue sky is dependent on the position of the sun. Since the eyes of the bee—unlike our eyes—can measure this direction of polarization, the bee can orient to that just as well as to the sun itself.

If a source of food is to be really efficiently exploited, its discoverer must communicate its location to the other foragers. The discovery of the way the honeybees do this is among the most exciting revelations of

Above: newly hatched males of the braconid *Apanteles* sp., on their communal pupal web. Lower left: the full-grown larvae of *Apanteles glomeratus* boring out of the body of a cabbage white caterpillar (*Pieris brassicae*) in order to pupate. Lower right: pupa of the mourning cloak (*Nymphalis antiopa*), cut open at the side to show the parasitic wasp pupa inside it.

modern biology. The 1973 Nobel Prize winner Karl von Frisch, to whom we owe our understanding of this achievement, has written about it as follows:

"The forager bee, having returned to the hive and disposed of its burden, begins a kind of round dance. It runs in tight circles with rapid, tripping steps, on whatever part of the comb it happens to be, often changing so that it runs now clockwise, now counterclockwise—alternating after one or two circuits in each direction. This dance is performed in the middle of a dense crowd of nestmates; it is particularly striking and charming to watch because it visibly affects the surrounding bees; those closest to the dancing bee trip along behind it, trying to keep their outstretched antennae in contact with its abdomen, and follow all its twists and turns, so that the dancer is trailed through its contortions by a long tail, as it seems, of other bees. This chaotic pattern can be maintained for a few seconds, half a minute, or even a whole minute; then the dancer suddenly stops and withdraws from its retinue, only (in many cases) to go to a second, and even a third, place on the comb; each time it regurgitates a droplet of honey and performs another dance. Finally, though, the dancer rushes precipitously back to the flight hole and flies once again to the food site to bring in a fresh load. The whole performance is repeated each time it returns. Under normal conditions, of course, the dance is done in the pitch darkness of a closed beehive, so that the dancer is invisible to its comrades. When they notice its activity and follow it through its tortuous course, they are relying entirely on their senses of touch and smell.

"What does this round dance mean? It is evident that it greatly excites the hivemates in the vicinity. One can also observe, if one keeps one or another of the followers of the dancer clearly in sight, that this follower makes preparations for flying out, quickly cleaning itself a bit, and then makes its way to the flight hole and leaves the nest. Not long afterward, the original discoverer of the food source is joined at the food source by the first newcomers. These, too, dance when they return to the hive with their burdens. The more dancers there are in the hive, the more new foragers can be observed to crowd around the food source. The connection cannot be doubted. The dance announces to the bees in the hive that a rich harvest has been located. But how do the bees, thus notified, find the place where the food can be gathered?

"One's first thought is that they must run to the flight hole with the dancer, when the dance is ended, and fly after it when it goes back to the food source. But careful observation shows us that this is certainly not so. The newly recruited foragers obviously have no idea where their goal lies. From the symbolic gesture of the round dance they have learned only that they should look somewhere around the hive, and that is what they do. While the original forager was sucking the sweet juice from the flowers, it acquired some of their scent, and this scent stayed with it during the subsequent recruiting dance. The comrades which danced after it, at the

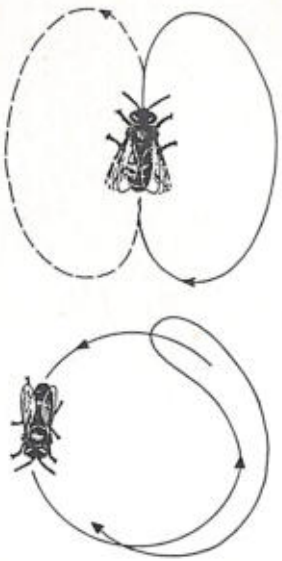


Fig. 18-40. The dances with which honeybees communicate: above, the waggle dance, and below, the round dance.

same time investigating it so actively with their antennae (where the olfactory sense organs are located), detected this scent, memorized it, and finally they look for it as they swarm about near the hive."

If the scent of the flowers should not be adequate, a worker can activate a scent organ on the back of the abdomen and thus mark a food place unambiguously. But in the event that a food source is at some distance from the hive, the round dance, which gives no indication of its direction, is not as effective. In this case, the bees use still another means of communication. We quote again from Karl von Frisch:

"Long-distance foragers perform 'waggle dances.' In this dance, the bee runs in a tight semicircle, then makes a sharp turn and runs in a straight line back to the starting point. Now it describes a second semicircle—toward the other side so as to complete the circle begun by the first—and again runs the straight course back to the starting point. And so it continues for minutes at a time, all in one place; a semicircle to the left, straight back, a semicircle to the right, straight back, a semicircle to the left, and so on. But the thing that most markedly distinguishes this dance from the round dance is a rapid waggling movement of the abdomen from side to side, which is done all during the straight run from the end of each semicircle back to the starting point. The waggle dance, just like the round dance, excites lively interest among the nearby bees, which fall in and try to follow along behind.

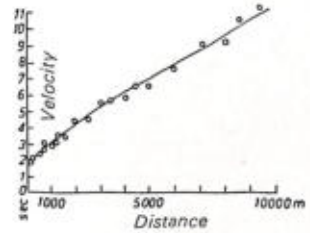


Fig. 18-41. The velocity of the waggle dance (vertical axis) as a function of the distance (horizontal axis) between feeding place and hive.

"If one displaces a nearby feeding place, step by step, to greater distances from the hive, the round dances of the foragers are found to change over to waggle dances at a distance of 50–100 m. Round dance and waggle dance are two distinct expressions in the language of the bees, which indicate close or distant sources of food. And—as can be shown—they are understood in this sense by the hivemates. However, the information 'closer or further than 100 m' is of little use to the bees, for their flying range extends for several kilometers in all directions from the hive. By stepwise displacement of the food place up to the boundaries of the range, one can demonstrate a particular feature of the waggle dance which gives both the human observer and the bees in the hive much more exact information about the source of the harvest. When the distance is 100 m, the turns of the waggle dance follow in quick succession and the dances are hastily performed. The greater the distance, the more sedate the dance becomes; the turns follow one another more slowly, but the linear waggle run takes more time and is more emphasized. With a watch in one's hand, one can determine that the runs through the straight part of the dance occur about nine or ten times in a quarter of a minute when the food source is 100 m away; with the food source at 500 m it runs only six times, at 1000 m four or five times, and at 5000, just twice.



Fig. 18-42. The relationship between the flight angle with respect to the sun and the dance angle in the hive with respect to gravity; the latter is diagrammed below for the three feeding sites shown.

"It would do the bee colony little good to learn that 2 km away from the hive a linden is in bloom, if the direction in which it is to be found were not communicated as well. In fact, the waggle dance also contains

this very information. Food-source direction is conveyed in the figure described by the dance—to be precise, in the direction of the straight part of the waggle dance. Within the beehive it is pitch dark, and moreover the comb surfaces are vertical. The bees relate the angle between the sun and the direction of the food site to the angle between the straight-line part of the dance and the direction of gravity. They do this according to the following code: runs upward mean that the food source lies in the direction of the sun; runs downward imply the opposite direction; and runs at other angles to the vertical (for example, 60° left of upward) indicate corresponding directions (i.e., 60° left of the direction of the sun). What the recruited foragers learn in the darkness of the hive—from the dance and their fine sense of the direction of gravity—they transfer to the direction of the sun as they fly out from the hive."

But the dance language has uses other than the communication of the location of food sources. Martin Lindauer has shown that it is also employed during swarming: the advance party tells the bees which are to follow it where they have found a likely site for a nest.

All these abilities, bordering on the miraculous yet almost entirely instinctive, have been discovered in studies of the domestic honeybee (*Apis mellifera*), whose many subspecies have been distributed by man throughout the world. In structure and habits the Indian subspecies *Apis mellifera cerana* is quite similar. The bees *A. m. dorsata* and *A. m. florea*, both of which also live in southeastern Asia, represent a somewhat lower level of evolution. Each of these species builds only one comb and hangs it in the open on a branch. *A. m. dorsata* is as large as a hornet, and its sting is feared; its comb can measure 2 m and contain 100 kg of honey. The nest of the tiny *A. m. florea* is barely 8 cm by 12 cm. These bees, too, use a dance language. The dwarf species, though, can dance only on a horizontal surface, which is provided by the roof over the comb, and they must have the sun or the blue sky in view; apparently the translation to gravity has not evolved. The giant species *A. m. dorsata* does dance on a vertical comb, but it, too, must have a view of the sky. Here again, as with the stingless bees already discussed, we can recognize certain parts of speech—though by no means the full syntax—of the subtle language of the honeybee.

Most feared of all is the aggressive, man-hating AFRICAN HONEYBEE (*A. m. adansonii*). In its native habitat in Africa its nest is constantly robbed by the native villagers who are guided to the hive in a dead tree by the honey guide (see Vol. IX), a relative of the woodpeckers. It was imported into Brazil in 1956 and is now spreading rapidly throughout northern South America. So severe and numerous are the stings of this bee that it may cause death among livestock. Brazil reports 300–400 human deaths a year caused by this bee.

19 Diptera: I. The Mosquitoes and Their Relatives

Order: Diptera, by P. Rietschel

The members of the next order of Mecopteroidea to be discussed have only two wings, the hindwings having been modified into halteres. This characteristic is reflected in the name of the order, Diptera. The members of the order will be discussed in two chapters, the mosquitoes and their relatives here, and the flies in Chapter 20.

Distinguishing characteristics

The Diptera are of small to moderate size (L 1 mm to 5.5 cm). The mouthparts depart widely from the basic form; in the imagoes they have been modified for licking or piercing and sucking and in the larvae, for biting or sucking, and they may be regressed in either the adult or larval form. Metamorphosis is complete. The larvae are always legless and live in a variety of ways, quite different from the adults. The earliest dipterans known are from the Jurassic (Lias, about 190 million years ago), but it is probable that the group is descended from mecopterans living during the Triassic (about 230 million years ago). About 85,000 present-day species have been described.

Common characteristics and variability

The best-known representatives of the Diptera, the mosquito and the house fly, are quite different in appearance; one is slender, with long, delicate antennae and very thin legs, while the other is compact, with sturdy legs and antennae so short that they are hardly discernible to the naked eye. On the basis of antenna length, we classify the mosquitoes in the suborder Nematocera (from the Greek for thread and antenna) and the house flies in the suborder Brachycera (Greek for short antenna). The larvae of mosquitoes and flies also differ in appearance: mosquito larvae have clearly recognizable heads, whereas in the fly larva the head is usually less distinct, since the capsule is regressed and the head is recessed into the thorax. In the extreme case, one speaks of acephalous (headless) larvae. Dipteran larvae are no less varied than the imagoes, in form and habits, and many elements of their structure represent departures from the basic plan, adaptations to particular requirements of larval life. One example of this divergence is the hover fly *Microdon* sp., which is so similar to its relatives that even a beginner in entomology can easily recognize it as a hover fly.

Its larvae, however, live with ants and are so unlike insect larvae that they can easily be mistaken for slugs! Another example is provided by the net-winged midges found near mountain brooks; even one entirely untrained in the field will call this insect a midge or mosquito, so closely does it resemble the basic type. But the larvae and pupae, attached by suction or glue to stones in the raging brooks, are such aberrant creatures that one would never think that they were related to the larvae and pupae of mosquitoes. Only by taking into account the entire course of development from the egg through larva and pupa to the adult does one obtain a complete picture of a dipteran—and this picture is often a fascinating one. Whereas in many insect orders the larvae are simply less developed preliminary stages of the adult, among the Diptera the modifications often depart considerably from a direct line of development to the adult. These roundabout paths of development serve only to meet the temporary needs of the larva; when the time comes for metamorphosis to the imago, all traces of them are lost. This variety in larval form among Diptera provides the systematist with useful characteristics by which to distinguish species, and it is of obvious value to use the larvae in setting up a system of classification. A particularly helpful characteristic is the distribution of hairs on the body of midge and mosquito larvae. The study of chaetotaxis (the arrangement of hairs or bristles) has proved fruitful here as well as with the young larvae of aphids. Nevertheless, even today a "natural" system of classification of Diptera—that is, a classification taking into account their evolutionary history—is not established in all respects. Zoologists divide the order into either two or three suborders. On the basis of antennal structure one can distinguish two groups, the mosquitoes and their relatives (Nematocera) and the flies (Brachycera). On the other hand, there is a dichotomy in the way the imago bursts the pupal case; some make a longitudinal slit along the back (orthorrhapha) and others make a transverse or circular one at the anterior end (cyclorrhapha). But this second dichotomy does not correspond to the first. All the Nematocera are orthorrhapha, but so are quite a few flies. For this reason many entomologists feel that there should be three suborders: the Nematocera, the Brachycera (flies which split the pupal case longitudinally) and the Cyclorrhapha (flies which make a circular split). The following discussion will be based on a division into only two suborders, the Nematocera (27% of dipteran species) and the Brachycera (73% of dipteran species—31% orthorrhapha and 42% cyclorrhapha).

Suborder: Nematocera

The suborder Nematocera contains mostly slender dipterans with long, thin legs and threadlike antennae with many segments (short antennae are found only in the Melusinidae and certain crane flies). The mouthparts of the imago are of the piercing-sucking type, very much modified. The mandibles are present in both sexes only in the families Melusinidae and Heleidae; in the other families they are regressed except for blood-sucking females, in which they have become piercing stylets. The maxillae are

Distinguishing characteristics

also greatly transformed, in the biting insects becoming piercing stylets in a sheath formed by the labium. The larvae live either in the ground (some crane flies and March flies) or in the water. If the head capsule is complete the larva is termed eucephalous; this is the case for all except the hemicephalous larvae of the ground-dwelling crane flies and the gall midges. The larval antennae are usually small; the mouthparts are less strongly modified than are those of the imagoes, and in some cases there are biting mandibles. The spiracles of the larvae and pupae are found either only at the anterior end (on horns, as in the pupae of most families), only at the posterior end (on a tubule, or siphon, as in the larvae of most families), or at both ends (as in the larvae of the Psychodidae). The spiracles in the middle of the body are closed, being opened only transiently at molting. In the larvae of the lake flies, all the spiracles are closed.

Family: Culicidae

Although they are not at the beginning in the systematic classification, we shall first consider the MOSQUITOES (family Culicidae; see Color plates, pp. 385 and 393). There are four other families with more species, but the mosquitoes, with about 1500 species, are not a small family; some of these species are such bloodthirsty nuisances that they make whole regions of countryside unpleasant or even—where they transmit diseases—uninhabitable. As an example of the life cycle of a mosquito we shall choose

The northern house mosquito

the most familiar species, the NORTHERN HOUSE MOSQUITO (*Culex pipiens*; L 6 mm; see Color plate, p. 393), which belongs to the subfamily Culicinae. In summer, we find this unwelcome guest on the walls, windows, and ceilings of our houses; it always holds the abdomen parallel to the substrate, a behavior which distinguishes it from the malaria mosquitoes, *Anopheles* spp. The hindlegs are raised and held back. The males are easy to recognize by the tufted appearance of the plumed antennae; those of the females are less feathery. In winter we encounter these mosquitoes in the cooler rooms of houses, in barns, and in cellars, but then we are only

Egg laying and larval development

seeing the females, for the males die in the fall. The previously inseminated females lay their eggs in spring; they are deposited on water; where they float upright, together forming a little boat, about 7 mm long and somewhat less wide, that drifts about on the surface. There may be 200–400 eggs in this mass or, if the female has had no opportunity to drink blood before laying, there may be only forty to eighty. Shortly after the eggs are laid the larvae hatch. They are heavier than water and must therefore swim to the surface by whipping their bodies into S-shaped curves. The surface is their real home; when danger threatens they let themselves sink, only to work their way up again soon afterward. The head is relatively small, but the thorax is broad and powerful. The delicate abdomen seems to end in a fork, because the last (ninth) segment is bent downward and the eighth bears an upward-pointing respiratory siphon. At the tip of this tube are the openings of the two main tracheal branches. Since these are greatly expanded inside the tube, the air contained in them makes this part of the body sufficiently buoyant that the respiratory siphon is always pointed

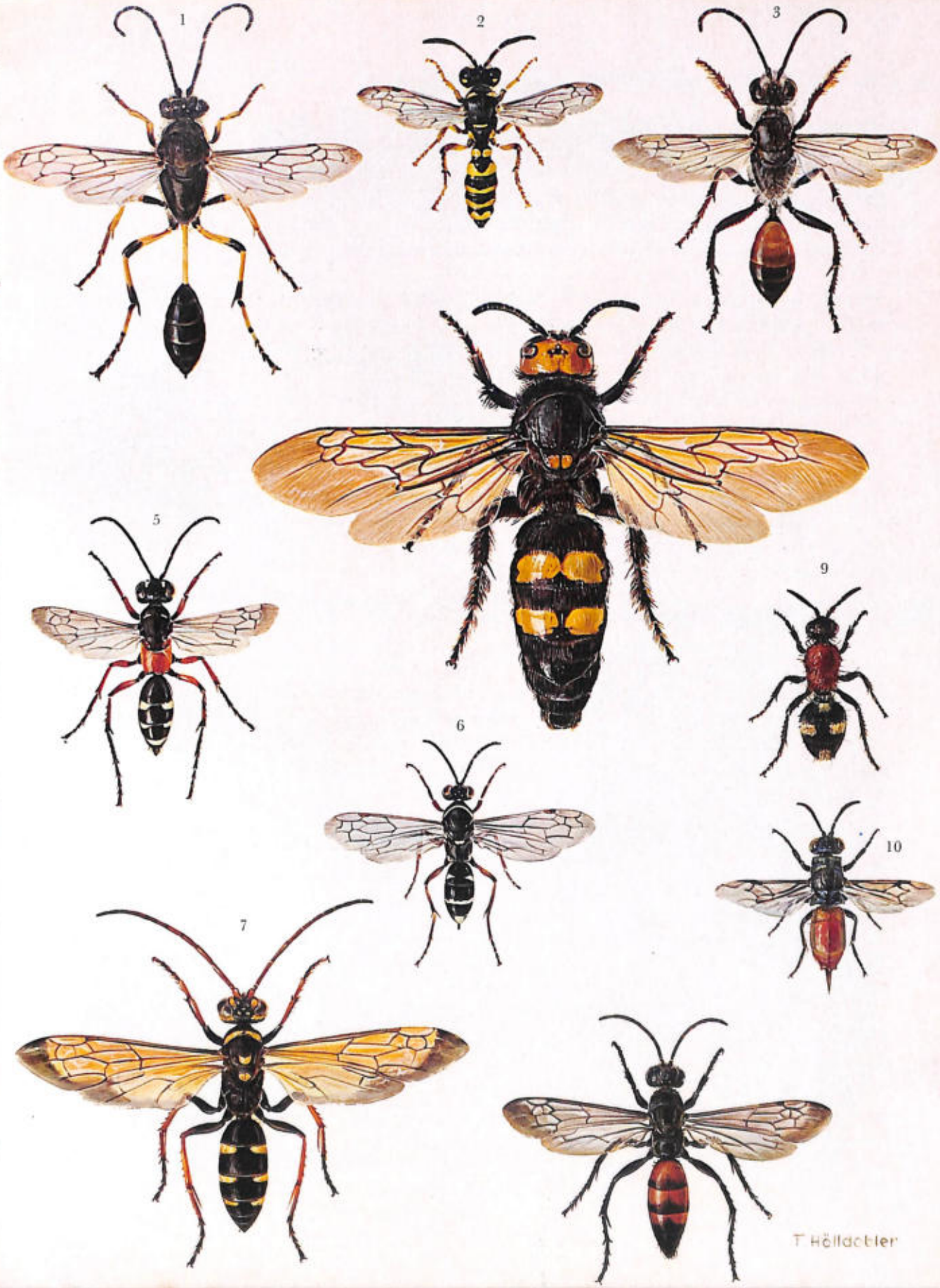
upward. The last abdominal segment bears little lamellae within which are a number of tracheoles and which have therefore been interpreted as gills. Organs like this are also found in the larvae of other families, particularly the Tendipedidae. But it is doubtful whether they really do serve a respiratory function, since they are smallest in larvae living in brackish water and largest in those living in water which is entirely salt-free. Evidently they operate to take up salt into the body of the larva, where the NaCl concentration is ordinarily 0.3%.

Although heavier than water, the mosquito larvae hang at the surface, held there by the action of surface tension on a ring of hairs surrounding the tracheal openings at the rear end. If the surface tension is reduced to half by a soap solution or by another of the household detergents, the larva can no longer maintain its position—it sinks and drowns. Otherwise it can hang there motionless for hours, the body pointing down at an angle; the only movement is that of the mouthparts, which bear combs of hairs. With this movement, the mosquito larva population of an aquarium or of a natural pond can set the entire body of water into regular circulation. A single mosquito larva can filter a whole liter of water per day. It swallows primarily unicellular siliceous and green algae, but also eats the floating and sinking materials produced by the decay of dead organisms. If one puts mosquito larvae into water made green and cloudy by algae, the water will be seen to clear as the larvae and their excrement turn green.

Pupation

During the period of growth the larva molts three times; the duration of this period depends on temperature and food supply, but on the average amounts to about three weeks. Then, at the fourth molt, it transforms itself into a pupa. The pupae of the various species resemble one another more than the larvae did, and the imagoes, still more. In contrast to the larva, the pupa is lighter than water, so that it floats at the surface without dependence upon surface tension. At this stage, the head and thorax appear to form a unit, since the head is drawn back between the large wing sheaths. But this anterior section is not at all as massive as it looks, for between the head and wing sheaths there is a cavity like a pocket, which carries a large air bubble. The middle part of the dorsal side of the thorax bears a pair of respiratory horns standing up like two little ears, at the tips of which are the anterior spiracles. The posterior spiracles, open in the larva, are closed in the pupa. The respiratory horns of the pupa are buoyant so that the anterior end of the body is up and the horns touch the surface. They are flexibly joined to the thorax, so that if there are ripples on the water surface the tubes can bob up and down while the larva remains motionless. Also remaining at the water surface is a pair of peculiar hairs on the back of the first abdominal segment. The head of the pupa has already acquired the large lateral compound eyes of the imago; they are covered by the pupal case, but this so transparent that the pupa can detect light through it. When suddenly exposed to light, or when otherwise

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Sphecid wasps: 1. *Sceliphron spirifex*; 2. *Cerceris arenaria*; 3. *Sphex maxillosus*. Scoliid wasp: 4. The yellow-fronted digger wasp (*Scolia flavifrons*). Pompilid wasps: 5. *Cryptochilus variegatus*; 6. *Ceropales maculatus*; 7. *Batozonus lacerticida*; 8. *Anoplius fuscus*. Mutillid wasp: 9. *Dasylabris maura*. Chrysilid wasp: 10. The fire cuckoo wasp (*Chrysis ignita*).


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T. Hölldobler


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disturbed, the pupa flees into the depths, but it soon floats back up to the surface. Despite this ability to move, the mosquito pupa spends most of its short existence at the water surface. It takes no food, for the mouthparts are being altered during this period from the stirring-filtering type to the piercing-sucking type; inside the animal, too, the larval organs are being changed into a form better adapted to the quite different life of the imago.

Emergence of the imago

After a resting period of only a few days, the imago emerges from the pupal case, an adult mosquito capable of flight. Before emergence, a layer of air is formed between the pupal case and the outside of the imago. The abdomen of the pupa, curved ventrally until then, extends, and its tip adheres from below to the water surface. Shortly thereafter, the pupal case splits along the back, and the thorax, head, and finally abdomen of the mosquito force their way out. The foregut, with its two caeca, fills with air, enlarging the animal so that it is essentially pushed out of the case. Soon almost the whole body is standing upright, outside the case; then the animal falls forward onto the legs, which now are extended from the body for the first time. The whole process of emergence requires three to five minutes. In this sort time, the lumpy pupa has transformed itself into the delicate, winged, long-legged mosquito.

These processes of development, in which the mosquito is changed from egg or larva to flying imago, are so breathtaking that every admirer of nature should see them with his or her own eyes. This can be done with no more elaborate equipment than a jar of water from a pond where mosquitoes live, a few larvae or a floating egg mass, a plate or piece of glass for covering the jar, a magnifying lens of moderate strength, open eyes, and finally that most priceless of present-day commodities, a little time. Anyone who can organize all these things will be richly rewarded.

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Sphecidae: 1. The female of the sand wasp *Ammophila adriaansei* drags a paralyzed geometrid caterpillar to her nest. The entrance (left) is closed with little stones before each hunting expedition. Vespidae: 2. The potter wasp *Eumenes* sp. flies with a paralyzed moth caterpillar to her urn-shaped nest of clay. 3. The nest of the giant hornet (*Vespa crabro*) is built of paper made of chewed-up splinters of wood mixed with saliva. In the picture, part of the outer wall has been removed to show the layers of comb, separated by pillars. 3a. View of the underside of one comb plate from a hornets' nest. The worker above feeds a larva; in the middle the queen is approving a cell before laying an egg in it; below her are cells covered by lids of silk. The emerging adult hornets chew through this lid (left).

Habits of the imago

The rest of the life of a mosquito cannot be observed indoors. In the evening hours the males gather in swarms and dance in the air over prominent points of reference in the landscape, repeatedly rising and falling. The location for the dance may be a church tower, a tree, or a bush; often it is even a person walking along a road—over whom, and with whom, the swarm of males dances. Anyone who has been chosen as an orientation point can confirm that all the mosquitoes dance in the same direction, with the head toward the wind; the hunter can use them as a reliable indicator of wind direction. Sometimes one can see a swarm of somewhat larger mosquitoes dancing closer to the ground; these are the females. From time to time one of the females flies horizontally into the swarm of males; for a moment the insects crowd together and then a pair separates and sinks to the ground. How do the males in their swarm detect the female that has flown in? They hear her wingbeat tone with their antennae. The male antennae are precisely tuned to this frequency, so that it causes them to oscillate in resonance, and this oscillation is detected by a

sense organ in the second antennal segment. The male does not hear his own flight tone, nor the identical tone of the other males in the swarm, for his antennae do not resonate with sound of that frequency. Excitation of the sense cells in the antennal organ (Johnston's organ) elicits from the male the whole sequence of actions necessary for mating; one can even release the sequence with a tuning fork set at this frequency.

Only the female mosquitoes bite. The piercing proboscis used for the purpose consists of a bundle of no less than six stylets enclosed in a sheath formed by the modified labium. During the bite the sheath does not penetrate the skin but rather bends backward as the stylet bundle passes through its tip, guided by a pair of lobes. Of the six stylets, two are unpaired structures: the labrum and the hypopharynx. The labrum, with its edges rolled in toward the underside, encloses the food channel through which the blood is sucked up. The hypopharynx is hollowed out longitudinally to form the saliva channel; the secretions of the salivary glands are carried through this to the tip of the proboscis. There the saliva mixes with the blood and prevents clotting, since otherwise the narrow food channel would soon be obstructed. The needlelike laciniae of the maxillae and the equally needlelike mandibles form the paired piercing stylets. The actual process of biting starts with the maxillary stylets, barbed at the end; these are pushed alternately into the skin and anchored there, so that their retractor muscles can force the remaining stylets after them. In the male, the stylets are regressed. It has long been unclear whether the female mosquitoes must drink blood in order that the eggs ripen. Even for the house mosquito there were contradictory reports, which are now accounted for by the finding that there are two subspecies of this mosquito. *Culex pipiens molestus* does not need blood in order that the eggs mature, but *C. p. pipiens* does require it. The two mosquitoes also differ in certain other respects, so that some researchers regard them as different species: *C. pipiens* and *C. molestus*.

Other mosquito species

The mosquito just described is only one of several species that annoy us, at home or outdoors. In central Europe alone there are dozens of mosquito species, and in the city of Frankfurt on the River Main, and its immediate surroundings, Christoph Scherpner counted twenty-seven species! They differ in external characteristics, the times of their appearance, the number of broods per year, the time of day that they bite, the way the eggs are deposited, the shape and patterning of the eggs, the structure and habits of the larvae, and in still other respects. The most striking among these species is the large European *Culiseta annulata* (L 10 mm), with tarsal segments ringed in black and white. The females of this species, too, are often found in houses in the winter, and they often bite even in midwinter. The larvae may be encountered in countless masses in very dirty water. Several species of mosquito that can destroy the pleasure of outdoor life for even the most enthusiastic nature lover belong to the genus *Aedes*. Among the European and North American species are *A. communis*

(L 9 mm), the gray *A. cinereus* (L 6 mm), and the spotted European and North American *A. rusticus* (L 9 mm). Their larvae live in the shallow ponds in woods, the bottoms of which are covered with rotting leaves. The water-meadows along rivers are the haunts of the small, widespread *A. vexans* —a most vexatious creature indeed! The *Aedes* females die in the fall, after laying their eggs on the ground near the water. The eggs winter on dry land, resting until the mountain snow melts in the spring. Then the rivers overflow their banks, submerging the mosquito eggs so that they can develop. The plague of biting adults therefore begins some time after the flood season. The meadows along the Rhine in Hesse, the Rhine island of Kühkopf, and the adjacent meadows, ordinarily very attractive for the observer of nature, then become barely habitable in some years. But this annoyance is trivial in comparison with the violence of the mosquito plagues in the far north. The limnologist A. Thienemann investigated the causes of the enormous outbreaks of species of *Aedes* mosquitoes in Lapland and discovered that five factors are involved, each of which is an essential contributing element: 1. The structure of the ground is such that there are numerous depressions with very poor drainage. 2. The precipitation is sufficient to fill these basins. For about two-thirds of the year the land is covered with snow, and then in April and May the thaw sets in and turns the accumulated precipitation of eight months into water. 3. The ground can draw off such quantities of water only slowly, since it is still frozen just beneath the surface; at depths of more than 60–80 cm, the permafrost layer, it never thaws at all. Thus the mosquito ponds remain for four to eight weeks. 4. This time is sufficient for complete development of the mosquitoes only if the water in the pond is warm enough. After the spring equinox the days in the north are longer than in more southern regions, eventually lasting twenty-four hours. Thus even in the early spring the stagnant water warms up to 20°C or more, even though the air above it falls below freezing at night. 5. Before they lay their eggs, these mosquitoes require a meal of warm blood. Although the numbers of humans and reindeer in the thinly settled tundra are far from adequate to meet the demand, voles and lemmings can supply the necessary blood for any number of mosquito females.

The malaria mosquitoes

Mosquito species of the genus *Anopheles* (see Color plates, pp. 385 and 393), among which are the MALARIA MOSQUITOES, have mandibular palps, as long as the proboscis, which together with the piercing proboscis, form what looks like a three-pronged fork. Anopheline mosquitoes can easily be distinguished from the other mosquitoes sitting on wall or window by their posture: proboscis and body lie in a straight line at an angle to the substrate. The malaria mosquitoes are without doubt the most intensively investigated of all, because of the profound effect thay have had as transmitters of human disease in the past and in many countries even today (see Chapter 1). They are by no means restricted to warm countries, but form part of the fauna of temperate zones as well. Scherpner carried out

his previously mentioned investigations at fifty-four points in the city of Frankfurt and its immediate surroundings, and at twenty-nine of these he observed one to four species of *Anopheles*. Among these were all six sampling points in the city center. In its manner of life *Anopheles* differs very much from the house mosquito. The delicate spindle-shaped eggs are kept afloat by a girdle containing air chambers. They float singly, but often close together in great numbers, on the water surface. The larvae float horizontally just below the surface, with the back up. With their mouthparts beating through the water, they filter out spores of algae, pollen scattered by the wind, bacteria, and the many small animals which also feed on these things. Water standing for long periods, which ordinarily would soon be covered by a film of bacteria, maintains a clear surface as a result of their activity. For the larvae to do this, the underside of the head must face the water surface. The head is turned with a jerk, and it turns back just as quickly when the work of filtration is interrupted. When disturbed, the larvae flee very rapidly into the depths, lying there with the light-colored underside up and soon rising again with snakelike movements of the body. Since they feed from the surface, they prefer clear water to cloudy and a smooth surface to a rippled one. The position of the body relative to the surface, quite different from that of the larvae of species of *Culex* and *Aedes*, requires that the respiratory siphon on the back of the eighth abdominal segment be very short. The Anopheline pupae, on the other hand, are similar in form and way of life to those of the Culicines.

As air-breathers, all the larvae discussed so far must spend most of their time at the surface of the water. But the larvae and pupae of species of the genus *Mansonia* have become independent of the air at the water surface. There are about fifty species of this genus, living primarily in the warmer countries; only one of these, *Mansonia richardii*, is found in northern parts of Europe and Asia, where it is not uncommon in permanent bodies of water with rich plant growth. This is a requirement of both the larvae and the pupae, for they obtain the air they breathe deep under water, from the roots of the aquatic plants. The respiratory siphon of the larva is provided with strong spurs which anchor the animal to the plant where it has bored into a root. The pupa uses the two thoracic respiratory horns similarly; their ends point toward each other, forming a point. To drive this point into the plant tissue, the pupa needs something to push against. A bearing is provided by the respiratory siphon at the posterior end, which has not yet pupated; only after the anterior end has become firmly attached to the plant is the molt to form the pupa completed at the other end. It is not known how the pupa frees itself from the plant when the imago is ready to emerge. C. Wesenberg-Lund, the Danish student of fresh-water fauna, reports that at the surface of the water one can find empty pupal cases with respiratory horns, the tips of which are broken off. Larvae and pupae of species of *Mansonia* are rarely seen, since they live submerged, attached to

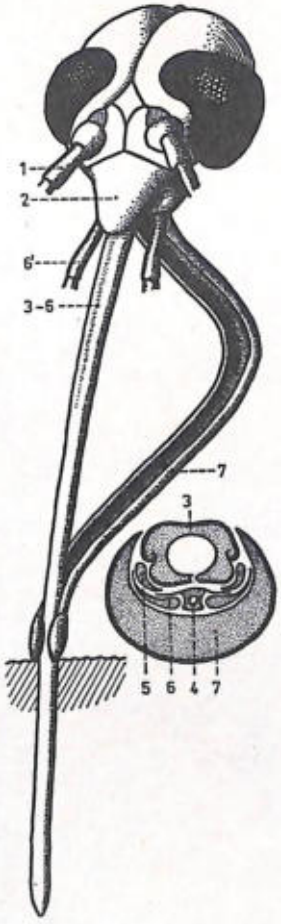


Fig. 19-1. Head of a mosquito in the act of biting, with schematic cross section through the proboscis. 1, Antennae (cut off); 2, Clypeus, fused with the frons; 3, Labrum enclosing the food channel; 4, Hypopharynx with salivary channel; 5, Mandible; 6, Maxilla; 6′, Maxillary palp (cut off); 7, Labium (stylet sheath).

the roots of aquatic plants, but the adults, ever eager to bite, can be very annoying in their favorite localities.

The yellow-fever mosquito

The *Aedes* subgenus *Stegomyia*, sometimes regarded as a distinct genus, has attained notoriety because it includes the YELLOW-FEVER MOSQUITO (*Aedes aegypti*). This is one of several hundred species of the genus, which inhabits the hot climatic zones of both the old and the New Worlds. Human commerce brought the yellow-fever mosquito to the New World, and in both places the mosquito has caused the deaths of many people, since it transmits the virus responsible for yellow fever.

Subfamily: Corethrinae

The closest relatives of the mosquitoes are the non-biting LAKE FLIES (subfamily Corethrinae). They resemble the mosquitoes but the two are easy to tell apart because the lake flies lack the long proboscis between the antennae. The larvae are very striking: stick-shaped and completely transparent, they float horizontally in the water. A pair of gas-filled vesicles at the anterior end and another at the posterior end—the only remnants of the regressed respiratory system—matches their density to that of the water, so that they neither rise nor fall. The glassy transparency of the larvae enables us to observe all the details of their internal structure with a strong lens or microscope; nevertheless, these larvae still present a number of questions. For example, K. Berg discovered that these creatures from time to time disappear from the open water and bury themselves in the mud at the bottom. The reason that they spend long periods there, without oxygen or suitable food, is unknown. At any depth in the water, the larva is capable of rapidly adjusting its weight so as to maintain that depth. To accomplish this, it must set the gas pressure within its gas vesicles at a new level, and the way this is done is also as yet unexplained. Lake fly larvae live by hunting small crustaceans, catching them with the downward-bent antennae. The mouthparts are not adapted for stirring the water like those of mosquitoes, but rather simply serve to tear the prey apart. This is the only instance in the insect kingdom of the modification of antennae as prehensile arms. Another unique aspect of these larvae is that they have large lateral compound eyes; in all other insects which undergo complete metamorphosis these are reserved for the imago. The pupae of the lake flies are also able to hang suspended in a vertical position in the water. They resemble mosquito pupae except that their abdomens are not bent ventrally but rather held out straight. In contrast to the preceding larval stage, the pupae have a well-developed system of tracheae and have lost the air-filled vesicles at either end; nevertheless, they are still able to achieve neutral buoyancy in the water—another unsolved puzzle. The pupa does not rise to the surface until the imago is about to emerge. Swarms of lake flies can be enormous. C. Wesenberg-Lund described a swarm at Lake Esrom, Denmark, around seven o'clock at night: "At about this time Schiffer Avenue and the whole park of Fredensborg Palace rang with a single very high tone which came from huge swarms of lake flies; the swarms, though, were hovering at such a height that one could hardly see them. At half

past eight the ringing stopped; now there were such enormous swarms hovering by the shore that the air was—so to speak—full of the flies, but they made no further sound." Lake flies, then, can either hum in flight or fly noiselessly—still another puzzle!

Family: Anisopodidae

Following the above detailed consideration of the Culicidae, the remaining nematoceran families will be taken up in their proper systematic sequence. Despite their rather doubtful position in this sequence, we begin with the WOOD-GNATS (family Anisopodidae). Their roughly seventy species are distributed throughout the world. They are an old, quite primitive group, evidence of which has been found as early as the Jurassic (upper Lias, about 180 million years ago). The best-known of the few European and North American species is *Sylvicola fenestralis* (L 6–7 mm), a gray insect with brown-spotted wings, the tip of each wing bearing a triangular brown mark. They do not bite, which is fortunate since they are frequently found at the windows in spring and summer. These gnats are not dependent on the presence of water; the larvae live in and feed on rotting materials and moldy wood and may be found under bark. They are elongated, like a worm, because there are extra segments between the ordinary segments of the abdomen. The well-developed head capsule is by far the most primitive among dipteran larvae. The pupae are found in the same places as the larvae; they have only short respiratory horns.

Family: Bibionidae

The MARCH FLIES (family Bibionidae) are conspicuous animals, quite different in appearance from the mosquitoes. They are compactly built, usually covered with bristly hairs, and their antennae, wings, and legs are relatively short. The veins of the anterior wing margin are much more prominent than those further back and are usually black. The two sexes often vary considerably in appearance, so that one might believe himself confronted with two different species. The males have large eyes, almost covering the whole head, with the ommatidia at the top larger than those lower down. The casual observer who does not study the antennae under a lens would consider these insects, because of their shape, to be flies, and their common names reflect this. The March fly *Bibio marci* (L 13 mm) appears in March or April, and St. John's fly (*Bibio johannis*; L 5 mm), somewhat later. At the same time as *B. marci* appears, one may see the GARDEN MARCH FLY (*Bibio hortulana*; L 11 mm; see Color plate, p. 394), the males black with brown legs and the females, brown with yellow legs. All these hairy creatures present an unmistakable appearance, flying laboriously with the long hindlegs hanging down. They lay their eggs in the ground, where the elongated larvae live, eating the roots of grass and the decomposing remains of plants.

Most species of FUNGUS GNATS (Mycetophilidae) are small, with long antennae and coxae, and spurs on the tibiae. The gnats themselves are of interest to at most a few specialists, but the grublike, black-headed larvae annoy and disappoint many collectors of mushrooms. Even though a

young mushroom may still be almost completely hidden in the ground, a fungus gnat has often been there first, and its larvae have made holes all through it.

Family: Sciaridae

Close relatives of the fungus gnats are the DARK-WINGED FUNGUS GNATS (family Sciaridae). The larvae, similar to those of the Bibionidae, live under leaves and in the humus-rich earth on the forest floor, under the bark of rotting tree stumps, and in other similar places. There they feed on molding plant remains and networks of fungi. The larvae (L up to 11 mm) of some species (*Sciara militaris*, *Sciara thomae*) in earlier times were frequently a disquieting spectacle to the superstitious, for they occasionally gather in thousands and migrate over the floor of the forest in long, dense columns. This apparition was thought to herald the approach of war, failed harvests, plagues, and other evils.

Family: Cecidomyidae

Just as inconspicuous and unnoticed as adults, though widely known for the activity of the larvae, are the GALL MIDGES (family Cecidomyidae). These little midges, only a few millimeters long, are very fragile; one can hardly catch them without injuring them. The larvae are colorless at first but soon become yellow, orange, or reddish. The first thoracic segment bears on its underside a hard longitudinal ridge, the sternal spatula, which permits the identification of at least the older larvae. The gall midge larvae are capable of long, high jumps. According to H. Prell, they jump by bending the end of the abdomen forward until the little teeth there catch in the spatula. Then they contract the dorsal longitudinal muscles, increasing the tension in the bowed abdomen until it breaks free and springs back, shooting the larva forward. The larva is also said to be able to burrow rapidly into the ground when it is ready to pupate. The gall midge larvae live in many different ways. Some of them are parasites on other insects, others live by hunting aphids, mites, or other gall midge larvae, and still others live on decaying plant materials; but most of them feed on fresh plants. Among these, many produce galls on the plants—hence the family name. Other species save themselves this work by simply moving into the galls of their relatives; these are known as inquilines. Of the numerous types of midge galls, only a few of the more striking formations on beeches and willows will be mentioned. On the upper sides of beech tree leaves in the spring one often finds dainty, pointed galls like little hazelnuts, each containing a yellow midge larva. This larva belongs to the species *Mikiola fagi*. Later, in July, other galls appear, covered with brownish hairs but not pointed. These are due to the gall midge *Hartigiola annulipes*. Both types of gall detach from the leaves and fall to the ground before the tree loses its leaves in the autumn, and the pupae spend the winter in the galls. The midge emerges the next year, leaving the gall by the narrow channel which joins the cavity with the underside of the leaf. The female midge lays her red eggs on the buds in the spring; the young larvae burrow between the scales enclosing the bud, down to the young, still-folded leaves. The larvae, not their mother, cause the beech leaf to

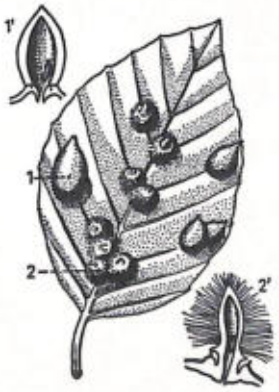


Fig. 19-2. Midge galls on a beech leaf. 1, Gall of *Mikoila fagi*; 1', the same, cut open longitudinally so that the opening to the underside of the leaf is visible; 2, Gall of *Hartigiola annulipes*; 2', the same, cut open longitudinally, also opening on the underside of the leaf.

form a gall. For the beech the gall is a malformation, but for the larva it is a perfect house, offering both food and protection. The twigs of willow trees are often seen to be swollen; in the following year their surface is densely covered with the circular holes through which the WILLOW-SHOOT HOLE MIDGE (*Helicomyia saliciperda*) has emerged. The fibrous tissue hanging down around the hole has not been loosened by the larva, but by the woodpeckers and tits which try to dig out the larvae in the winter. We find these galls both on young shoots and on branches as thick as one's arm. Shorter swellings on year-old willow shoots come from another gall midge, *Rhabdophaga salicis* known from Germany and New York; this larva also spends the winter in the gall. Of the great number of German gall midges there is one species which makes no galls; this is the HESSIAN FLY (*Mayetiola destructor*). This species is said to have been introduced to America in 1776/7 along with the straw the Hessian soldiers brought with them. These Hessians were sold as mercenaries by their ruler to pay for the magnificent structures he was building in Kassel. As early as 1778 the Hessian fly began to destroy the North American grain fields; the devastation reached a peak between 1850 and 1857. In Germany, too, this insect does severe damage to grain crops in some years. The larva lives between the stalk and leaf sheath of grains and grasses, near the lowest or next-to-lowest nodes, causing the parts of the plant above this level to die off. There are only two larval stages; the second stage pupates, and the pupa, which looks like a flax seed, remains encased in the old larval skin (the puparium). In Germany the average temperature over the year is high enough to permit a second generation, which lives just above the roots of the winter crop and produces gall-like thickenings there.

Family: Trichoceridae

The WINTER CRANE FLIES (family Trichoceridae) were once counted as Tipulidae, for they strongly resemble them. But the winter gnats have ocelli at the front of the head, and their larvae are actually more similar to those of the wood gnats; in both larvae the head capsule is complete (they are eucephalous). The larvae live in the ground, often in communities, feeding on decaying plant materials. An encounter with the European and the American *Trichocera hiemalis* (L 5 mm) can be a memorable experience: on cold but sunny winter days, the swarms of males dance in forest clearings.

Family: Ptychopteridae

With the PHANTOM CRANE FLIES (family Ptychopteridae), we turn to those families with aquatic larvae. As a rule, the slender, long-legged, non-biting flies are inconspicuously colored, though they may be prettily patterned; *Ptychoptera contaminata* (L 10 mm), for example, has rusty-yellow bands on the abdomen and the same color on the back of the thorax and the brown-striped wings. But the larva and pupa are very unusual. The larva bears on the posterior end a respiratory siphon which can be extended like a telescope; when it is extended, the overall length of the larva is 7 cm. Like the mosquito pupa, that of the phantom crane fly has paired respiratory horns on the thorax, one of which is short, while

the other is more than twice as long as the body. Both larva and pupa live in the mud under stagnant water, and the long siphon of the larvae reaches up to the surface like a snorkel. The long horn of the pupa serves the same purpose, but at its tip it is closed by a capsule of peculiar structure. The way that this odd "tubular gill" works is not understood.

Families: Psychodidae and Blepharoceridae

Some of the MOTH FLIES and SANDFLIES (family Psychodidae; see Color plate, p. 394) are familiar to us because they share our houses. They are small, compact animals, with hairy bodies and almost woolly wings, held together like a roof over the back. They look very much like tiny moths. Their larvae live in the regions between water and land, where they find both moisture and food. Their food consists primarily of the slimy bacterial coatings found in this region. R. Heymons reported in Brehm's *Tierleben* that in the Berlin sewage filtration plants the larvae of *Psychoda sexpunctata* (L 2–3.5 mm) live in vast numbers on the bits of excrement caught in the filters. Rural outhouses also offer favorable conditions for these insects. In the 1930's it once happened that these larvae occupied a filter of quite a different sort in a film factory, an installation which cleaned the air for the rooms where the emulsions were poured. Instead of dust-free air, the filters poured forth air full of moth flies. This was brought to an end by pouring boiling water through the filter system. The MOTH FLIES (subfamily Psychodinae) do not bite, but the SANDFLIES (subfamily Phlebotominae) are notorious for the annoyance and even widespread illness that they cause in warm regions. In the Mediterranean and even as far north as central France (Somme, Oise, Loire) four species are found, of which the PAPATASI SANDFLY (*Phlebotomus papatasii*; L 2.5 mm) is the best known. During the day the sandflies rest in hidden crannies, coming out only at night. Ordinary mosquito nets and screens are no hindrance to these tiny creatures.

The NET-WINGED MIDGES (family Blepharoceridae) are slender, long-legged midges, which may be encountered near mountain brooks. The females have piercing-sucking mouthparts, used for sucking out the bodies of other insects. A distinctive characteristic is the wings, which in addition to the usual venation have a network of folds running in all directions; this is the consequence of the peculiar conditions under which the imago emerges, described below. The females lay their eggs on the stones just above the water on the banks of rapidly flowing streams; the larvae which hatch find their way into the water, where they attach themselves to stones. The attachment is produced by six powerful suckers arranged in a row along the ventral midline. At the base of each sucker is a structure like a pump piston which can be pulled up by means of a strong, V-shaped muscle. This causes the sucker to stick firmly to the substrate, and it is difficult to remove an attached larva from its stone without damaging it. This anchorage is vital to the larva, for it would otherwise be swept into the quiet lower regions of the brook, where the water is warmer and poorer in oxygen; there the larva would perish. It feeds on the gelatinous

coating of siliceous algae on the stones. In order to graze in fresh algal pastures, the larva must regularly move to a new site. In so doing, it can release only a few of its suckers at a time or it would be swept away.

This contraint also applies when the larva molts. The suckers consist entirely of cuticle, so that the larva must slip out of all six of the old suckers, one after another. In order to do this without drifting away, it must accomplish two things which seem nearly impossible: each of the old suckers must remain firmly attached to the substrate until the last moment, when the larva casts it off, and the new sucker which replaces it must be capable of attaching firmly when it first appears. The new sucker has twice the surface area of the old one; nevertheless, it must have room to develop and even harden under the old sucker without impairing its activity. The author must admit that he could not think of a way of reconciling these contradictory requirements. Only after he had investigated these larvae did he learn the ingenious solution nature had found. The new sucker, with its double-sized surface, lies within the old one like a closed umbrella; the reinforcing ribs, which correspond to those of an umbrella except that there are many more in a sucker, harden before the molt begins. After the molt, when the umbrella is unfolded, these ribs form the suction surface. But how is the umbrella opened? The cuticle which forms the whole sucker is split into an outer and an inner lamella in the region of the stalk and the upper side of the suction disc, and between these two lamellae there is a cavity running around the whole sucker. Into it on either side there opens a large gland. At the moment of molting, the two glands empty a fluid into the cavity, thus pumping up the new sucker.

The blepharocerid pupa, arched dorsally and flattened ventrally, attaches itself not by suckers, but by a sort of glue which hardens in water. The respiratory horns on the anterior end are divided into lamellae and have no opening for the entry of air. The pupa can of course not reach up to the water surface, but it can happen from time to time that the water level in the brook falls and exposes the pupa. Then it is in the same situation as the pupae of the Melusinidae (see below). In the pupae of both these families there is a permanent film of air (a plastron, see Chapter 1) enclosing the cuticle of the respiratory horns; this permits an exchange of gases in the water as well as in the air. In contrast to the mosquito pupa, the blepharocerid pupa cannot rise to the surface for the imago to emerge. Therefore, when it is time for emergence, a layer of air forms around the imago inside the pupal case; surrounded by this air bubble, the freshly emerged midge floats to the surface. The buoyancy of the bubble accelerates the midge so that when it reaches the surface of the turbulent water it breaks through into the air and flies away on its already-hardened wings. This midge has no time, as other insects do, to rest after emergence while spreading and hardening its wings; it must make its wings ready for flight while still in the pupal case. For this reason, the folds imposed on the wings by this confined space are retained for life. Blepharocerid larvae in-



Fig. 19-3. Ventral side of the larva (above) and dorsal side of the pupa (below) of a blepharocerid (L 7 and 6 mm, respectively). Both attach the ventral surface to stones in turbulent mountain brooks, the larva with the six suckers and six pairs of leg stumps (not true legs), the pupa with glue.

habit primarily the raging streams of the Alps. There is a sequence of species, arranged in order of their temperature and oxygen requirements, from the altitude of the glaciers down to the valley bottoms. But even brooks in the lower mountain ranges of Germany are inhabited by another species, *Liponeura belgica*, less sensitive to warmth and with a lower oxygen requirement; the full-grown larvae and pupae are to be found in springtime, when the mountain brooks are still cold and full of water.

Family: Ceratopogonidae

The family following the net-winged midges in the systematic series is that of the mosquitoes (Culicidae), discussed at the outset. Following it is another family of most unpleasant blood-suckers, the BITING MIDGES (family Ceratopogonidae). These midges are small to minute (L in some cases less than 1 mm); the males have plumose antennae and the females have antennae sparsely covered with hairs. The legs are moderately long; the wings may or may not be hairy. The larvae live either in water, in which case they are much elongated (the main genera are *Helea* and *Culicoides*), or on land, where they are more compact and provided with leg stumps at the front and hind ends (main genus *Forcipomyia*). The slender, bristly pupa of the species with aquatic larvae floats motionless on the surface of the water, whereas the more compact pupa of the purely terrestrial forms remains half inside the last larval skin, with the large thorax projecting out. The midges themselves are bloodthirsty only in the evening, when they attack their human victims primarily at the edges of their clothing. The bites sting intensely, and when one slaps at the tiny culprit there is usually nothing recognizable on one's fingers. *Helea* spp. prefer cold-blooded animals, but *Culicoides* spp. feed on all warm-blooded animals and in addition—as has been demonstrated—on mosquitoes. Whether the target of the midge is the mosquito blood or the vertebrate blood in its gut is an open question. Other midges suck from caterpillars, butterflies and moths, and even earthworms. Still others attack the non-biting midges and suck out their contents. Like the sandflies, these midges cannot be kept away by ordinary mosquito netting; they slip through the mesh. Ultraviolet light attracts them strongly.

Family: Chironomidae

In contrast to this extremely troublesome group, the family Chironomidae contains only harmless species. These NON-BITING MIDGES are similar to mosquitoes, and, like them, the males have very feathery antennae. Some species tend to repose on the middle and hind legs, stretching the forelegs up into the air like antennae. The larvae of the non-biting midge species all resemble one another; they are slender, and the head is clearly demarcated. Of their twelve body segments, the most anterior and posterior each bear a pair of leg stumps, though in some cases either the anterior stumps or, less commonly, both pairs may be absent. The eleventh segment of the body has two pairs of so-called "blood gills" on the underside, but, as with the similar organs of mosquito larvae; it is still questionable whether these blood-filled tubes actually serve as gas-exchangers. Some species, particularly those living in oxygen-poor mud, are red in

color. The same respiratory pigment that is found in the red blood cells of vertebrates, hemoglobin, is dissolved in their blood. It is surprising that these larvae, so uniform in structure, show great variety in their ways of life. There are species which live in the mud, in tubes they spin for themselves; others spin grains of sand, parts of plants, algae, and so forth into the tubes. Still others live in passages they make in the calcium deposits precipitated by algae from hard water; others again cover the tubes they spin in hard waters with a crust of calcium deposits, so that eventually they are living in a house of calcium. Some larvae burrow long galleries in the leaves of aquatic plants, usually species of the genera *Stratiotes* and *Sparganium*. The larvae also differ widely in their requirements with respect to the oxygen and nutrient contents of the water. Oxygen-poor but nutrient-rich lakes are occupied by the larvae of the European and North American *Chironomus plumosus*, whereas oxygen-rich, nutrient-poor lakes contain *Tanytarsus* spp. larvae. In fact, limnologists even speak of "plumosus lakes" and "tanytarsus lakes," and have named a number of other types of lakes by the midge larvae which inhabit them. Midges have become quite an important descriptor in limnological research. Of course, considerable professional knowledge is required for reliable identification of the vast number of midge species and their larvae, but this expertise is indispensable to the limnologist.



Fig. 19-4. Larva of a midge (Chironomidae).

Family: Simuliidae

The next family, the Simuliidae (see Color plate, p. 394) presents us once again with some troublesome pests. These are small, compact insects, commonly called BLACK FLIES or BUFFALO GNATS. Their appearance is more like that of flies than midges. The wings are broad, with thickened veins at the anterior edge. Both sexes have piercing mouthparts, but here again only the females make use of them. Among the many European species three are particularly noteworthy: in the flat regions, *Simulium ornata*; by small rivers, *S. erythrocephala*; and in other regions, *S. reptans*. In the Danube lowlands, the species *S. columbaczensis* is the scourge of cattle, causing considerable injury to the herds. Similar species of the genus occur in North America.

The breeding area of these black flies is above the Iron Gate (a gorge through which the Danube flows); from there, swarms of males and females migrate out into a large region including parts of Bulgaria, Rumania, Hungary, and Yugoslavia. Over extensive areas, the migration is assisted by the wind. The damage the swarms do is great: in 1923 the poisonous bites and blood sucking of the black flies killed 17,474 horses, donkeys, cattle, buffalo, sheep, goats, and pigs in Rumania, and in 1934, in Yugoslavia, 11,901 of these animals. Baranoff, to whom we are indebted for these figures, did not learn of a single human fatality as a result of black-fly bites, but they certainly caused illnesses lasting for days. It also happens that there are mass outbreaks of black flies which are not at all bothersome, so that one may assume that the readiness to bite differs among the various species.

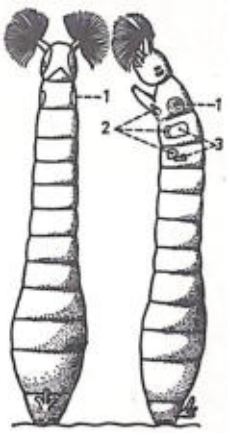


Fig. 19-5. Larva of a black fly, dorsal and lateral aspects (L up to 15 mm). 1, Primordium of the pupal gills; 2., Primordium of the legs of the imago; 3, Primordium of the wings and halteres of the imago.



Fig. 19-6. Relatively old pupa of a black fly in the slipper-shaped pupal case spun by the larva before pupation.

The black fly larvae are found only in flowing waters, but there they may be encountered in great numbers. They are peculiarly constructed; the body is club-shaped, swollen at the hind end, and when full grown is about 1.5 cm long. On the head there are outgrowths of the labrum in the form of a pair of stalks bearing a fan of long, curved bristles. In contrast to the stirring-type mouthparts of other nematoceran larvae, these fans do not serve to agitate the water, for the larvae live only in flowing water. Rather, the fans are devices for catching the small particles carried past them by the water. Brushes on the mandibles then comb these bits of food from the fans, and the other mouthparts carry them to the mouth opening. The fans are folded in by muscles, but they open without the aid of muscles by their springy connection with the labrum. The silk glands, which run through the body to the hind end as a pair of tubules, and there turn and run forward again, open on the hypopharynx. The enlarged hind end is armed with a dense circlet of barbed hooks; in the center of the circlet the body wall can be pulled inward by muscles so that the tip of the abdomen attaches to the substrate by suction. The barbs then anchor the larva securely. The first thoracic segment has a leg stump on the underside, and this too is equipped with rows of hooks. This appendage can also be used to attach the larva to the substrate, so that by alternately attaching and releasing the two ends of the body it can move about like an inchworm (see Chapter 15). On the last abdomina segment, above the circlet of hooks, there are bundles of gills penetrated by tracheoles and filled with blood. Thus these serve both as tracheal gills and as blood gills. The respiratory system is entirely closed; this is understandable, since this larva, living in running water, cannot rise to the surface for air. If it detached itself from the substrate, it would drift with the current down to a region of still water or into some quiet corner, and there its food-catching fans would no longer serve their purpose.

In more slowly flowing brooks one can observe another remarkable achievement of the black fly larvae. Sitting close together, the larvae spin threads which wave back and forth in the water, forming a network downstream. Here other black fly larvae can gain a foothold and attach themselves. In this way very many more larvae can settle in the brook than can find room on the stones at the bottom. The black fly pupae are just as unusual as the larvae. They, too, are attached firmly to the substrate resting in a conical structure of spun threads. The tip of the cone is upstream, and its broad opening points downstream. The gills of the pupa project out of this case, divided on either side into a few or many fine branches. At their free ends the gills are closed, and they contain neither blood nor tracheoles, but the cavities within them are connected with the anterior spiracle. The cuticular wall of the tubes consists of two layers, between which is a permanent film of air. Gills of this sort, made only of cuticle, are called cuticular gills. They occur in other sessile dipteran pupae as well; for example, they are found in the Blepharoceridae and

the Asian and North American Deuterophlebiae. These gills act as a plastron in the water and also permit airbreathing on land. The pupae are forced to use the latter form of respiration if the water in which they live temporarily dries up.

Family: Tipulidae

The CRANE FLIES (family Tipulidae) with over 11,000 species, are quite like mosquitoes and midges in appearance, but they greatly exceed most of these in size. The largest German crane fly, the GIANT CRANE FLY (*Tipula maxima*), is 35 mm long, and the limoniine *Pedicia rivulosa*, which lives in the same areas, is its equal in length. But the most conspicuous thing about the crane flies is the long legs; in this respect they belong to the same life-form type (see Chapter 7) as the daddy long-legs (see Vol. I). According to C. Wesenberg-Lund, the extremely long legs give them the advantage that when they walk in grass they can hold on to several blades at once and cannot be shaken off even though they may be blown about by the wind. Of course, the long legs put them in danger of being seized by a predator. In that case, the crane fly discards the imprisoned leg, just as a daddy long-legs does in the same situation.

Some crane fly larvae live in the water, others in damp ground; the larvae of species of the genus *Ctenophora* occupy rotting wood. All are elongated and have a distinct head which can, however, be drawn far back into the thorax. The head capsule is still complete in front, but toward the back it is not, so that the larva is called hemicephalous (Greek for half-headed). Such a regression of the head capsule is common among fly larvae. At the hind end of the body there are two large spiracles surrounded by six fleshy retractile processes—two dorsal, two lateral, and two ventral. If one seizes a crane fly larva at the anterior end between three fingertips, pressing gently so that the hind end becomes taut, a grotesque "devil's mask" stares out, like something from a medieval puppet show (see Color plate, pp. 51/52). The upper fleshy lobes form the horns of the devil, the spiracles are the eyes, the anus takes the place of a mouth, and the four remaining lobes surround the "face" as ears and beard. The slender pupae bear short respiratory horns at the anterior end and are recognizable by the long sheaths in which the mandibular palps of the imago are formed. The crane flies are among the most common and conspicuous of the insects.

Subfamily: Tipulinae

The best-known of the subfamily Tipulinae is the COMMON CRANE FLY (*Tipula oleracea*; L 25 mm; see Color plate, p. 394, cf. Color plate, pp. 51/52); the more yellowish swamp-dweller *Tipula paludosa* (L 25 mm) is not uncommon. The most beautiful of all the German crane flies is the red-legged *Ctenophora atrata* (see Color plate, p. 394). The female (L 32 mm) has a bit of rusty yellow on the abdomen, which bears a long, saberlike ovipositor. Her antennae are deeply notched, even sawtoothed, while those of the smaller male (L 25 mm) have combs in three rows. The crane flies have no significance with respect to human health, nor, in most cases, to human economy. Only when there is a mass outbreak of

larvae can they do appreciable damage; this once happened to the recreation grounds at a Frankfurt swimming pool, where they made bald spots in the lawn.

Subfamily: Limoniinae

Another subfamily of CRANE FLIES is the Limoniinae. With approximately 4000–5000 species, this is the largest, subfamily of the group. The winged adults look like the other crane flies, but the limoniines lack the whiplike extension of the mandibular palps characteristic of the Tipulinae. The wing venation is also different and the limoniines are usually considerably smaller than the tipulines. But the stately *Pedicia rivulosa* (L 3.5 cm) is as large as the giant crane fly. The larvae of the two subfamilies differ from one another more markedly than do the adults. Moreover, those of the Tipulinae are all very similar, whereas there is great variety among the limoniine larvae. Their spiracles are surrounded by only five lobes, the two dorsal ones having become fused. The body of the larva, plain in the tipulines, can have several kinds of appendages in the limoniines. The impressively large larvae of *P. rivulosa* bear, on the eighth to the eleventh segments, locomotor papillae, which can be everted and withdrawn; the smaller (L *ca.* 2 cm) larvae of *Dicranota bimaculata* have similar papillae on the sixth to the tenth segments. In the latter species these are provided with hooks, like the abdominal feet of the lepidopteran caterpillars, and the back of the larva is covered with soft black hairs. The habits of the larvae are equally varied. For example, the aquatic larvae of *Trichosticha flavescens* breathe by drawing air from the ventilation tissue (aerenchyma) of the submerged parts of swamp and aquatic plants; in this, they resemble the larvae of species of the beetle genus *Donacia* and the mosquito genus *Mansonia*. The margins of their spiracles are prolonged into a spur on one side, and with this they pierce the air-conducting parts of the plants. The respiratory horns of the pupae are also sharp, so that one may well assume that they obtain air in the same manner. On the other hand, the larvae of *Antocha vitripennis* live where there is more than enough oxygen; they build galleries of silk threads, 4–5 cm long, on the stones in foaming mountain brooks. There they feed on the siliceous algae coating the stones. The spiracles on the hind end are closed, and the oxygen dissolved in the water is absorbed through the skin. The hairy, leechlike, flattened larvae of species of *Dactylolabis* also inhabit mountain brooks. A close relative of *Antocha* spp. also capable of spinning as a larva, is *Thaumastoptera calceata*. The larva lives in the dirty water of filtration plants, where it spins an hourglass-shaped case which it carries about. Larvae of the many species of *Dicranomyia* also spin out threads of silk in the water. Some species of this genus have become independent of water; their larvae live under the bark of trees, and some mine in leaves.

But the most unusual tipulid larvae are those of the subfamily Cylindrotominae, which is considered a separate family by many researchers. These larvae live on damp ground or in the water on mosses;

the Asian and North American Deuterophlebiae. These gills act as a plastron in the water and also permit airbreathing on land. The pupae are forced to use the latter form of respiration if the water in which they live temporarily dries up.

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But the most unusual tipulid larvae are those of the subfamily Cylindrotominae, which is considered a separate family by many researchers. These larvae live on damp ground or in the water on mosses;

their shape and the green coloration of the body appendages are so perfectly matched to the environment that even a practiced observer can easily overlook them. The appendages of the aquatic larvae serve not only as camouflage, but also as gills. It is still a matter of debate whether this odd group, with its few species is closer to the tipulines or to the limoniines. This uncertainty suggests that the Cylindrotominae separated from one of these two branches near the time that they separated from one another. Moreover, the close association of many species of the subfamily with the phylogenetically old mosses lends credence to the great age of the fly species themselves.

20 Diptera: II. The Flies

Suborder: Brachycera, by P. Rietschel

Distinguishing characteristics

The FLIES (suborder Brachycera) include both small and rather large Diptera. The antennae are short, generally consisting of the two basal segments and the very large first segment of the flagellum. The remaining segments of the flagellum are attached to the end or upper surface of the first one, as a segmented or unsegmented bristle or tuft of bristles called the arista. The mouthparts are basically of the sponging-sucking type, with the labium modified into a sponging proboscis and its palps forming a pair of labella. In some cases the mouthparts are modified into piercing-sucking organs, the labium being employed as a sheath for the piercing proboscis (horseflies) or as the piercing organ itself (the biting muscid flies). The palps of the mandibles and maxillae each consist of one or two segments; they are directed forward. The mandibles are often regressed. The body is usually compact, and the legs are shorter and stronger than those of the Nematocera. Most of the larvae are maggots, with the head capsule partly or completely regressed (hemicephalous or acephalous). The mandibles of the larvae are modified into hooks which operate vertically. The tracheae of the larvae usually open only at the very anterior part of the thorax and far posterior, in the eighth abdominal segment. The pupae have short antennal sheaths, and often remain inside the last larval skin (the puparium). Some open the pupal case by means of a longitudinal slit and others, by making a slit around the anterior end.

The housefly

Here, as in the last chapter, we shall introduce the flies with a discussion of the most familiar one, although it is not first in the systematic sequence. This is the HOUSEFLY (*Musca domestica*; L 7.5 mm; see Color plate, p. 403). It is sometimes called the large housefly to distinguish it from the LITTLE HOUSEFLY (*Fannia canicularis*; L 5.5 mm). Its appearance is probably so familiar to most of us that description is superfluous. But it would be worth the reader's while to take a look through a strong magnifying lens at the face of this common, despised creature. Enlargement reveals an entirely new picture of the animal we thought we knew so well; the large, brown-red eyes are faceted; between them are set the antennae, ending in

enlarged third segments which bear the aristae on their upper sides. Above the bases of the antennae one can see a suture like an inverted U, called the frontal suture, and below this is a swelling of the same shape, the frontal lunule. Along the margins of the suture the body wall is invaginated to form the ptilinum, a structure which is everted when the fly is ready to emerge from the pupal case and which serves to lift off the end of the case. Once the fly has emerged, it pulls the ptilinum in again, and only the suture remains visible. The vertex extends as a thin-skinned area between the eyes down to the frontal suture. Under the antennae is the sponging proboscis, its sides supported by struts which are vestiges of the maxillae and bear the maxillary palps. The stalk of the proboscis is bent back at an angle. On the anterior side at the point of the bend there arise the pointed, triangular labrum and, covered by the labrum, the hypopharynx. The opening of the fly's mouth is in the angle between labrum and hypopharynx. The proboscis is formed by the labium from the bend to its tip. The sponging surface consists of the two labella, formed from the labial palps. With these, the fly sponges up fluid food; they are covered with a network of branching grooves stiffened by cuticular struts. The latter, in the form of incomplete rings, give the grooves a resemblance to tracheae, which are also kept from collapsing by stiff rings. For this reason the labellar grooves are called pseudotracheae. At this point, of course, we have gone beyond the range of magnification of a hand lens; the details of the pseudotracheae can be observed only under a microscope.

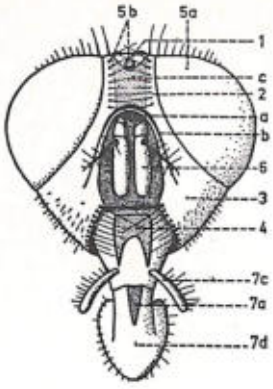


Fig. 20-1. Head of the housefly, from the front. 1, Vertex; 2, Frons; 3, Gena; 4, Clypeus; 5a, Compound eyes; 5b, Ocelli; 6, Antenna, with arista; 7a, Labrum (mandibles are regressed); 7c, Maxillary palps; 7d, Labium (forms the sponging proboscis); a, Frontal lunula; b, Frontal suture; c, Thin-skinned part of vertex.

Of the three thoracic segments—prothorax, mesothorax, and metathorax—only the mesothorax is visible on the dorsal surface. It is divided into three sections, the prescutum, scutum, and scutellum. The first two are each decorated with four black stripes running from front to back on a gray background, while the most posterior plate, the scutellum, has one such stripe. The many black bristles on the thoracic segment are arrayed in a strictly regular pattern which provides the systematist with a useful guide to classification. At the posterior margin of the wing, near its base, there is a notch demarcating a lobe called the alula. This is part of the wing and, like it, is transparent. Closer to the body there are one or two further lobes; that nearest the thorax, the squama, is yellowish and opaque. Hidden under it, but visible from the underside, is the hindwing, which in the Diptera is no longer a wing but is modified to form a haltere. In flight, the wings of the housefly beat about 200 times per second. Each of the hairy legs has two claws and two lobes, the pulvilli, on the tarsus, which enable the fly to walk on walls and even on the ceiling. Although we can observe this behavior any summer day, the problem of just how the feet adhere to the substrate is still unsolved.

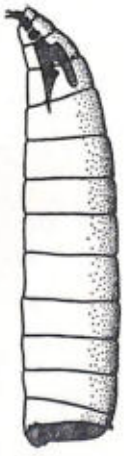


Fig. 20-2. Larva of a fly with regressed head; at the front end (above) are the mandibular sclerites and the cephalopharyngeal skeleton, visible through the skin; at the hind end (below) are the paired, large posterior spiracles and the anus.

From above, we can see four segments in the abdomen of the housefly; the first one is a fusion of two segments, so that we are really looking at the first five segments. If the fly is a female, which is indicated by the

smaller eyes, a light pressure on the body will cause three more narrow segments to appear at the hind end; the abdomen is terminated by the ninth abdominal segment, which is at the end of this ovipositor. Between the eighth segment and this terminal structure is the female genital opening. During copulation, the female inserts the ovipositor into the male genital opening, at the bottom of which is the male copulatory organ.

The housefly larva is a soft-skinned, legless maggot, in which there is no apparent separation of head, thorax, and abdomen. The head capsule is regressed, and its vestiges are drawn back into the thorax, so that the fly maggot is one of the acephalous larvae. The supporting structure of the mouthparts, the cephalopharyngeal skeleton, is within the head; it and the mandibular sclerites, or mouth-hooks, can be seen as vague black structures through the skin at the pointed anterior end. The fat body and the silvery, air-filled branches of the tracheae can also be seen through the thin skin. At the posterior end, which is broad and terminated by a flat surface lying at an angle, there are two black dots, the posterior spiracles. The anterior spiracles, located close to the anterior end, are very much smaller and difficult to see. There are no eyes as such, but near the anterior end there is a simple photoreceptor with which the maggot detects light. The fly pupa is entirely surrounded by the last larval skin, which forms the puparium.

Let us now go through the life cycle of a housefly, beginning with the egg; the provident mother lays it where the larva will find appropriate food. Such places include piles of dung, particularly that of horses, stable manure, the contents of latrines, rotting household garbage, droppings of all sorts, carrion, and other accumulations of material most unappetizing to us. From the rather elongated eggs, about 1 mm long, the little larvae develop in twelve to twenty-four hours. After only one to one and one-half days the first-stage larva molts, and a few days later there is another molt, producing the third-stage larva. In three to four days, this larva pupates. In the warm, fermenting part of a dung heap, the pupa needs only three days for metamorphosis, but usually the larva withdraws to a cooler part for pupation, and then requires four or five days to complete the transformation. Three days after emergence, the female imago is ready to lay eggs; one generation, then, lasts approximately two weeks. There are about 100 eggs in each batch laid, and one fly can produce four to six such batches in her lifetime, which spans about two months in summer. The short generation time and the large number of progeny permit the housefly to multiply at an enormous rate. The reproductive season in Europe begins in June and ends in October, but in warm countries (and in permanently warm places in cold countries, such as barns, kitchens, and inns) the winter imposes no limit to reproduction. Accumulated filth can thus rapidly become densely infested by the offspring of a single female fly. Faichne, in India, managed to get 4000 houseflies out of 5 l of latrine contents; and in California Herms counted, in 1 kg of dung taken from a heap,

1540 almost or completely full-grown larvae. The American entomologist L. O. Howard calculated that one female which survives the winter and begins to lay eggs on April 15 would have 5600 billion offspring on September 10 of the same year, if all eggs laid produced a fly which reproduced without hindrance. Since a fly weighs about 1/70 of a gram, that would amount to 80,000 metric tons of flies!

The housefly imago is entirely dependent on fluid, or at least soluble, food. Fluid food is sponged up with the proboscis, and the pseudotracheae (comparable to those of crickets; see Chapter 5) convey it to the mouth. Solid materials are liquified by a drop of saliva and then sponged up in the same way. If one offers the fly an abundance of dissolved food, it takes a full load into the crop in less than a minute. After this drink the fly becomes rather sluggish, and one can observe that a dozen times or more a thick drop will come out of the crop onto the end of the proboscis and then be sucked back in again. One can tell that this drop is not just saliva if one has presented the fly with colored sugar water; then the color of the drop shows that it consists of the contents of the crop. Evidently this is mixed with saliva by alternate regurgitation and sucking back, so that it becomes predigested. C. G. Hewitt, who made a thorough study of the housefly, has remarked upon the similarity of this process to the cud-chewing of ruminants.

Another remarkable aspect of housefly behavior is their manner of mating. This was first described in 1738 by the French naturalist R. A. Réaumur. It never occurs in flight, but often is begun by the male seizing the female while they are still in the air and making a (sometimes rather rough) landing with her. Then he jumps on her back with a well-judged leap, holds onto her head with the anterior tarsi, and with his proboscis "kisses" her on the back of the head between the eyes. At the same time the male lowers the end of his abdomen. After these preliminary maneuvers his role is at an end, and the female takes over. She stretches out her abdomen so that the ovipositor appears, and then she inserts it into the vestibule of the male's reproductive chamber. The copulatory organ is within this opening. As a rule, the two are joined only for a few moments, though copulation may last for a longer time. Other forms of housefly behavior also reward observation; for example, they devote much attention to cleaning themselves. H.-J. Heinz, who investigated the toilet activities of the housefly in detail, determined that there are seven different types of cleaning: head cleaning, proboscis cleaning, foreleg cleaning, hindleg cleaning, wing cleaning, abdomen cleaning, and finally, middle leg cleaning. The last of these never occurs by itself; to do it, the fly pushes one of its middle legs between the pair of fore or hindlegs which are making reciprocal cleaning movements. U. Jander, who compared the cleaning behavior of members of various insect orders, noted the great similarity between the actions of the fly and those of the scorpionfly; he interpreted it as an indication of close relationship. Thus it is not only

physical characteristics, but forms of behavior as well, that reveal evolutionary relationships in the animal kingdom.

Another feature of fly behavior, the way they land on ceilings, has only recently been explained by use of an electronic flash apparatus. The fly approaches the ceiling at a shallow angle, with forelegs extended forward and upward, and as soon as the forelegs touch it makes a somersault over them in the flight direction, coming to rest on the ceiling with the head pointing in the direction from which it came.

The life span of the housefly depends upon the season: in summer flies can reach an age of several weeks, whereas the last flies to emerge in fall take up winter quarters in cool, dark places and stay there until spring, without eating. But only a few flies escape the widespread mortality caused every autumn by the fungus *Empusa muscae*. One often finds its victims on windowpanes, surrounded by a white halo of spores (conidia) thrown out by the fungus.

The housefly, constantly engaged in cleaning itself, may seem a symbol of cleanliness, but this view ignores the places it chooses to lay eggs and feed. In spite of the continual cleaning, countless bacteria stick to the fly's feet, among them some which cause disease. In their constant search for something palatable, flies often land on our food and dirty it with their excrement as well. Flies also like to land on the moist lips of sleeping people, to take a drink. All this is not only annoying and unappetizing to us, but actually dangerous. Typhus, dysentery, tuberculosis, trachoma, and poliomyelitis are only a few of the diseases for which the housefly is implicated as a transmitter. That is reason enough not to tolerate the reproduction of flies in the vicinity of human settlements. To control them, one must know how far a fly can go from its breeding grounds. Flies marked with paint at the place where they emerged as imagoes have been recovered for the most part within a radius of a few hundred meters; certain individuals in rural areas were found to cover 1.3 km, but inside the city none strayed farther than 650 m. The introduction of communal sewage systems, refuse removal, and general cleanliness have already markedly restricted the summer plagues of flies in the more highly developed countries. The contrast with areas of the world where flies are not controlled is striking; one can still see walls of rooms which are black with flies.

Family: Xylophagidae

In the systematic sequence given at the end of the volume, the Nematocera—all of which split the pupal case longitudinally (they are orthorrhapha)—are followed by those flies which are also orthorrhapha, beginning with the family Xylophagidae. This quite primitive family, including only forty-five species, is represented in Germany by three species, whose members are all about the same size (L 13 mm): the black *Xylophagus atra* (see Color plate, p. 394), the black-red *X. cincta*, and the rust-red *Coenomyia ferruginea*, which smells like cheese; they also occur in North America. They are hairless, slender, long-legged flies with rather long antennae.

Since the third antennal segment has ringlike indentations, the antennae appear to consist of many segments like those of the Nematocera. The head capsule of the larva is complete and not retractable into the thorax. The larvae hunt in rotting wood.

Family: Rhagionidae

With about 350 species, the family containing the SNIPE FLIES (Rhagionidae) is larger than the Xylophagidae. Snipe flies are slender, almost hairless, and dusky in color; the mouthparts are of the piercing-sucking type, used to suck out other insects. Species of the American genus *Symphoromyia* and the Tasmanian *Spaniopsis*, however, suck the blood of warm-blooded animals, as do their close relatives, the horseflies. Their larvae, too, feed on animals; the maggotlike larvae of the many species of *Rhagio* live in the soil and suck insect larvae and small annelids, while the larva of the Mediterranean *Vermileo vermileo* builds a funnel-shaped trap in dry soil and feeds on the animals which slide into it. *Vermileo* spp. thus trap their prey in a manner quite similar to that of the antlion larva (see Chapter 12). But in appearance it is not at all like an antlion. Its slender anterior part twines around the victim, holding it fast with the mobile pseudopod on the ventral surface of the fourth body segment. The well-developed end of the abdomen bears spurs on the last segments, which also assist in holding the prey. The most remarkable snipe fly is found in Germany; this is *Atherix ibis* (L 11 mm). Its glassy wings are decorated with three dark crossbands and the legs are red-yellow. The caterpillarlike larvae have eight pairs of stumpy legs and at the hind end a pair of appendages bordered at the sides with hairs. The larva hunts in water, and nearby one can find the adult flies. The females, ready to lay eggs, gather in great clumps on branches hanging over the water and under bridges. There they lay their eggs and then die, still clumped together. Soon the young larvae hatch; first they feed on the bodies of their dead mothers, and then let themselves fall into the water, where they develop as predators. The mass of flies from which they have fallen continues to attract new females, which remain on its wet, sticky surface. Such a mass, looking like a bunch of grapes, consists of an outer layer of dead, partly decomposed flies and within it a core of nests with fly eggs and living fly larvae, each a few millimeters long. The brood masses of one American species were baked like bread and eaten by the Indians in Oregon and California.

Family: Tabanidae

The extensive family Tabanidae, with about 3000 species, includes the HORSEFLIES, large Diptera which feed on the blood of warm-blooded animals. These are powerful flies, not bristly, having large eyes and antennae. The third segment of the antenna has a ring at the tip but no arista. The piercing mouthparts of the female rest within the labium and are arranged like those of the nematoceran family Heleidae (see Chapter 19). But here they are much larger; the mandibles are broad, toothed daggers, and the galeae of the maxillae are similar but narrower. Together with the sharply triangular labrum and the hypopharynx, through which the

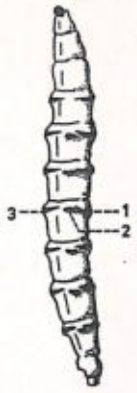


Fig. 20-3. Larva of a horsefly (*Tabanus* sp.; L 30–40 mm) with dorsal (1), lateral (2), and ventral (3) pseudopods.

salivary canal runs, they form a tool capable of producing considerable wounds. Since the blood is prevented from clotting by the action of the saliva, horsefly bites tend to bleed for some time.

The largest horseflies belong to the genus *Tabanus*. *Tabanus sudeticus* (L 19–24.5 mm) is actually one of the largest of all the flies found in Germany, and *Tabanus bovinus* (L 18–20 mm; see Color plate, p. 394) is only slightly smaller. We are lucky that these giants among the blood-sucking insects leave us alone, though cattle and horses must suffer that much more from them. But on hot, sunny days, humans can be bitten quite painfully by species of flies of the genus *Chrysops* (L 10 mm). The name of one species, *Chrysops caecutiens*, is rather misleading (*caecutiens* means blinding); with its shimmering eyes patterned in emerald green and purple, and its spotted wings, these tormentors are actually rather beautiful (see Color plate, p. 394). In shady places near the water, when the sky is overcast, there appears in their place the homely gray *Haematopota pluvialis* (L 5.7–11 mm; see Color plate, p. 394). At outdoor swimming pools it can be a great nuisance, and it attacks cattle as well as people. The long, spindle-shaped larvae of the horseflies have circles of fleshy pseudopods around the anterior margins of the fourth to tenth body segments; on each segment there are two pseudopods dorsally, two at the sides, and four ventrally. These structures enable the larva to push itself with agility through wet soil and the thickets of algae in open water. All horsefly larvae live by hunting, those of *Haematopota pluvialis* remaining on land, while species of *Chrysops* and *Tabanus* prefer the water. Their prey is primarily the larvae of other insects; the large *Tabanus* spp. larvae concentrate especially on the large larvae of the crane flies. As blood-suckers, the horseflies also play a role in spreading disease. In India, they transmit the flagellates (see Vol. I) causing the horse sleeping sickness called surra from one horse to another. Moreover, the *Chrysops* species called mangrove flies, *C. silaceus* and *C. dimidiatus*, are transmitters of a nematode, the African eye worm (*Loa loa*; see Vol. I), which wanders through human subcutaneous tissues, causing swellings in the skin.

Family: Stratiomyidae

There are about 1500 species of SOLDIER FLIES (family Stratiomyidae). The flies themselves are varied in form. Some of them are not sharply distinguished from the Xylophagidae. Their most distinctive characteristic is the flattened larva, in whose cuticle calcium salts are embedded so that it gives the impression of a coat of armor. The basic habitat of the larvae is the soil, and their usual food there is decaying materials. But both habitat and food of many species have been altered; some live in rotting fruits or trees, in latrines, or in water. The amateur naturalist encounters most frequently the aquatic larvae of the subfamily Stratiomyinae; their spindle-shaped bodies narrow toward the hind end, where the two spiracles are encircled by a large wreath of water-repellent hairs. This wreath enables the larva to hold itself at the surface of the water, so that the two spiracles stay quite dry. These spiracles do not lead directly to the two main branches of the

tracheae; they open first into an atrium which expands and contracts rhythmically. With the same rhythm, about once very two seconds, the spiracles open and shut. In this way the larva continually renews its air supply. The large soldier fly larvae (see Fig. 20-4) are often seen at the water surface, with the body twisting from side to side in a peculiar way; but any vibration on the shore may cause them to flee into the depths for a while. The pupa, on the other hand, floats motionless at the surface. It is enclosed in a puparium, the calcified last larval skin, which affords it protection. But the pupa is much smaller than the larva which preceded it (L *ca.* 10 mm), so that there is room for it to lie in an inner case it has spun within the puparium. Soldier fly species of the genus *Stratiomyia* (L 13–17 mm; see Color plate, p. 394) are quite striking, with their very broad abdomens, usually black and yellow, and their rather long antennae, the third segment of which is ringed. Despite their militant name, the soldier flies do not bite, but rather feed on the flowers which grow near the water.

▷
The wasp *Paravespula germanica*.

Fewer species (about 670) are included in the family Therevidae; about 75 species of these STILETTO FLIES are found in Germany. They are slender, usually with a woolly covering of hair; they are armed with a powerful piercing proboscis and probably live as predators as do the robber flies (see below). Their extremely thin larvae are curious animals; they live in the ground and move about with a snakelike motion. Their segmentation departs from the ordinary rules: the small, well-defined head and the three thoracic segments are followed by seventeen more segments. Each of the first six abdominal segments has divided into two toward the back, so that twelve segments are formed. Then come the unchanged seventh and eighth segments, the latter bearing the spiracles, and then three more segments the origin of which is unexplained. The stiletto fly larvae feed on the larvae of other soil-dwelling insects and therefore are considered "useful." But they are occasionally reputed to damage the roots of cultivated plants, in which case they become "pests." The attributives "beneficial" and "destructive" clearly depend upon the point of view one happens to have at the moment.

Family: Omphralidae

Close relatives of the stiletto flies are the OMPHRALIDS (family Omphralidae). Their larvae show the same unusual segmentation of the body as the stiletto fly larvae. The most common species in Germany has a name meaning the "hump-backed window fly" (*Omphrale fenestralis*; L 4.5–6.5 mm), because of one of its preferred resting places. The larvae of this species live in the dust under rugs, in the nests of sparrows and swallows, in chicken coops and dovecotes, and have even been found in spoiled flour stores. All of these are places where the larvae can hunt vermin. Thus, when these flies appear, the housewife should look for their breeding place and join the larvae there in the war against their prey.

Family: Asilidae

The ROBBER FLIES (family Asilidae) are familiar to every observant person who goes for walks in the woods. With about 4200 species, they are one of the most extensive families. Because of their size (L up to 25 mm)





◁ Ants of the subfamily Myrmicinae visiting a colony of aphids of the family Aphidae (see Chapter 9).

and their bold method of hunting, they are not easy to overlook. In appearance, though, they are not uniform. Some (subfamily Leptogastrinae) are slender and fragile, reminiscent of dragonflies, while others (subfamily Asilinae; see Color plate, p. 394) are also slender but much more strongly built, and still others (subfamily Laphriinae; see Color plate, p. 394) are large and bulky, like bumblebees or, in the smaller species, like little bees. The members of a fourth subfamily (Dasypoginae) are also bulky-bodied, even humpbacked in some cases, but their legs are as long as those of spiders. Despite the great differences in appearance of the eighty or so German robber fly species, they have a number of characteristics in common, all associated with their lives as hunters of flying insects. The large, protuberant eyes, between which the head is indented, allow a broad field of view. The neck and the front part of the dorsal thorax are movable, enabling the fly to turn its head in a wide arc when searching for prey. The two anterior pairs of legs are built for holding prey. The proboscis, angled downward, is short but powerful. Thick tufts of hair, like whiskers and moustache, give the face of the robber flies a piratical appearance. The cylindrical larvae live in soil, sand, and rotted wood. It has been demonstrated that some of them suck out the larvae and pupae of insects, at least as a supplementary food; it is not certain to what extent they also take vegetable food and decomposing substances. The adult flies are often encountered on the stumps or trunks of trees in the woods, lying in wait for prey to fly past. The large *Asilus* and *Laphria* species thus serve to eliminate the weaker individuals in the insect fauna. But one should not—as some do—regard that as a service; for the biotic balance of the forest to be maintained, their effect in counteracting mass outbreaks of single species is more important. In a natural forest, which never permits overpopulation by a single species, the robber flies are common. For example, the forest zoologist Karl Escherich wrote: "In the Bialowieza Forest I saw the robber flies swarming about in surprising numbers and in a really obtrusive manner. Everywhere one encountered various species of the large, pretty *Laphria* flying or sitting on tree trunks, copulating or sucking on a captured animal; and the same was true of the various large *Asilus* species."

The larvae of many flies, both orthorrhapha and cyclorrhapha, are internal parasites, feeding on the blood and the organs of their hosts. But the "calculated restraint" which characterizes perfected parasitism, designed to keep the host alive indefinitely, is evident only initially with these larvae; toward the end of their development they secrete enzymes which digest even the vital organs, killing the host. The larvae of the brachyceran families next mentioned are predatory parasites of this sort.

Family: Nemestrinidae

We shall begin our discussion of this group with the small family (about 150 species) Nemestrinidae, sometimes called TANGLE-VEINED FLIES because of the complexity of the wing venation. They are large insects with long proboscises, inhabitants of warm arid regions. There they hover

above flowers, dipping the proboscis into the nectar. Of the fourteen species found in Mediterranean countries, only one, *Hirmoneura obscura* (L 14 mm), has moved as far north as lower Austria. The female lays her eggs in coniferous trees, but the larvae do not remain there; rather, they let themselves fall to the ground, and proceed to hunt out the larvae and pupae of June beetles. How they find these hosts is still not known.

Family: Acroceridae

The SMALL-HEADED FLIES (Acroceridae) comprise few species; the flies are small, with large eyes almost covering the head, a humpbacked thorax, unusually large squamae, and the abdomen swollen into a ball. The larvae live as parasites in or on spiders. The small likelihood that any given larva will manage to find a host spider is compensated for by the large number of very small eggs laid. For example, a single female has been known to lay 4000 eggs. The larvae have dorsal and ventral plates covered with little lamellae or spines, and at the hind end there is a pair of long bristles with which the larvae can jump. Some flies of this family (genus *Acrocera*) have been observed to emerge from spider cocoons, where they presumably fed on the young of the spider, but others (genus *Astomella*) emerge from the abdomens of adult spiders. In this case the larva obtains the necessary air supply by boring its abdomen from inside the spider into its lung books.

Family: Bombyliidae

The BEE FLIES (family Bombyliidae) are a third family with parasitic larvae, but in contrast to the previous families this one includes species frequently encountered outdoors by the amateur entomologist. In particular, the large *Bombylius* species (L 9–13 mm; see Color plate, p. 394) are impossible to overlook. On warm spring days they hover in the air, in sunny places at the edges of woods. Now and then they dart suddenly a short distance forward, backward, or sideways, and then hover for a few seconds in the new position. They also hover over flowers while dipping in their proboscises, which are almost as long as the body. The larvae of species of the bee fly genus *Bombylius* are parasites in the structures made by certain species of bee genera (*Andrena*, *Colletes*, *Halictus*; see Chapter 18). The species *Villa hottentotta* (L 13 mm) is of economic significance to forestry. Its light-colored wings are brownish at the anterior margin and at the base. The larvae live in the caterpillars of two moths, the pine beauty and the turnip dart, and they are therefore welcomed by the forester and farmer. But this is not true of the two species of *Hemipenthes* common in Germany, *H. maurus* (L 11 mm) and *H. morio* (L 13 mm; see Color plate, p. 394), whose wings are deep black with a pattern of transparent areas. The larvae of these species do live in the caterpillars of the pine beauty and black arches, which are notorious for the devastation they cause in forests. However, they do not feed on these caterpillars, but rather on the parasites inside them, the larvae of larvivorid flies and parasitic wasps. That is, they are parasites of parasites, or hyperparasites. When there is an outbreak of pine beauties, but the majority of the caterpillars are infested by larvae of the larvivorid *Ernestia rudis*, the forester has hopes for the

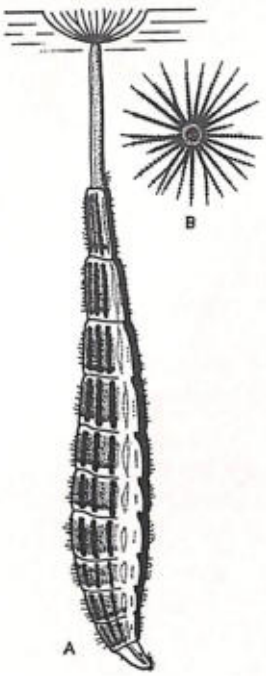


Fig. 20-4. Larva of a soldier fly (*Stratiomyia* sp.; L 40–50 mm). A, from the side; B, surface view of the wreath of hairs surrounding the spiracles.

safety of his woods. But if then—as once happened in such a situation in Bohemia—eighty-three percent of the *E. rudis* larvae are themselves attacked by *Hemipenthes* spp. larvae, this markedly retards the multiplication of the tachinid. It is then the pine beauties that have hopes of success. But one should be cautious about drawing a black-and-white distinction between the "destructive" *Hemipenthes* spp. and the "beneficial" *Villa hottentotta*. In any wooded area where there is something approaching a natural balance, both species have their place and their right to exist. The *Hemipenthes* spp. larvae attack not only the larvivorid larvae parasitic in the caterpillars but also the larvae of the parasitic wasps, especially species of the genera *Ophion* and *Banchus*. Once the larvirorid or wasp larva has reached its full growth, it leaves its host, the caterpillar, and pupates. The *Hemipenthes* spp. larva (the hyperparasite) is still inside it, also ready to pupate, and it too must leave its host. At the tip of the head it has two large horns and a number of small ones; with these it easily breaks its way out of the puparium of the tachinid fly. But it takes more work to escape if the *Hemipenthes* spp. pupa is in the cocoon in which the wasp pupates. The forest zoologist H. Gäbler discovered that the *Hemipenthes* spp. pupae which come out of wasp cocoons have larger horns than those coming from the puparia of flies, a thoroughly practical arrangement; the mechanism which determines the size of the horns is still a puzzle. The free pupae are astonishingly movable; they burrow into the ground, where they may rest for up to a year before emerging.

The next two families, the dance flies and the long-legged flies, according to the studies of W. Hennig, are closely related not only to one another but also—even though they are orthorrhapha—to the cyclorrhapha. For this reason he places them at the end of the series of orthorrhapha, just preceding the cyclorrhapha.

Family: Empidae

The DANCE FLIES (family Empidae) comprise about 2800 species, distributed throughout the world and numerous in Europe. Almost all dance flies are small, only rarely exceeding 10 mm in length, with a small, round, movable head on a thin neck, a long downward-pointing piercing proboscis, and rather long legs. Most dance flies feed by sucking out other insects, but there are some which drink plant juices. The larvae, living in the ground or rotten wood, are wormlike, with a small head whose capsule is largely regressed. Many have pseudopods which assist their locomotion. The larvae of some species live in water. In other respects rather easily ignored, the dance flies fascinate an observant naturalist by their manner of courtship The males, or in some cases both sexes, gather in swarms, the males carrying captured insects as "wedding presents." The male offers his gift to a female, which sits quietly sucking it out while the male inseminates her (see Color plate, p. 388). As soon as copulation is completed, the female drops what remains of her present. This simplest form of courtship has been observed in species of the genus *Empis*; in the species *Hilara maura* it is elaborated by the male's spinning a fine veil, with

the glands on his anterior tarsae, in which the wedding gift is wrapped. The North American *Empis aerobatica* surrounds the prey to be offered with a delicate balloon of silk. Males of other species dance with an insect held in a web. The very sight of this dance produces in the female a readiness to mate; the offering need not be eaten. Finally, the males of some species need not bother to catch an insect as a gift, for the waving of a veil alone is sufficient to make the female ready for copulation. But not all dance flies perform with veils. The species of small flies of the genus *Tachydromia* fly only rarely; usually one sees them running about on the trunks of trees, often carrying an aphid.

Family: Dolichopodidae

A rather larger family is that of the LONG-LEGGED FLIES (Dolichopodidae); it contains over 3500 species, many of them native to Germany. Most of these flies are small and many are colored a metallic green; they feed on small soft insects like springtails and aphids. One species has been observed to land on the surface of the water, fish out mosquito larvae, and fly away with them. Some species are restricted to the seacoast.

All the rest of the brachyceran families are cyclorrhapha; they do not cast off the last larval skin when they pupate, but rather pupate within it. Then the larval skin, previously soft, hardens to form a protective puparium. The first two families to be mentioned, the Platypezidae and Phoridae, are closely related and are included in the superfamily Lonchopteroidea.

Family: Platypezidae

The family Platypezidae comprises about 120 species of small flies with few hairs. They are sometimes called FLAT-FOOTED FLIES because the tibiae and adjacent tarsal segments of the hindlegs of the males are oddly broadened. These flies are noticeable for their habit of running hastily in a circle on leaves. All the larvae which are known live in fungi.

Family: Phoridae

At the midpoint in this series of families is the large family of the HUMPBACKED FLIES (Phoridae; see Color plate, p. 394), with about 1500 species. The humpbacked flies often display behavior like that of the flat-footed flies described above, and their wings are often more or less regressed. They have an inconspicuous gray-black or yellowish coloration. As their name implies, the thorax is highly arched; the abdomen tapers sharply. These flies are often encountered on the decaying remains of plants, but other species live in the colonies of termites, ants, or bees. Some species are parasites in honeybee larvae. This infestation becomes apparent to the beekeeper when he sees the light-brown puparia (L 3–4 mm), rather wedge-shaped at the sides, in the refuse on the floor of the beehive. From these, after about twelve days, the small flies emerge. Some of the flies live on corpses; *Conicera tibialis* could be called the coffin fly. A few species live as larvae in the "pitchers" of the pitcher plant *Nepenthes*. The fluid secreted by the plant, with which it digests insects which fall into the pitchers, is their feeding place; they eat the bodies of insects partially digested by the fluid. The TERMITE FLIES (*Termitoxenia* spp.), parasitic in termite colonies, have no wings, but only two vestiges shaped like cup



Fig. 20-5. *Termitoxenia* sp., a termite fly, in the early, male stage (above) and the later, female stage (below).

handles. They are so greatly modified in form that some researchers assign them to a family of their own, the Termitoxenidae. The imagoes of these remarkable insects change form and sex as they grow older: initially they are stenogastric males (with short abdomens), and then they become physogastric females (with swollen abdomens). As females they lay only one large egg at a time, from which the full-grown larva soon hatches. A few minutes later it has pupated. This means that all the nutrients for production of the adult fly must be included in the egg; this requirement determines the size of the egg, which in turn determines the size of the mother's abdomen. Although the termite flies feed on the eggs of termites, they are tolerated in the colony because they have tufts of yellow hairs (trichomes) at the end of the abdomen, carrying a secretion which is offered to the termites; the termites evidently prize this as a delicacy. Beetles living in ant colonies ingratiate themselves in a similar way (see Chapter 13). Another guest in termite nests, *Thaumatoxena wasmanni*, is practically invulnerable to the attacks of termites because of its rounded body. This modification has altered the characteristic fly shape so drastically that zoologists at first took this humpbacked fly for a bug.

The next two families, the big-headed flies and the hover flies, are also closely related to one another; together they form the group Syrphoidea. The smaller of the two families is the Pipunculidae; it includes almost 400 species of flies, usually small and black, with eyes so large that the head appears to consist of nothing else. The eyes have crowded the antennae down to the middle of the head, and the mouthparts are small and hidden. All the larvae are parasitic in cicadas and their relatives.

Family: Syrphidae

The HOVER FLIES (family Syrphidae) comprise one of the largest of the fly families, for as long ago as 1952 W. Hennig estimated that over 4600 species had been described. Of these 939 are native to the U.S.A. Most are of moderate to large size (L up to 20 mm), with a lively patterning of black and yellow which gives them a similarity to bees or wasps. They visit flowers, often hovering over them as their name suggests. The proboscis, though, is shorter than that of the bee flies, which sip from flowers in much the same way. A reliable identifying characteristic of the hover flies is the wing venation, but to study this one must use a lens. The large, closed wing cell near the posterior margin of the wing (the anal cell) has a stalklike extension out to the wing margin, and a fold (the vena spuria), with the appearance of a longitudinal vein, runs through two of the cells in the middle of the wing. There is a surprising resemblance between some hover flies and the stinging Hymenoptera. For this reason the DRONE FLY (*Eristalis tenax*; L 14 mm; see Color plate, p. 394) is colloquially called the "dung bee" in Germany. The species *Volucella bombylans* (L 16 mm; see Color plate, p. 394), with its black-and-yellow abdomen, is very like the bumblebee *Bombus lapidarius*, and its subspecies *V. b. mystacea* has a white tip to the abdomen which gives it a deceptive resemblance to *Bombus terrestris*. The small, slender hover flies of the genus *Eristalis* (formerly

Helophilus and *Tubifera*), with the abdomen patterned in black and yellow, are almost always to be found on sunny days among the many visitors to large umbelliferous plants. Although all the adult flies feed on the nectar of flowers, the habits of their larvae are quite varied. The pits beneath rural outhouses and stagnant waters provide homes for the "rat-tailed larvae" of the drone fly. The hind end of this larva is extended to form a long snorkel through which it obtains fresh air from above the oxygen-poor waters in which it lives. The snorkel consists of three parts, nested as in a telescope, that can be extended or collapsed. The length of the tube can thus be matched to the depth at which the larva is resting. The tube is extended by means of blood pressure and shortened by the action of muscles. Anyone who can overcome his distate for these creatures and take a closer look will discover another apparatus at the anterior end, which "with its fortunate combination of practical design and incomparable elegance is among the finest known in the insects." This was written by the Danish limnologist C. Wesenberg-Lund about the esophageal filter of the rat-tailed larva. This organ has been justifiably compared with the sievelike structure in the upper jaw of a whale. Firm balls of food are formed in it, the water being pressed out and expelled from the gullet by way of a special chamber. But how different in appearance from the drone fly larvae are the hover fly larvae in the subfamily Syrphinae! Their lively green, yellow, and brown coloration—due to the fat body—is rare among fly larvae. They have become flattened so as to resemble small leeches, and they move through foliage in a leechlike manner. There they hunt aphids, and usually they need not look for long; the mother takes care to lay her eggs in the vicinity of an aphid colony (see Color plate, p. 386). When one of these hover fly larvae encounters an aphid, it spears it with its mouthparts, raises the front part of its body up so that the aphid is lifted into the air, and then retracts the anterior end into the thorax "so that the unfortunate aphid sits in the depression thus formed like a cork in the neck of a bottle," as K. Escherich writes. "This renders the victim completely helpless; usually its legs are on top and it cannot escape the enemy, which with gulping and pumping movements draws out the fluid contents of the aphid's body." Since the remaining aphids pay no attention to what is happening, the larva can suck them out one after another. S. Bombosch observed one larva of *Syrphus corollae*, which during its ten days of development consumed 421 bean aphids (*Aphis fabae*; see Chapter 11). One might think that performances like this would control the population of aphids; but that is not the case, for the aphids begin to multiply early in spring, when the number of egg-laying hover fly females is small. One reason for this situation may be the cultivation of the soil, which kills many of the hover fly larvae that pass the winter there in a dormant state.

Of the hover fly larvae in the subfamily Volucellinae, some eat the stems and leaves of plants. But the species of *Volucella* native to Germany live in the nests of wasps and bumblebees, feeding on the larvae. One is

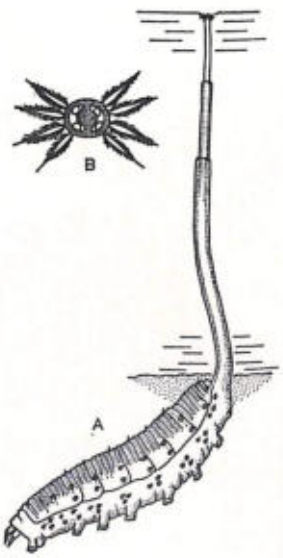


Fig. 20-6. "Rat-tailed larva" of the drone fly (*Eristalis tenax*; L 20 mm); A, lateral aspect of the larva, buried in mud with the snorkel reaching to the water surface; B, surface view of the spiracles, surrounded by a wreath of hairs.

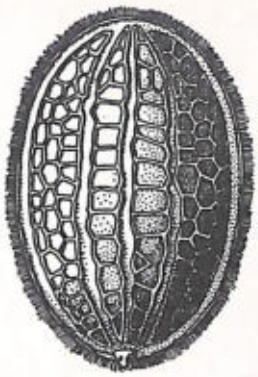


Fig. 20-7. Larva of *Microdon* sp., a hover fly which develops as a parasite in ant colonies.

tempted to regard the striking similarity of the adults to bumblebees as a correlate of this behavior. But this could be of use only outside the bees' nest, for their appearance can have no effect in the darkness within the nest. Moreover, the same flies lay their eggs in the nests of wasps, which they do not resemble, and they are equally successful despite the strict guard kept by the wasps.

Hover fly larvae of species of the genus *Microdon*, which belongs to the subfamily Microdontinae, live in the colonies of ants and feed on their young; thanks to their extremely slow movements and their very hard, ridged, hemispherical surface, they are not recognized as enemies by the ants. The pupa resembles the larva, since it is enclosed in the last larval skin.

These three methods of obtaining food by no means exhaust the variety of behavior to be found among hover fly larvae. The larvae of species of *Rhingia* live in cow manure, and the larvae of the species of the closely related genus, *Brachiopa*, live in the flowing sap of diseased trees. Larvae of two subfamilies, the NARCISSUS BULB FLY (*Merodon equestris*; subfamily Eristalinae) and the ONION BULB FLY (*Eumerus strigatus*; subfamily Milesiinae), have acquired a taste for the juice of onions and other bulbs. Both of these bulb-lovers belong to subfamilies in which most of the larvae feed on rotting materials. The two subfamilies have switched independently from this food to the bulbs of plants. The narcissus bulb flies do considerable damage in ornamental-plant nurseries, as do the onion bulb flies in fields of onions.

All of the families to be discussed next differ from the preceding ones in that they emerge from the puparium by lifting the lid at the anterior end with a special structure, the ptilinum, which is everted from the head for the purpose; after emergence it is retracted and then remains invisible, though its location is still marked by the frontal suture. With a lens one can examine this distinctive characteristic of the family-series SCHIZOPHORA just above the bases of the antennae of a housefly or, still better, a blowfly. And to see an example of a dipteran lacking this characteristic, look at the front of the head of a large hover fly.

Family: Conopidae

The THICK-HEADED FLIES (family Conopidae) comprise about 500 species, of which about sixty are native to Germany. The range of sizes is appreciable (L 4–18 mm for the German species); most of these flies look like wasps. The head is often greatly enlarged and the abdomen is constricted at the base, forming a stalk. The larvae are parasites in the posterior part of the body of both social and solitary bees and wasps. The females lay their eggs on the abdomen of the future host. Often they do this in flight, a feat requiring considerable skill. The eggs are equipped with hooks, threads, and other attachment devices. The regressed state of the larval mouthparts makes it probable that the larvae feed only by drinking the blood of their hosts. They pupate inside the host, and leave it only as imagoes. The imago emerges by making a hole in the joint membrane behind one of the anterior dorsal plates, and lifting up the plate.

Family: Trypetidae

The FRUIT FLIES (family Trypetidae), with about 1500 species, are distributed throughout the world. The name is extensively, though erroneously, applied to the Drosophilidae, but the larvae of the latter actually eat the yeasts and fungi in decomposing fruit, and not the fruit itself. The trypetids are characterized by light-colored wings with dark bands or spots, and by the female's long ovipositor, which is used to lay eggs in plant tissue. The larvae feed on plants, some doing damage to crops. Among them is the dreaded MEDITERRANEAN FRUIT FLY (*Ceratitis capitata*; L 5 mm). It has long been a pest in Africa, Australia, South America, and on the Hawaiian and Bermuda Islands, destroying peaches, apricots, pears, oranges, tangerines, and other cultivated fruits. The common name is somewhat misleading, since the fly was introduced into the Mediterranean relatively recently. It was soon realized that there was great danger of the flies being carried into central Europe along with imported fruit, and the border-control authorities did everything they could to prevent this. Nevertheless, by 1937 the fly appeared in orchards near Frankfurt, and in 1939 it destroyed the peach harvest in that area. Evidently it withstood the cold winter of 1939/40, although ordinarily it requires a warm climate; in 1952 it again destroyed the peach harvest in the same orchards. Thus it must now be regarded as established in Germany, although it multiplies sufficiently to be destructive only in very hot summers. In some fruit-growing regions near Basel, Paris, and Geneva, according to J. Baas, it has caused the cessation of the cultivation of peaches. The yellowish-white, active maggots (L 8 mm) turn the flesh of the fruit into a brown viscous mass. The maggot bends itself into an arch on a smooth surface, and then, with a snapping noise, jumps about 10 cm high and twice as far along the ground.

▷
A bumblebee, *Bombus* sp., flying up to a willow catkin. The pollen on the yellow stamens is an important source of protein for the bumblebees in spring.

▷▷
Honeybees (*Apis mellifera*) on the comb. The queen has been marked with a yellow spot. Such marks are used by researchers to identify certain bees in the study of their behavior.

The ASPARAGUS FLY (*Platyparea poeciloptera*; L 5.5–7 mm) lays its eggs under the scales of young asparagus heads. After hatching there, the young maggots crawl through the stalks to the woody parts, damaging them irreparably. The most common fruit fly in Germany is *Rhagoletis cerasi* (L 3.5 mm; see Color plate, p. 403); its larva is the well-known cherry maggot. The female lays its eggs with the ovipositor in ripening cherries, particularly sweet cherries. As it grows, the maggot turns the parts of the cherry next to it into a fetid liquid. By the time the cherry has become quite ripe, the maggot has completed its growth; it leaves the cherry, falls to the ground, and pupates there. The next spring, when the cherries are beginning to ripen, the imago leaves the pupa and puparium. So far no effective method of control has been discovered; in fact, infestation of cherries with these maggots is increasing, since the high cost of labor often means that the cherries are not picked. The maggots, which used to be distributed to consumers over a wide area and thus killed, then stay in the orchard, and the army of flies emerging the following year is even greater.

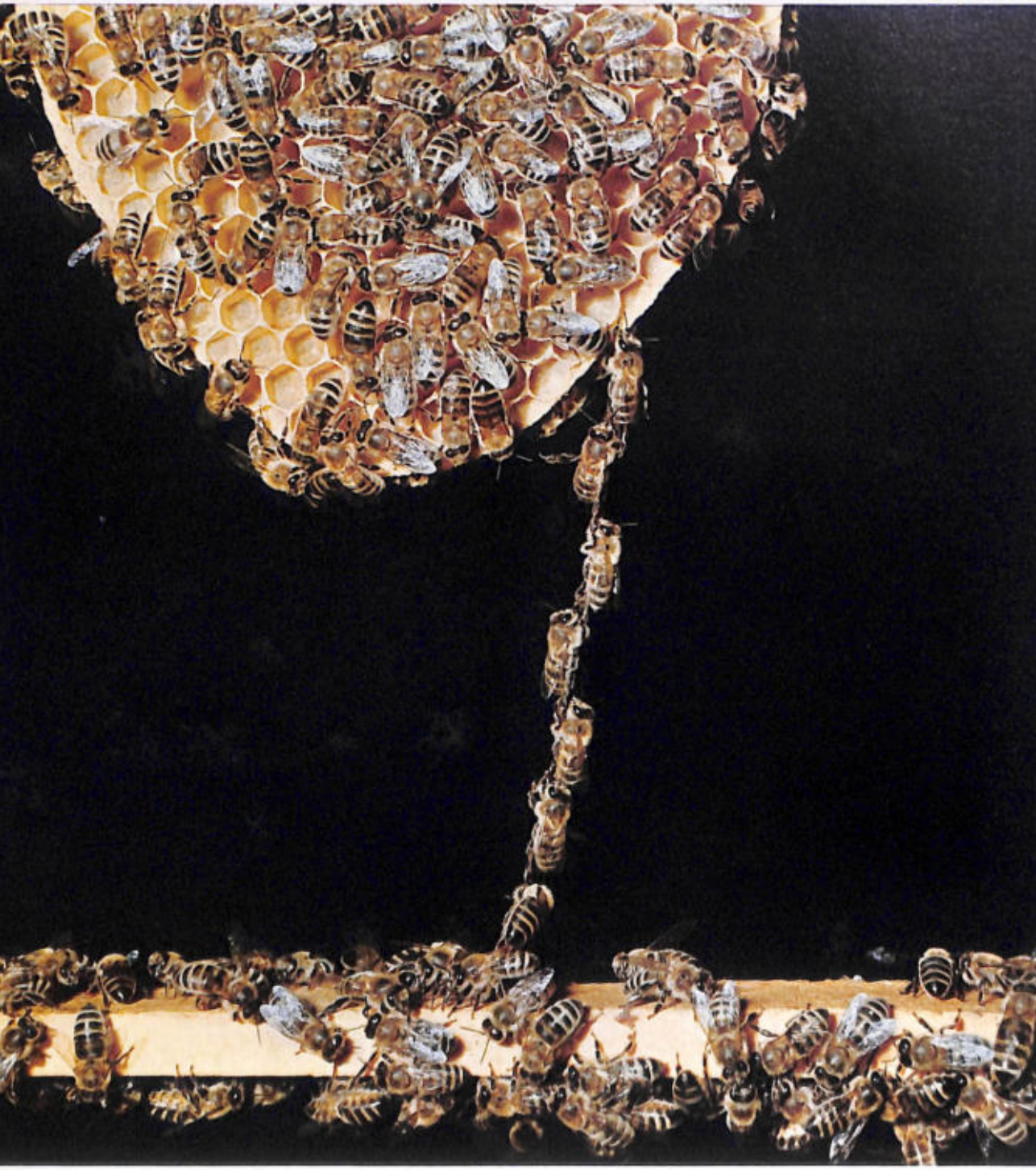
Family: Psilidae

Some of the RUST FLIES (family Psilidae) are also enemies of cultivated plants. For example, the twisting tunnels in carrots are made by the larvae









Honeybees (*Apis mellifera*) building a comb. Workers hang on to one another, forming a chain between the comb under construction and the framework below.

of the CARROT RUST FLY (*Psila rosae*; L 4 mm). In Germany, one finds the larvae in the carrots in both May and August; that is, the fly has two generations per year. It is shiny black with a red-yellow head and yellow legs. Close relatives of the rust flies are the predominantly African STALK-EYED FLIES (family Diopsidae). The head is broadened by long stalks, on which the eyes sit far apart from one another. The larvae of South African species have been found in corn stalks, and other larvae live in decomposing matter.

Family: Piophilidae

The few species of SKIPPER FLIES (family Piophilidae) all are small flies, the best-known of which is the cosmopolitan *Piophila casei* (L 4–5 mm). The larvae live primarily in cheese, but also in smoked and pickled meat including bacon and ham, and in carrion, rotting fungi, and feces. They are known for their ability to jump, which they do by hooking the mouthparts into the end of the abdomen and then pulling on the attachment until it breaks free; thus they straighten out with a jerk, shooting themselves through the air. Skipper flies prefer high-quality varieties of rich cheese, and there are even human gourmets who particularly prize maggoty cheese. But in eating such cheese, caution is recommended; the maggots are extremely hardy, and the digestive juices of the human stomach and intestines do not harm them. They go on living in the digestive tract and eventually leave it, usually still alive. Meanwhile, though, they can cause severe inflammations of the mucous lining. The astonishing thing is that these lively animals can manage without oxygen when they are in the gut; they can even live for a day and a half if one submerges them entirely in wax with a low melting point.

Family: Chloropidae

The roughly 1200 species of FRIT FLIES (family Chloropidae) are small, hairless flies, whose larvae live primarily in grass stalks. Grain fields often suffer severe damage from the yellow *Chlorops pumilionis* (L 3–4 mm) and the FRIT FLY (*Oscinella frit*; L 3 mm) of Europe, Canada, and the U.S.A. The flies of some species, such as *Thaumatomyia notata* (L 2 mm) may move into houses in large numbers to pass the winter, causing great annoyance. Some species have sharp little spines on the sponging surface of the proboscis, which cause small wounds when they touch the human mucous membranes, opening the way to pathogenic organisms. In India, *Siphunculina funiculi* transmits conjunctivitis and other eye diseases. In the West Indies and Central America, species of *Hippolates* transmit the tropical disease called yaws, which is produced by a spirochaete and is characterized by raspberrylike excrescences on the skin.

Family: Milichiidae

The family Milichiidae is represented in Europe and North America by one species, *Carnus hemapterus* (L up to 1 mm), with another approximately fifty species in North America. This tiny fly, whose abdomen is markedly swollen in both sexes, lives in bird nests and sucks blood. After the imago emerges, its wings break off, so that it looks more like a louse than a fly.

Family: Agromyzidae

In contrast to the rare Milichiidae, there are many species of LEAF

MINERS (family Agromyzidae) and about 600 species in the family as a whole. The flies are small to minute and may be easily overlooked, but the sharp observer can see traces of the activity of the larvae wherever he goes. They mine in leaves; that is, they cut out tunnels within the green spongy tissue between the cellular epidermis which forms the two surfaces of the leaf. Sooner or later these mines turn a brownish color which contrasts distinctly with the green of the leaf. Young larvae produce narrow tunnels and older larvae, broader ones, so that a single mine is quite small at one end and gradually broadens over its winding course, until finally the larva, ready to pupate, chews a hole to the outside. Then it falls to the ground, where it enters pupation. Some larvae construct mines not in the form of tunnels, but rather by expanding in two dimensions, forming blotch mines. Some begin with tunnel but end up making a blotch mine. If one holds a mined leaf to the light, dark stripes can be seen along the middle or the edge of the tunnel; these are due to the larvae depositing their excrement, each species in a characteristic way. But not every such mine has been made by a fly. There are also leaf-mining larvae in many species of Lepidoptera and in some Coleoptera and Hymenoptera. If the larva is still in the mine it is easy to decide whether it is a fly or some other insect; other larvae have dark head capsules, whereas the larva of the leaf-mining fly has a pointed anterior end with only the cephalopharyngeal skeleton which bears the mouth-hooks visible below the surface. The influence of these largely ignored insects on the balance of nature was demonstrated about the turn of the century when a Central American ornamental shrub, *Lantana* spp. (family Verbenaceae), was introduced to Hawaii. There, in the absence of its natural enemies, it grew wild to such an extent that it interfered with the cultivation of sugar cane. Once again, the German-American Koebels (see Chapter 10) came to the rescue with his "biological pest control." He procured enemies of *Lantana* spp. from the land of origin of the weed, and it was a leaf-mining fly which was decisive in putting an end to the massive spread of the plant.



Fig. 20-8. The milichiid fly *Carnus hemapterus* (L up to 1 mm), which lives in feathers.



Fig. 20-9. Mine made by the larva of *Phytomyza brunnipes* in a *Sanicula* sp. leaf; just one example of the many types of passages made by the larvae of leaf-mining flies.

The SMALL DUNG FLIES (family Sphaeroceridae) comprise about 250 species of flies, usually small and black. Their larvae live in rotting masses of plants, in decaying seaweed on the beach, in fungi, in diseased trees, and in excrement. Species of the genus *Anatalanta*, which inhabits the Kerguelens, a group of islands in the southernmost part of the Indian Ocean, are wingless. Hereditary lack of wings also occasionally appears in European fly species but is soon eliminated as a result of natural selection. On these islands, however, which are constantly swept by violent storms, it is the wingless flies that survive, since an insect in flight can fall victim to the storms. A mutation that in other places counts as a fatal malformation is here a vital characteristic, favored by natural selection.

Family: Sphaeroceridae

There is only one species of BEELOUSE (*Braula coeca*, family Braulidae; L 1–1.5 mm), which lives in beehives in Europe, Africa, and North and South America. It is a wingless fly, but not at all blind (as the Latin name

Family: Braulidae

coeca suggests). The larvae feed on the pollen-containing wax of the comb, particularly the wax covering the honey cells. The imago is found primarily on the queen bee; the Erlangen bee researcher Enoch Zander reported a case in which 187 were counted on a single queen. When the queen is fed by the worker bees, the imagoes sit on her head and suck the food from her tongue. When the infestation is heavy, though, the parasites attack the worker bees as well.

Family: Drosophilidae

The POMACE FLIES (family Drosophilidae) are a large family, with about 700 species. These small flies, patterned in yellow and dark gray with red eyes, are probably familiar to everyone. They appear on overripe fruit in kitchens (hence the inaccurate but nearly universal common name, fruit flies), they swarm in thousands about the residue produced by the pressing of grapes or apples for wine, they nibble on marmalade and other preserves, and wherever vinegar is standing open, they are there. The greatest fame has been earned by the species *Drosophila melanogaster* (L 2 mm; see Color plate, p. 403), as a result of investigations by the American T. H. Morgan and his colleagues C. B. Bridges, A. H. Sturtevant, and H. J. Miller, which led to fundamental discoveries in genetics. The results have proved valid not only for the fly, but for other animals (including humans) and plants. *Drosophila* spp. were chosen for these studies because they combine several advantages: (1) The generations follow one another in rapid succession, under favorable conditions with a period of about a week. (2) The number of offspring produced in each generation is large. (3) Culture and cross-breeding of the flies is easily done, since they mate even in small containers and the larvae are easy to feed. (4) There are only four pairs of chromosomes in each cell nucleus, so that these carriers of the hereditary material are relatively easy to identify and study. (5) The chromosomes in the salivary glands of the larvae are recognizable not only during nuclear division, but even in the intervening periods; moreover, they are very large (giant chromosomes). (6) In cultures of drosophila, many hereditary changes (mutations) occur spontaneously and are identifiable in the coloration of the eyes and the body, the arrangement of bristles, the shape of the wings, and other externally visible characteristics.

Family: Ephydridae

The SHORE FLIES (family Ephydridae) are small and dark in color, close relatives of the Drosophilidae; there are about 1000 species. The larvae are aquatic, many of them preferring salt water. For example, the larvae of BRINE FLY species of the genus *Ephydra* are found in great numbers in pools at mineral baths, where the salt concentration of the brine is greatly increased by evaporation. The larvae of *Ephydra riparia* (L 4 mm) a nearly cosmopolitan species, require a salt concentration in the range 2% to 20.9%; the range of acceptable concentrations is thus quite wide. In contrast, the range acceptable to the European species *E. scholtzi* is only 0.67% to 12.44%. Adaptation to life in salty inland waters has made available to these insects a habitat in which lower plants (algae) produce an abundance of food and in which there are practically no predators. The shore flies are

particularly adept at fitting themselves into ecological niches of this sort, initially free of animal life and accessible to it only through special adaptations. One such niche was the hot springs of Iceland, Japan, Kamchatka, New Zealand, and Yellowstone Park (U.S.A.). Species of the genus *Scatella* live in these warm waters, at temperatures as high as 55°C. But the most remarkable niche has been colonized by the larvae of the PETROLEUM FLY (*Helaeomyia petrolii*) in the petroleum pools of California. Here they live entirely surrounded by crude oil, with only the respiratory tube connecting them with the air. They feed on dead insects that fall into the oil, sucking out the contents of their bodies. In the process, they cannot avoid swallowing a good deal of oil, but the inner surface of the gut, where digestion takes place, remains free of it. The peritrophic membrane (see Chapter 1) forms an impermeable tube around the swallowed oil, and only the food materials pass through it to the wall of the gut. The pupae of the brine flies lie in a puparium with a peculiar attachment structure; between the last two pairs of pseudopods of the larvae there is a deep groove, and when the last larval skin hardens to form the puparium this indentation becomes a rigid, almost circular vise. Even before pupation this structure is used to grasp a plant stalk under water, or another puparium; the puparia are often seen floating on the water, attached to one another in great numbers. On lakes, a wind of long duration can drive the larvae and pupae over the surface to the lee shore, where they pile up in masses. According to J. M. Aldrich, the Indians in the neighborhood of the Great Salt Lake in Utah prized these as food. In addition to all these odd groups, the shore fly family includes many species which live in fresh water and on the land, as leaf miners.

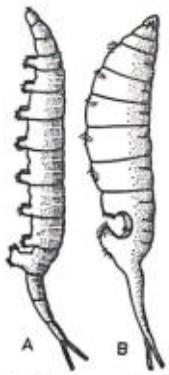


Fig. 20-10. Larva (A) and pupa (B) of a brine fly.

In the families which follow, the characteristics of the cyclorrhapha are particularly pronounced; these include the frontal suture, the thin-skinned vertex, the lid of the puparium, and the alula and squama. The latter is here sufficiently enlarged that it covers the haltere, and is called a calypter, so that this group of families has been given the name Calyptrata. We shall begin with the ANTHOMYIID FLIES (family Anthomyiidae, including the subfamily Scatophagidae). These slender flies are hunters of other insects, but the larvae feed on plant food or rotting substances. In water-lily leaves, the mines of the European *Hydromyza livens* (L 8 mm) are conspicuous. Even commoner is *Scatophaga stercoraria* (L 9 mm), covered with yellow to red hairs, which one almost always finds on animal and human excrement outdoors. This species lives throughout Europe, Asia, and North America. It is astonishing how quickly the dung flies arrive at freshly deposited dung; they must have an extraordinarily sensitive sense of smell for this odor. Dung is important to them in two respects. First, the females lay their eggs there; the whitish maggots live in and feed on dung and contribute to its rapid decomposition. They certainly deserve the generic name *Scatophaga* (dung-eater). Second, it is in the dung that the adult flies find their prey, other insects associated with excrement, such

Family: Anthomyiidae

as the numerous small dung flies (family Sphaeroceridae); occasionally they even attack *Lucilia* sp., a fly much larger than themselves.

Family: Muscidae

The Muscidae is a family of many closely similar species, with 622 species occurring in the U.S.A. A group formerly thought to be a part of this family, the Anthomyiidae, is now treated separately, as noted previously. The best-known species by far, the HOUSEFLY or LARGE HOUSEFLY (*Musca domestica*) was discussed in detail at the beginning of this chapter. In most houses, in the summer, one also finds the LITTLE HOUSEFLY (*Fannia canicularis*; L 5.5 mm; see Color plate, p. 403). This fly orients its outdoor swarming dances around the crowns of trees, whereas indoors it chooses ceiling lights for the same purpose. It differs from the large housefly not only in its smaller size, but in the venation of the wings and even more clearly in the form of the larva. The maggot of the large housefly is smooth, whereas that of the little housefly bears, on the back and sides of each body segment, pairs of appendages armed with little spines. In habits and habitat the two species are similar, but they differ fundamentally in the annual number of generations. In the case of the large housefly the number of generations is limited only by the temperature of the environment; the little housefly, however, never exceeds four generations per year even under the most favorable conditions, for the last larval stage of the fourth generation always enters diapause and becomes active again only in the following spring.

The third common companion of humans in their settlements is the STABLE FLY (*Stomoxys calcitrans*; L 6.5 mm; see Color plate, p. 403). Its bites are quite painful, since it drives even the labium into the skin. It prefers to bite people on the legs, and pursues this goal with such stubborness that often even thick stockings are no deterrent. The larvae of stable flies are like those of the large housefly; they live primarily in cow barns. Since the stable fly cannot fly very far, it is limited to rural areas where cattle are kept, and is not found in cities. The practiced eye can distinguish the stable fly from the housefly by the more widespread wings of the former, its piercing proboscis which stands out from the front of the head, the somewhat steeper angle at which the body is held, and—it is claimed—the resting orientation on vertical walls. The stable fly is said to tend to sit with the head up and the housefly, with the head down. But neither species keeps strictly to this rule.

The small biting fly species of the genus *Haematobia* are relatives of the stable fly. They hold their wings even less widely spread than does the housefly, so that they overlap over about three-quarters of their width. *Haematobia stimulans* (L 5.5 mm), from Europe, is as large as the little housefly, while *H. irritans* (L 4 mm), of Europe and North America, is smaller. Both of these flies may torment grazing cattle from June to September.

Some relatives of the housefly do agricultural damage through the feeding activities of the larvae; those of *Hylemya coarctata* mine in the

stalks of grain plants, and those of the European and North American *Pegomya hyoscyami* are pests in fields of fodder and sugar beets.

The tsetse flies

Stable flies and other biting flies can transmit diseases when they bite. This situation has become a matter of life and death for an entire region in the case of the TSETSE FLIES (*Glossina* spp.; see Color plate, p. 403, and Chapter 1) of Africa. They transmit the pathogen for the deadly sleeping sickness of humans and the corresponding disease of domestic animals, called nagana. For this reason, scientists have investigated this biting fly more intensively than any other. There are about thirty species, each of which has particular, rigid requirements for its habitat. Some require high humidity and others, low; some need heat and others, moderate temperatures; some prefer briery savanna, others, the fringes of forest along rivers, and still others, the tropical rain forests. They also differ in their choice of hosts: some bite humans and others do not, some depend on the blood of the larger wild animals and cattle, while others are content with small mammals, birds, crocodiles, and other reptiles. But the remarkable way in which the larvae develop is common to all these flies: they actually grow inside the body of the adult female until they are ready to pupate. The mother provides all the materials needed for the larva to develop into an imago. She obtains these from the blood she sucks and, as is true of all insects which feed exclusively on blood, from symbiosis (see Chapter 1) with microorganisms housed in her anterior midgut. Only one larva at a time develops in the mother's body, and it pupates immediately after birth. A similar relationship was discovered in the termite flies discussed earlier, and it occurs in three other families of flies; these are therefore grouped under the heading Pupipara (see below). The mothers bear the larvae in shady spots where the ground is soft enough that the larvae can burrow in. This shady brood area is always separate from the hunting area of the adult flies. There, the victim is recognized visually at a distance, particularly on the basis of movement, and the predator flies up to it. At close range the sense of smell also plays a role, as has been demonstrated in experiments with extracts of skin glands. Grassland quite free of woody plants is avoided by tsetse flies. The creation of a two-mile-wide cleared belt around a nature preserve will therefore prevent the tsetse flies from migrating out into the adjacent pasture land. The gestation period of tsetse females lasts one to two weeks, if the temperature is sufficiently high and the food supply adequate, so that during her lifetime a female can bear about eight, or at most ten larvae. This extremely low number of progeny, for an insect, suggests that the tsetse fly has few enemies. Since the connection between the flies and disease was discovered, the main enemy has been man. At first the flies were combatted with butterfly nets and sticky cloths carried on people's backs, but the fly trap invented by Harris was more successful. Even this, though, could reduce only a dense population of flies, and could not eradicate a reduced population. By 1940, 26,000 of these devices were in use in South Africa.

At about this time tsetse flies began to be destroyed in certain parts of Africa, such as Southern Rhodesia (now Rhodesia) and Zululand (in South Africa), by elimination of their hosts, the large wild mammals (cf. Chapter 1 and Vol. XIII). This approach was successful only with those species which were dependent on the blood of these animals. This method of control, unworthy of humanity, became outmoded in 1947 when du Toit, of the veterinary laboratory in Onderstepoort, first dusted the brood areas of the fly with contact poisons by helicopter. Since then, the nature preserves of Zululand and other tsetse regions have been cleared of the infestation while the hosts were spared. Now still another method has been found, which eliminates the tsetse flies while sparing even the rest of the insect fauna: male pupae are collected and sterilized by radiation in laboratories. They are then set free in the tsetse regions. They have not lost their mating instinct, and since each male copulates with several females, he removes them from the reproductive population. But since there are always other, untreated males which are fertile, the population declines only gradually. Sterilization and poisoning of course cost a great deal of money, but they do not cost the lives of the indispensable and irreplaceable wild mammals of Africa.

The pupiparous families

The members of the next three fly families have acquired the same form of larval development as the tsetse flies; the larvae come into the world ready to pupate. The families containing the louse flies (Hippoboscidae) and the bat flies (Nycteribiidae and Streblidae) were therefore once grouped as Pupipara. In contrast to the tsetse flies, the imagoes are not temporary parasites, visiting the host from time to time, but permanent (stationary) parasites living on the skin of the host and resembling lice more than flies. The similarities between the members of these three families are due more to their shared "life-form type" (see Chapter 5), as animals which walk over the skin, than to any close phylogenetic relationship.

Family: Hippoboscidae

The LOUSE FLIES (Hippoboscidae) live in the feathers of numerous species of birds and the fur of some mammalian species. The European species *Lipoptena cervi* (L 5–6 mm; see Color plate, p. 403) sucks the blood of red deer, fallow deer, roe deer, and elk, and very frequently attacks humans in the woods. This insect has been introduced into northern North America. If one seizes such a louse fly, the wings break off close to the body. The wings are also lost when the fly reaches the host on which it remains. The tough exoskeleton withstands the roughest treatment, so that the deer's defense of scratching the body or trying to bite the fly is ineffective. The newborn (already full-grown) larvae pupate in the ground. Only the sheep parasite *Melophagus ovinus* (L 5–6 mm) is wingless from the outset. The pupae of this species are attached to the sheep wool, so that the imagoes which emerge need not seek out a host. The close contact between the sheep in a herd provides a quite sufficient opportunity for dispersal of the species. The two European bird parasites *Stenopteryx hirun-*

dinis (L 5 mm), on swallows, and *Crataerhina pallida* (L 6 mm; cf. Vol. VIII), on swifts, both have small narrow wings which are inadequate for flight. The European horse parasite *Hippobosca equina* (L 7.5 mm), for which the family was named, and the numerous other louse flies infesting European birds are equipped with normally formed wings which do not break off. The BAT FLIES of the family Nycteribiidae (see Color plate, p. 403) live primarily in the Old World; seven species live on German bats, and five species live on North American bats. They are blind and wingless. When at rest, the bats hang close together in a bunch like grapes, so that the flies can easily move from one to another. Bat flies of the family Streblidae live predominantly in the New World tropics, with only one small species (*Nycteribosca kollari*; L 3 mm) on the bats of southern Europe. The wings of these bat flies break off easily. The bat flies which have gone the furthest in adaptation to a parasitic life are the species of the genus *Ascodipteron*, of eastern India and Queensland, Australia. Initially winged, these flies lose both wings and legs as soon as they have found a host. They burrow into the host's skin, behind the ear, and there assume the appearance of a bottle-shaped sack.

Families: Nycteribiidae and Streblidae

The BLOWFLIES (family Calliphoridae) took quite a different road to parasitism; here it is not the imagoes, but the larvae which are parasites. This development from a saprophagous (eating rotting materials) to an endoparasitic way of life is still going on before our eyes. There are species in this family whose larvae feed only on decayed matter; others are parasites which are still harmless to their hosts (the beginners in parasitism); still others feed on the hosts voraciously (the dangerous half-way stage); and finally there are parasites which have developed the art of feeding indefinitely on the host while sparing its life. Flies at this last, most highly adapted level, follow the principle that one does not saw off the branch on which one is sitting. This sequence of levels, described by the master of medical entomology, E. Martini, is particularly well illustrated by the example of the blowflies. The larvae of the European, African, and American BLUE-BOTTLE FLY (*Calliphora vomitoria*; L 14 mm; see Color plate, p. 403) and of the European *Lucilia caesar* (L 11 mm; see Color plate, p. 403) feed on rotting animal or vegetable matter. A similar American species; *L. illustris*, has the same diet. The mother ensures that the larvae will have a suitable food supply by laying the eggs on such food. Thus the larvae are even found in suppurating wounds, but they feed only on the necrotic tissue and on the pus, which contains plasma and white blood cells. Their excretions actually facilitate the healing of wounds, so that at one time larvae of this species which had been disinfected were used to clean wounds. An American variety of the closely related cosmopolitan *Phoenicia sericata* also proved valuable for this purpose, but the English form of this species is less appropriate, for it also attacks healthy tissue. Even the English *Phoenicia sericata*, though, is still a relatively "harmless beginner" at parasitism. Among those at the "dangerous half-way stage" are without

Family: Calliphoridae

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Ants: 1. *Dinoponera grandis*, one of the largest living ants (subfamily Ponerinae); 2. Worker of the army ant *Eciton vagans*; 3. *Strongylognathus testaceus*, a social parasite of the pavement ant; 4. *Formica polyctena*; a, section through the nest; b, a nest seen from outside; c, female with eggs; d, a worker adds another larva to a group of larvae; e, male with male pupae.









4 a

4 b

4c

4d



4e


1☿


3 ♀


2 ♀


4 ♂


4☿


4 a
4 b
4 l
4 c
4 l
4 ♀
4 e
4 p
4 e
T. Hölldobler

Bees: 1. Worker of the bumblebee *Bombus terrestris*; 2. Parasitic bee (*Nomada* sp.); 3. The mason bee *Chalicodoma muraria* at its nest; 4. The honeybee (*Apis mellifera*); ☿ worker with pollen-filled corbiculum; ♂ drone; ♀ queen laying eggs; 3, eggs, *l*, larvae of various ages; p, pupa; a, honey in a cell of the comb; b, pollen in another cell; c, water drop on the upper wall of a cell, placed there by the bees to maintain the high humidity of the nest.

doubt the larvae of species of the genus *Protocalliphora*, which attack the young of birds in the nest and often kill them. Another member of this group is the widespread *Bufolucilia silvarum* (L 9 mm), which lives as a larva in the nasal cavity of species of the toad genus *Bufo*, at first destroying the nasal mucosa and eventually the whole front of the head. There are horrifying pictures of the destruction of the human face as a result of attack by fly maggots (myiasis) of the SCREWWORM (*Cochliomyia hominivorax*) in North America. This fly may be confused with its very close relative the SECONDARY SCREWWORM (*C. macellaria*), but the latter is in the category of "harmless beginners." Recent advances in the biological control of insects is exemplified by the work of E. F. Knipling of the U.S. Department of Agriculture, who developed a system of irradiating male screwworm flies, rendering them sterile. Since the female mates only once, if one is inseminated by a sterile male, her eggs are not viable. Thus the release of millions of sterile males has resulted in the control of this serious livestock pest in the southern United States.

Closely related to the Calliphoridae is the somewhat larger family, the FLESH FLIES (Sarcophagidae). It contains another dangerous genus, *Wohlfahrtia*; *W. magnifica* (L 9 mm) is distributed throughout central and southern Europe and bears its larvae in the auditory canal, the nose, the mouth, and in wounds of humans and other mammals; infestation can be lethal. Other species of the genus live in the same way in northern Africa and North America (*W. vigil*). A step beyond these in the progress of adaptation has been made by the African TUMBU FLY (*Cordylobia anthropophaga*), the females of which lay their eggs in the urine- and sweat-soaked earth in the camping or resting places of humans and animals. The larvae remain close below the surface and when stimulated by warmth or vibration they emerge and raise themselves upright; they sway back and forth with the upper end of the body until they contact the warm skin of their victim. Then they burrow in and produce swellings like boils. After about two weeks the larvae, now full-grown, burrow back out of the skin and pupate in the ground. The German GRAY FLESH FLY (*Sarcophaga carnaria*; L 17 mm; see Color plate, p. 403) does not have a metallic sheen like that of the blue-bottle fly; it shines more like damask, and its abdomen is patterned like a checkerboard. In the U.S.A., too, the larvae of some flesh fly species, such as *Sarcophaga haemorrhoidalis*, are found in wounds, in sores, and in the intestines of humans.

Family: Oestridae

Examples of the most perfect form of parasitism, in which the host is spared any severe injury, are offered by the BOT FLIES (family Oestridae). In the warm parts of Central and South America the young larva of the pretty metallic-blue, yellow-legged *Dermatobia hominis* (L 12 mm) burrows into the skins of humans and cattle. Here it grows to a length of about 2.5 cm in a very painful swelling. It maintains contact with the outside air by way of the abdominal spiracles, which are placed at the entrance hole. When it is ready to pupate, the larva falls out of the wound and

undergoes metamorphosis in the soil. These fly maggots are popularly called mosquito worms, and are thought to be the larvae of mosquitoes; there is in fact a connection between them and the mosquitoes, especially some species of the genus *Psorophora*, which transmit the bot fly eggs to the hosts. When ready to lay eggs, *D. hominis* females swarm with mosquitoes in the air, and during this flight attach their eggs to the abdomens of the mosquitoes. Six days later the larvae in them are ready to hatch, but they actually do so only when the mosquito bites a human or a cow; then they leave the eggshell and move onto the skin.

The other species of bot flies are also characterized by precise methods of egg deposition, but in these relationships the inherited behavior of the host with respect to the parasites has reached a high level of development. Even though the bot fly females fly up to their victims more quietly than do the large horseflies, and even though, in contrast to the bite of a horsefly, the eggs are deposited quite painlessly, the cattle, deer, and horses respond to the approach of a bot fly with excited defense and flight behavior which is never elicited by a horsefly. HORSE BOT FLIES (*Gastrophilus* spp.; see Color plate, p. 403) usually live as larvae in the stomach and intestines of their hosts. The females of the *Gastrophilus intestinalis* (L 11–13 mm) lay their eggs mainly on the inside of the front legs, which the horse can easily reach with its tongue. After hatching, the little larvae burrow in the skin, irritating it so that the horse licks the spot. But then the larvae burrow into the tongue and wander through the mucous membranes to the throat. Here they break through the mucous membrane and are swallowed. They settle in the stomach, where one can commonly find 50–100 larvae close together. The closely related *G. nasalis* lays its eggs on the lower jaw of the horse, where the larvae hatch and move to the lips. Then they burrow in and take the same route as the previous species, except that they pass through the stomach and stop only in the small intestine. The eggs of the *G. haemorrhoidalis*, on the other hand, are laid around the mouth, at the base of the tactile hairs, and their journey ends in either the stomach or the rectum. Here they grow, but they leave four to five days before pupation and hang in the region of the anus. These three cosmopolitan species, as well as other horse bot flies, leave the host highly sensitized to their protein; if it is injected it can elicit a fatal shock. Parasitism by the MOUTH FLY (*Cephenomyia* spp.) of red deer, fallow deer, roe deer, and elk is just as highly developed. The males form swarms at elevated sites, such as lookout towers and mountain peaks. The females bear large numbers of young larvae and spray them accurately into the nostrils of the deer. But each host receives only some of a female's offspring; the 500 larvae a female contains would certainly kill a single host and thus would themselves be condemned to death. The larvae grow on the mucous membranes of the mouth and upper throat, and them move into the nasal cavity. The irritation they cause to the nasal mucosa causes violent sneezing which expels the larvae so that they can pupate in the

ground. Bot flies which live in the nose include the widely distributed SHEEP BOT FLY (*Oestrus ovis*; L 10–12 mm) and *Rhinoestrus purpureus* (L 8–11 mm). The latter infects horses in eastern and southern Europe and in northern Africa. Both these species spray their young larvae not only into the nose but into the eyes of their victims as well. From there, they move through the lacrimal duct to the nasal cavity. Both flies also attack humans, and their larvae, covered with numerous little spines, cause great pain in the conjunctiva of the eye. Since man is only a secondary host of these parasites, he lacks defensive behavior, and the consequences of infestation are even more severe for humans than for the primary host, to which the parasite is best adapted. The last group of bot flies to be discussed is the WARBLE FLIES (*Hypoderma* spp.) These have perhaps reached the highest level of parasitism among all bot flies, for they undertake extensive migrations through the bodies of their hosts, without causing excessive damage to health. The eggs of *Hypoderma bovis* (L 13 mm), a species occurring throughout Europe and North America, are laid on the hindlegs of cattle. The young larva bores through the skin of the leg and moves along the large leg nerves to the spinal cord. Its path then leads forward, along the vertebral canal and finally out through one of the openings between the vertebrae. Just under the skin the larva stops and bores a hole through which it can breathe with the spiracles of the hind end, and which it eventually enlarges so that it falls out and pupates in the ground. The "boils" thus produced on the skin are inflamed areas which become surrounded with a capsule of connective tissue. The boil contains pus and lymphatic fluid, on which the larva feeds. Another warble fly parasitic on cattle, the cosmopolitan *Hypoderma lineatum*, is found as a young larva in the esophagus, between the mucosa amd the muscular lining; from there it too eventually finds its way to a place under the skin. The boils produced by warble flies leave wounds which soon heal. Wild animals in Europe suffer from warble flies as well; red deer, roe deer, and elk are attacked by *H. diana* (L 12 mm), and the red deer is also a host of *H. actaeon* (L 13 mm). The reindeer of northern Europe and North America are greatly plagued by the bot fly *Oedemagena tarandi*. People in charge of domestic animals attacked by bot flies can limit the flies' reproduction by opening the boils in the skin before the larvae can leave of their own accord. But this procedure must be carried out with great caution. If the larvae are crushed in the skin, the foreign protein produces a feverish reaction in the host. Both cattle owners and hunters are hurt economically by bot flies, because the boils leave permanent scars which reduce the value of the skin. Game wardens can diminish the numbers of bot flies in their areas if in March and April, when the full-grown larvae are leaving the skin, they examine the soil at the feeding places for the fly pupae and destroy them. The insect collector can also count on a good harvest in such places.

Family: Tachinidae

Finally, we shall describe the family Tachinidae, by far the largest family of flies, with 1281 species in Canada and the U.S.A. As imagoes

they are dark animals, like blowflies but even more bristly; the puparia also have no striking peculiarities. But the larvae are particularly well adapted to a way of life at first parasitic and then ruthlessly lethal to the host; they are predator-parasites of other insects. The hosts of one subfamily (Phasiinae) are Hemiptera, Coleoptera, and Orthoptera, while those of a second (Dexiinae) are the larvae of lamellicorn beetles (see Chapter 13). The subfamily with the most species (Tachininae) includes larvae most of which live in lepidopteran caterpillars, while a small number live in the larvae of Hymenoptera. Those living in caterpillars are by far the most common in the U.S.A. A butterfly collector who gathers caterpillars and cares for them, hoping to obtain butterflies for his collection, often finds that his charges die when they are ready to pupate, and next to their collapsed bodies there lies the puparium of a larvivorid fly. He may not appreciate this outcome of his attempt at caterpillar culture, but it has introduced him to an insect which, next to the parasitic wasps, makes the greatest contribution toward maintaining the balance of nature. Lepidopteran caterpillars are enormously wasteful of their food plants; their mass reproduction often leaves trees and shrubs entirely bare, so that they die. Here, if natural conditions have not been too greatly altered by man, the larvivorids play a regulatory role. In his study of this family, W. Baer lists eighteen species of larvivorids which parasitize the browntail moth, twenty-one for the moths called black arches, and thirty for the gypsy moth. Some larvivorids are entirely or primarily restricted to one species of caterpillar, thus becoming particularly effective at keeping their numbers down. For example, in North America the tachinid *Mericia ampelus* (a species related to *Ernestia rudis* of Europe, not to be confused with the cluster fly, *Pollenia rudis*) is a parasite of the fall webworm (*Hyphantria cunea*), and of the caterpillars of *Parasetigena agilis*.

The larvae of the CLUSTER FLY (*Pollenia rudis*) live in earthworms. The adults are most noticeable in the fall of the year when they enter houses to hibernate, or in the spring when they cluster around windows, especially in attics, trying to get out. Other tachinid species have a broad range of acceptable hosts. For *Compsilura concinnata*, two hundred host caterpillars are known, and in this tachinid, according to W. Baer, "in warm summers the generations can follow one another like the months." Thus, in a wood composed of natural elements, the tachinids prevent mass outbreaks of the insects which devastate the plants, but their activity is only apparent when the forest has already lost its state of equilibrium and the outbreak of a lepidopteran is followed by an outbreak of a larvivorid.

There are three ways in which a tachinid larva can enter the host caterpillar. The fly may lay her eggs on the caterpillar, and the larvae burrow into it through the skin. Alternatively, the fly may lay her eggs near the caterpillar, on its food plant, so that the caterpillar eats them with its food. Finally, the females of some flies have a sharp ovipositor which they use to insert the eggs into the caterpillar. The first method was described

for *Parasetigena agilis* by the forest zoologist Heinrich Prell; "Hurrying past the caterpillar, she takes up a position beside its anterior end, at a distance of 1 or 2 cm. Her posture is very characteristic: the legs are spread wide, with the forelegs more extended than the others, so that she looks as if she is quite ready to jump and only looking for a suitable target. . . . As the caterpillar moves forward, the female fly follows, jumping sideways like a crab with her head always toward the caterpillar. . . . Suddenly she flies or jumps onto the caterpillar and, apparently without having actually settled on it, flies away again. . . . In most cases this brief interval has been sufficient for her to attach an egg to the caterpillar." Often only one maggot develops in a caterpillar, while the others perish. The tachinids have solved the problem of obtaining the necessary air for respiration while inside the caterpillar in various ways. The thin-skinned young larvae can obtain enough air from the dense network of caterpillar tracheae which surrounds them. Older larvae become covered with a sort of scab formed at the hole through which they entered. If the caterpillar is successful in this defensive procedure, it will completely encapsulate the parasite and kill it. But usually the covering tissue remains incomplete, forming not a capsule but a funnel through which the larva can remain in communication with the outside air. Other larvivorid larvae make their own connection to the exterior by boring a hole from within through the body wall or one of the large tracheae of the caterpillar. In this case, too, the caterpillar forms a funnel to the outside air. At first the fly larva in the caterpillar feeds on the surrounding blood and the blood corpuscles suspended in it. At this stage it is a true parasite. After the second molt, which produces the third-stage larva, this gentle treatment of the host is abandoned. The larva secretes an enzyme which liquefies the cells and tissues of the host, turning the entire body contents of the caterpillar into a brownish, viscous fluid. But there is no sign of putrefaction; in fact, according to J. Pantel, there is a fruity smell like that of rennet apples. The tachinid larva now feeds on this thick soup, for it is still entirely dependent on fluid food. Finally it burrows out of the lifeless shell of its former host and pupates in the ground. In rare cases the host lives long enough to pupate, and sometimes even manages to emerge as an imago.

The significance of the Diptera

Let us conclude by reviewing once again the role of the Diptera in the balance of nature. The hunters, the parasites, and the predator-parasites are clearly important in regulating biotic communities. On the other hand, the dipteran larvae which feed on rotting materials and plants may be regarded as the most successful representatives of the primary consumer level, serving in turn as food for the higher-level consumers. Some species are annoying parasites of man, others are dangerous and a few have even brought death to human populations, as the transmitters of epidemic diseases.

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21 The Fleas

Order: Siphonaptera, by F. Zumpt

An easily recognizable and well-defined order of insects is that of the FLEAS (Siphonaptera, formerly also called Suctoria or Aphaniptera). They are distributed worldwide; thus far about 1400 species have been described, divided by some zoologists into five families and by others into fifteen.

Distinguishing characteristics

They are small, wingless insects with complete metamorphosis. The larvae lack legs and look like maggots; they feed on dead animal and plant materials. The imagoes are blood-suckers, ordinarily living as temporary, but occasionally as permanent, ectoparasites in the coats of mammals and the plumage of birds. The mouthparts are of the piercing-sucking type. The body is greatly flattened laterally, and the hindlegs are specialized for jumping. Fundamentally parasitic on mammals, they did not arise before the mammals; that is, they must have lived no earlier than the beginning of the Tertiary (about 65 million years ago).

Family: Pulicidae

The family of greatest interest to us is the PULICIDS (Pulicidae), which includes the human flea (*Pulex irritans*; see Color plate, p. 404), the dog flea (*Ctenocephalides canis*), the cat flea (*Ctenocephalides felis*), and the Oriental rat flea (*Xenopsylla cheopis*; cf. Chapter 1).

Because the members of this family are so uniform, the identification of genera and species is quite difficult. Many species can only be identified by the male individuals. All fleas are blood-suckers as adults, restricted to birds and mammals (including man). There are no fleas on reptiles, amphibia, or fish; the "water flea" (*Daphnia* spp. and others) known to every aquarium owner is neither a flea nor any other sort of insect, but a crustacean (see Vol. I).

Reproduction and development

Female fleas lay a few hundred eggs, from which hatch hairy, legless larvae, similar in appearance to some fly larvae. This is one reason for assuming that the non-parasitic ancestors of the fleas were close relatives of the Diptera and, like them, had two wings. It is quite certain that the fleas have become wingless secondarily, and do not belong to the originally wingless "primitive insects" (the Apterygota; see Chapter 2). The

larvae molt three times, the last molt resulting in a pupa which lies in a cocoon. The larvae of fleas are not parasites, but rather feed on dead plant and animal materials which they find in the nests and burrows of the hosts of their parents. They also eat the undigested blood excreted by the adult fleas. Development from the egg to the newly emerged imago lasts three to six weeks, depending on temperature and humidity, or even several months. When the flea is ready to emerge it remains in the pupal case until a host animal approaches. The vibration of the ground associated with this approach releases the emergence behavior. In rooms which are not used for long periods, there can accumulate quite a large brood of fleas, all waiting for this signal; the unsuspecting person who is then the first to enter the room is attacked by hundreds of newly emerged fleas, starved by the long waiting period. Fleas are so well adapted to an irregular food supply that they can make up for starvation by sucking blood several times in one day. Under such conditions the excrement often contains undigested blood, which the larvae eat. Thus one can find blood in the gut of a larva, although it is not a blood-sucker.

Body structure

The external structure of fleas is to a great extent adapted to the necessity of moving through the thickets of fur and hair on the skin of the host. These insects are the main examples of the "snow-plow" type, to which the bat bugs (see Chapter 10) also belong. The latter are dorsoventrally flattened, wheres the fleas are flattened laterally so that they are much higher than they are wide (see Color plate, p. 404). Because of this, they can easily make their way between the hairs or feathers. There are strong combs of spines on the head and thorax, with their tips directed backward; these prevent the flea from falling out of the fur or feathers. There are no adhesive pads on the feet, but there are rather strong double claws, which catch hold on the skin as well as on the hairs and feathers. When the animal plows through the thicket, the forelegs serve to pull it, whereas the middle and hind legs push it forward. The head opens the path; it is helmet-shaped, and the antennae can be recessed into grooves. The head is thus comparable to the streamlined prow of a ship. The tough exoskeleton of a flea is relatively resistant to biting, as is that of the louse flies (see Chapter 20). The host is therefore not always able to defend itself from its tormentors with its teeth, and even humans need a certain amount of skill to crack fleas between the edges of the fingernails.

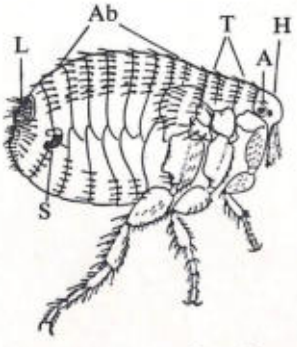


Fig. 21-1. Oriental rat flea (female): H, Head; A, Antennae; T, Thorax, with the three pairs of legs; Ab, Abdomen; L, Last abdominal segments (pygidium); S, Spermatheca.

The majority of fleas stay on the host only when they are feeding. When outside fur or feathers they use a characteristic method of locomotion: the jump. The jumping legs are the hindlegs, and the joints involved are the hip (coxa-femur) and knee joints. Because they contain the jumping muscles, the coxae and femora are very well developed. Fleas combine the jumping technique of cicadas and aphids (extension at the coxa; see Chapter 11) with that of grasshoppers (extension at the joint between femur and tibia; see Chapter 5). But their performance, about which so much has been said, is the result not only of the leg structure, but

also of their very small weight. The force involved in a jump increases as a function of the cross section of the muscle—that is, as the square of linear body dimensions—while the mass to be lifted in a jump increases with the volume—a cubic function. Thus in general the ratio of force to mass becomes smaller as the size of an animal increases, and the jumping performance becomes worse.

A third group of flea characteristics is related to their blood-sucking manner of feeding: the mouthparts are so drastically modified for this purpose that it has only recently been possible to interpret them. The mandibles are regressed; piercing stylets are formed by the laciniae of the maxillae and an elongation (the epipharynx) of the roof of the mouth. The stylet sheath, which does not penetrate the skin during a bite, is formed from the two labial palps. The head capsule of many fleas is flexible because of the interantennal groove which crosses it; this sort of "broken head" is also found in other blood-suckers—the bat bugs (see Chapter 10), some louse flies (see Chapter 20), and the bat flies of the family Streblidae (see Chapter 20). This flexibility permits the head to make better contact with the skin while it sucks.

The best-known species of flea, to the non-zoologist, is the HUMAN FLEA (*Pulex irritans*; L 2–3 mm; see Color plate, p. 404). It is a good jumper, with powerful hindlegs which can propel it up to 35 cm (over 1 foot) along the ground, and as much as 20 cm up into the air.

The original host of the human flea was not man, but rather is presumed to have been the badger of Europe and Asia. It was not until people began to build huts that this flea found suitable conditions with the new host. The humans transported it all over the world, making this flea a true cosmopolite.

But plagues of fleas in human houses are caused not by the human flea alone, but also—and in some regions primarily—by the DOG FLEA (*Ctenocephalides canis*), the CAT FLEA (*Ctenocephalides felis*), and a number of other species which usually live on rats and mice. Among these, the ORIENTAL RAT FLEA (*Xenopsylla cheopis*), a common parasite on the domesticated rats in tropical and subtropical regions, has achieved an unpleasant sort of fame because of its leading role in the spread of epidemics of plague among humans.

The bubonic plague, produced by the bacterium *Pasteurella pestis* (cf. Chapter 1), was originally epidemic among wild rodents (see Vol. XI). Particularly mice of the subfamily Murinae (to which the rats also belong), voles (Microtinae), and gerbils (Gerbillinae) are carriers of the plague, but squirrels (Sciuridae) and even hares (Leporidae, a family which belongs to a quite different order of mammals; see Vol. XII) also play a role. These small wild mammals serve as a reservoir for the plague; transmission is accomplished by the species-specific fleas associated with them, which belong to several genera (the most important is *Xenopsylla*). From time to time there are epidemics of plague (forest plague and steppe plague)

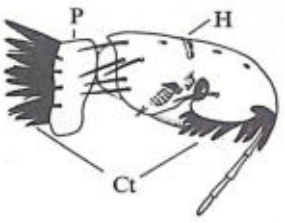


Fig. 21-2. Head (H) and prothorax (P) of the dog and cat flea (*Ctenocephalides* spp.); the combs of bristles (ctenidia, Ct) serve to anchor the animal in the fur of the host.

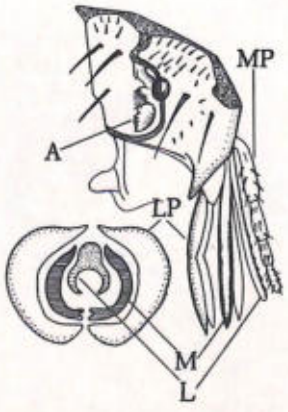


Fig. 21-3. Head of a jigger; below it, cross section through the piercing proboscis: A, Antenna; L, Labrum; M, Mandible; MP, Maxillary palp; LP, Labial palp.

among these wild animals; these may take many lives but do not kill the fleas.

Fleas as disease transmitters

Infection of humans can occur in regions of forest or steppe plague if the fleas, their original hosts having died, jump onto the men (hunters, etc.) there and transmit the bacteria to them. In such a situation the disease usually spreads to only a few individuals. But if domestic rats and brown rats or other rodents which live in close association with humans (for example, the Natal rat [*Praomys natalensis*], of South Africa) are attacked by the fleas which have lost their primary hosts, the epidemic spreads to these rats and eventually from them to humans. Presently the most important "plague flea" for mankind is the previously mentioned rat flea *Xenopsylla cheopis*. The human flea (*Pulex irritans*) can also acquire plague bacteria from infected humans, but in the epidemiology of human plague it plays a subordinate role. It is of much greater significance that the bacteria also infect the lungs of humans (pneumonic plague), so that they are readily transmitted directly from one person to another by the breath; this is an extremely lethal form of plague, which can lead to death in only a few days.

In the 14th Century, particularly in the plague years 1347 to 1350, about 25 million people died of plague in Europe alone—amounting then to a quarter of the population of that part of the world. Extensive control measures, directed against the rats as well as their fleas, have essentially banished the plague from Europe. But there are still many regions of the world where the disease occurs and, at intervals, breaks out in an epidemic; this happens in India, in eastern Asia, in central and southern Africa, in South America, and even in the U.S.A.

Another disease transmitted to people by rodent fleas is murine typhus, caused by a microorganism called *Rickettsia mooseri*. Here again one must regard the rat flea *Xenopsylla cheopis* as the most important agent in spreading the pathogenic organism. Fortunately, murine typhus is not nearly as severe as the plague, the Black Death of the Middle Ages, and it appears only occasionally and in restricted areas. The syndrome is relatively mild.

But even if human fleas do not transmit disease in human dwellings, they are an annoyance and are of significance with respect to hygiene. Many people are very sensitive to flea bites; they react with swellings which itch fiercely, sometimes for days, destroying both sleep and all enthusiasm for waking activities. In houses severely infested with fleas, the human inhabitants often get used to their troublesome tenants. But there are some people who are allergic to flea bites and react more and more strongly to them. Fortunately it is simple nowadays to eliminate such an infestation in a short time, by the application of modern methods of control.

Family: Tungidae; the jigger

In the tropical and subtropical regions of America and Africa there is a species of flea which occasionally sucks human blood; more serious,

though, is the fact that the females burrow into the skin and produce dangerous inflammation of the adjacent tissue. This is the JIGGER or CHIGOE FLEA (*Tunga penetrans*; see Color plate, p. 404). It belongs to another family, the Tungidae. The males and females which emerge from the pupal case are only about 1 mm long. They have the usual appearance of a flea; the males can be identified by the genital organs, which project far out from the body. There are a great many wild and domesticated mammals which can serve as hosts of the jigger, but humans and domestic pigs are preferred. The male is content to sink his sucking proboscis into the skin and take a brief meal of blood. But the female forces her way under the outer horny layer of the epidermis, head foremost. In humans, she prefers the feet and hands, especially the soft places under the nails, under and between the toes, and between the fingers.

Here, with the end of the abdomen at the surface of the skin, the female waits to be inseminated. In the next few days after insemination she becomes extraordinarily swollen, stretching the membranes between the abdominal segments until she has reached the size of a pea. The surrounding host tissue becomes inflamed, itches, and hurts. Now the female produces a steady stream of eggs which fall out of the swelling. How many eggs she can lay, and how long such a female can stay in the skin of the host under the most favorable circumstances, are not yet known. Some authorities have assumed that several thousand eggs can come to maturity. Under natural circumstances this is probably rarely the case, since the human or other host will sooner or later succeed in squashing or scratching out the swollen flea.

There can be an additional (secondary) infection due to disease pathogens, fatal to the host. Such cases are even known among humans, who succumbed to gas gangrene or tetanus as a consequence of the presence of a jigger. But this is a rare occurrence, for wherever jiggers are common, people learn to find the insect soon after it has invaded the skin and to remove it with a needle. The jigger larvae prefer sandy places for their development; these are common near houses and huts. These larvae, like those of other fleas, feed on dead plant and animal substances.

Other species of flea

In tropical and subtropical regions there is a species of flea parasitic on chickens, the STICKTIGHT FLEA (*Echidnophaga gallinacea*), which lives in a manner halfway between that of the jigger and the other, free-living fleas. Great numbers of females of this species anchor themselves close together in the skin by their mouthparts, choosing primarily the bare places on the head, but they do not penetrate further. They are so bothersome to their hosts that the distracted chickens no longer eat enough and become susceptible to other diseases. The original hosts of this species, remarkably, are not chickens, but rats and other rodents. The sticktight flea is frequently found on these animals, but never in such numbers as infest domestic chickens. Humans, too, are sometimes attacked by the sticktight flea. The original home of this flea species is the Mediterranean region.

Fleas are definitely nest parasites. Their larvae require sheltered places to develop, with plenty of rubbish on which to feed. Almost all mammals which make or live in burrows are therefore hosts to one or more species of flea. Other mammals, on the other hand, which manage without "nests," have for that reason no fleas or only occasional ones which have got onto them by mistake; such animals include, for example, the majority of ungulates. Even apes and monkeys do not naturally have fleas, but they may acquire them through association with humans, either from the people themselves or from their domestic animals.

Apes have no fleas

There are fleas in bird nests as well, but they are by no means so common and widespread as one might think. Ordinarily these fleas are of particular species which have specialized in certain types of nests. It is likely that the fleas began their "conquest" of bird nests by way of their association with mammals. An example of such a transition is apparent in the flea genus *Parapsyllus*, members of which live with penguins and other sea birds; this genus can be derived from flea species which parasitize South American rodents.

Flea circuses, by B. Grzimek

In the first half of this century there was much talk of flea circuses with supposedly trained fleas. But these fleas had not actually been taught anything; they were simply fastened by an invisibly thin bit of gold wire around the metathorax, which hampered their movements so that they could no longer jump, but only creep along. In this way one could take advantage of their urge to move—presumably an instinct to flee from bright light—by making them pull little wagons and perform other tricks.

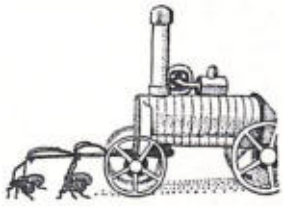


Fig. 21-4. In a flea circus female fleas are hitched to tiny vehicles . . .

The first and probably best-known flea-circus director was the Czech Raimund Otawa. He presented his little "artists" in inns and at fairs, traveled through country after country, and appeared before crowned heads and dictators. In the course of decades Otawa continued to expand the program of his circus. For example, a flea was turned onto its back and juggled a white ball of elder-pith on its feet; "on command," it kicked the ball far into the air. Actually, of course, it paid no attention to the command; rather, the "ringmaster" turned the flea more horizontally so that the load became effectively lighter and the small creature was able to toss it away. As another trick, the circus director, with a pair of forceps, removes from a can small, gaily dressed ballerinas made of tinfoil. Under the skirt of each there is a female flea, and when set down the dancers skip and twirl about together. (For such a circus, only the female fleas are suitable, since the smaller males are too weak.)



. . . and made to juggle with balls of elder-pith.

The fleas must be fed with human blood; dog fleas are not usable in such a presentation. "I let my fleas suck on my arms or legs," explained Otawa, "ordinarily once a day, though when they are working they may eat twice. It takes from two to fifteen minutes for the flea to drink its fill." Otawa reacted with itching and swelling only to the bites of dog fleas.

Nowadays the human flea has become very rare in countries that employ modern hygienic techniques.

Systematic Classification

Because of the great number of insect species, not all of the genera and species treated in the text have been named in the Systematic Classification of this volume. Rather, only a few particularly important forms in each group are mentioned here. Most insect orders include very many more families than are named in the text or in this summary. The page numbers with asterisks (*) refer to Color plates; the other numbers designate pages in the text on which the group or some of its members are discussed most extensively.

Particular genera and species may be found in the text by consulting the Index.

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On the Zoological Classification and Names

For many years, zoologists and botanists have tried to classify animals and plants into a system which would be a survey of the abundance of forms in fauna and flora. Such a system, of course, may be established under very different aspects. Since Charles Darwin, his predecessors, and his successors have found that all creatures have evolved out of common ancestors, species of animals and plants have been classified according to their natural relationships. Our knowledge about the phylogeny, and thus the relationship of each living being to the other, is augmented every year by new discoveries and insights. Old ideas are replaced with more recent and more appropriate ones. Therefore, the natural classification of the animal kingdom (and the plant kingdom) is subject to changes. Furthermore, the opinions of zoologists, who are working on the classification of animals into the various groups, are anything but uniform. These differences and changes are usually insignificant. The classification of vertebrates into the classes of fish, amphibians, reptiles, birds, and mammals has been fixed for many decades. Only the Cyclostomata were recently separated from the fish and all other classes of vertebrates as the "jawless" Agnatha (comp. Vol. 4).

The animal kingdom has been split into several subkingdoms and these were again divided into further sections, subsections, and so on. The scale of the most important systematic categories follows in a descending rank order:

Kingdom
Subkingdom
Phylum
Subphylum
Class
Subclass
Superorder
Order
Suborder
Infraorder
Family
Subfamily
Tribe
Genus
Subgenus
Species
Subspecies

The scientific names of the animals and their spelling follow the international rules for the zoological nomenclature as agreed upon by the XV International Congress for Zoology and are obligatory for all zoological publications. The name of the genus, which is a Latin or Latinized noun, is singular and capitalized. After the name of the genus follows the name of the species and of the subspecies. The names of the species and subspecies may be nouns or adjectives, and they are spelled in the lower case. The name of a subgenus, which is formed in the same manner as a genus, may be added in brackets following the name of the genus. The names of the tribes, subfamilies, families, and superfamilies are plural capitalized nouns. They are formed from the name of a given genus by adding to the principal word the endings -ini for the tribe, -inae for the subfamily, -idae for the family, and -oidea for the superfamily. The names of the authors who were the first to describe and to name a species, subspecies, or group of animals should be cited with the year of this naming at least once in each scientific publication. The name of the author and year are not enclosed in brackets when the species or subspecies is classified as belonging to the same genus with which the author had originally classified it. They are in brackets when another genus name is used in the present publication. The scientific names of the genus, subgenus, species, and subspecies are supposed to be printed with different letters, usually italics.

Animal Dictionary

1. English—German—French—Russian

For scientific names of species see the German-English-French-Russian section of this dictionary or the index.

N. A. after English names means that the name is used exclusively in North America.

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Adelgids	Tannenläuse	Puceron des sapins	Хермесы
African Tumbu Fly	Tumbufliege	Cordylobia africaine	
Alder Dogger	Erleneule	Noctuide d'aune	Ольховая стрельчатка
– Fly	Schlammfliege	Sialis de la vase	Обыкновенная вислокрылка
Alpines	Mohrenfalter	Erébia	Глазки-чернушки
Ambrosia Beetles	Kernkäfer	Platypodidés	
Ambush Bugs (N. A.)	Fangwanzen	Phymatidés	
American Ant-loving Crickets	Amerikanische Ameisengrille	Grillon myrmécophile de l'Amérique	
– Cockroach	– Großschabe	Blatte américaine	Американский большой таракан
Animal Lice	Tierläuse	Poux des animaux	Животные вши
Ant Lions	Ameisenlöwen	Fourmis-lions	Муравьиные львы
Ant-loving Crickets	Ameisengrillen	Grillons myrmécophiles	
Ants	Ameisen	Formicidés	Муравьи
Aphids	Blattläuse	Pucerons	Тли
Apocrites	Taillenwespen	Apocrites	
Apollo	Apollofalter	Apollon	Аполлон
Apple Blossom Weevil	Apfelblütenstecher	Anthonome du pommier	Яблонный цветоед
– Capsid Bug	Apfelwanze	Capsid du pommier	Яблонный клоп
– Psylla	Apfelblattsauger	Psylle du pommier	Яблонная медяница
Armoured Scales	Deckelschildläuse	Diaspididés	Щитовки
Asparagus Fly	Spargelfliege	Mouche des asperges	Спаржевая бурилка
Assasin Bugs	Raubwanzen	Réduviidées	Хищнецы
– Flies	Jagdfliegen	Asilidés	Ктыри
Atlas Moth	Atlasspinner	Bombyx atlas	
Australian Cockroach	Südliche Großschabe	Blatte d'Australie	
Back-swimmers	Rückenschwimmer	Notonectidés	Гладыши
Bag-worm Moths (N. A.)	Sackspinner	Psychides	Мешочницы
Balsam Twig Aphid	Tannentrieblaus	Puceron du sapin	Пихтовая тля
Band-winged Grasshoppers	Schnarrheuschrecken	Oedipodinés	Кобылки
Banded Agrion	Gebänderte Prachtlibelle	Caloptéryx brillant	Блестящая красотка
Bed Bug	Bettwanze	Punaise des lits	Постельный клоп
Bee-Flies	Wollschweber	Bombylidés	Жужжалы
Bee-hunting Wasp	Bienenwolf	Philanthe apivore	Пчелиный волк
Bee-»Lice«	Bienenläuse	Braulidés	Пчелиные паразиты
Beech Aphid	Buchenzierlaus	Puceron du hêtre	Буковая тля
Bees	Bienen	Apoidés	Пчелиные
Beetbugs	Meldenwanzen	Piésmides	
Beetles	Käfer	Coléoptères	Жуки
Big-headed Flies	Augenfliegen	Dorilaidés	Цикадоедки
Big Pear Psylla	Birnblattsauger	Psylle du poirier	Грушевая медяница
Birch Leaf Roller	Birkenblattroller	Coléoptère du bouleau	Березовый слоник
– Sawfly	Breitfüßige Birkenblattwespe, Große Pelzblattwespe	Tenthrède du bouleau, Trichosome géant	Северный березовый пилильщик, —
Bird Flies	Lausfliegen	Hippoboscidés	Кровососки
– Wings	Vogelfalter		Птицекрылки
Biting Midges	Gnitzen	Heléides	Мокрецы
Black Arches	Nonne	Nonne	Монашенка
– Bean Aphid	Bohnenlaus	Puceron de la fève	Свекловичная тля
– Currant Sawfly	Gelbe Stachelbeer-Blattwespe	Némate du groseillier	Желтый крыжовниковый пилильщик
– Flies	Kriebelmücken	Mélusinides	Мошки
Black-veined White	Baumweißling	Piéride d'aubépine	Боярышница
Blinding Breeze Flies	Blindbremsen	Chrysops	Златоглазки
Blister Beetles	Blasenkäfer, Ölkäfer	Mylabris, Méloidés	Нарывники
Blood-red Ant	Blutrote Raubameise	Fourmi sanguine	Кровавый муравей
Blossom Weevils	Blütenstecher	Anthonomes	Цветоеды
Blow Flies	Schmeißfliegen	Calliphoridés	
Blue-bottle Fly	Blaue Schmeißfliege	Mouche bleue de la viande	Синяя мясная муха
Blue Cattle Louse	Langköpfige Rinderlaus	Pou de veau	Длинноголовая коровья вошь
Blue-winged Waste-land Grasshopper	Blauflüglige Ödlandschrecke		Голубокрылая кобылка

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Blues	Bläulinge	Lycénides	Голубянки
Body Louse	Kleiderlaus	Pou de vêtement	Платяная вошь
Bombardier Beetles	Bombardierkäfer	Bombardiers	Жужелицы-бомбардиры
Book lice	Staubläuse	Poux de livres	Сеноеды
Book-louse	Bücherlaus	Pou devin	Книжная вошь
Bordered White	Kiefernspanner	Fidonie du pin	Сосновая пяденица
Boring Thrips	Bohr-Fransenflügler	Térébrants	Яйцекладные трипсы
Bot Flies	Dasselfliegen	Œstridés	Оводы
Braconid Flies	Brackwespen	Braconides	Бракониды
Brassica Bug	Kohlwanze	Punaise des potagers	Рапсовый щитник
Brentid Beetles (N. A.)	Langkopfkäfer		Долготелы
Brimstone	Zitronenfalter	Citron	Крушинница
Bristle-tails	Borstenschwänze	Thysanoures	Щетинохвостки
Broad-bodied Libellula	Plattbauch	Libellule à déprimé	Плоская стрекоза
Broad Bordered Bee Hawk-moth	Hummelschwärmer	Sphinx-gazé	
Brown-banded Cockroach	Braunband- oder Möbelschabe	Blatte des meubles	
Brown Lacewings	Taghafte	Hémérobidés	Стрекозки
Brown-tail	Goldafter	Cul doré	Златогузка
Bugs	Wanzen	Hétéroptères	Клопы
Bulldog Ants	Bulldoggenameisen	Myrmécinés	
Bumble Bee	Erdhummel	Bourdon de terre	Земляной шмель
Burnets	Widderchen	Zygénides	Пестрянки
Burying Beetles	Aaskäfer	Silphidés	Мертвоеды
Bush-crickets	Heupferde, Langfühlerschrecken, Laubheuschrecken	Tettigonides, Sauterelles à longues antennes, Tettigonides	Обыкновенные кузнечики, Кузнечиковые и Сверчковые, Настоящие кузнечиковые
Butterflies and Moths	Schmetterlinge	Lépidoptères	Чешуекрылые или Бабочки
Cabbage Moth	Kohleule	Noctuelle du chou	Капустная совка
– Root Fly	Blumenfliegen	Anthomyiinés	
– Thrips	Schmalkopfthrips	Thrips à tête étroite	Узкоголовый трипс
Caddice Flies	Köcherfliegen	Trichoptères	Ручейники
Camberwell Beauty	Trauermantel	Morio	Траурница
Carabids	Laufkäfer	Carabidés, Carabiques	Жужелицы
Carnivorous Water beetles	Schwimmkäfer	Dytiscides	Плавунцы
Carpet Beetle	Kabinettkäfer, Teppichkäfer	Anthrène du cabinet, Anthrène de la scophulaire	Кабинетные кожееды, Ковровый кожеед
Carrion Beetles	Aaskäfer	Silphidés	Мертвоеды
Carrionfly	Uferaas	Polymitarcis vierge	Береговая поденка
Carrot Rust Fly	Möhrenfliege	Mouche des carottes	Морковная муха
Case Bearers	Sackmotten	Coléophoridés	
Case-making Clothes Moth	Pelzmotte	Teigne des fourrures	Шубная моль
Caterpillar Hunter	Puppenräuber		Пахучий красотел
Cat Flea	Katzenfloh	Puce du chat	Кошачья блоха
Cat-louse	Katzenhaarling	Pou du chat	Кошачий власоед
Cattle-lice	Rinderhaarlinge	Poux des boeufs	Коровий власоед
Cattle Warble Fly	Rinderbiesfliege	Hypoderme du boeuf	Бычий овод
Cave- and Camel-crickets	Grillenschrecken	Sauterelle grillon	Ненастоящие кузнечиковые
Cave Cricket	Höhlenschrecke	Troglophile	
Cellar Beetles	Autokratkäfer	Trictenotomdiés	
Checkered Beetles	Buntkäfer	Clairons	Пестряки
Cheese Skipper	Käsefliege	Mouche du fromage	Сырная муха
Chewing Dog-louse	Hundehaarling	Pou du chien	Собачий власоед
– Lice	Kieferläuse	Mallophages	Пухоеды
Cicadas	Zikaden	Cigales	Цикадовые
Cimbicid Sawflies	Knopfhorn-Blattwespen	Cimbicidés	Булавоусы
Citrus Black Fly	Schwarze Citrusfliege	Mouche noire des Aurantiacées	Темнокрылая белая мушка
– White Fly	Weiße Citrusfliege	Mouche blanche des Aurantiacées	Цитрусовая мушка
Clairwings	Glasflügler	Sésies	Стеклянницы
Clear-winged Bugs	Pflanzensauger	Homoptères	Равнокрылые хоботные
Click-beetles	Schnellkäfer	Taupins	Проволочники или Щелкуны
Clothes Moths	Echte Motten	Teignes	Моли
Clouded Yellow	Postillion	Souci	
– Yellows	Gelblinge	Colias	Желтушки
Club-tail Dragonflies	Flußjungfern	Gomphides	
Cluster Fly	Eulentachine	Mouche des greiners	Совковая ежемуха
Coccids	Schildläuse	Cochenilles	Кокциды
Cochineal Insect	Cochenille-Laus	Cochenille	Мексиканская коншель
Cockchafers	Blatthornkäfer, Echte Maikäfer	Scarabés, Hannetons	Пластинчатоусые или Навозники, Майские хрущи
Cockroaches	Schaben	Blattes	Таракановые
Coffin Flies	Buckelfliegen	Phoridés	Горбатки

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Colletid Bees	Seidenbienen	Colletidés	Шелковые пчелы
Colorado Beetles	Kartoffelkäfer		Колорадский картофельный жук
Comb-claw Beetles	Pflanzenkäfer	Alleculidés	
Comma	C-Falter	Gamma	Голубянка икар
Common Blue	Hauheche' Bläuling		
– Clothes Moth	Gewöhnliche Kleidermotte	Mite des vêtements	Мебельная моль или Платяная моль
– Cockroach	Küchenschabe	Blatte des Cuisines	Черный таракан
– Crane Fly	Graue Kohlschnake	Tipule du chou	Огородная долгоножка
– Earwig	Gemeiner Ohrwurm	Forficule auriculaire	Обыкновенная уховертка
– Glowworm	Großer Leuchtkäfer	Lampyre noctiluque	Большой светляк
– Hide Beetle	Gemeiner Speckkäfer	Dermeste commun	Ветчинный кожеед
– Lackey	Ringelspinner	Livrée	Кольчатый коконопряд
– Magpie Moth	Harlekin	Zérène mouchetée du groseillier	Крыжовниковая пяденица
– Oak Gallfly	Gemeine Eichengallwespe	Cynips du chêne	Обыкновенная дубовая орехотворка
– Silver Moth	Gammaeule	Lettre grecque	Совка гамма
– Swallowtail	Schwalbenschwanz	Grand porte-queue	Махаон
– Web-spinning Sawfly	Gesellige Birnblattwespe	Lyde du poirier	Общественный грушевый пилильщик-ткач
– Willow Sawfly	Gemeine Weidenblattgallen-Wespe	Pontanie commune	Обыкновенный ивовый пилильщик
– Yellow Underwing	Hausmutter	Hibou	
Cone-heads	Kegelköpfe, Schwertschrecken	Conocéphalides	Конусоголовые кузнечики
Conifer Sawflies	Buschhorn-Blattwespen	Diprionides	
Convolvulus Hawk	Windenschwärmer	Sphinx du ciseron	Вьюнковый бражник
Coppers	Feuerfalter	Lycènes	
Corixids	Wasserzikaden	Corixidés	Гребляки
Cotton Stainer	Dunkle Baumwollwanze	Punaise grise du Cotton	
Cottony-cushion Scale	Wollsackschildlaus	Cochenille australienne	Австралийский желобчатый червец
Crab Louse	Schamlaus	Pou de feutre	Лобковая вошь
Crane Flies	Stelzschnaken, Wiesenschnaken	Limoniidés, Tipulidés	Долгоножки
Crickets	Grillen	Gryllides	Сверчковые
Cryptophagid Beetles (N. A.)	Schimmelkäfer	Cryptophagidés	
Cuckoo Wasps	Goldwespen	Chrysidides	Блестянки
Damsel Bugs	Sichelwanzen	Nabidés	
Damselflies	Kleinlibellen	Libellules	Стрекозы
Dance-flies	Tanzfliegen	Empididés	Толкунчики
Death's-head Hawk	Totenkopfschwärmer	Sphinx tête du mort	Мертвая голова
Deer Ked	Hirschlausfliege	Lipoptène du cerf	Оленья кровососка
– Warble Fly	Rehdasselfliege	Hypoderme du chevreuil	Косулий овод
Demoiselle Agrion	Gemeine Seejungfer	Demoiselle	Обыкновенная лютка
Demoiselles	Prachtlibellen	Caloptéryx	Красотки
Desert Locust	Wüstenschrecke	Sauterelle pélerin	Пустынная саранча
Devil-hoppers	Buckelzirpen	Membracidés	Горбатки
Diamond-back Moth	Kohlmotte	Teigne du Colza	Капустная моль
Digger Wasps	Dolchwespen	Scoliides	Сколии
Dil Beetles	Maiwürmer	Méloés	Майские букашки
Dog Flea	Hundefloh	Puce du chien	Собачья блоха
– Louse	Hundelaus	Pou du chien	Собачья вошь
Dor Beetles	Mistkäfer		Настоящие навозники
Dracaena Thrips	Drazänenthrips	Thripide dracaene	
Dragonflies	Libellen, Großlibellen	Libellules, Anisoptères	Стрекозы, Разнокрылые стрекозы
Drone Fly	Schlammfliege	Eristale gluante	Ильница
Drugstore Beetles	Klopfkäfer	Vrillettes	Точильщики
Duke of Burgundy	Würfelfalter	Lucine	Лесная пеструшка
Dun-bar	Mondraupeneule	Trapèze	
Dung Beetles	Dungkäfer, Kotfresser, Kotkäfer, Mondhornkäfer, Pillendreher	Aphodiinés, Onthophagus, Coprins, Copris, Scarabées	Пометокопатели, Калоеды, Копры, Лунные копры, Скарабеи
– Flies	Kotfliegen	Cordyluridés	Колосковые мухи
Dusty Wings	Staubhafte	Conioptérygidés	
Earwigs	Ohrwürmer	Dermaptères	Кожистокрылые
Eastern subterranean Termite	Gelbfüßige Termite	Termite aux pieds jaunes	Желтоногий термит
Embiids	Fersenspinner		Эмбии
Emperor Dragonfly	Königslibelle	Anax empéreur	
– Moth	Kleines Nachtpfauenauge	Petit paon de nuit	Малый ночной павлиний глаз
– Moths	Augenspinner	Saturniides	Павлиноглазки
Ensign Flies	Hungerwespen	Evaniides	Эваниды
Erratic Ants	Rasenameise	Fourmi des prés	
European Ant-loving Crickets	Europäische Ameisengrille	Grillon myrmécophile de l'Europe	

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
– Apple Sawfly	Apfelsägewespe	Hoplocampe du pommier	Яблонный плодовый пилильщик
– Fruit Lecanium	Zwetschgen-Napfschildlaus	Cochenille du cornouiller	Акациевая ложнощитовка
– House Mosquito	Gemeine Stechmücke	Moustique commun	Обыкновенный комар
– Lantern-fly	Europäischer Laternenträger	Fulgoride européen	Обыкновенная светоноска
– Mantis	Gottesanbeterin	Mante prie-Dieu	Обыкновенный богомол
– Velvet-ant	Europäische Ameisenwespe	Mutille d'Europé	Европейская немка
– Wheat Stem Sawfly	Getreidehalmwespe	Cèphe du blé	Хлебный пилильщик
Eyed Hawk	Abendpfauenauge	Demi-paon	Глазчатый бражник
False Click Beetles (N. A.)	Schienenkäfer	Eucnémidés	
– Crane Flies	Faltenmücken	Liriopeidés	
– Darkling Beetles (N. A.)	Düsterkäfer	Serropalpidés	
– Pine Webworm	Stahlblaue Kiefernschonungs – Gespinstblattwespe	Lyde bleue	
– Powder-post Beetles (N .A.)	Kapuzinerkäfer	Bostryches	
Fat Flies	Spinnenfliegen		
Field-cricket	Feldgrille	Grillon des champs	Шаровки
Field Tiger Beetles	Feld-Sandlaufkäfer	Cicindèle des champs	Полевой сверчок
Fig Insects	Feigenwespen	Cynips du figuier	Полевой скакун
Firebrat	Ofenfischchen		
Firebug	Feuerwanze	Punaise sans ailes	Бескрылый красноклоп
Fire Cuckoo Wasp	Feuergoldwespe	Chrysis enflammée	Обыкновенная блестянка
Fir Web-spinning Sawfly	Fichten-Gespinstblattwespe	Lyde de l'épicéa	
Flat Bark Beetles (N. A.)	Plattkäfer	Rhizophagidés	Плоскотелки
– Bugs	Rindenwanzen	Aradidés	Подкорники
Flat-footed Flies (N. A.)	Rollfliegen	Clythiidés	
Fleas	Flöhe	Puces	Блошиные
Flies	Zweiflügler	Diptères	Двукрылые
Flower Bugs	Blumenwanzen	Punaises des fleurs	Цветочные клопы
– Tree-cricket	Weinhähnchen		Трубачик
Fly Bug	Kotwanze	Punaise masqué	Грязный хищнец
Foresters	Grünwidderchen	Procris	
Four-banded Mining Bee	Viergürtlige Schmalbiene	Halicte des sillons à quatre bandes	
Four-spotted Libellula	Vierflecklibelle	Libellule à quatre taches	Пятнистая стрекоза
Frit Fly	Fritfliege	Oscinie frit	Овсяная шведская мушка
Fritillaries	Perlmutterfalter	Nacrés	Перламутровки
Frog-hoppers	Schaumzikaden	Cercopidés	Пенницы
Fungus Gnats	Pilzmücken	Mycetophilidés	Грибные комарики
– Weevils (N. A.)	Breitrüßler	Anthribidés	Ложнослоники
Gall Midges	Gallmücken	Cécidomyus	Галлицы
– Wasps	Gallwespen	Cynipides gallicoles	Настоящие орехотворки
Garden March Fly	Gartenhaarmücke	Bibion des jardins	Садовая мошка
– Tiger	Brauner Bär	Ecaille martre	Бурая медведица
Gemmet Shoot	Kieferntriebwickler	Tordeuse des pousses	Сосновая плодожорка
Geometers	Spanner	Géométrides	Пяденицы
German Cockroach	Hausschabe	Blatte d'Allemagne	Рыжий таракан
– Grasshopper	Rotflüglige Ödlandschrecke		Краснокрылая кобылка
Ghost Swift	Hopfenwurzelbohrer	Hépiale du'houblon	Хмелевый тонкопряд
Giant Crane Fly	Riesenschnake	Tipule géante	Большая долгоножка
– Termites	Riesentermiten	Termites géantes	
– Water Bugs	Riesenwanzen	Belostamatidés	
Gipsy	Schwammspinner	Bombyx disparate	Непарный шелкопряд
Gladiolus Thrips	Gladiolenthrips	Thrips du gladiole	Гладиолусовый трипс
Glowworms	Leuchtkäfer	Lampyridés	Светляки
Goat Louse	Ziegenlaus	Pou du chèvre	Козья вошь
– Moth	Weidenbohrer	Cossus gâte-bois	Пахучий древоточец
Golden Braconid Fly	Goldfliegen-Brackwespe	Alysia dorée	
Golden-ringed Dragonflies	Quelljungfern	Cordulégastrides	
Gold Swift	Heidekraut-Wurzelbohrer	Hépiale de la fougère	
Goliath Beetle	Goliathkäfer		Вересковый тонкопряд
Gout Fly	Gelbe Halmfliege	Chlorops du blé et de l'onge	Жук-голиаф
Grain Ants	Getreideameisen	Fourmi moissonneuse	Желтая зеленоглазка
– Thrips	Getreidethripse	Thrips du blé	Муравьи-жнецы
Grasshoppers	Feldheuschrecken	Acridiens	Хлебные трипсы
Grass Moths	Graszünsler	Crambides	Настоящие саранчовые
Grayling	Ockerbindiger Samtfalter	Agreste	
Great Birch Sawfly	Große Birkenblattwespe	Cimbex du bouleau	Сатир семеле
– Green Bush-cricket	Grünes Heupferd	Grande sauterelle verte	Березовый булавоус
– Pine Web-spinning Pine-sawfly	Große Kiefernbestands-Gespinstblattwespe	– lyde champêtre	Обыкновенный зеленый кузнечик
– Silver Water-beetle	Großer Kolbenwasserkäfer	Grand Hydrophile	Большой сосновый пилильщик-ткач
– Viceroy	– Eisvogel	– Sylvain	Черный большой водолюб
– Water Beetle	Gelbrandkäfer	Dytisque bordé	Тополевая ленточница
Green Lacewing	Goldauge	Chrysops commun	Окаймленный плавунец
			Простая златоглазка

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
– Sawfly	Grüne Blattwespe	Rhogogaster vert	Большой зеленый пилильщик
– Shieldbug	– Stinkwanze	Punaise verte	Зеленый древесный щитник
Green-veined White	Rübenweißling	Piéride du navet	Горчичная белянка
Greenhouse Camel-cricket	Gewächshausschrecke	Sauterelle grillon de serre	Оранжерейный кузнечик
– Thrips	Treibhausthrips	Thrips des serres	Оранжерейный трипс
– White Fly	Weiße Gewächshausfliege	Mouche blanche des serres	Тепличная белокрылка
Grey Flesh Fly	Graue Fleischfliege	– grise de la viande	Серая мясоедка
Grint Hornet	Hornisse	Frelon	Шершень
Ground Beetles (N. A.)	Schwarzkäfer	Ténébrionidés	Чернотелки
– Bugs	Langwanzen	Lygaeidés	Тощеклопы
Grouse Locusts	Dornschrecken	Tetrigides	Тетригиды
Hair-streaks	Zipfelfalter	Théclines	
Hairy Dragonfly	Mosaiklibellen	Aeschna à abdomen court	Коромысло
Hairylegged Mining Bees	Hosenbiene	Abeilles à pantalon	Мохноножки
Harvest Flies	Singzikaden	Cigales	Певчие цикады
Hawk-moth	Schwärmer	Sphingides	Бражники
Hazel Leaf Roller	Haselblattroller	Apodère du noisettier	Орешниковый трубковерт
– Scale	Haselschildlaus	Lécanium du noisettier	
Head Louse	Kopflaus	Pou de la tête	Головная вошь
Hessian Fly	Hessenfliege	Mouche d'Hesse	Гессенская муха
Hide Beetles	Sägekäfer, Speckkäfer	Heteroceridés, Dermestes	—, Кожееды
Hister Beetles	Stutzkäfer	Histénidés	Карапузики
Homeless Bees	Schmarotzerbienen	Abeilles parasites	
Honey Bee	Honigbiene	Abeille domestique	Обыкновенная медоносная пчела
Hornets	Echte Wespen	Vespides	Общественные осы
Horn-tails	Holzwespen	Siricidés	Настоящие рогохвосты
Horse Bot Flies	Magendasseln	Gastrophiles	Желудочные оводы
Horse-flies	Bremsen	Taons	Слепни
House-cricket	Hausgrille	Gryllon domestique	Домовый сверчок
House Fly	Große Stubenfliege	Mouche domestique	Большая комнатная муха
– Flies	Echte Fliegen	Muscidés	Настоящие мухи
– Longhorn	Hausbockkäfer	Hylotrupe	Домовый усач
Hover Flies	Schwebfliegen	Syrphidés	Журчалки
Human Flea	Menschenfloh	Puce de l'homme	Человеческая блоха
Humming-bird Hawk-moth	Taubenschwänzchen	Moro-sphinx	Языкан
Ichneumons	Eigentliche Schlupfwespen	Ichneumonides	Настоящие наездники
Insects	Insekten	Insectes	Насекомые
Italian Locust	Italienische Schönschrecke	Criquet italien	Обыкновенный прус
Jet Ant	Glänzendschwarze Holzameise	Fourmi fuligineuse	Муравей-древоточец
Jigger	Sandfloh	Chique	Вредная блоха
Katydids (N. A.)	Sattelschrecken	Ephippigérides	
Lacebugs	Netzwanzen	Tingidés	Кружевницы
Lace-wings	Hafte	Planipennes	Сетчатокрылые
Lackeys and Eggars	Glucken	Bombyx feuilles	Коконопряды
Ladybird	Siebenpunkt-Marienkäfer	Coccinelle à sept points	Семиточечная коровка
Lake Flies	Büschelmücken	Corethrines	Перистоусики
Lantern-flies	Laternenträger	Fulgoridés	Светоноски
Larch Sawfly	Große Lärchenblattwespe	Grand Pritisphore du larix	Большой лиственничный пилильщик
– Web-spinning Sawfly	Lärchen-Gespinstblattwespe	Lyde étoilée du laryx	
Large Blue	Arion-Bläuling	Alcon	
– Cabbage-white	Großer Kohlweißling	Piéride du chou	Капустная белянка
Large Carpenter Bees	Holzbienen	Abeille charpentièro	Пчелы-древогнезды
– Fruit Flies	Fruchtfliegen	Mouches des fruits	Пестрокрылки
– Horse Fly	Rinderbremse	Taon des bœufs	Бычий слепень
– Pine Weevil	Fichtenrüßler	Grand Charançon du sapin	Большой сосновый долгоносик
– Woodwasp	Riesenholzwespe	Sirex géant	Большой рогохвост
Largely-winged Insects	Fluginsekten	Ptérygotes	Высшие насекомые или Крылатые насекомые
Leaf Beetles	Blattkäfer	Chrysomélidés	Листоеды
Leaf-cutting Ants	Blattschneiderameisen	Les Atta	Атты
– – Bees	Blattschneiderbienen	Mégachiles	Пчелы-листорезы
Leaf-footed Bugs	Lederwanzen	Coréidés	Краевики
Leaf-insect	Wandelndes Blatt		Листотел
Leaf Miners	Minierfliegen	Agromyzidés	Минирующие мушки
– Rollers (Moths)	Wickler	Tortricides	Листовертки
Leaf-rollers (Wasps)	Gespinst-Blattwespen	Pamphilides	Паутинные пилильщики
Lesser Bulb Fly	Zwiebelfliegen	Mouches des oignons	Луковичные мухи
– House Fly	Kleine Stubenfliege	Petite mouche domestique	Малая комнатная муха
– Water-boatmen	Zwergrückenschwimmer	Pleidés	
Little Fir Sawfly	Kleine Fichtenblattwespe	Petit Pritisphore du pin	Малый еловый пилильщик
Lobster Moth	Buchenspinner	Écureuil	Буковый вилохвост

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Long-horned Beetles	Bockkäfer	Capricorines	Усачи или Дровосеки
Long-legged Flies	Langbeinfliegen	Dolichopodidés	
Long-nosed Oxlouse	Langköpfige Rinderlaus	Pou du veau	Длинноголовая коровья вошь
Long-winged Cone-head	Langflügelige Schwertschrecke	Conocéphalus brun	
Lucerne Flea	Luzernefloh	Sminthure vert	
Machilids	Felsenspringer	Machilides	Махилисы
Many-combed Bugs (N. A.)	Kammwanzen	Polycténidés	Клопы летучих мышей
Many-plume Moth	Geistchen	Orneodidés	Веерницы
Marbled White	Schachbrett	Demi-deuil	Шашечница
March-flies	Haarmücken	Bibionidés	Комары-толстоножки
Maroccan Grasshopper	Marokkanische Wanderheuschrecke	Criquet marocain	Марокккская саранча
Mason Bees	Mauerbienen	Abeille des murailles	Стенные пчелы
– Wasp	Wespe	Guêpe des murailles	Стенная оса
May Beetles	Maikäfer	Hannetons	Майские жуки
Mayflies	Eintagsfliegen	Ephémères	Поденки
Meadow-brown	Großes Ochsenauge	Myrtil	Воловий глаз
Mealworm	Mehlkäfer	Ténébrion meunier	Мучной хрущак
Mealy Bugs	Schildläuse	Cochenilles	Кокциды
Mediterranean Flour Moth	Mehlmotte	Teigne de la farine	Мельничная огневка
– Fruit Fly	Mittelmeerfruchtfliege	Mouche des oranges	Средиземноморская плодовая муха
– Stick-insect	Mittelmeer-Stabschrecke		Стеблевидка
Men-louse	Kopf- und Kleiderlaus	Pou de l'homme	Человеческая вошь
Metallic Wood-borers (N. A.)	Prachtkäfer	Buprestes	Златки
Migratory Locusts	Wanderheuschrecken	Sauterelles de passage	
Mole-cricket	Maulwurfsgrille	Taupe-gryllon commun	Обыкновенная медведка
Monarch (N. A.)	Monarchfalter	Monarque	
Morphos	Morphofalter	Morphos	
Mosquitoes	Fiebermücken, Stechmücken	Anophèles, Moustiques	Малярийные комары, Настоящие комары или Кровососущие комары
Mossy Rose Gall	Gemeine Rosengallwespe	Diplolepis du rosier	Розанная орехотворка
Moth Flies	Schmetterlingsmücken	Phlébotonies	Бабочницы
Mould Beetles	Moderkäfer	Lathriidés	
Mouth Flies	Rachendasseln	Cephenomyes	Глоточные оводы
Museum Beetle	Museumskäfer		Кабинетные кожееды
Mussel Scale	Kommaschildlaus	Cochenille des arbres fruitiers	Запятовидная щитовка
Net-winged Beetles (N. A.)	Schnabelkäfer	Lycidés	
– – Midges	Lidmücken	Blépharocéridés	Сетчатокрылки
Noctuids	Eulenfalter	Noctuelles	Совки или Ночницы
Non-biting Midges	Zuckmücken	Tendipédidés	Звонцы или Комары-дергуны
Nut Weevil	Haselnußbohrer		Ореховый долгоносик
Oak-apple Gallfly	Eichen-Schwammgallwespe	Biorhiza du chêne	Губчатая дубовая орехотворка
Oak Bush-cricket	Eichenschrecke	Méconema	Дубовый кузнечик
– Eggar	Eichenspinner	Minime à baudes jaunes	Дубовый кокономряд
– Leaf Roller	Eichenblattroller	Attelabe du chêne	Дубовый трубковерт
Oedemerid Beetles (N. A.)	Scheinböcke	Oedéméridés	Узконадкрылки
Onion Thrips	Tabakthrips	Thrips de l'oignon et du tabac	Табачный трипс
Orchid Wasp	Orchideenwespe	Guêpe des orchidées	Орхидеевый семеед
Ostomatid Beetles	Jagdkäfer	Ostomidés	
Oystershell Scale	Kommaschildlaus	Cochenille des arbres fruitiers	Запятовидная щитовка
Painted Lady	Distelfalter	Belle-dame	Репейница
Pale Clouded Yellow	Gemeiner Heufalter	Soufré	Луговая желтушка
Papatasi Sandfly	Papatacimücke	Phlébotome de Papatau	
Parasite Flies	Raupenfliegen	Larvivoridés	Ежемухи
Parasitic Earwigs	Doppelzüngler	Diploglossates	
Parasitical Hymenoptera	Legwespen	Parasites	
Passalid Beetles (N. A.)	Zuckerkäfer	Passalidés	Сахарные жуки
Peach-potato Aphid	Pfirsichblattlaus	Puceron vert du pêcher	Персиковая тля
Peacock	Tagpfauenauge	Paon de jour	Дневной павлиний глаз
Pea-green Oak Twist	Eichenwickler	Tordeuse du chêne	Дубовая листовертка
Pebble Prominents	Zickzackspinner, Kamelspinner	Notodontides, Bois veinés	Хохлатки
Peppered Moth	Birkenspanner	Phalène du bouleau	Березовая пяденица
Periodical Cicadas	Siebzehnjahr-Zikade	Cigale de 17ans	Цикада семнадцатилетка
Phyllids	Blattflöhe	Psyllines	Листоблошки или Медяницы
Piercer	Apfelwickler	Pyrale des pommes	Яблонная плодожорка
Pig Louse	Schweinelaus	Pou du porc	Свиная вошь
Pigeon-lice	Taubenfederlinge	Poux de colombes	Голубиные пероеды
Pigmy Cockroaches	Kleinschaben	Petit Blattes	
– Mole-crickets	Dreifingerschrecken	Tridactylides	Триперстовые

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Pill Beetles	Pillenkäfer	Byrrhidés	Пилюльщики
Pine Beauty	Kieferneule	Varié de gris	Сосновая совка
Pine-feeding Processionary Caterpillar	Pinien-Prozessionsspinner	Processionnaire du pin	Пиниевый походный шелкопряд
Pine Lappet	Kiefernspinner	Feuille morte du pin	Сосновый кокономряд
– Sawfly	Gemeine Kiefernbuschhorn-Blattwespe	Diprion du pin	Сосновый пилильщик
Pit Scales	Pockenschildläuse	Cochenille des véroles	
Plant Bugs	Schmalwanzen	Miridés	Клопы-слепняки
Plumes	Federmotten	Ptérophores	Пальцекрылки
Polished Horntail	Gemeine Holzwespe	Sirex commun	Обыкновеный сосновый рогохвост
Pollen Beetle	Rapsglanzkäfer	Méligèthe bronzé	Рапсовая блестянка
Pond Weed Bugs	Hüftwasserläufer	Mesoveliidées	
Pondskaters (N. A.)	Wasserläufer	Gerridés	Водомерки
Poplar Hawk	Pappelschwärmer	Sphinx du peuplier	Тополевый бражник
– Hornet Clearwing	Hornissenschwärmer	Sésie du peuplier	Большая тополевая стеклянница
Potter Flower Bees	Pelzbienen	Anthophores	Антофоры
– Wasps	Lehmwespen	Euménines	Одиночные осы
Powder-post Beetles	Splintholzkäfer	Lyctidés	
Praying Mantids	Fangschrecken	Mantides	Богомолы
Predatory	Jagdthripse	Thrips à chasse	Сиреневый бражник
Privet Hawk	Ligusterschwärmer	Sphinx du troène	Хоботковые пухоеды
Proboscis Lice	Rüsselläuse	Poux à trompes	Походные шелкопряды
Processionary Caterpillars	Prozessionsspinner	Processionnaires	
Proctotrupoids	Zehrwespen	Proctotrupoidés	Хохлатки
Prominents	Zahnspinner	Notodontides	Бессяжковые насекомые
Proturans	Halbinsekten	Protoures	
Pseudogall Coccids	Eichennapfläuse	Cochenilles du chêne	Апатуры
Purple Emperor	Schillerfalter	Apatura	Вилохвосты
Pusses	Gabelschwänze	Petites-queues-fourchues	Красноклопы
Pyrrhocorid Bugs	Feuerwanzen	Pyrrhocoridés	Адмирал
Red Admiral	Admiral	Vulcain	
– Locust	Rote Wanderheuschrecke	Criquet nomade	Тополевый листоед
– Poplar Leaf Beetle	Pappelblattkäfer		Красная ленточница
– Underwing	Rotes Ordensband	Mariée	Трескучая кобылка
Red-winged Grasshopper	Rotflügelige Schnarrschrecke		Исполинские жуки
Rhinoceros Beetles	Nashornkäfer	Dynastinés	Рододендроновый клоп
Rhododendron Bug	Rhododendron-Netzwanze	Tigre du rhododendron	Сенницы
Ringlets	Heufalter		
Rolling Wasps	Rollwespen i. e. S.	Tiphides	Бронзовки
Roses Chafers	Rosenkäfer	Cetonines	Розанная цикадка
Rose Leafhopper	Rosenzikade	Cicadelle du rosier	Розанный пилильщик
– Sawfly	Rosen-Bürsthornwespe	Hylotome de la rose	Розанный пилильщик-ткач
– Web-spinning Sawfly	Rosen-Gespinstblattwespe	Lyde du rosier	Настоящие коротко-надкрылые жуки
Rove Beetles	Kurzflügler	Staphylins	Голотелки
			Священный навозник
Rust Flies	Nacktfliegen	Psilidés	Прыгающие прямокрылые
Sacred Scarab	Heiliger Pillendreher		Калифорнийская щитовка
Saltatoria	Schrecken	Sauterelles	Обыкновенный пескорой
San Jose Scale	San-José-Schildlaus	Pou de San José	Москиты
Sand Wasp	Sandwespe	Guêpe des sables	Блестянки
Sandflies	Sandmücken i. e. S.	Phlébotomines	
Sap-beetles	Glanzkäfer	Nitidulidés	
Saucer Bugs	Schwimmwanzen	Naucoridés	Сидячебрюхие перепончатокрылые
Sausage Ants	Treiberameisen	Dorylinés	Кистехвост
Sawflies	Pflanzenwespen, Sägewespen	Symphytes	Заболонники
			Скорпионницы
Scarce Vapourer	Bürstenbinder	Scolytes	
Scolytid Beetles	Borkenkäfer	Panorpides	Зерновки
Scorpion Flies	Skorpionsfliegen	Hygrobiidés	Цикада семнадцатилетка
Screech Beetles	Schlammkäfer	Bruches	Могильщики
Seed Beetles	Samenkäfer	Cigale de 17 ans	
Seventeen year Locust	Siebzehnjahr-Zikade	Nécrophores	Овечий овод
Sexton Beetles	Totengräber	Noctuelle d'armoise	Овечья кровососка
Sharks	Grauer Beifußmönch	Œstre du mouton	Овечья вошь
Sheep Gadfly	Schaf-Nasendassel	Mélophage du mouton	Щитники
– Ked	Schafslausfliege	Pou du mouton	
– Louse	Schafslaus	Punaises à bouclier	Береговые клопы
Shield Bugs	Schildwanzen	Machilide du littoral	
Shore Bristle-tail	Küstenspringer	Saldidés	
– Bugs	Uferwanzen	Ephydridés	
– Flies	Sumpffliegen		

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Short-horns	Fliegen	Brachycères	Мухи или Короткоусые двукрылые
Short-tentacled Grasshoppers	Kurzfühlerschrecken	Sauterelles de palpes courtes	Саранчовые и Трипер-стовые
Siberian Grasshopper	Sibirische Keulenschrecke	Sauterelle de Sibérie	Сибирская саранча
Silk-moths	Echte Spinner	Bombycides	Настоящие шелкопряды
Silverfish	Silberfischchen	Poisson d'argent	Чешуйницы
Silver-studded Blue	Argusbläuling	Azuré	
Silver-washed Fritillary	Kaisermantel	Tabac d'Espagne	Большая лесная перламутровка
Six-spot Burnet	Blutströpfchen	Zygène-de-la-filipendule	Таволговая пестрянка
Skippers	Dickkopffalter	Hespérides	Толстоголовки
Sloebug	Beerenwanze	Punaise des baies	Ягодный клоп
Small Black Ant	Schwarze Wiesenameise	Fourmi noire des prés	Черный луговой муравей
– Earwig	Zwergohrwurm	Perce-oreille nain, Forficule nain	Малая уховертка
– Ermines	Gespinstmotten	Hyponomeutidés	Горностаевые моли
– Fruit Flies	Taufliegen	Drosophilidés	Дрозофилы
– Tortoiseshell	Kleiner Fuchs	Petite tortue	Крапивница
– White	– Kohlweißling	Piéride de rave	Репная белянка
Smaller Larch Sawfly	Kleine Lärchenblattwespe	Petit Pritisphore du milize	Малый лиственичный пилильщик
Snake Flies	Kamelhalsfliegen	Raphididés	Верблюдки
Snipe-flies	Schnepfenfliegen	Rhagionidés	Бекасоноски
Snout Moths	Zünsler	Pyralididés	Огневки
Snow Scorpion Flies	Winterhafte	Boréides	
Soft Scales	Schalenschildläuse	Lécanines, Coccidés	Подушечницы или Ложнощитовки
Soldier-beetles	Weichkäfer	Cantharidés	Мягкотелки
Soldier Flies	Waffenfliegen	Stratiomyidés	Львинки
Solitary Bees	Sandbienen	Andrenidés	Андрены
Southern Aeshna	Blaugrüne Mosaikjungfer	Aeschna bleue	
Spanish Flies	Spanische Fliegen	Mouches d'Espagne	Шпанские мухи
Sphagnum Bugs	Zwergwasserläufer	Hébridés	
Spider Beetles	Diebskäfer	Ptinidés	Притворяшки
Spider-wasps	Wegwespen	Pompilidés	Дорожные осы
Spined Rat Louse	Rattenlaus	Pou du rat	Крысиная вошь
Spittle Bugs	Schaumzikaden	Cercopidés	Пенницы
Springtails	Springschwänze	Collemboles	Ногохвостки или Вилохвостки
Spruce	Europäische Fichtenblattwespe	Tenthride du pin	Европейский еловый пилильщик
Squash Bugs	Lederwanzen	Coréidés	Краевики
Stable Fly	Wadenstecher	Mouche des étables	Жигалка
Stag Beetle	Hirschkäfer	Lucane cerf-volant	Жук-олень
Stalk-eyed Flies	Stielaugenfliegen	Diopsides	
Stem Sawflies	Halmwespen	Céphidés	Стеблевые пилильщики
Stick- and Leaf-insects	Gespenstschrecken	Phasmes	Привиденьевые
Stiletto Flies	Stilettfliegen	Thérévidés	Ктыревидки
Stilt Bugs	Stelzenwanzen	Bérytidés	
Stingless Bees	Stachellose Bienen	Abeilles sans aiguillon	
St. John's Fly	Johannisfliege	Bibion de St. Jean	
St. Mark's Fly	Märzfliege	– St. Marc	Черная мошка
Stoneflies	Steinfliegen	Plécoptères	Веснянки
Strawberry Blossom Weevil	Beerenstecher		Ягодный цветоед
Sucking Horse Louse	Pferdelaus	Pou de l'âne	Лошадиная вошь
– Lice	Echte Läuse	Anoplurés	Настоящие вши
Sugar-cane Borer	Zuckerrohrzünsler	Pyrole de la canne à sucre	
Surinam Cockroach	Gewächshausschabe	Blatte de serre	Суринамский таракан
Swallow Bug	Schwalbenwanze	Punaise d'hirondelle	Ласточковый клоп
– Louse Fly	Schwalbenlausfliege	Mouche des hirondelles	Ласточковая кровососка
Swallowtail Family	Ritterfalter	Papilionidés	Парусники или Кавалеры
Swallowtails	Echte Schwalbenschwänze	Papilios	
Swift Louse Fly	Mauersegler-Lausfliege	Mouche des martinets	Стрижиная кровососка
Swifts	Wurzelbohrer	Hépialides	Тонкопряды
Tapestry Moth	Gemeine Tapetenmotte	Teigne des tapis	Ковровая моль
Termite Flies	Termitenfliegen	Mouches des termitières	
Termites	Termiten	Termites	Термиты
Thick-headed Flies	Dickkopffliegen	Conopidés	Толстоголовки
Thread-horns	Mücken	Nématocères	Комары
Thread-waisted Wasps	Grabwespen	Sphécidés	Роющие осы
Three-horned Dor Beetles	Dreihorn-Mistkäfer	Minotaure typhée	Трехрогие навозники
Three-pronged Bristle-tails	Zangenschwänze	Japyx	
Thrips	Fransenflügler	Thrips	Бахромчатокрылые
Tiger Beetles	Sandlaufkäfer	Cicindèles	Скакуны
Tiger-moths	Bärenspinner	Arctiidés	Медведицы
Timber Beetles [N. A.]	Werftkäfer	Lymexylonidés	Жуки-матросы

ENGLISH NAME	GERMAN NAME	FRENCH NAME	RUSSIAN NAME
Timberman	Zimmermannsbock		Домовый дровосек
Tingids	Netzwanzen	Tingidés	Кружевницы
Tiny Wasps	Zwergwespen	Mymaridés	
Tiphiid Wasps	Rollwespen	Tiphides	Тифии
Tortoise Beetles	Schildkäfer	Cassidinés	Щитоноски
Tree-crickets	Baumgrillen		Стеблевые сверчки
Tree-hoppers	Buckelzirpen	Membracidés	Горбатки
Tree Locust	Ägyptische Knarrschrecke	Criquet d'Egypte	Египетская саранча
– Wasp	Sächsische Wespe, Waldwespe	Guêpe de Saxe, Guêpe sylvestre	Саксонская оса, Лесная оса
Tropical Ratflea	Indischer Rattenfloh		Южная крысиная блоха
True Bugs	Schnabelkerfe	Hémiptères	Настоящие полужестко-крылые
Tsetse Flies	Tsetsefliegen	Mouches tsé-tsé	Мухи це-це
Tubuliferae	Röhren-Fransenflügler	Tubulifères	Трубкохвостые трипсы
Tumbling Flower Beetles [N. A.]	Stachelkäfer	Mordellidés	Шипоноски или Горбатки
Turnip Sawfly	Runkelrüben-Blattwespe	Athale de la betterave	Рапсовый пилильщик
– Dart	Saateule	Noctuelle des moissons	Озимая совка
– Mud Beetles	Furchenwasserkäfer	Helophoridés	
Tussock-moths	Trägspinner	Lymantriides	Волнянки
Twisted-winged Insects	Fächerflügler	Strepsitères	Веерокрылки
Two-pronged Bristle-tails	Doppelschwänze	Diploures	Двухвостки
Underwings	Ordensbänder	Linchénées	Ленточницы
Variable Coenagrion	Fledermaus-Azurjungfer	Agrion joli	
Velvet-ants	Ameisenwespen	Mutillides	Немки
Vine Louse	Reblaus	Phylloxéra	Виноградная филоксера или Виноградная тля
Violin Beetles	Gespenstlaufkäfer		Лиственные жужелицы
Warble Flies	Hautdassel	Hypodermes	Кожные оводы
Wart-biter	Warzenbeißer	Dectique verrucivore	Серый кузнечик
Water-beetles	Eigentliche Wasserkäfer	Hydrophiles	Водолюбы
Water Bugs	Wasserwanzen	Punaises d'eau	Водяные клопы
Water-crickets	Bachläufer	Véliidées	
Water-measurers	Teichläufer	Hydrométridés	Водомерки
Water-scorpions	Skorpionswanzen, Wasserskorpione	Népidés, Népa roux	Водяные скорпионы
Water Springtail	Wasser-Kugelspringer	Sminthuride d'eau	
– Stick-insect	Stabwanze	Punaise linéaire	Ренатра
Wax Moth [N. A.]	Wachsmotte	Taupe teigne des ruches	Восковая моль или Большая пчелиная огневка
Web-spinning Pine-sawfly	Kiefernkultur-Gespinstblattwespe	Lyde champêtre	Одиночный сосновый пилильщик-ткач
Weevils [N. A.]	Rüsselkäfer	Charançons	Долгоносики
Whirling Beetles	Taumelkäfer	Gyrins	Вертячки
White Flies	Mottenschildläuse	Aleurodinés	Алейродиды
– Grub	Feldmaikäfer	Ver blanc	Западный майский хрущ
Whites	Weißlinge	Piérides	Беляики
Willow-shoot Hole	Weidenholzgallmücke	Moustique des saules	Ивовая галлица
Window Fly	Buckelige Fensterfliege, Fenstermücke	Mouche des fenêtres, Phryne des fenêtres	Оконная муха
Winter Gnat	Winterschnake	Trichocère hivernal	
Wood Ant	Große Rote Waldameise	Fourmi rousse	Лесной рыжий муравей
– Cockroaches	Waldschaben	Blattes des bois	Лесные тараканы
Wood-cricket	Waldgrille	Grillon des bois	
Wood Leopard	Kastanienbohrer	Zeuzère du marronnier	Въедливая древесница
Wool Carder Bees	Wollbienen	Abeille cotonnière	
Woolly Aphids	Blutläuse		Кровяные тли
– Apple Aphid	Blutlaus	Puceron laineux	Кровяная тля
Yellow Dung Fly	Kotfliege	Mouche des bouses	
– Fever Mosquito	Gelbfiebermücke	Moustique de la fièvre jaune	Желтолихорадный комар
Yellow-fronted Digger Wasp	Gelbstirnige Dolchwespe	Scolia à front jaune	Желтолобая сколия
Yellow Jackets	Faltenwespen	Vespides	Складчатокрылые осы
Yellow-necked Termite	Gelbhalstermite	Termite à cou jaune, Flavicolle	Желтошеий термит
Zoropterons	Bodenläuse	Poux de terre	

2. German—English—French—Russian

N. A. bei englischen Namen bedeutet, daß dieser Name nur in Nordamerika gebräuchlich ist.

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Aaskäfer	Carrion Beetles, Burying Beetles	Silphidés	Мертвоеды
Abendpfauenauge	Eyed Hawk	Demi-paon	Глазчатый бражник
Abraxas grossulariata	Common Magpie Moth	Zérène mouchetée du groseillier	Крыжовниковая пяденица
Acanthocinus aedilis	Timberman		Домовый дровосек
Acantholyda erythrocephala	False Pine Webworm	Lyde bleue	
– *hieroglyphica*	Web-spinning Pine-sawfly	– champêtre	Одиночный сосновый пилильщик-ткач
–*posticalis*	Great Pine Web-spinning Pine-sawfly	Grande lyde champêtre	Большой сосновый пилильщик-ткач
Acherontia atropos	Death's-head Hawk	Sphinx tête du mort	Мертвая голова
Acheta domestica	House-cricket	Gryllon domestique	Домовый сверчок
Acrididae	Grasshoppers	Acridiens	Настоящие саранчовые
Acronycta alni	Alder Dagger	Noctuide d'aune	Ольховая стрельчатка
Aculeata		Guêpes piqueuses	Жалоносные перепончато-крылые
Adelgidae	Adelgids	Puceron des sapins	Хермесы
Admiral	Red Admiral	Vulcain	Адмирал
Aedes cinereus		Aedes cendré	Серый комар-кусака
– *communis*		– commun	Обыкновенный комар-кусака
– *maculatus*		– tacheté	Пятнистый комар-кусака
Aegeria apiformis	Poplar Hornet Clearwing	Sésie du peuplier	Большая тополевая стеклянница
Aegeriidae	Clairwings	Sésies	Стеклянницы
Aelia		Punaise du blé	Остроголовые клопы
Aeschna	Hairy Dragonfly	Aeschna à abdomen court	Коромысло
– *cyanea*	Southern Aeshna	– bleue	
Agaonidae	Fig Insects	Cynips du figuier	
Agapetes galathea	Marbled White	Demi-deuil	Шашечница
Agelastica alni		Galeruque de l'aulne	Ольховая козявка
Aglais urticae	Small Tortoiseshell	Petite tortue	Крапивница
Aglia tau		Hachette	Рыжий ночной павлиний глаз Кошачий глаз
Agrion pulchellum	Variable Coenagrion	Agrion joli	
Agromyzidae	Leaf Miners	Agromyzidés	Минирующие мушки
Agrotis segetum	Turnip Dart	Noctuelle des moissons	Озимая совка
Ägyptische Knarrschrecke	Tree Locust	Criquet d'Egypte	Египетская саранча
Ahornspringlaus		Puceron du platane	Кленовая тля
Aleurocanthus woglumy	Citrus Black Fly	Mouche noire des Aurantiacées	Темнокрылая белая мушка
Aleurodina	White Flies	Aleurodinés	Алейродиды
Alpen-Apollo		Petit Apollon	Альпийский аполлон
Alysia manducator	Golden Braconid Fly	Alysia dorée	
Amazonenameise		Fourmi Amazon	Муравей-амазонка
Amblycera		Poux à tentacle cônes	Короткоусиковые пухоеды
Ameisen	Ants	Formicidés	Муравьи
Ameisengrillen	Ant-loving Crickets	Grillons myrmécophiles	
Ameisenlöwen	Ant Lions	Fourmis-lions	Муравьиные львы
Ameisenwanze		Punaise de la fourmi	Муравьиный клоп
Ameisenwespen	Velvet-ants	Mutillides	Немки
Amerikanische Ameisengrille	American Ant-loving Crickets	Grillon myrmécophile de l'Amérique	
– Großschabe	American Cockroach	Blatte américaine	Американский большой таракан
Ammophila adriaansei	Sand Wasp	Guêpe des sables	Обыкновенный пескорой
Anacridium aegyptium	Tree Locust	Criquet d'Egypte	Египетская саранча
Anasa tristis	Squash Bug	Punaise de courge	Тыквенный клоп
Anax imperator	Emperor Dragonfly	Anax empéreur	
Andrena	Solitary Bees	Andrenidés	Андрены
Anisoptera	Dragonflies	Anisoptères	Разнокрылые стрекозы
Anobiidae	Drugstore Beetles	Vrillettes	Точильщики
Anopheles	Mosquitoes	Anophèles	Малярийные комары
Anoplura	Sucking Lice	Anoplurés	Настоящие вши
Antarctophthirus microchir		Pou du lion marin	Сивучовая вошь
Anthidium	Wool Carder Bees	Abeille cotonnière	
Anthocoridae	Flower Bugs	Punaises des fleurs	Цветочные клопы
Anthomyiinae	Cabbage Root Fly	Anthomyiinés	
Anthonomus	Blossom Weevils	Anthonomes	Цветоеды
– *pomorum*	Apple Blossom Weevil	Anthonome du pommier	Яблонный цветоед
– *rubi*	Strawberry Blossom Weevil		Ягодный цветоед
Anthophora	Potter Flower Bees	Anthophores	Антофоры
Anthophorinae		Anthophores	Антофоры
Anthrenus	Carpet Beetle	Anthrène du cabinet	Кабинетные кожееды

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
– *museorum*	Museum Beetle		Кабинетные кожееды
– *scrophulariae*	Carpet Beetle	Anthrène de la scrophulaire	Ковровый кожеед
Anthribidae	Fungus Weevils (N. A.)	Anthribidés	Ложнослоники
Apanteles glomeratus	Braconid Fly	Ichneumon	Капустничный апантелес
Apatura	Purple Emperor	Apatura	Апатуры
– *iris*	– –	Grand mars changeant	Мерцательница
Apfelblattsauger	Apple Psylla	Psylle du pommier	Яблонная медяница
Apfelblütenstecher	– Blossom Weevil	Anthonome du pommier	Яблонный цветоед
Apfelsägewespe	European Apple Sawfly	Hoplocampe du pommier	Яблонный плодовый пилильщик
Apfelwanze	Apple Capsid Bug	Capsid du pommier	Яблонный клоп
Apfelwickler	Piercer	Pyrale des pommes	Яблонная плодожорка
Aphididae	Aphids	Aphididés	Настоящие тли
Aphidiidae	Ichneumons	Aphidiidés	Тлиные наездники
Aphidina	Aphids	Pucerons	Тли
Aphis fabae	Black Bean Aphid	Puceron de la fève	Свекловичная тля
Aphodiinae	Dung Beetles	Aphodiinés	Пометокопатели
Aphrophora salicina		Cigale du saule	Ивовая пенница
Apidae	Bumble Bees	Abeille domestique	Настоящие пчелы
Apis cerana	Honey Bee	– de l'Inde	Индийская медоносная пчела
– *dorsata*	– –	– naine	Исполинская пчела
– *florea*			Карликовая пчела
– *mellifica*	– –	– domestique	Обыкновенная медоносная пчела
Apocrita	Apocrites	Apocrites	
Apoderus coryli	Hazel Leaf Roller	Apodère du noisettier	Орешниковый трубковерт
Apoidea	Bees	Apoidés	Пчелиные
Apollofalter	Apollo	Apollon	Аполлон
Aporia crataegi	Black-veined White	Piéride d'aubépine	Боярышница
Aprilfliege	St. Mark's Fly	Bibion de St. Marc	Черная мошка
Aradidae	Flat Bugs	Aradidés	Подкорники
Araschnia levana		Carte géographique	Весенняя Пестрокрыльница
Arctia caja	Garden Tiger	Ecaille martre	Бурая медведица
Arctiidae	Tiger-moths	Arctiidés	Медведицы
Arge ochropus	Rose Sawfly	Hylotome de la rose	Розанный пилильщик
Argusbläuling	Silver-studded Blue	Azuré	
Argynnis	Fritillaris	Nacrés	Перламутровки
– paphia	Silver-washed Fritillary	Tabac d'Espagne	Большая лесная перламутровка
Arion-Bläuling	Large Blue	Alcon	
Ascalaphidae		Ascalaphidés	Аскалафы
Asilidae	Assasin Flies	Asilidés	Ктыри
Asterolecanidae	Pit Scales	Cochenille des véroles	
Asterolecanium variolosum		– du chêne	Дубовый червец
Athalia rosae	Turnip	Athale de la betterave	Рапсовый пилильщик
Atlasspinner	Atlas Moth	Bombyx atlas	
Atta	Leaf-cutting Ant	Les Atta	Атты
Attacus atlas	Atlas Moth	Bombyx atlas	
Attelabus nitens	Oak Leaf Roller	Attelabe du chêne	Дубовый трубковерт
Augenfalter	Meadow Browns	Satyrides	Сатиры
Augenfliegen	Big-headed Flies	Dorilaidés	Цикадоедки
Augenspinner	Emperor Moths	Saturniides	Павлиноглазки
Autographa gamma	Common Silver Y Moth	Lettre grecque	Совка гамма
Autokratkäfer	Cellar Beetles	Trictenotomdiés	
Bachläufer	Water-crickets	Véliidées	
Bacillus rossii	Mediterranean Stick-insect		
Bärenspinner	Tiger-moths	Arctiidés	Стеблевидка
Baumgrillen	Tree-crickets		Медведицы
Baumthripse			Стеблевые сверчки
Baumweißling	Black-veined White	Thrips d'arbres	Древесные трипсы
Beerenstecher	Strawberry Blossom Weevil	Piéride d'aubépine	Боярышница
Beerenwanze	Sloebug		Ягодный цветоед
Beintastler	Proturans	Punaise des baies	Ягодный клоп
Bellicositermes bellicosus		Protoures	Бессяжковые насекомые
Belostomidae	Giant Water Bugs	Termite militaire	Воинственный термит
Bembecia hylaeiformis		Belostamatidés	
Bergzikade		Sésie du framboisier	Малинная стеклянница
Berytidae	Stilt Bugs	Cigale de montagne	Горная цикада
Bestachelte Hautflügler		Bérytidés	
		Guêpes piqueuses	
Bettwanze	Bed Bug	Punaise des lits	Жалоносные перепончатокрылые
Biberlaus		Platypsylles	Постельный клоп
Bibio hortulana	Garden March Fly	Bibion des jardins	Бобровые блохи
– *johannis*	St. John's Fly	– de St. Jean	Садовая мошка
– *marci*	St. Mark's Fly	– de St. Marc	Черная мошка

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Bibionidae	March-flies	Bibionidés	Комары-толстонотки
Bienen	Bees	Apoidés	Пчелиные
Bienenläuse	Bee-»Lice«	Braulidés	Пчелиные паразиты
Bienenwolf	Bees Wool	Philanthe apivore	Пчелиный волк
Biesfliegen i. e. S.	Warble Flies	Hypodermes	Подкожные оводы
Biorhiza pallida	Oak-apple Gallfly	Biorhiza du chêne	Губчатая дубовая орехотворка
Birkenblattroller	Birch Leaf Roller	Coléoptère du bouleau	Березовый слоник
Birkenspanner	Peppered Moth	Phalène du bouleau	Березовая пяденица
Birnblattsauger	Big Pear Psylla	Psylle du poirier	Грушевая медяница
Birnen-Netzwanze		Tigre du poirier	Грушевая кружевница
Birnensägewespe		Hoplocampe du poirier	Грушевый пилильщик
Birnentriebwespe		Janus du poirier	Грушевый стеблевой пилильщик
Birnenwurzellaus		Schizonèvre laineux	Пузырная тля
Biston betularia	Peppered Moth	Phalène du bouleau	Березовая пяденица
Blasenkäfer	Blister Beetles	Mylabris	Нарывники
Blatta orientalis	Common Cockroach	Blatte des Cuisines	Черный таракан
Blattariae	Cockroaches	Blattes	Таракановые
Blattella germanica	German Cockroach	Blatte d'Allemagne	Рыжий таракан
Blattflöhe	Phyllids	Psyllines	Листоблошки или Медяницы
Blatthornkäfer	Cockchafers	Scarabés	Пластинчатоусые
Blattia	Cockroaches	Blattes	Таракановидные
Blattkäfer	Leaf Beetles	Chrysomélidés	Листоеды
Blattläuse	Aphids	Pucerons	Тли
Blattlaus-Schlupfwespen	Ichneumons	Aphidiidés	Тлиные наездники
Blattschneiderameisen	Leaf-cutting Ant	Les Atta	Атты
Blattschneiderbienen	— — Bees	Mégachiles	Пчелы-листорезы
Blattwespen	Sawflies	Tenthrédinidés	Пилильщики
Blaue Schmeißfliege	Blue-bottle Fly	Mouche bleue de la viande	Синяя мясная муха
Blauer Erlenblattkäfer		Galeruque de l'aulne	Ольховая козявка
Blauflüglige Ödlandschrecke	Blue-winged Waste-land Grasshopper		Голубокрылая кобылка
Blaugrüne Mosaikjungfer	Southern Aeshna	Aeschna bleue	
Bläulinge	Blues	Lycénides	Голубянки
Blausieb	Wood Leopard	Zeuzère du marronnier	Въедливая древесница
Blepharoceridae	Net-winged Midges	Blépharocéridés	Сетчатокрылки
Blindbremsen	Blinding Breeze Flies	Chrysops	Златоглазки
Blindwanzen	Plant Bugs	Miridés	Клопы-слепняки
Blumenfliegen	Cabbage Root Fly	Anthomyiinés	
Blumengrille	Flower Tree-cricket		Трубачик
Blumenwanzen	— Bugs	Punaises des fleurs	Цветочные клопы
Blütenstecher	Blossom Weevils	Anthonomes	Цветоеды
Blutlaus	Woolly Apple Aphid	Puceron laineux	Кровяная тля
Blutrote Raubameise	Blood-red Ant	Fourmi sanguine	Кровавый муравей
Blutströpfchen	Six-spot Burnet	Zygène-de-la-filipendule	Таволговая пестрянка
Blutzikade		Cigale sanguinolent	Кровавая пенница
Bockkäfer	Long-horned Beetles	Capricorines	Усачи или Дровосеки
Bodenläuse	Zorapterons	Poux de terre	
Bohnenlaus	*Black Bean Aphid*	Puceron de la fève	Свекловичная тля
Bohr-Fransenflügler	Boring Thrips	Térébrants	Яйцекладные трипсы
Bombardierkäfer	Bombardier Beetles	Bombardiers	Жужелицы-бомбардиры
Bombus terrestris	Bumble Bee	Bourdon de terre	Земляной шмель
Bombycidae	Silk-Moths	Bombycides	Настоящие шелкопряды
Bombyliidae	Bee-Flies	Bombylidés	Жужжалы
Bombyx mori	Silk-Moth	Bombyx du mûrier	Тутовый шелкопряд
Boreidae	Snow Scorpion Flies	Boréides	
Borkenkäfer	Scolytid Beetles	Scolytes	Заболонники
Borstenschwänze	Bristle-tails	Thysanoures	Щетинохвостки
Bostrychidae	False Powder-post Beetles (N. A.)	Bostryches	
Bovicola	Cattle-lice	Poux des bœufs	Коровий власоед
Brachycera	Short-horns	Brachycères	Мухи
Brachyninae	Bombardier Beetles	Bombardiers	Жужелицы-бомбардиры
Brachytron	Hairy Dragonfly	Aeschna à abdomen court	Коромысло
Brackwespen	Braconid Flies	Braconides	Бракониды
Braconidae	— —	—	Бракониды
Braulidae	Bee-»Lice«	Braulidés	Пчелиные паразиты
Braunband- oder Möbelschabe	Brown-banded Cockroach	Blatte des meubles	
Braune Wiesenameise		Fourmi brune des prés	Темнобурый луговой муравей
Brauner Bär	Garden Tiger	Ecaille martre	Бурая медведица
Breitfüßige Birkenblattwespe	Birch Sawfly	Tenthrède du bouleau	Северный березовый пилильщик
Breitrüßler	Fungus Weevils (N. A.)	Anthribidés	Ложнослоники
Bremsen	Horse-flies	Taons	Слепни

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Brenthidae	Brentid Beetles (N. A.)		Долготелы
Brombeergallwespe		Diastrophus de la ronce	Ежевичная орехотворка
Bruchidae	Seed Beetles	Bruches	Зерновки
Bruchophagus gibbus		Brachophage du trèfle	Клеверный семеед
Buchenspinner	Lobster Moth	Écureuil	Буковый вилохвост
Buchenzierlaus	Beech Aphid	Puceron du hêtre	Буковая тля
Bücherlaus	Book-louse	Pou devin	Книжная вошь
Buckelfliegen	Coffin Flies	Phoridés	Горбатки
Buckelige Fensterfliege	Window Fly	Mouche des fenêtres	Оконная муха
Buckelzirpen	Tree-hoppers, Devil-hoppers	Membracidés	Горбашки
Bulldoggenameisen	Bulldog Ants	Myrmécinés	
Buntkäfer	Checkered Beetles	Clairons	Пестряки
Bupalus piniarius	Bordered White	Fidonie du pin	Сосновая пяденица
Buprestidae	Metallic Wood-borers (N. A.)	Buprestes	Златки
Bürstenbinder	Scarce Vapourer		Кистехвост
Büschelmücken	Lake Flies	Corethrines	Перистоусики
Buschhorn-Blattwespen	Conifer Sawflies	Diprionides	
Byctiscus betulae		Cigarier	Виноградный слоник
Byrrhidae	Pill Beetles	Byrrhidés	Пилюльщики
Caelifera	Short-tentacled Grasshoppers	Sauterelles de palpes courtes	Саранчовые и Трипер-стовые
			Синяя мясная муха
Calliphora vomitoria	Blue-bottle Fly	Mouche bleue de la viande	
Calliphoridae	Blow Flies	Calliphoridés	Обыкновенный прус
Calliptamus italicus	Italian Locust	Criquet italien	Лютки
Calopterygidae	Demoiselles	Caloptérygides	Красотки
Calopteryx	–	Caloptéryx	Блестящая красотка
– splendens	Banded Agrion	– brillant	Обыкновенная лютка
– virgo	Demoiselle Agrion	Demoiselle	Пахучий красотел
Calosoma sycophanta	Caterpillar Hunter		Муравьи-древоточцы
Camponotus		Camponotus	Мягкотелки
Cantharidae	Soldier-beetles	Cantharidés	Жужелицы
Carabidae	Carabids	Carabidés, Carabiques	Соколиная кровососка
Carnus hemapterus		Mouche mineuse	Щитоноски
Cassidinae	Tortoise Beetles	Cassidinés	Ленточницы
Catocala	Underwings	Lichénées	Красная ленточница
– nupta	Red Underwing	Mariée	Обыкновенная горбатка
Centrotus cornutus	Devil-hopper		
Cephalicia abietis	Fir Web-spinning Sawfly	Lyde d l'épicéa	
– alpina	Larch Web-spinning Sawfly	– étoilée du laryx	Глоточные оводы
Cephenomyia	Mouth Flies	Cephenomyes	Стеблевые пилильщики
Cephidae	Stem Sawflies	Céphides	Стеблевые пилильщики
Cephoidea	– –	Céphidés	Хлебный пилильщик
Cephus pygmaeus	European Wheat Stem Sawfly	Cèphe du blé	Усачи или Дровосеки
Cerambycidae	Long-horned Beetles	Capricorines	Средиземноморская плодовая муха
Ceratitis capitata	Mediterranean Fruit Fly	Mouche des oranges	Пенницы
			Кровавая пенница
Cercopidae	Spittle Bugs, Frog-hoppers	Cercopidés	Вилохвосты
Cercopis sanguinolenta		Cigale sanguinolent	Большая тополевая гарпия
Cerura	Puss	Petites-queues-fourchues	Бронзовки
– vinula	–		
			Злаковые мушки
Cetoninae	Rose-chafers	Cetonines	Желтая зеленоглазка
C-Falter	Comma	Gamma	Блестянки
Chloropidae	Gout Flies	Chloropidés	Обыкновенная блестянка
Chlorops pumilionis	– Fly	Chlorops du blé et de l'onge	Листоеды
Chrysididae	Cockoo Wasps	Chrysidides	Простая златоглазка
Chrysis ignita	Fire Cuckoo Wasp	Chrysis enflammée	Златоглазки
Chrysomelidae	Leaf Beetles	Chrysomélidés	Златоглазки
Chrysopa carnea	Green Lacewing	Chrysops commun	Дождевка
Chrysopidae	– Lacewings	Chrysopides	Ясеневая цикада
Chrysops	Blinding Breeze Flies	Chrysops	Горная цикада
Chrysozona pluvialis		Taon des pluies	Певчие цикады
Cicada orni		Cigale du frêne	Цикадовые
Cicadetta montana	Cicadas, Harvest Flies	– de montagne	Певчие цикадовые
Cicadidae	Cicadas	Cigales	Шеститочечная цикадка
Cicadina	–	–	Полевой скакун
Cicadoidea		Cicadidés	Скакуны
Cicadula sexnotata	Field Tiger Beetles	Cigale à six taches	Березовый булавоус
Cicindela campestris	Tiger Beetles	Cicindèle des champs	Булавоусы
Cicindelidae	Great Birch Sawfly	Cicindèles	Постельный клоп
Cimbex femoratus	Cimbicid Sawflies	Cimbex du bouleau	Постельные клопы
Cimbicidae	Bed Bug	Cimbicidés	Булавчики
Cimex lectularius	– Bugs	Punaise des lits	Блестянки
Cimicidae		Cimicidés	
Clavigeridae		Clavigéridés	
Cleptidae		Cleptides	

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Bibionidae	March-flies	Bibionidés	Комары-толстонотки
Bienen	Bees	Apoidés	Пчелиные
Bienenläuse	Bee-»Lice«	Braulidés	Пчелиные паразиты
Bienenwolf	Bees Wool	Philanthe apivore	Пчелиный волк
Biesfliegen i. e. S.	Warble Flies	Hypodermes	Подкожные оводы
Biorhiza pallida	Oak-apple Gallfly	Biorhiza du chêne	Губчатая дубовая орехотворка
Birkenblattroller	Birch Leaf Roller	Coléoptère du bouleau	Березовый слоник
Birkenspanner	Peppered Moth	Phalène du bouleau	Березовая пяденица
Birnblattsauger	Big Pear Psylla	Psylle du poirier	Грушевая медяница
Birnen-Netzwanze		Tigre du poirier	Грушевая кружевница
Birnensägewespe		Hoplocampe du poirier	Грушевый пилильщик
Birnentriebwespe		Janus du poirier	Грушевый стеблевой пилильщик
Birnenwurzellaus		Schizonèvre laineux	Пузырная тля
Biston betularia	Peppered Moth	Phalène du bouleau	Березовая пяденица
Blasenkäfer	Blister Beetles	Mylabris	Нарывники
Blatta orientalis	Common Cockroach	Blatte des Cuisines	Черный таракан
Blattariae	Cockroaches	Blattes	Таракановые
Blattella germanica	German Cockroach	Blatte d'Allemagne	Рыжий таракан
Blattflöhe	Phyllids	Psyllines	Листоблошки или Медяницы
Blatthornkäfer	Cockchafers	Scarabés	Пластинчатоусые
Blattia	Cockroaches	Blattes	Тарakановидные
Blattkäfer	Leaf Beetles	Chrysomélidés	Листоеды
Blattläuse	Aphids	Pucerons	Тли
Blattlaus-Schlupfwespen	Ichneumons	Aphidiidés	Тлиные наездники
Blattschneiderameisen	Leaf-cutting Ant	Les Atta	Атты
Blattschneiderbienen	— — Bees	Mégachiles	Пчелы-листорезы
Blattwespen	Sawflies	Tenthrédinidés	Пилильщики
Blaue Schmeißfliege	Blue-bottle Fly	Mouche bleue de la viande	Синяя мясная муха
Blauer Erlenblattkäfer		Galeruque de l'aulne	Ольховая козявка
Blauflüglige Ödlandschrecke	Blue-winged Waste-land Grasshopper		Голубокрылая кобылка
Blaugrüne Mosaikjungfer	Southern Aeshna	Aeschna bleue	
Bläulinge	Blues	Lycénides	Голубянки
Blausieb	Wood Leopard	Zeuzère du marronnier	Въедливая древесница
Blepharoceridae	Net-winged Midges	Blépharocéridés	Сетчатокрылки
Blindbremsen	Blinding Breeze Flies	Chrysops	Златоглазки
Blindwanzen	Plant Bugs	Miridés	Клопы-слепняки
Blumenfliegen	Cabbage Root Fly	Anthomyiinés	
Blumengrille	Flower Tree-cricket		Трубачик
Blumenwanzen	— Bugs	Punaises des fleurs	Цветочные клопы
Blütenstecher	Blossom Weevils	Anthonomes	Цветоеды
Blutlaus	Woolly Apple Aphid	Puceron laineux	Кровяная тля
Blutrote Raubameise	Blood-red Ant	Fourmi sanguine	Кровавый муравей
Blutströpfchen	Six-spot Burnet	Zygène-de-la-filipendule	Таволговая пестрянка
Blutzikade		Cigale sanguinolent	Кровавая пенница
Bockkäfer	Long-horned Beetles	Capricorines	Усачи или Дровосеки
Bodenläuse	Zorapterons	Poux de terre	
Bohnenlaus	Black Bean Aphid	Puceron de la fève	Свекловичная тля
Bohr-Fransenflügler	Boring Thrips	Térébrants	Яйцекладные трипсы
Bombardierkäfer	Bombardier Beetles	Bombardiers	Жужелицы-бомбардиры
Bombus terrestris	Bumble Bee	Bourdon de terre	Земляной шмель
Bombycidae	Silk-Moths	Bombycides	Настоящие шелкопряды
Bombyliidae	Bee-Flies	Bombylidés	Жужжалы
Bombyx mori	Silk-Moth	Bombyx du mûrier	Тутовый шелкопряд
Boreidae	Snow Scorpion Flies	Boréides	
Borkenkäfer	Scolytid Beetles	Scolytes	Заболонники
Borstenschwänze	Bristle-tails	Thysanoures	Щетинохвостки
Bostrychidae	False Powder-post Beetles (N. A.)	Bostryches	
Bovicola	Cattle-lice	Poux des bœufs	Коровий власоед
Brachycera	Short-horns	Brachycères	Мухи
Brachyninae	Bombardier Beetles	Bombardiers	Жужелицы-бомбардиры
Brachytron	Hairy Dragonfly	Aeschna à abdomen court	Коромысло
Brackwespen	Braconid Flies	Braconides	Бракониды
Braconidae	— —	—	Бракониды
Braulidae	Bee-»Lice«	Braulidés	Пчелиные паразиты
Braunband- oder Möbelschabe	Brown-banded Cockroach	Blatte des meubles	
Braune Wiesenameise		Fourmi brune des prés	Темнобурый луговой муравей
Brauner Bär	Garden Tiger	Ecaille martre	Бурая медведица
Breitfüßige Birkenblattwespe	Birch Sawfly	Tenthrède du bouleau	Северный березовый пилильщик
Breitrüßler	Fungus Weevils (N. A.)	Anthribidés	Ложнослоники
Bremsen	Horse-flies	Taons	Слепни

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Brenthidae	Brentid Beetles (N. A.)		Долготелы
Brombeergallwespe		Diastrophus de la ronce	Ежевичная орехотворка
Bruchidae	Seed Beetles	Bruches	Зерновки
Bruchophagus gibbus		Brachophage du trèfle	Клеверный семеед
Buchenspinner	Lobster Moth	Écureuil	Буковый вилохвост
Buchenzierlaus	Beech Aphid	Puceron du hêtre	Буковая тля
Bücherlaus	Book-louse	Pou devin	Книжная вошь
Buckelfliegen	Coffin Flies	Phoridés	Горбатки
Buckelige Fensterfliege	Window Fly	Mouche des fenêtres	Оконная муха
Buckelzirpen	Tree-hoppers, Devil-hoppers	Membracidés	Горбашки
Bulldoggenameisen	Bulldog Ants	Myrmécinés	
Buntkäfer	Checkered Beetles	Clairons	Пестряки
Bupalus piniarius	Bordered White	Fidonie du pin	Сосновая пяденица
Buprestidae	Metallic Wood-borers (N. A.)	Buprestes	Златки
Bürstenbinder	Scarce Vapourer		Кистехвост
Büschelmücken	Lake Flies	Corethrines	Перистоусики
Buschhorn-Blattwespen	Conifer Sawflies	Diprionides	
Byctiscus betulae		Cigarier	Виноградный слоник
Byrrhidae	Pill Beetles	Byrrhidés	Пилюльщики
Caelifera	Short-tentacled Grasshoppers	Sauterelles de palpes courtes	Саранчовые и Трипер-стовые
Calliphora vomitoria	Blue-bottle Fly	Mouche bleue de la viande	Синяя мясная муха
Calliphoridae	Blow Flies	Calliphoridés	
Calliptamus italicus	Italian Locust	Criquet italien	Обыкновенный прус
Calopterygidae	Demoiselles	Caloptérygides	Лютки
Calopteryx	–	Caloptéryx	Красотки
– splendens	Banded Agrion	– brillant	Блестящая красотка
– virgo	Demoiselle Agrion	Demoiselle	Обыкновенная лютка
Calosoma sycophanta	Caterpillar Hunter		Пахучий красотел
Camponotus		Camponotus	Муравьи-древоточцы
Cantharidae	Soldier-beetles	Cantharidés	Мягкотелки
Carabidae	Carabids	Carabidés, Carabiques	Жужелицы
Carnus hemapterus		Mouche mineuse	Соколиная кровососка
Cassidinae	Tortoise Beetles	Cassidinés	Щитоноски
Catocala	Underwings	Lichénées	Ленточницы
– nupta	Red Underwing	Mariée	Красная ленточница
Centrotus cornutus	Devil-hopper		Обыкновенная горбатка
Cephalicia abietis	Fir Web-spinning Sawfly	Lyde d l'épicéa	
– alpina	Larch Web-spinning Sawfly	– étoilée du laryx	
Cephenomyia	Mouth Flies	Cephenomyes	Глоточные оводы
Cephidae	Stem Sawflies	Céphides	Стеблевые пилильщики
Cephoidea	– –	Céphidés	Стеблевые пилильщики
Cephus pygmaeus	European Wheat Stem Sawfly	Cèphe du blé	Хлебный пилильщик
Cerambycidae	Long-horned Beetles	Capricorines	Усачи или Дровосеки
Ceratitis capitata	Mediterranean Fruit Fly	Mouche des oranges	Средиземноморская плодовая муха
Cercopidae	Spittle Bugs, Frog-hoppers	Cercopidés	Пенницы
Cercopis sanguinolenta		Cigale sanguinolent	Кровавая пенница
Cerura	Puss	Petites-queues-fourchues	Вилохвосты
– vinula	–		Большая тополевая гарпия
Cetoninae	Rose-chafers	Cetonines	Бронзовки
C-Falter	Comma	Gamma	
Chloropidae	Gout Flies	Chloropidés	Злаковые мушки
Chlorops pumilionis	– Fly	Chlorops du blé et de l'onge	Желтая зеленоглазка
Chrysididae	Cockoo Wasps	Chrysidides	Блестянки
Chrysis ignita	Fire Cuckoo Wasp	Chrysis enflammée	Обыкновенная блестянка
Chrysomelidae	Leaf Beetles	Chrysomélidés	Листоеды
Chrysopa carnea	Green Lacewing	Chrysops commun	Простая златоглазка
Chrysopidae	– Lacewings	Chrysopides	Златоглазки
Chrysops	Blinding Breeze Flies	Chrysops	Златоглазки
Chrysozona pluvialis		Taon des pluies	Дождевка
Cicada orni		Cigale du frêne	Ясеневая цикада
Cicadetta montana	Cicadas, Harvest Flies	– de montagne	Горная цикада
Cicadidae	Cicadas	Cigales	Певчие цикады
Cicadina	–	–	Цикадовые
Cicadoidea		Cicadidés	Певчие цикадовые
Cicadula sexnotata	Field Tiger Beetles	Cigale à six taches	Шеститочечная цикадка
Cicindela campestris	Tiger Beetles	Cicindèle des champs	Полевой скакун
Cicindelidae	Great Birch Sawfly	Cicindèles	Скакуны
Cimbex femoratus	Cimbicid Sawflies	Cimbex du bouleau	Березовый булавоус
Cimbicidae	Bed Bug	Cimbicidés	Булавоусы
Cimex lectularius	– Bugs	Punaise des lits	Постельный клоп
Cimicidae		Cimicidés	Постельные клопы
Clavigeridae		Clavigéridés	Булавчики
Cleptidae		Cleptides	Блестянки

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Cleridae	Checkered Beetles	Clairons	Пестряки
Clythiidae	Flat-footed Flies (N. A.)	Clythiidés	
Clytra		Clythres	Клитры
Coccidae	Soft Scales	Lécanines, Coccidés	Полущечницы
Coccina	Coccids, Mealy Bugs	Cochenilles	Кокциды
Coccinella septempunctata	Ladybird	Coccinelle à sept points	Семиточечная коровка
Coccinellidae	Ladybirds	Coccinellidés, Coccinelles	Божьи коровки
Cochenille-Laus	Cochineal Insect	Cochenille	Мексиканская конишель
Cochylis ambiguella		Teigne de la grappe	Виноградная вертунья
Coelioxys		Abeille à abdomen conique	Пчелы-остробрюхи
Coenomyia ferruginea		Mouche rouge du bois	Рыжая древесная муха
Coenonympha	Ringlets		Сенницы
Coleophoridae	Case bearers	Coléophoridés	
Coleoptera	Beetles	Coléoptères	Жуки
Coleopteria	–	Coléoptérides	Жесткокрылые
Colias	Clouded Yellows	Colias	Желтушки
– *croceus*	– Yellow	Souci	
– *hyalae*	Pale Clouded Yellow	Soufré	Луговая желтушка
Collembola	Springtails	Collemboles	Ногохвостки
Colletes	Colletid Bees	Colletidés	Шелковые пчелы
Colletidae	– –	–	Шелковые пчелы
Columbicola	Pigeon-lice	Poux de colombes	Голубиные пироеды
Coniopterygidae	Dusty Wings	Conioptérygidés	
Conocephalidae	Cone-heads	Conocéphalidés	Конусоголовые кузнечик
Conocephalus	–	Conocéphalus	
– *fuscus*	Long-winged Cone-head	– brun	
Conopidae	Thick-headed Flies	Conopidés	Толстоголовки
Coprinae	Dung Beetles	Coprins	Копры
Copris	– –	Copris	Лунные копры
Cordulegasteridae	Golden-ringed Dragonflies	Cordulégastrides	
Cordylobia anthropophaga	African Tumbu Fly	Cordylobia africaine	
Cordyluridae	Dung Flies	Cordyluridés	Колосковые мухи
Corethrinae	Lake Flies	Corethrines	Перистоусики
Coreidae	Leaf-footed Bugs, Squash Bugs	Coréidés	Краевики
Coreus marginatus		Punaise bordée	Обыкновенный краевик
Corixidae	Corixids	Corixidés	Гребляки
Cosmia trapezina	Dun-bar	Trapèze	
Cossidae	Goat Moths	Cossides	Древоточцы
Cossus cossus	Goat Moth	Cossus gâte-bois	Пахучий древоточец
Crambinae	Grass Moths	Crambides	
Craterhina pallida	Swift Louse Fly	Mouche des martinets	Стрижиная кровососка
Croesus septentrionalis	Birch Sawfly	Tenthrède du bouleau	Северный березовый пилильщик
Cryptophagidae	Cryptophagid Beetles (N. A.)	Cryptophagidés	
Ctenocephalides canis	Dog Flea	Puce du chien	Собачья блоха
– *felis*	Cat Flea	– – chat	Кошачья блоха
Ctenophora atrata		Cténophore obscur	Гребневая долгоножка
Cucujidae	Flat Bark Beetles (N. A.)	Rhizophagidés	Плоскотелки
Cucullia artemisiae	Sharks	Noctuelle d'armoise	
Culex pipiens	European House Mosquito	Moustique commun	Обыкновенный комар
Culicidae	Mosquitoes	Moustiques	Настоящие комары
Curculio nucum	Nut Weevil		Ореховый долгоносик
Curculionidae	Weevils (N. A.)	Charançons	Долгоносики
Cyclorrhapha		Cyclorhaphes	Круглошовные мухи
Cynipidae	Gall Wasps	Cynipoides	
Cynipinae	– –	Cynipides gallicoles	Настоящие орехотворки
Cynips quercusfolii	Common Oak Gallfly	Cynips du chêne	Обыкновенная дубовая орехотворка
Cyrtidae	Fat Flies		Шаровки
Dactylopius coccus	Cochineal Insect	Cochenille	Мексиканская конишель
Danais plexippus	Monarch (N. A.)	Monarque	
Darwin-Termite		Mantis de Darwin	Дарвинов термит
Dasselfliegen	Bot Flies	Œstridés	Оводы
Dasypoda	Hairylegged Mining Bees	Abeilles à pantalon	Мохноножки
Deckelschildläuse	Armored Scales	Diaspididés	Щитовки
Deckelschlüpfer		Cyclorhaphes	Круглошовные мухи
Deckflügler	Beetles	Coléoptérides	Жесткокрылые
Decticus verrucivorus	Wart-biter	Dectique verrucivore	Серый кузнечик
Deltocephalus striatus		Cigale à abdomen	Полосатая цикадка
Dendroctonus		Dendroctones	Большие лубоеды
Dendrolimus pini	Pine Lappet	Feuille morte du pin	Сосновый коконопряд
Dendrothrips		Thrips d'arbres	Древесные трипсы
Deporaus betulae	Birch Leaf Roller	Coléoptère du bouleau	Березовый слоник
Dermaptera	Earwigs	Dermaptères	Кожистокрылые
Dermestes	Hide Beetles	Dermestes	Кожееды
– *lardarius*	Common Hide Beetle	Dermeste commun	Ветчинный кожеед

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Dermestidae	Common Hide Beetles	Dermestidés	Кожееды
Deutsche Schabe	German Cockroach	Blatte d'Allemagne	Прусак
Dialeurodes citri	Citrus White Fly	Mouche blanche des Aurantiacées	Цитрусовая мушка
Diaspididae	Armored Scales	Diaspididés	Щитовки
Diastrophus rubi		Diastrophus de la ronce	Ежевичная орехотворка
Diatraea saccharalis	Sugar-cane Borer	Pyrole de la canne à sucre	
Dickkopffalter	Skippers	Hespérides	Толстоголовки
Dickkopffliegen	Thick-headed Flies	Conopidés	Толстоголовки
Diebskäfer	Spider Beetles	Ptinidés	Притворяшки
Diebswespen		Cleptides	Блестянки
Diopsidae	Stalk-eyed Flies	Diopsides	
Diploglossata	Parasitic Earwigs	Diploglossates	
Diplolepis rosae	Mossy Rose Gall	Diplolepis du rosier	Розанная орехотворка
Diplura	Two-pronged Bristle-tails	Diploures	Двухвостки
Diprion pini	Pine Sawfly	Diprion du pin	Сосновый пилильщик
Diprionidae	Conifer Sawflies	Diprionides	
Diptera	Flies	Diptères	Двукрылые
Distelfalter	Painted Lady	Belle-dame	Репейница
Dolchwespen	Digger Wasps	Scoliides	Сколии
Dolichopodidae	Long-legged Flies	Dolichopodidés	
Dolichuvespula media	Tree Wasp	Guêpe moyenne	Средняя оса
– *saxonica*	– –	– de Saxe	Саксонская оса
– *sylvestris*	Sloebug	– sylvestre	Лесная оса
Dolycoris baccarum	Two-pronged Bristle-tails	Punaise des baies	Ягодный клоп
Doppelschwänze	Parasitic Earwigs	Diploures	Двухвостки
Doppelzüngler	Big-headed Flies	Diploglossates	
Dorilaidae	Grouse Locusts	Dorilaidés	Цикадоедки
Dornschrecken	Devil-hopper	Tetrigides	Тетригиды
Dornzikade	Sausage Ants		Обыкновенная горбатка
Dorylinae	Dracaena Thrips	Dorylinés	
Drazänenthrips	Pigmy Mole-crickets	Thripide dracaene	
Dreifingerschrecken	Three-horned Dor Beetles	Tridactylides	Триперстовые
Dreihorn-Mistkäfer		Minotaure typhée	Трехрогие навозники
Drepanosiphum californicum		Puceron de Californie	Калифорнийская кленовая тля
– *platanoides*	Small Fruit Flies	– du platane	Кленовая тля
Drosophilidae		Drosophilidés	Дрозофилы
Dryinidae	Dung Beetles	Dryinides	Дриины
Dukatenfalter	Cotton Stainer	Argus satiné	Огненный червонец
Dungkäfer		Aphodiinés	Пометокопатели
Dunkle Baumwollwanze	False Darkling Beetles (N. A.)	Punaise grise du Cotton	
Dünnfühlerläuse		Poux aux tentacles minces	Тонкоусиковые пухоеды
Düsterkäfer	Rhinocers Beetles	Serropalpidés	
Dynastes	Carnivorous Water Beetles	Dynastes hercule	Жук-геркулес
Dynastinae	Great Water Beetles	Dynastinés	Исполинские жуки
Dytiscidae	– – Beetle	Dytiscides	Плавунцы
Dytiscus	Bumble Bees	Dytiscidés	Плавунцы
– *marginalis*	Blues	Dytisque bordé	Окаймленный плавунец
Echte Bienen	Mouse Flies	Abeille domestique	Настоящие пчелы
– Bläulinge	Sucking Lice	Plébiines	
– Fliegen	Cockchafers	Muscidés	Настоящие мухи
– Läuse	Dor Beetles	Anoplurés	Настоящие вши
– Maikäfer		Hannetons	Майские хрущи
– Mistkäfer	Clothes Moths	Géotrupes	Настоящие навозные жуки
– Motten	Swallowtails	Teignes	Моли
– Schwalbenschwänze	Silk-moths	Papilios	
– Spinner	Whites	Bombycides	Настоящие шелкопряды
– Weißlinge	Hornets	Piérides	Настоящие белянки
– Wespen	Silk-moth	Vespides	Общественные осы
Echter Seidenspinner	Wood Cockroaches	Bombyx du mûrier	Тутовый шелкопряд
Ectobius	Oak Leaf Roller	Blattes des bois	Лесные тараканы
Eichenblattroller	Pseudogall Coccids	Attelabe du chêne	Дубовый трубковерт
Eichennapfläuse		Cochenilles du chêne	
Eichenpockenschildlaus		Cochenille du chêne	Дубовый червец
Eichenprozessionsspinner		Processionnaire du chêne	Дубовый походный шелкопряд
Eichenrindenlaus	Oak Bush-cricket	Puceron du chêne	Дубовая тля
Eichenschrecke	Oak-apple Gallfly	Méconema	Дубовый кузнечик
Eichen-Schwammgallwespe		Biorhiza du chêne	Губчатая дубовая орехотворка
Eichenspinner	Oak Eggar	Minime à baudes jaunes	Дубовый коконопряд
Eichenwickler	Pea-green Oak Twist	Tordeuse du chêne	Дубовая листовертка
Eigentliche Blattwespen	Sawflies	Tenthrédinidés	Настоящие пилильщики
– Gallwespen	Gall Wasps	Cynipides gallicoles	Настоящие орехотворки
– Ohrwürmer	Earwigs	Forficulides	Уховертки

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– Schlupfwespen	Ichneumons	Ichneumonides	Настоящие наездники
– Termiten	Termites	Termes	
– Wasserkäfer	Water Beetles	Hydrophiles	Водолюбы
Einbindiger Traubenwickler		Teigne de la grappe	Виноградная вертунья
Eintagsfliegen	Mayflies	Ephémères	Поденки
Elateridae	Click-beetles	Taupins	Проволочники или Щелкуны
Elefantenlaus		Pou d'éléphant	Слоновая вошь
Embiia	Embiids		Эмбии
Empidae	Dance-flies	Empididés	Толкунчаки
Ensifera	Bush-crickets	Sauterelles à longues antennes	Кузнечиковые и Сверчковые
Ephemera vulgata	Mayfly	Ephémère commune	Обыкновенная поденка
Ephemoptera	Mayflies	Ephémères	Поденки
Ephestia kuehniella	Mediterranean Flour Moth	Teigne de la farine	Мельничная огневка
Ephippiger vitium	Katydid (N. A.)	Ephippigère des vignes	
Ephippigeridae	Katydids (N. A.)	Ephippigérides	
Ephydridae	Shore Flies	Ephydridés	
Erannis		Phalins défeuillantes	Зимняя пяденица
Erdhummel	Bumble Bee	Bourdon de terre	Земляной шмель
Erebia	Alpines	Erébia	Глазки-чернушки
Erinnidae		Erinniés	Древесные мухи
Eriosoma	Woolly Aphids		Кровяные тли
– *lanigerum*	– Apple Aphid	Puceron lainеux	Кровяная тля
Eristalis tenax	Drone Fly	Eristale gluante	Ильница
Erleneule	Alder Dagger	Noctuide d'aune	Ольховая стрельчатка
Ernestia rudis	Cluster Fly	Mouche des greiners	Совковая ежемуха
Ernteameisen		Fourmi des récoltes	Муравьи-земледельцы
Eschenzikade		Cigale du frêne	Ясеневая цикада
Espenbockkäfer		Petite saperde du peuplier	Малый осиновый усач
Eucnemidae	False Click Beetles (N. A.)	Eucnémidés	
Eudia pavonia	Emperor Moth	Petit paon de nuit	Малый ночной павлиний глаз
Eulecanium corni	European Fruit Lecanium	Cochenille du cornouiller	Акациевая ложнощитовка
– *coryli*	Hazel Scale	Lécanium du noisetier	
Eulenfalter	Noctuids	Noctuelles	Совки или Ночницы
Eulentachine	Cluster Fly	Mouche des greiners	Совковая ежемуха
Eumenes	Potter Wasps	Eumènes	Эвмены
Eumeninae	– –	Euménines	Одиночные осы
Eumerus	Lesser Bulb Fly	Mouches des oignons	Луковичные мухи
Euphyllura olivina		Puce d'olivier	Оливковая медяница
Euproctis chrysorrhoea	Brown-tail	Cul doré	Златогузка
Eupteryx atropunctata		Cigale à tache noire	Черноточечная цикадка
Europäische Ameisengrille	European Ant-loving Crickets	Grillon myrmécophile de l'Europe	
– Ameisenwespe	European Velvet-ant	Mutille d'Europe	Европейская немка
– Fichtenblattwespe	Spruce	Tenthride du pin	Европейский еловый пилильщик
Europäischer Laternenträger	European Lantern-fly	Fulgoride européen	Обыкновенная светоноска
Eurydema oleraceum	Brassica Bug	Punaise des potagers	Рапсовый щитник
Eurytoma orchidearum	Orchid Wasp	Guêpe des orchidées	Орхидеевый семеед
Evaniidae	Ensign Flies	Evaniides	Эваниды
Evetria buoliana	Gemmet Shoot	Tordeuse des pousses	Сосновая плодожорка
Fächerflügler	Twisted-winged Insects	Strepsitères	Веерокрылки
Fächerkäfer		Rhipiphoridés	Веероносцы
Fadenfühler	Thread-horns	Nématocères	Длинноусые двукрылые
Falkenlausfliege		Mouche mineuse	Соколиная кровососка
Faltenmücken	False Crane Flies	Liriopeidés	
Faltenwespen	Yellow Jackets	Vespides	Складчатокрылые осы
Fangschrecken	Praying Mantids	Mantides	Богомолы
Fangwanzen	Ambush Bugs (N. A.)	Phymatidés	
Fannia canicularis	Lesser House Fly	Petite mouche domestique	Малая комнатная муха
Federflügler		Ptiliidés	Перокрылки
Federmotten	Plumes	Ptérophores	Пальцекрылки
Feigenwespen	Fig Insects	Cynips du figuier	
Feldgrille	Field-cricket	Grillon des champs	Полевой сверчок
Feldheuschrecken	Grasshoppers	Acridiens	Настоящие саранчовые
Feldmaikäfer	White Grub	Ver blanc	Западный майский хрущ
Feld-Sandlaufkäfer	Field Tiger Beetle	Cicindèle des champs	Полевой скакун
Felicola subostratus	Cat-louse	Pou du chat	Кошачий власоед
Felsenspringer	Machilids	Machilides	Махилисы
Fenstermücke	Window Fly	Phryne des fenêtres	
Fersenspinner	Embiids		Эмбии
Feuerfalter	Coppers	Lycènes	
Feuergoldwespe	Fire Cuckoo Wasp	Chrysis enflammée	Обыкновенная блестянка
Feuerwanze	Firebug	Punaise sans ailes	Бескрылый красноклоп

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Feuerwanzen	Pyrrhocorid Bugs	Pyrrhocoridés	Красноклопы
Fichten-Gespinstblattwespe	Fir Web-spinning Sawfly	Lyde de l'épicéa	
Fichtenkotsack-Gespinstblattwespe	— — —	— — —	
Fichtenquirlschildläuse		Cochenille de verticille du sapin	Еловая ложнощитовка
Fichtenrüßler	Large Pine Weevil	Grand Charançon du sapin	Большой сосновый долгоносик
Fiebermücken	Mosquitoes	Anophèles	Малярийные комары
Filzlaus	Crab Louse	Pou de feutre	Площица
Fischchen	Firebrats	Lépismatidés	
Fleckenfalter	Fritillaries	Nymphalides	Многоцветницы
Fledermaus-Azurjungfer	Variable Coenagrion	Agrion joli	
Fliegen	Short-horns	Brachycères	Мухи или Короткоусые двукрылые
Flöhe	Fleas	Puces	Блошиные
Florfliegen	Green Lacewings	Chrysopides	Златоглазки
Fluginsekten	Largely-winged Insects	Ptérygotes	Высшие насекомые или Крылатые насекомые
Flußjungfern	Club-tail Dragonflies	Gomphides	
Forficula auricularia	Common Earwig	Forficule auriculaire	Обыкновенная уховертка
Forficulidae	Earwigs	Forficulides	Уховертки
Formica rufa	Wood Ant	Fourmi rousse	Лесной рыжий муравей
Formicidae	Ants	Formicidés	Муравьи
Fransenflügler	Thrips	Thrips	Бахромчатокрылые
Französische Feldwespe		Poliste française	Французская бумажная оса
Fritfliege	Frit Fly	Oscinie frit	Овсяная шведская мушка
Frostspanner		Phalins défeuillantes	Зимняя пяденица
Fruchtfliegen	Large Fruit Flies	Mouches des fruits	Пестрокрылки
Frühlingsscheckenfalter	Duke of Burgundy	Lucine	Лесная пеструшка
Fulgora europaea	European Lantern-fly	Fulgoride européen	Обыкновенная светоноска
Fulgoridae	Lantern-flies	Fulgoridés	Светоноски
Fungivoridae	Fungus Gnats	Mycetophilidés	Грибные комарики
Furchenwasserkäfer	Turnip Mud Beetles	Helophoridés	
Gabelmücken	Mosquitoes	Anophèles	Малярийные комары
Gabelschwänze	Pusses	Petites-queues-fourchues	Вилохвосты
Galerucella luteola	Wax Moth (N. A.)	Galérucelle d'orme	Ильмовая козявка
Galleria mellonella		Taupe teigne des ruches	Восковая моль или Большая пчелиная огневка
Gallmücken	Gall Midges	Cécidomyus	Галлицы
Gallwespen i. e. S.	Gall Wasps	Cynipoides	
Gammaeule	Common Silver Y Moth	Lettre grecque	Совка гамма
Gartenhaarmücke	Garden March Fly	Bibion des jardins	Садовая мошка
Gasteruptiidae		Gastéruptionidés	Гастерупциониды
Gastrophilus	Horse Bot Flies	Gastrophiles	Желудочные оводы
Gebänderte Prachtlibelle	Banded Agrion	Caloptéryx brillant	Блестящая красотка
Gefleckte Waldschnake		Aedes tacheté	Пятнистый комар-кусака
Gefleckter Birnblattsauger		Puce tacheté du poirier	Пятнистая грушевая медяница
Geistchen	Many-plume Moth	Orméodidés	Веерницы
Gelbbraune Pflaumensägewespe		Hoplocampe jaune du prunier	Желтый сливовый пилильщик
Gelbe Halmfliege	Gout Fly	Chlorops du blé et de l'onge	Желтая зеленоглазка
– Stachelbeer-Blattwespe	Black Currant Sawfly	Némate du groseillier	Желтый крыжовниковый пилильщик
Gelbfiebermücke	Yellow Fever Mosquito	Moustique de la fièvre jaune	Желтолихорадный комар
Gelbfüßige Termite	Eastern subterranean Termite	Termite aux pieds jaunes	Желтоногий термит
Gelbhalstermite	Yellow-necked Termite	– à cou jaune, Flavicolle	Желтошеий термит
Gelblinge	Clouded Yellows	Colias	Желтушки
Gelbrandkäfer	Great Water Beetle	Dytisque bordé	Окаймленный плавунец
Gelbstirnige Dolchwespe	Yellow-fronted Digger Wasp	Scolia à front jaune	Желтолобая сколия
Gemeine Eichengallwespe	Common Oak Gallfly	Cynips du chêne	Обыкновенная дубовая орехотворка
– Eintagsfliege	Mayfly	Ephémère commune	Обыкновенная поденка
– Holzwespe	Polished Horntail	Sirex commun	Обыкновенный сосновый рогохвост
– Kiefernbuschhorn-Blattwespe	Pine Sawfly	Diprion du pin	Сосновый пилильщик
– Kriebelmücke		Mélusine commun	Обыкновенная мошка
– Rosengallwespe	Mossy Rose Gall	Diplolepis du rosier	Розанная орехотворка
– Schaumzikade		Cicadelle écumeuse	Слюнявая пенница
– Schlupfwespe		Ichneumon commun	Обыкновенный наездник
– Seejungfer	Demoiselle Agrion	Demoiselle	Обыкновенная лютка
– Staublaus		Pou de fropper	Домовый сеноед
– Stechmücke	European House Mosquito	Moustique commun	Обыкновенный комар
– Tapetenmotte	Tapestry Moth	Teigne des tapis	Ковровая моль
– Waldschnake		Aedes commun	Обыкновенный комар-кусака

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– Weidenblattgallen-Wespe	Common Willow Sawfly	Pontanie commune	Обыкновенный ивовый пилильщик
Gemeiner Heufalter	Pale Clouded Yellow	Soufré	Луговая желтушка
– Ohrwurm	Common Earwig	Forficule auriculaire	Обыкновенная уховертка
– Speckkäfer	– Hide Beetle	Dermeste commun	Ветчинный кожеед
Geocorisa		Punaises de terre, Géocorises	Наземные клопы
Geometridae	Geometers	Géométrides	Пяденицы
Geotrupes	Dor Beetles	Géotrupes	Настоящие навозные жуки
Geotrupinae	Dor Beetles		Настоящие навозники
Geradflügler		Orthoptères	Прямокрылые
Gerridae	Water-striders, Pondskater's [N. A.]	Gerridés	Водомерки
Gesellige Birnblattwespe	Common Web-spinning Sawfly	Lyde du poirier	Общественный грушевый пилильщик-ткач
Gespenstlaufkäfer	Violin Beetles		Лиственные жужелицы
Gespenstschrecken	Stick- and Leaf-Insects	Phasmes	Привиденьевые
Gespinst-Blattwespen	Leaf-rollers	Pamphilides	Паутинные пилильщики
Gespinstmotten	Small Ermines	Hyponomeutidés	Горностаевые моли
Gestreifter Pillendreher		Scarabée à corselet large	Полосатый скарабей
Getreideameisen	Grain Ants	Fourmi moissonneuse	Муравьи-жнецы
Getreidehalmwespe	European Wheat Stem Sawfly	Cèphe du blé	Хлебный пилильщик
Getreidethripse	Grain Thrips	Thrips du blé	Хлебные трипсы
Getreidewanzen		Punaise du blé	Остроголовые клопы
Gewächshausschabe	Surinam Cockroach	Blatte de serre	Суринамский таракан
Gewächshausschrecke	Greenhouse Camel-cricket	Sauterelle grillon de serre	Оранжерейный кузнечик
Gewöhnliche Kleidermotte	Common Clothes Moth	Mite des vêtements	Мебельная моль или Платяная моль
Gichtwespen		Gastéruptionidés	Гастерупциониды
Gilpinia hercyniae	Spruce	Tenthride du pin	Европейский еловый пилильщик
Gladiolenthrips	Gladiolus Thrips	Thrips du gladiole	Гладиолусовый трипс
Glänzendschwarze Holzameise	Jet Ant	Fourmi fuligineuse	Муравей-древоточец
Glanzkäfer	Sap-beetles	Nitidulidés	Блестянки
Glasflügler	Clairwings	Sésies	Стеклянницы
Gleichflügler	Termites	Isoptères	Термиты
Gletscherfloh		Puce du glacier	Глетчерная блоха или Снежная блоха
Glossina	Tsetse Flies	Mouches tsé-tsé	Мухи це-це
Glucken	Lackeys and Eggars	Bombyx feuilles	Коконопряды
Gnitzen	Biting Midges	Heléides	Мокрецы
Goldafter	Brown-tail	Cul doré	Златогузка
Goldauge	Green Lacewing	Chrysops commun	Простая златоглазка
Goldene Acht	Pale Clouded Yellow	Soufré	Луговая желтушка
Goldfliegen-Brackwespe	Golden Braconid Fly	Alysia dorée	
Goldwespen	Cuckoo Wasps	Chrysidides	Блестянки
Goliathkäfer	Goliath Beetle		Жук-голиаф
Goliathus meleagris	– –		Жук-голиаф
Golofa porteri		Coléoptère de Columbie	Колумбийский жук-носорог
Gomphidae	Club-tail Dragonflies	Gomphides	
Gomphocerus sibiricus	Siberian Grasshopper	Sauterelle de Sibérie	Сибирская саранча
Gonepteryx rhamni	Brimstone	Citron	Крушинница
Gottesanbeterin	European Mantis	Mante prie-Dieu	Обыкновенный богомол
Grabwespen	Thread-waisted Wasps	Sphécidés	Роющие осы
Graphosoma italicum		Punaise d'Italie	Итальянский щитник, Полосатый клоп
Graszünsler	Grass Moths	Crambides	
Graue Fleischfliege	Grey Flesh Fly	Mouche grise de la viande	Серая мясоедка
– Kohlschnake	Common Crane Fly	Tipule du chou	Огородная долгоножка
– Waldschnake		Aedes cendré	Серый комар-кусака
Grauer Beifußmönch	Sharks	Noctuelle d'armoise	
Grillacridoidea	Cave and Camel-crickets	Sauterelle grillon	Ненастоящие кузнечиковые
Grillen	Crickets	Gryllides	Сверчковые
Grillenschrecken	Cave and Camel-crickets	Sauterelle grillon	Ненастоящие кузнечиковые
Große Birkenblattwespe	Great Birch Sawfly	Cimbex du bouleau	Березовый булавоус
– Kiefernbestands-Gespinstblattwespe	– Pine Web-spinning Pine-sawfly	Grande lyde champêtre	Большой сосновый пилильщик-ткач
– Lärchenblattwespe	Larch Sawfly	Grand Pritisphore du larix	Большой лиственничный пилильщик
– Pelzblattwespe	Birch Sawfly	Trichosome géant	
– Rote Waldameise	Wood Ant	Fourmi rousse	Лесной рыжий муравей
– Stubenfliege	House Fly	Mouche domestique	Большая комнатная муха

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Großer Eisvogel	Great Viceroy	Grand Sylvain	Тополевая ленточница
– Kohlweißling	Large Cabbage-white	Piéride du chou	Капустная белянка
– Kolbenwasserkäfer	Great Silver Water-beetle	Grand Hydrophile	Черный большой водолюб
– Leuchtkäfer	Common Glowworm	Lampyre noctiluque	Большой светляк
– Schillerfalter	Purple Emperor	Grand mars changeant	Мерцательница
Großes Nachtpfauenauge		– paon de nuit	Большой ночной павлиний глаз
– Ochsenauge	Meadow-brown	Myrtil	Воловий глаз
Großflügler	Snake Flies	Mégaloptères	Большекрылые
Großlibellen	Dragonflies	Anisoptères	Разнокрылые стрекозы
Großschaben	Cockroaches	Blattes vagabonds	
Grüne Blattwespe	Green Sawfly	Rhogogaster vert	Большой зеленый пилильщик
– Stinkwanze	– Shieldbug	Punaise verte	Зеленый древесный щитник
Grünes Heupferd	Great Green Bush-cricket	Grande sauterelle verte	Обыкновенный зеленый кузнечик
Grünwidderchen	Foresters	Procris	
Grylloidea	Crickets	Gryllides	Сверчковые
Gryllotalpa gryllotalpa	Mole-cricket	Taupe-gryllon commun	Обыкновенная медведка
Gryllus campestris	Field-cricket	Grillon des champs	Полевой сверчок
Gyrinidae	Whirling Beetles	Gyrins	Вертячки
Haarmücken	March-flies	Bibionidés	Комары-толстоножки
Haematomyzus elephantis		Pou d'éléphant	Слоновая вошь
Haematopinus asini	Sucking Horse Louse	– de l'âne	Лошадиная вошь
– *suis*	Pig Louse	– du porc	Свиная вошь
Hafte	Lace-wings	Planipennes	Сетчатокрылые
Halbinsekten	Proturans	Protoures	Бессяжковые насекомые
Halictus quadricinctus	Four-banded Mining Bee	Halicte des sillons à quatre bandes	
Halmfliegen	Gout Flies	Chloropidés	Злаковые мушки
Halmwespen	Stem Sawflies	Céphides	Стеблевые пилильщики
Halomachilis maritimus	Shore Bristle-tail	Machilide du littoral	
Harlekin	Common Magpie Moth	Zérène mouchetée du groseillier	Крыжовниковая пяденица
Haselblattroller	Hazel Leaf Roller	Apodère du noisettier	Орешниковый трубковерт
Haselnußbohrer	Nut Weevil		Ореховый долгоносик
Haselschildlaus	Hazel Scale	Lécanium du noisettier	
Hauhechel-Bläuling	Common Blue		Голубянка икар
Hausbockkäfer	House Longhorn	Hylotrupe	Домовый усач
Hausgrille	House-cricket	Gryllon domestique	Домовый сверчок
Hausmutter	Common Yellow Underwing	Hibou	
Hausschabe	German Cockroach	Blatte d'Allemagne	Рыжий таракан
Hautdassel	Warble Flies	Hypodermes	Кожные оводы
Hautflügler	Sawflies, Wasps	Hyménoptères	Перепончатокрылые
Hebridae	Sphagnum Bugs	Hébridés	
Heidekraut-Wurzelbohrer	Gold Swift	Hépiale de la fougère	Вересковый тонкопряд
Heiliger Pillendreher	Sacred Scarab		Священный навозник
Heimchen	House-cricket	Gryllon domestique	Домовый сверчок
Heleida	Biting Midges	Heléides	Мокрецы
Helicomyia saliciperda	Willow-shoot Hole	Moustique des saules	Ивовая галлица
Heliothrips haemorrhoidalis	Greenhouse Thrips	Thrips des serres	Оранжерейный трипс
Helophorus	Turnip Mud Beetles	Helophoridés	
Hemaris fuciformis	Broad Bordered Bee Hawk-moth	Sphinx-gazé	Стрекозки
Hemerobiidae	Brown Lacewings	Hémérobidés	Настоящие
Hemipteria	True Bugs	Hémiptères	Огненный червонец
Heodes virgaureae		Argus satiné	Тонкопряды
Hepialidae	Swifts	Hépialides	Вересковый тонкопряд
Hepialus hecta	Gold Swift	Hépiale de la fougère	Хмелевый тонкопряд
– *humili*	Ghost Swift	– du houblon	Жук-геркулес
Herkuleskäfer		Dynastes hercule	Вьюнковый бражник
Herse convolvuli	Convolvulus Hawk	Sphinx du ciseron	Толетоголовки
Hesperiidae	Skippers	Hespérides	Гессенская муха
Hessenfliege	Hessian Fly	Mouche d'Hesse	
Heteroceridae	Hide Beetles	Heteroceridés	Разнокрылые бабочки
Heteroneura		Hétéroneures	Клопы
Heteroptera	Bugs	Hétéroptères	Сенницы
Heufalter	Ringlets		Обыкновенные кузнечики
Heupferde	Bush-crickets	Tettigonides	Малинная стеклянница
Himbeer-Glasflügler		Sésie du framboisier	Сатир семеле
Hipparchia semele	Grayling	Agreste	Лошадиная кровососка или Паутка
Hippobosca equina		Mouche du cheval	Кровососки
Hippoboscidae	Bird Flies	Hippoboscidés	Олений овод
Hirschdasselfliege		Hypoderme du cerf	Жук-олень
Hirschkäfer	Stag Beetle	Lucane cerf-volant	Оленья кровососка
Hirschlausfliege	Deer Ked	Lipoptène du cerf	

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Histeridae		Histétidés	Карапузики
Höhere Schmetterlinge		Hétéroneures	Разнокрылые бабочки
Höhlenschrecke	Cave-cricket	Troglophile	
Hololampra	Pigmy Cockroaches	Petites Blattes	
Holzbienen	Large Carpenter Bees	Abeille charpentière	Пчелы-древогнезды
Holzbohrer	Goat Moths	Cossides	Древоточцы
Holzfliegen		Erinniés	Древесные мухи
Holzwespen	Horn-tails	Siricidés	Настоящие рогохвосты
Homoneura		Homoneures	Равнокрылые бабочки
Homoptera	Clear-winged Bugs	Homoptères	Равнокрылые хоботные
Honigbiene	Honey Bee	Abeille domestique	Обыкновенная медоносная пчела
Hopfenwurzelbohrer	Ghost Swift	Hépiale du houblon	Хмелевый тонкопряд
Hoplocampa	Sawflies	Hoplocampes	
– *brevis*		Hoplocampe du poirier	Грушевый пилильщик
– *flava*		– jaune du prunier	Желтый сливовый пилильщик
– *minuta*		– noir du prunier	Сливовый пилильщик
– *testudinea*	European Apple Sawfly	– du pommier	Яблоневый плодовый пилильщик
Hoplopus spinipes	Mason Wasp	Guêpe des murailles	Стенная оса
Hornisse	Grint Hornet	Frelon	Шершень
Hornissenschwärmer	Poplar Hornet Clearwing	Sésie du peuplier	Большая тополевая стеклянница
Hosenbiene	Hairylegged Mining Bees	Abeilles à pantalon	Мохноножки
Hüftwasserläufer	Pond Weed Bugs	Mesoveliidées	
Hummelschwärmer	Broad Bordered Bee Hawk-moth	Sphinx-gazé	
Hummelschwebfliege		Volucelle bourdon	Шмелевидная мохнатка
Hundefloh	Dog Flea	Puce du chien	Собачья блоха
Hundehaarling	Chewing Dog-louse	Pou du chien	Собачий власоед
Hundelaus	Dog Louse	– – –	Собачья вошь
Hungerwespen	Ensign Flies	Evaniides	Эваниды
Hydrocorisa	Water Bugs	Punaises d'eau	Водяные клопы
Hydrometridae	Water-measurers	Hydrométridés	Водомерки
Hydrophilidae	Water-beetles	Hydrophiles	Водолюбы
Hydrus piceus	Great Silver Water-beetle	Grand Hydrophile	Черный большой водолюб
Hygrobiidae	Screech Beetles	Hygrobiidés	
Hylaeus		Hylaeus	Пчелы-лесовки
Hylobius abietis	Large Pine Weevil	Grand Charançon du sapin	Большой сосновый долгоносик
Hylotrupes bajulus	House Longhorn	Hylotrupe	Домовый усач
Hymenoptera	Sawflies, Wasps	Hyménoptères	Перепончатокрылые
Hypoderma	Warble Flies	Hypodermes	Кожные оводы
– *actaeon*		Hypoderme du cerf	Олений овод
– *bovis*	Cattle Warble Fly	– – bœuf	Бычий овод
– *diana*	Deer Warble Fly	– – chevreuil	Косулий овод
Icerya purchasi	Cottony-cushion Scale	Cochenille australienne	Австралийский желобчатый червец
Ichneumonidae	Ichneumons	Ichneumonides	Настоящие наездники
Idolum diabolicum		Mante de diable	Чертов цветок
Immenkäfer		Trichodés	Пчеложуки
Inachis io	Peacock	Paon de jour	Дневной павлиний глаз
Indische Biene	Honey Bee	Abeille de l'Inde	Индийская медоносная пчела
Indischer Rattenfloh	Tropical Ratflea		Южная крысиная блоха
Insecta	Insects	Insectes	Насекомые
Insekten	–	–	Насекомые
Iphlicides podalirius		Flambé	Подалирий
Ischnocera		Poux aux tentacles minces	Тонкоусиковые пухоеды
Isoptera	Termites	Isoptères	Термиты
Isotoma saltans		Puce du glacier	Глетчерная блоха, Снежная блоха
Italienische Schönschrecke	Italian Locust	Criquet italien	Обыкновенный прус
Itoniidae	Gall Midges	Cécidomyus	Галлицы
Jagdfliegen	Assasin Flies	Asilidés	Ктыри
Jagdkäfer	Ostomatid Beetles	Ostomidés	
Jagdthripse	Predatory	Thrips à chasse	
Janus compressus		Janus du poirier	Грушевый стеблевой пилильщик
Japyx	Three-pronged Bristle-tails	Japyx	
»Jigger«	Jigger	Chique	Вредная блоха
Johannisfliege	St. John's Fly	Bibion de St. Jean	
Kabinettkäfer	Carpet Beetle	Anthrène du cabinet	Кабинетные кожееды
Käfer	Beetles	Coléoptères	Жуки
Kaisermantel	Silver-washed Fritillary	Tabac d'Espagne	Большая лесная перламутровка

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Kalifornische Ahornspringlaus		Puceron de Californie	Калифорнийская кленовая тля
Kalotermes flavicollis	Yellow-necked Termite	Termite à cou jaune, Flavicolle	Желтошеий термит
Kamelhalsfliegen	Snake Flies	Raphidiidés	Верблюдки
Kamelspinner	Pebble Prominent	Bois veiné	
Kammwanzen	Many-combed Bugs (N. A.)	Polycténidés	Клопы летучих мышей
Kapuzinerkäfer	False Powder-post Beetles (N. A.)	Bostryches	
Kartoffelkäfer	Colorado Beetles		Колорадский картофельный жук
Käsefliege	Cheese Skipper	Mouche du fromage	Сырная муха
Kastanienbohrer	Wood Leopard	Zeuzère du marronnier	Въедливая древесница
Katzenfloh	Cat Flea	Puce du chat	Кошачья блоха
Katzenhaarling	Cat-louse	Pou du chat	Кошачий власоед
Kegelbienen		Abeille à abdomen conique	Пчелы-остробрюхи
Kegelköpfe	Cone-heads	Conocéphalidés	Конусоголовые кузнечики
Kerbtiere	Insects	Insectes	Насекомые
Kermidae	Pseudogall Coccids	Cochenilles du chêne	
Kernkäfer	Ambrosia Beetles	Platypodidés	
Keulenkäfer		Clavigéridés	Булавчики
Kieferläuse	Chewing Lice	Mallophages	Пухоеды
Kieferneule	Pine Beauty	Varié de gris	Сосновая совка
Kiefernkultur-Gespinstblattwespe	Web-spinning Pine-sawfly	Lyde champêtre	Одиночный сосновый пилильщик-ткач
Kiefernspanner	Bordered White	Fidonie du pin	Сосновая пяденица
Kiefernspinner	Pine Lappet	Feuille morte du pin	Сосновый коконопряд
Kieferntriebwickler	Gemmet Shoot	Tordeuse des pousses	Сосновая плодожорка
Kirschfliege		Mouche des cerises	Вишневая муха
Kleesamenwespe		Brachophage du trèfle	Клеверный семеед
Kleiderlaus	Body Louse	Pou de vêtement	Платяная вошь
Kleine Fichtenblattwespe	Fir Sawfly	Petit Pritisphore du pin	Малый еловый пилильщик
– Lärchenblattwespe	Smaller Larch Sawfly	– – – milize	Малый лиственничный пилильщик
– Stubenfliege	Lesser House Fly	Petite mouche domestique	Малая комнатная муха
Kleiner Fuchs	Small Tortoiseshell	– tortue	Крапивница
– Kohlweißling	– White	Piéride de rave	Репная белянка
Kleines Nachtpfauenauge	Emperor Moth	Petit paon de nuit	Малый ночной павлиний глаз
Kleinlibellen	Damselflies	Zygoptères	Равнокрылые стрекозы
Kleinschaben	Pigmy Cockroaches	Petites blattes	
Klopfkäfer	Drugstore Beetles	Vrillettes	Точильщики
Knopfhorn-Blattwespen	Cimbicid Sawflies	Cimbicidés	Булавоусы
Köcherfliegen	Caddice Flies	Trichoptères	Ручейники
Kohleule	Cabbage Moth	Noctuelle du chou	Капустная совка
Kohlmotte	Diamond-back Moth	Teigne du Colza	Капустная моль
Kohlwanze	Brassica Bug	Punaise des potagers	Рапсовый щитник
Kolumbianischer Nashornkäfer		Coléoptère de Columbie	Колумбийский жук-носорог
Kommaschildlaus	Mussel Scale, Oystershell Scale	Cochenille des arbres fruitiers	Запятовидная щитовка
Königslibelle	Emperor Dragonfly	Anax empéreur	
Kopflaus	Head Louse	Pou de la tête	Головная вошь
Kopf- und Kleiderlaus	Men-louse	– – l'homme	Человеческая вошь
Kotfliege	Yellow Dung Fly	Mouche des bouses	
Kotfliegen	Dung Flies	Cordyluridés	Колосковые мухи
Kotfresser	– Beetles	Onthophagus	Калоеды
Kotkäfer	– Beetles	Coprins	Копры
Kotsack-Blattwespen	Leaf-rollers	Pamphilides	Пилильщики-ткачи
Kotwanze	Fly Bug	Punaise masqué	Грязный хищнец
Kriebelmücken	Black Flies	Mélusinides	Мошки
Kriegertermite		Termite militaire	Воинственный термит
Küchenschabe	Common Cockroach	Blatte des Cuisines	Черный таракан
Kugelfliegen	Fat Flies		Шаровки
Kürbiswanze	Squash Bug	Punaise de courge	Тыквенный клоп
Kurzflügler	Rove Beetles	Staphylins	Настоящие коротконадкрылые жуки
Kurzfühlerschrecken	Short-tentacled Grasshoppers	Sauterelles de palpes courtes	Саранчовые и Трипер-стовые
Küstenspringer	Shore Bristle-tail	Machilide du littoral	
Labia minor	Small Earwig	Perce-oreille nain, Forficule nain	Малая уховертка
Labidura riparia	Earwig	– des rivages	Прибрежная уховертка
Lampyridae	Glowworms	Lampyridés	Светляки
Lampyris noctiluca	Common Glowworm	Lampyre noctiluque	Большой светляк
Landkärtchen		Carte géographique	Весенняя пестрокрыльница
Landwanzen		Punaises de terre, Géocorises	Наземные клопы
Langbeinfliegen	Long-legged Flies	Dolichopodidés	
Langflügelige Schwertschrecke	Long-winged Cone-head	Conocéphalus brun	

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Langfühlerschrecken	Bush-crickets	Sauterelles à longues antennes	Кузнечиковые и Сверчковые
Langköpfige Rinderlaus	Long-nosed Oxlouse, Blue Cattle Louse	Pou du veau	Длинноголовая коровья вошь
Langkopfkäfer	Brentid Beetles (N. A.)		Долготелы
Langwanzen	Ground Bugs	Lygaeidés	Тощеклопы
Laothoe populi	Poplar Hawk	Sphinx du peuplier	Тополевый бражник
Lappländische Kriebelmücke		Mélusine de Laponie	Лапландская мошка
Lärchen-Gespinstblattwespe	Larch Web-spinning Sawfly	Lyde étoilée du laryx	
Larvivoridae	Parasite Flies	Larvivoridés	Ежемухи
Lasiocampa quercus	Oak Eggar	Minime à baudes jaunes	Дубовый коконопряд
Lasiocampidae	Lackeys and Eggars	Bombyx feuilles	Коконопряды
Lasius fuliginosus	Jet Ant	Fourmi fuligineuse	Муравей-древоточец
– *niger*	Small Black Ant	– noire des prés	Черный луговой муравей
– *umbratus*		– brune des prés	Темнобурый луговой муравей
Laspeyresia pomonella	Piercer	Pyrale des pommes	Яблонная плодожорка
Laternenträger	Lantern-flies	Fulgoridés	Светоноски
Lathridiidae	Mould Beetles	Lathriidés	
Laubheuschrecken	Bush-crickets	Tettigonides	Настоящие кузнечиковые
Laufkäfer	Carabids	Carabidés, Carabiques	Жужелицы
Läuseverwandte	Psocids	Psocidés	Вшевидные
Lausfliegen	Bird Flies	Hippoboscidés	Кровососки
Lederwanzen	Leaf-footed Bugs, Squash Bugs	Coréidés	Краевики
Ledra aurita		Cigale à oreilles	Ушастая цикадка
Legwespen	Parasitical Hymenoptera	Parasites	
Lehmwespen	Potter Wasps	Euménines	Одиночные осы
Lepidophthirius macrorhini		Pou d'éléphant marin	Вошь морских слонов
Lepidoptera	Butterflies and Moths	Lépidoptères	Чешуекрылые или Бабочки
Lepidosaphes ulmi	Mussel Scale, Oystershell Scale	Cochenille des arbres fruitiers	Запятовидная щитовка
Lepisma	Silverfish	Poisson d'argent	Чешуйницы
Lepismatidae	Firebrats	Lépismatidés	
Leptinotarsa decemlineata	Colorado Beetles		Колорадский картофельный жук
Lestes viridis		Leste vert	Зеленая лютка
Leuchtkäfer	Glowworms	Lampyridés	Светляки
Leuchtschnellkäfer		Coléoptères luisants, Pyrophores	Щелкуны-светляки
Leucophaea surinamensis	Surinam Cockroach	Blatte de serre	Суринамский таракан
Libellen	Dragonflies and Damselflies	Libellules	Стрекозы
Libellula depressa	Broad-bodied Libellula	Libellule déprimé	Плоская стрекоза
– *quadrimaculata*	Four-spotted Libellula	– à quatre taches	Пятнистая стрекоза
Libythea celtis		Échancré	Носатка
Libytheidae		–	Носатки
Lichtscheue Termite		Termite photophobe	Темнобурый термит
Lidmücken	Net-winged Midges	Blépharocéridés	Сетчатокрылки
Ligusterschwärmer	Privet Hawk	Sphinx du troène	Сиреневый бражник
Limenitis populi	Great Viceroy	Grand Sylvain	Тополевая ленточница
Limoniidae	Crane Flies	Limoniidés	Долгоножки
Limothrips	Grain Thrips	Thrips du blé	Хлебные трипсы
Linognathus ovillus	Sheep Louse	Pou du mouton	Овечья вошь
– *setosus*	Dog Louse	– – chien	Собачья вошь
– *stenopsis*	Goat Louse	– – chèvre	Козья вошь
– *vituli*	Long-nosed Oxlouse, Blue Cattle Louse	– – veau	Длинноголовая коровья вошь
Lipoptena cervi	Deer Ked	Lipoptène du cerf	Оленья кровососка
Liposcelis divinatorius	Book-louse	Pou devin	Книжная вошь
Liriopeidae	False Crane Flies	Liriopeidés	
Lucanidae	Stag Beetles	Lucanes	Рогачи
Lucanus	– –	Lucane cerf-volant	Жуки-олени
Luzernefloh	Lucerne Flea	Sminthure vert	
Lycaena	Coppers	Lycènes	
Lycenidae	Blues	Lycénides	Голубянки
Lycidae	Net-winged Beetles (N. A.)	Lycidés	
Lycoriidae		Sciaridés	Грибные комарики
Lyctidae	Powder-post Beetles	Lyctidés	
Lygaeidae	Ground Bugs	Lygaeidés	Тощеклопы
Lymantria dispar	Gipsy	Bombyx disparate	Непарный шелкопряд
– *monacha*	Black Arches	Nonne	Монашенка
Lymantriidae	Tussock-moths	Lymantriides	Волнянки
Lymexylonidae	Timber Beetles (N. A.)	Lymexylonidés	Жуки-матросы
Lytta	Spanish Flies	Mouches d'Espagne	Шпанские мухи
Machilidae	Machilids	Machilides	Махилисы
Macroglossum stellatarum	Humming-bird Hawk-moth	Moro-sphinx	Языкан
Macrotermes	Giant Termites	Termites géantes	
Maculinea arion	Large Blue	Alcon	

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Magenbremsen	Horse Bot Flies	Gastrophiles	Желудочные оводы
Magendasseln	– – –	– –	Желудочные оводы
Magicicada septendecim	Periodical Cicadas, Seventeen year Locust	Cigale de 17 ans	Цикада семнадцатилетка
Maikäfer	May Beetles	Hannetons	Майские жуки
Maiwürmer	Dil Beetles	Méloés	Майские букашки
Malachiidae		Malachidés	Малашки
Malacosoma neustria	Common Lackey	Livrée	Кольчатый коконопряд
Mallophaga	Chewing Lice	Mallophages	Пухоеды
Mamestra brassicae	Cabbage Moth	Noctuelle du chou	Капустная совка
Maniola jurtina	Meadow-brown	Myrtil	Воловий глаз
Mantis religiosa	European Mantis	Mante prie-Dieu	Обыкновенный богомол
Mantodea	Praying Mantids	Mantides	Богомолы
Marienkäfer	Ladybirds	Coccinellidés, Coccinelles	Божьи коровки
Marokkanische Wanderheuschrecke	Maroccan Grasshopper	Criquet marocain	Марокккская саранча
Märzfliege	St. Mark's Fly	Bibion de St.-Marc	Черная мошка
Maskenbienen		Hylaeus	Пчелы-лесовки
Mastotermes darwiniensis		Mantis de Darwin	Дарвинов термит
Mauer-, Mörtel- und Blattschneiderbienen	Leafcutting Bees	Abeille décaupeuse des feuilles	Мегахилиды
Mauerbienen	Mason Bees	– des murailles	Стенные пчелы
Mauersegler-Lausfliege	Swift Louse Fly	Mouche des martinets	Стрижиная кровососка
Maulbeerspinner	Silk Moth	Bombyx du mûrier	Тутовый шелкопряд
Maulwurfsgrille	Mole-cricket	Taupe-gryllon commun	Обыкновенная медведка
Mayetiola destructor	Hessian Fly	Mouche d'Hesse	Гессенская муха
Meconema thalassinum	Oak Bush-cricket	Méconema	Дубовый кузнечик
Mecoptera	Scorpion Flies	Mécoptères	Скорпионовые мухи
Mecopteria	– –	–	Мухи
Megachile	Leaf-cutting Bees	Mégachiles	Пчелы-листорезы
Megachilidae	– –	Abeille décaupeuse des feuilles	Мегахилиды
Megaloptera	Snake Flies	Mégaloptères	Большекрылые
Mehlkäfer	Mealworm	Ténébrion meunier	Мучной хрущак
Mehlmotte	Mediterranean Flour Moth	Teigne de la farine	Мельничная огневка
Melasoma populi	Red Poplar Leaf Beetle		Тополевый листоед
Meldenwanzen	Beetbugs	Piésmides	
Meligethes aeneus	Pollen Beetle	Méligèthe bronzé	Рапсовая блестянка
Meliponini	Stingless Bees	Abeilles sans aiguillon	
Meloe	Dil Beetles	Méloés	Майские букашки
Meloidae	Blister Beetles	Méloidés	Нарывники
Melolontha	Cockchafers	Hannetons	Майские хрущи
– *melolontha*	White Grub	Ver blanc	Западный майский хрущ
Melolonthinae	May Beetles	Hannetons	Майские жуки
Melophagus ovinus	Sheep Ked	Mélophage du mouton	Овечья кровососка
Melusina ornata		Mélusine commun	Обыкновенная мошка
Melusina reptans		– de Laponie	Лапландская мошка
Melusinidae	Black Flies	Mélusinides	Мошки
Membranacidae	Tree-hoppers, Devil-hoppers	Membracidés	Горбатки
Menschenfloh	Human Flea	Puce de l'homme	Человеческая блоха
Mesoveliidae	Pond Weed Bugs	Mesoveliidées	
Messor	Grain Ants	Fourmi moissonneuse	Муравьи-Жнецы
Micropterygidae		Microptérygidés	Первичные моли
Mindarus abietinus	Balsam Twig Aphid	Puceron du sapin	Пихтовая тля
Minierfliegen	Leaf Miners	Agromyzidés	Минирующие мушки
Miridae	Plant Bugs	Miridés	Клопы-слепняки
Mistkäfer	Dor Beetles		Настоящие навозники
Mittelmeerfruchtfliege	Mediterranean Fruit Fly	Mouche des oranges	Средиземноморская плодовая муха
Mittelmeer-Stabschrecke	– Stick-insect		Стеблевидка
Mittlere Wespe		Guêpe moyenne	Средняя оса
Moderkäfer	Mould Beetles	Lathriidés	
Mohrenfalter	Alpines	Erébia	Глазки-чернушки
Möhrenfliege	Carrot Rust Fly	Mouche des carottes	Морковная муха
Monarchfalter	Monarch [N. A.]	Monarque	
Mondhornkäfer	Dung Beetles	Copris	Лунные копры
Mondraupeneule	Dun-bar	Trapèze	
Mordellidae	Tumbling Flower Beetles [N. A.]	Mordellidés	Шипоноски или Горбатки
Mordwanzen		Punaise du meurtre	Хищнецы
Mormolyce	Violin Beetles		Листовенные жужелицы
Morphidae	Morphos	Morphos	
Morphofalter	–	–	
Mosaiklibellen	Hairy Dragonfly	Aeschna à abdomen court	Коромысло
Mottenschildläuse	White Flies	Aleurodinés	Алейродиды
Mücken	Thread-horns	Nématocères	Комары
Musca domestica	House Fly	Mouche domestique	Вольшая комнатная муха
Muscidae	House Flies	Muscidés	Настоящие мухи

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Museumskäfer	Museum Beetle		Кабинетные кожееды
Mutilla europaea	European Velvet-ant	Mutille d'Europe	Европейская немка
Mutillidae	Velvet-ants	Mutillides	Немки
Mylabris	Blister Beetles	Mylabris	Нарывники
Mymaridae	Tiny Wasps	Mymaridés	
Myrmeciinae	Bulldog Ants	Myrmécinés	
Myrmecophila acervorum	European Ant-loving Crickets	Grillon myrmécophile de l'Europe	
– americana	American Ant-loving Crickets	– – – l'Amérique	
Myrmecophylidae	Ant-loving Crickets	Grillons myrmécophiles	
Myrmecoris gracilis		Punaise de la fourmi	Муравьиный клоп
Myrmeleon formicarius		Fourmis lion	Муравьиный лев
Myrmeleonidae	Ant Lions	Fourmis-lions	Муравьиные львы
Myzodes persicae	Peach-potatoe Aphid	Puceron vert du pêcher	Персиковая тля
Nabidae	Damsel Bugs	Nabidés	
Nachtpfauenaugen	Emperor Moths	Saturniides	Павлиноглазки
Nacktfliegen	Rust Flies	Psilidés	Голотелки
Nagelfleck		Hachette	Рыжий ночной павлиний глаз Кошачий глаз
Nasendasseln	Bot Flies	Œstres	Носоглоточные оводы
Nashornkäfer	Rhinoceros Beetles	Dynastinés	Исполинские жуки
Naucoridae	Saucer Bugs	Naucoridés	
Necrophorus	Sexton Beetles	Nécrophores	Могильщики
Nelkenthrips		Thrips d'œillet	Гвоздичный трипс
Nematocera	Thread-horns	Nématocères	Комары
Nematus ribesii	Black Currant Sawfly	Némate du groseillier	Желтый крыжовниковый пилильщик
Nemeobius lucina	Duke of Burgundy	Lucine	Лесная пеструшка
Nemestrinidae		Némestrinidés	Неместриниды
Nemobius sylvestris	Wood-cricket	Grillon des bois	
Nepa rubra	Water-scorpion	Népa roux	Водяной скорпион
Nepidae	Water-scorpions	Népidés	Водяные скорпионы
Nepticulidae		Nepticulidés	Моли-малютки
Nesselröhrenlaus		Cochenille de l'ortie	Крапивный червец
Netzfliegen		Némestrinidés	Неместриниды
Netzflüglerartige	Alder Flies	Neuroptéroïdés	Сетчатокрыловые
Netzmücken	Net-winged Midges	Blépharocéridés	Сетчатокрылки
Netzwanzen	Lacebugs, Tingids	Tingidés	Кружевницы
Neuropteria	Alder Flies	Neuroptéroïdés	Сетчатокрыловые
Neurotoma nemoralis		Lyde du pêcher	Вишневый паутинный пилильщик
– saltuum	Common Web-spinning Sawfly	– – poirier	Общественный грушевый пилильщик-ткач
Nitidulidae	Sap-beetles	Nitidulidés	Блестяники
Noctuidae	Noctuids	Noctuelles	Совки или Ночницы
Nomada	Homeless Bees	Abeilles parasites	
Nomadacris septemfasciatus	Red Locust	Criquet nomade	
Nonne	Black Arches	Nonne	Монашенка
Notodonta	Pebble Prominents	Notodontides	Хохлатки
– ziczak	– Prominent	Bois veiné	
Notodontidae	Prominents	Notodontides	Хохлатки
Notonectidae	Back-swimmers	Notonectidés	Гладыши
Nymphalidae	Fritillaries	Nymphalides	Многоцветницы
Nymphalis antiopsa	Camberwell Beauty	Morio	Траурница
Ockerbindiger Samtfalter	Grayling	Agreste	Сатир семеле
Odonata	Dragonflies and Damselflies	Libellules	Стрекозы
Oecanthidae	Tree-crickets		Стеблевые сверчки
Oecanthus pellucens	Flower Tree-cricket		Трубачик
Oeciacus hirundinis	Swallow Bug	Punaise d'hirondelle	Ласточковый клоп
Oedemeridae	Oedemerid Beetles (N. A.)	Oedéméridés	Узконадкрылки
Oedipodinae	Band-winged Grasshoppers	Oedipodinés	Кобылки
Oedipoda caerulescens	Blue-winged Waste-land Grasshopper		Голубокрылая кобылка
– germanica	German Grasshopper		Краснокрылая кобылка
Oestridae	Bot Flies	Œstridés	Оводы
Oestrus	– –	Œstres	Носоглоточные оводы
– ovis	Sheep Gadfly	Œstre du mouton	Овечий овод
Ofenfischchen	Fire-bat		
Ohrwürmer	Earwigs	Dermaptères	Кожистокрылые
Ohrzikade		Cigale à oreilles	Ушастая цикадка
Ölbaumblattsauger		Puce d'olivier	Оливковая медяница
Ölkäfer	Oil Beetles	Méloés	Майские букашки
Omphrale fenestralis	Window Fly	Mouche des fenêtres	Оконная муха
Onthophagus	Dung Beetles	Onthophagus	Калоеды
Orchideenwespe	Orchid Wasp	Guêpe des orchidées	Орхидеевый семеед
Ordensbänder	Underwings	Lichénées	Ленточницы

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Orgyia recens	Scarce Vapourer		Кистехвост
Orneodidae	Many-plume Moth	Ornéodidés	Веерницы
Orthezia urticae		Cochenille de l'ortie	Крапивный червец
Orthopteria		Orthoptères	Прямокрылые
Oscinis frit	Frit Fly	Oscinie frit	Овсяная шведская мушка
Osmia	Mason Bees	Abeille des murailles	Стенные пчелы
Ostomidae	Ostomatid Beetles	Ostomidés	
Oxycarenus hyalipennis	Cotton Stainer	Punaise grise du Cotton	
Palomena prasina	Green Shieldbug	– verte	Зеленый древесный щитник
Palpenkäfer		Pselaphidés	Ощупники
Pamphilidae	Leaf-rollers	Pamphilides	Паутинные пилильщики
Pamphilius inanitus	Rose Web-spinning Sawfly	Lyde du rosier	Розанный пилильщик-ткач
Panolis flammea	Pine Beauty	Varié de gris	Сосновая совка
Panorpidae	Scorpion Flies	Panorpides	Скорпионницы
Papatacimücke	Papatasi Sandfly	Phlébotome de Papatau	
Papilio	Swallowtails	Papilios	
– *machaon*	Common Swallowtail	Grand porte-queue	Махаон
Papilionidae	Swallowtail Family	Papilionidés	Парусники или Кавалеры
Pappelblattkäfer	Red Poplar Leaf Beetle		Тополевый листоед
Pappelschwärmer	Poplar Hawk	Sphinx du peuplier	Тополевый бражник
Paravespula rufa	Wasp	Guêpe rousse	Рыжая оса
Parnassius	Apollos	Apollons	
– *apollo*	Apollo	Apollon	Аполлон
– *mnemosyne*		Semi-apollon	Черный аполлон
– *phoebus*		Petit Apollon	Альпийский аполлон
Parthenothrips dracaenae	Dracaena Thrips	Thripide dracaene	
Passalidae	Passalid Beetles (N. A.)	Passalidés	Сахарные жуки
Pediculidae	Men-lice	Poux	Вши приматов
Pediculus humanus	Men-louse	Pou de l'homme	Человеческая вошь
– – *capitis*	Head Louse	– – la tête	Головная вошь
– – *humanus*	Body Louse	– – vêtement	Платяная вошь
Pegomyia hyoscyami		Mouche de la betterave	Свекловичная муха
Pelzbienen	Potter Flower Bees	Anthophores	Антофоры
Pelzmotte	Case-making Clothes Moth	Teigne des fourrures	Шубная моль
Pentatotomidae	Shield Bugs	Punaises à bouclier	Щитники
Periplaneta	Cockroaches	Blattes vagabonds	
– *americana*	American Cockroach	Blatte américaine	Американский большой таракан
– *australasiae*	Australian Cockroach	– d'Australie	
Perlaugen	Green Lacewings	Chrysopides	Златоглазки
Perlmutterfalter	Fritillaris	Nacrés	Перламутровки
Petaurista hiemalis	Winter Gnat	Trichocère hivernal	
Petauristidae	Winter Gnats	Trichocéridés	Зимние комары
Pfeifenräumer		Rhyssa persuasive	Рисса
Pferdelaus	Sucking Horse Louse	Pou de l'âne	Лошадиная вошь
Pferdelausfliege		Mouche du cheval	Лошадиная кровососка или Паутка
Pferde-Nasendassel		Œstre du cheval	Лошадиный овод
Pferde- und Rinderbremsen	Horse-flies	Taons	Слепни
Pfirsichblattlaus	Peach-potatoe Aphid	Puceron vert du pêcher	Персиковая тля
Pflanzenkäfer	Comb-claw Beetles	Alleculidés	
Pflanzensauger	Clear-winged Bugs	Homoptères	Равнокрылые хоботные
Pflanzenwespen	Sawflies	Symphytes	Сидячебрюхие перепончатокрылые
Phasmida	Stick- and Leaf-insects	Phasmes	Привиденьевые
Philaenus spumarius		Cicadelle écumeuse	Слюнявая пенница
Philanthus triangulum	Bees Wool	Philanthe apivore	Пчелиный волк
Phlebotominae	Sandflies	Phlébotomines	Москиты
Phlebotomus papatasii	Papatasi Sandfly	Phlébotome de Papatau	
Phoridae	Coffin Flies	Phoridés	Горбатки
Phoridea	– –		Форы
Phryne fenestralis	Window Fly	Phryne des fenêtres	
Phtiraptera	Animal Lice	Poux des animaux	Животные вши
Phthirus pubis	Crab Louse	Pou de feutre	Лобковая вошь
Phyllaphis fagi	Beech Aphid	Puceron du hêtre	Буковая тля
Phyllium	Leaf-insect		Листотел
Phylloxeridae		Puceron de Cooley	Филоксеры
Phymatidae	Ambush Bugs (N. A.)	Phymatidés	
Physakermes hemicryphus		Cochenille de verticille du sapin	Еловая ложнощитовка
Pieridae	Whites	Piérides	Белянки
Pierinae	–	–	Настоящие белянки
Pieris brassicae	Large Cabbage-white	Piéride du chou	Капустная белянка
– *napi*	Green-veined White	– – navet	Горчичная белянка
– *rapae*	Small White	– de rave	Репная белянка

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Piesmidae	Beetbugs	Piésmides	
Pillendreher	Dung Beetles	Scarabées	Скарабеи
Pillenkäfer	Pill Beetles	Byrrhidés	Пилюльщики
Pillenwespen	Potter Wasp	Eumènes	Эвмены
Pilzmücken	Fungus Gnats	Mycetophilidés	Грибные комарики
Pimpla instigator		Ichneumon commun	Обыкновенный наездник
Pinien-Prozessionsspinner	Pine-feeding Processionary Caterpillar	Processionnaire du pin	Пиниевый походный шелкопряд
Piophila casei	Cheese Skipper	Mouche du fromage	Сырная муха
Piophilidae	– Skippers	Mouches du fromage	Пиофилиды
Planipennia	Lace-wings	Planipennes	Сетчатокрылые
Plattbauch	Broad-bodied Libellula	Libellule déprimée	Плоская стрекоза
Plattkäfer	Flat Bark Beetles (N. A.)	Rhizophagidés	Плоскотелки
Platyparea poeciloptera	Asparagus Fly	Mouche des asperges	Спаржевая бурилка
Platypodidae	Ambrosia Beetles	Platypodidés	
Platypsyllus		Platypsylles	Бобровые блюхи
Plebeiinae	Blues	Plébiines	
Plebeius argus	Silver-studded Blue	Azuré	
Plecoptera	Stoneflies	Plécoptères	Веснянки
Pleidae	Lesser Water-boatmen	Pleidés	
Plesiocoris rugicollis	Apple Capsid Bug	Capsid du pommier	Яблочный клоп
Plutella maculipennis	Diamond-back Moth	Teigne du Colza	Капустная моль
Pockenschildläuse	Pit Scales	Cochenille des véroles	
Pogonomyrmex		Fourmi des récoltes	Муравьи-земледельцы
Polistes gallicus		Poliste française	Французскаябумажная оса
Polyctenidae	Many-combed Bugs (N. A.)	Polycténidés	Клопы летучих мышей
Polyergus rufescens		Fourmi Amazon	Муравей-амазонка
Polygonia c-album	Comma	Gamma	
Polymitarcis virgo	Carrionfly	Polymitarcis vierge	Береговая поденка
Polyommatus icarus	Common Blue		Голубянка икар
Polyplax spinulosa	Spined Rat Louse	Pou du rat	Крысиная вошь
Pompilidae	Spider-wasps	Pompilidés	Дорожные осы
Pontania proxima	Common Willow Sawfly	Pontanie commune	Обыкновенный ивовый пилильщик
Postillion	Clouded Yellow	Souci	
Prachtkäfer	Metallic Wood-borers (N. A.)	Buprestes	Златки
Prachtlibellen	Demoiselles	Caloptéryx	Красотки
Primatenläuse	Men-lice	Poux	Вши приматов
Pritisphora abietina	Fir Sawfly	Petit Pritisphore du pin	Малый еловый пилильщик
– erichsoni	Larch Sawfly	Grand Pritisphore du larix	Большой лиственничный пилильщик
– laricis	Smaller Larch Sawfly	Petit Pritisphore du milize	Малый лиственничный пилильщик
Procris	Foresters	Procris	
Proctotrupoidea	Proctotrupoids	Proctotrupoidés	Гороховый наездник
Protichneumon pisorius		Ichneumon reclus	Бессяжковые насекомые
Protura	Proturans	Protoures	Походные шелкопряды
Prozessionsspinner	Processionary Caterpillars	Processionnaires	Ощупники
Pselaphidae		Pselaphidés	Морковная муха
Psila rosae	Carrot Rust Fly	Mouche des carottes	Голотелки
Psilidae	Rust Flies	Psilidés	Вшевидные
Psocia	Psocids	Psocidés	Сеноеды
Psocoptera	Book Lice	Poux de livres	Трескучая кобылка
Psophus stridulus	Red-winged Grasshopper		Мешочницы
Psychidae	Bag-worm Moths (N. A.)	Psychides	Бабочницы
Psychodidae	Moth Flies	Phlébotonies	Яблонная медяница
Psylla mali	Apple Psylla	Psylle du pommier	Пятнистая грушевая медяница
– piricola		Puce tacheté du poirier	Грушевая медяница
– pirisuga	Big Pear Psylla	Psylle du poirier	Листоблошки или Медяницы
Psyllina	Phyllids	Psyllines	Пальцекрылки
Pterophoridae	Plumes	Ptérophores	Высшие насекомые, Крылатые насекомые
Pterygota	Largely-winged Insects	Ptérygotes	Перокрылки
Ptiliidae		Ptiliidés	Притворяшки
Ptinidae	Spider Beetles	Ptinidés	Человеческая блоха
Pulex irritans	Human Flea	Puce de l'homme	Пахучий красотел
Puppenräuber	Caterpillar Hunter		Огневки
Pyralididae	Snout Moths	Pyralididés	Щелкуны-светляки
Pyrophorus		Coléoptères luisants, Pyrophores	Красноклопы
Pyrrhocoridae	Pyrrhocorid Bugs	Pyrrhocoridés	Бескрылый красноклоп
Pyrrhocoris apertus	Firebug	Punaise sans ailes	Калифорнийская щитовка
Quadraspidiotus perniciosus	San Jose Scale	Pou de San José	
Quellfungfern	Golden-ringed Dragonflies	Cordulégastrides	
Rachendasseln	Mouth Flies	Cephenomyes	Глоточные оводы

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Ranatra linearis	Water Stick-insect	Punaise linéaire	Ренатра
Randwanze		– bordée	Обыкновенный краевик
Raphidia ophiopsis	Snake Fly	Raphide aux yeux d'un serpent	
Raphidides	– Flies	Raphididés	Верблюдки
Rapsglanzkäfer	Pollen Beetle	Méligèthe bronzé	Рапсовая блестянка
Raptiformica sanguinea	Blood-red Ant	Fourmi sanguine	Кровавый муравей
Rasenameise	Erratic Ants	– des prés	
Rattenlaus	Spined Rat Louse	Pou du rat	Крысиная вошь
Raubfliegen	Assasin Flies	Asilidés	Ктыри
Raubwanzen	– Bugs	Réduviidées	Хищнецы
Raupenfliegen	Parasite Flies	Larvivoridés	Ежемухи
Rebenstecher		Cigarier	Виноградный слоник
Reblaus	Vine Louse	Phylloxéra	Виноградная филоксера или Виноградная тля
Reduviidae	Assasin Bugs	Réduviidées	Хищнецы
Reduvius personatus	Fly Bug	Punaise masquée	Грязный хищнец
Regenbremse		Taon des pluies	Дождевка
Rehdasselfliege	Deer Warble Fly	Hypoderme du chevreuil	Косулий овод
Reticulitermes flavipes	Eastern subterranean Termite	Termite aux pieds jaunes	Желтоногий термит
– *lucifugus*		– photophobe	Темнобурый термит
Rhabdophaga salicis		Rhabdophage des saules	Ростковая ивовая галлица
Rhagionidae	Snipe-flies	Rhagionidés	Бекасоноски
Rhagoletis cerasi		Mouche des cerises	Вишневая муха
Rhinocoris		Punaise du meurtre	Хищнецы
Rhinoestrus purpureus		Œstre du cheval	Лошадиный овод
Rhipiphoridae		Rhipiphoridés	Веероносцы
Rhogogaster viridis	Green Sawfly	Rhogogaster vert	Большой зеленый пилильщик
Rhynchophthira	Probescis Lice	Poux à trompes	Хоботковые пухоеды
Rhysodidae		Rhysodidés	Ризоды
Rhyssa persuasoria		Rhyssa persuasive	Рисса
Riesenbastkäfer		Dendroctones	Большие лубоеды
Riesenholzwespe	Large Woodwasp	Sirex géant	Большой рогохвост
Riesenhonigbiene	Honey Bee		Исполинская пчела
Riesenschlupfwespe		Ichneumon reclus	Гороховый наездник
Riesenschnake	Giant Crane Fly	Tipule géante	Большая долгоножка
Riesentermiten	– Termites	Termites géantes	
Riesenwanzen	– Water Bugs	Belostamatidés	
Rindenwanzen	Flat Bugs	Aradidés	Подкорники
Rinderbiesfliege	Cattle Warble Fly	Hypoderme du bœuf	Бычий овод
Rinderbremse	Large Horse Fly	Taon des bœufs	Бычий слепень
Rinderhaarlinge	Cattle-lice	Poux des bœufs	Коровий власоед
Ringelspinner	Common Lackey	Livrée	Кольчатый коконопряд
Ritterfalter	Swallowtail Family	Papilionidés	Парусники или Кавалеры
Rhododendron-Netzwanze	Rhododendron Bug	Tigre du rhododendron	Рододендроновый клоп
Röhren-Fransenflügler	Tubuliferae	Tubulifères	Трубкохвостые трипсы
Röhrenläuse	Aphids	Aphididés	Настоящие тли
Rollfliegen	Flat-footed Flies (N. A.)	Clythiidés	
Rollwespen	Rolling Wasps	Tiphides	Тифии
Rosen-Bürsthornwespe	Rose Sawfly	Hylotome de la rose	Розанный пилильщик
Rosen-Gespinstblattwespe	– Web-spinning Sawfly	Lyde du rosier	Розанный пилильщик-ткач
Rosenkäfer	Rose-chafers	Cetonines	Бронзовки
Rosenzikade	Rose Leafhopper	Cicadelle du rosier	Розанная цикадка
Roßameise		Camponotus	Муравьи-древоточцы
Rostrote Holzfliege		Mouche rouge du bois	Рыжая древесная муха
Rote Wanderheuschrecke	Red Locust	Criquet nomade	
– Wespe	Wasp	Guêpe rousse	Рыжая оса
Rotes Ordensband	Red Underwing	Mariée	Красная ленточница
Rotflüglige Ödlandschrecke	German Grasshopper		Краснокрылая кобылка
– Schnarrschrecke	Red-winged Grasshopper		Трескучая кобылка
Rübenweißling	Green-veined White	Piéride du navet	Горчичная белянка
Rückenschwimmer	Back-swimmers	Notonectidés	Гладыши
Runkelrüben-Blattwespe	Turnip	Athale de la betterave	Рапсовый пилильщик
Runkelrübenfliege		Mouche de la betterave	Свекловичная муха
Runzelkäfer		Rhysodidés	Ризоды
Rüsselkäfer	Weevils (N. A.)	Charançons	Долгоносики
Rüsselläuse	Proboscis Lice	Poux à trompes	Хоботковые пухоеды
Saateule	Turnip Dart	Noctuelle des moissons	Озимая совка
Sächsische Wespe	Tree Wasp	Guêpe de Saxe	Саксонская оса
Sackblattkäfer		Clythres	Клитры
Sackmotten	Case Bearers	Coléophoridés	
Sackspinner	Bagworm Moths (N. A.)	Psychides	Мешочницы
Sägekäfer	Hide Beetles	Heteroceridés	
Sägewespen	Sawflies	Hoplocampes	
Saldidae	Shore Bugs	Saldidés	Береговые клопы

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Saltatoria	Saltatoria	Sauterelles	Прыгающие прямокрылые
Samenkäfer	Seed Beetles	Bruches	Зерновки
Sandbienen	Solitary Bees	Andrenidés	Андрены
Sandfloh	Jigger	Chique	Вредная блоха
Sandlaufkäfer	Tiger Beetles	Cicindèles	Скакуны
Sandmücken i. e. S.	Sandflies	Phlébotomines	Москиты
Sandohrwurm	Earwig	Perce-oreille des rivages	Прибрежная уховертка
Sandwespe	Sand Wasp	Guêpe des sables	Обыкновенный пескорой
San-José-Schildlaus	San Jose Scale	Pou de San José	Калифорнийская щитовка
Saperda populnea		Petite saperde du peuplier	Малый осиновый усач
Sarcophaga carnaria	Grey Flesh Fly	Mouche grise de la viande	Серая мясоедка
Sattelschrecken	Katydids (N. A.)	Ephippigérides	
Saturnia pyri		Grand paon de nuit	Большой ночной павлиний глаз
Saturniidae	Emperor Moths	Saturniides	Павлиноглазки
Satyridae	Meadow Browns	Satyrides	Сатиры
Scarabaeidae	Cockchafers	Scarabés	Пластинчатоусые или Навозники
Scarabaeus	Dung Beetles	Scarabées	Скарабеи
– *laticollis*		Scarabée à corselet large	Пластинчатоусые или Навозники
– *sacer*	Sacred Scarab		Священный навозник
Schaben	Cockroaches	Blattes	Таракановые
Schachbrett	Marbled White	Demi-deuil	Шашечница
Schaf-Nasendassel	Sheep Gadfly	Œstre du mouton	Овечий овод
Schafslaus	– Louse	Pou du mouton	Овечья вошь
Schafslausfliege	– Ked	Mélophage du mouton	Овечья кровососка
Schalenschildläuse	Soft Scales	Lécanines, Coccidés	Полушечницы или Ложнощитовки
Schamlaus	Crab Louse	Pou de feutre	Лобковая вошь
Schaumzikaden	Spittle Bugs, Frog-hoppers	Cercopidés	Пенницы
Scheinböcke	Oedemerid Beetles (N. A.)	Oedémérídés	Узконадкрылки
Schienenkäfer	False Click Beetles (N. A.)	Eucnémidés	
Schildkäfer	Tortoise Beetles	Cassidinés	Щитоноски
Schildläuse	Coccids, Mealy Bugs	Cochenilles	Кокциды
Schildwanzen	Shield Bugs	Punaises à bouclier	Щитники
Schillerfalter	Purple Emperor	Apatura	Апатуры
Schimmelkäfer	Cryptophagid Beetles (N. A.)	Cryptophagidés	
Schistocerca peregrina	Desert Locust	Sauterelle pélerin	Пустынная саранча
Schizoneura lanuginosa		Schizonèvre laineux	Пузырная тля
Schlammfliege	Alder Fly, Drone Fly	Sialis de la vase, Eristale gluante	Обыкновенная вислокрылка, Ильница
Schlammfliegen	Snake Flies	Mégaloptères	Большекрылые
Schlammkäfer	Screech Beetles	Hygrobiidés	
Schlangenäugige Kamelhalsfliege	Snake Fly	Raphide aux yeux d'un serpent	
Schlupf-und Gallwespen	Parasitical Hymenoptera	Parasites	
Schmalkopfthrips	Cabbage Thrips	Thrips à tête étroite	Узкоголовый трипс
Schmalwanzen	Plant Bugs	Miridés	Клопы-слепняки
Schmarotzerbienen	Homeless Bees	Abeilles parasites	
Schmeißfliegen	Blow Flies	Calliphoridés	
Schmetterlinge	Butterflies and Moths	Lépidoptères	Чешуекрылые или Бабочки
Schmetterlingshafte		Ascalaphidés	Аскалафы
Schmetterlingsmücken	Moth Flies	Phlébotonies	Бабочницы
Schnabelfliegen	Scorpion Flies	Mécoptères	Скорпионовые мухи
Schnabelhaftverwandte	– –	–	Мухи
Schnabelkäfer	Net-winged Beetles (N. A.)	Lycidés	
Schnabelkerfe	True Bugs	Hémiptères	Настоящие полужестокрылые
Schnarrheuschrecken	Band-winged Grasshoppers	Oedipodinés	Кобылки
Schnauzenfalter		Échancré	Носатки
Schnellkäfer	Click-beetles	Taupins	Проволочники или Щелкуны
Schnepfenfliegen	Snipe-flies	Rhagionidés	Векасоноски
Schrecken	Saltatoria	Sauterelles	Прыгающие прямокрылые
Schwalbenlausfliege	Swallow Louse Fly	Mouche des hirondelles	Ласточковая кровососка
Schwalbenschwanz	Swallowtail	Grand porte-queue	Махаон
Schwalbenwanze	Swallow Bug	Punaise d'hirondelle	Ласточковый клоп
Schwammspinner	Gipsy	Bombyx disparate	Непарный шелкопряд
Schwärmer	Hawk-moth	Sphingides	Бражники
Schwarze Citrusfliege	Citrus Black Fly	Mouche noire des Aurantiacées	Темнокрылая белая мушка
– Fliege	Greenhouse Thrips	Thrips des serres	Оранжерейный трипс
– Kammschnake		Cténophore obscur	Гребневая долгоножка
– Kiefernholzwespe		Xeris du pin	Черный рогохвост
– Pflaumensägewespe		Hoplocampe noir du prunier	Сливовый пилильщик
– Wiesenameise	Small Black Ant	Fourmi noire des prés	Черный луговой муравей

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Schwarzer Apollo		Semi-apollon	Черный аполлон
Schwarzgraue Hilfsameise		Fourmi noir cendré	Черный муравей
Schwarzkäfer	Ground Beetles (N. A.)	Ténébrionidés	Чернотелки
Schwarzpunktzikade		Cigale à tache noire	Черноточечная цикадка
Schwebfliegen	Hover Flies	Syrphidés	Журчалки
Schweinelaus	Pig Louse	Pou du porc	Свиная вошь
Schwertschrecken	Cone-heads	Conocéphalus	
Schwertwespen		Xiphydriidés	Ксифидрии
Schwimmkäfer	Carnivorous Water beetles	Dytiscides	Плавунцы
Schwimmwanzen	Saucer Bugs	Naucoridés	
Scolia flavifrons	Yellow-fronted Digger Wasp	Scolia à front jaune	Желтолобая сколия
Scoliidae	Digger Wasps	Scoliides	Сколии
Scolothrips	Predatory	Thrips à chasse	
Scolytidae	Scolytid Beetles	Scolytes	Заболонники
Scopeuma stercoraria	Yellow Dung Fly	Mouche des bouses	
See-Elefanten-Laus		Pou d'éléphant marin	Вошь морских слонов
Seelöwenlaus		– du lion marin	Сивучовая вошь
Segelfalter		Flambé	Подалирий
Seidenbienen	Colletid Bees	Colletidés	Шелковые пчелы
Seidenspinner	Silk Moths	Bombycides	Настоящие шелкопряды
Serropalpidae	False Darkling Beetles (N. A.)	Serropalpidés	
Serviformica fusca		Fourmi noir cendré	Черный муравей
Sialidae	Alder Flies	Sialides	Вислокрылки
Sialis lutaria	– Fly	Sialis de la vase	Обыкновенная вислокрылка
Sibirische Keulenschrecke	Siberian Grasshopper	Sauterelle de Sibérie	Сибирская саранча
Sichelwanzen	Damsel Bugs	Nabidés	
Siebenpunkt-Marienkäfer	Ladybird	Coccinelle à sept points	Семиточечная коровка
Siebzehnjahr-Zikade	Periodical Cicadas, Seventeen year Locust	Cigale de 17 ans	Цикада семнадцатилетка
Silberfischchen	Silverfish	Poisson d'argent	Чешуйницы
Silberstich	Silver-washed Fritillary	Tabac d'Espagne	Большая лесная перламутровка
Silphidae	Carrion Beetles, Burying Beetles	Silphidés	Мертвоеды
Singzikaden	Cicadas	Cigales	Певчие цикады
Siphonaptera	Fleas	Puces	Блошиные
Sirex juvencus	Polished Horntail	Sirex commun	Обыкновенный сосновый рогохвост
Siricidae	Horn-tails	Siricidés	Настоящие рогохвосты
Skorpionsfliegen	Scorpion Flies	Panorpides	Скорпионницы
Skorpionswanzen	Water-scorpions	Népidés	Водяные скорпионы
Smerinthus ocellata	Eyed Hawk	Demi-paon	Глазчатый бражник
Sminthurides aquaticus	Water Springtail	Sminthuride d'eau	
Sminthurus viridis	Lucerne Flea	Sminthure vert	
Spanische Fliegen	Spanish Flies	Mouches d'Espagne	Шпанские мухи
Spanner	Geometers	Géométrides	Пяденицы
Spargelfliege	Asparagus Fly	Mouche des asperges	Спаржевая бурилка
Speckkäfer	Hide Beetles	Dermestes	Кожееды
Sphecidae	Thread-waisted Wasps	Sphécidés	Роющие осы
Sphingidae	Hawk-moth	Sphingides	Бражники
Sphinx ligustri	Privet Hawk	Sphinx du troène	Сиреневый бражник
Spinnenfliegen	Fat Flies		Шаровки
Splintholzkäfer	Powder-post Beetles	Lyctidés	
Springschwänze	Springtails	Collemboles	Ногохвостки или Вилохвостки
Stabwanze	Water Stick-insect	Punaise linéaire	Ренатра
Stachelbeerspanner	Common Magpie Moth	Zérène mouchetée du groseillier	Крыжовниковая пяденица
Stachelkäfer	Tumbling Flower Beetles (N. A.)	Mordellidés	Шипоноски или Горбатки
Stachellose Bienen	Stingless Bees	Abeilles sans aiguillon	
Stahlblaue Kiefernschonungs-Gespinstblattwespe	False Pine Webworm	Lyde bleue	
Staphylinidenartige	Rove Beetles	Staphylins	Коротконадкрылые жуки
Staphylinidae	– –		Настоящие коротконадкрылые жуки
Staphylinoidea	– –		Коротконадкрылые жуки
Staubhafte	Dusty Wings	Conioptérygidés	
Staubläuse	Book lice	Poux de livres	Сеноеды
Staubwanze	Fly Bug	Punaise masquée	Грязный хищнец
Stauronotus maroccanus	Maroccan Grasshopper	Criquet marocain	Марокккская саранча
Stauropus fagi	Lobster Moth	Écureuil	Буковый вилохвост
Stechmücken	Mosquitoes	Moustiques	Настоящие комары или Кровососущие комары
Stechwespen		Guêpes piqueuses	Жалоносные перепончатокрылые
Stegomyia aegypti	Yellow Fever Mosquito	Moustique de la fièvre jaune	Желтолихорадный комар
Steinfliegen	Stoneflies	Plécoptères	Веснянки

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Steinobst-Gespinstblattwespe		Lyde du pêcher	Вишневый паутинный пилильщик
Stelzenwanzen	Stilt Bugs	Bérytidés	
Stelzmücken	Crane Flies	Limoniidés	Долгоножки
Stelzschnaken	– –	–	Долгоножки
Stenopteryx hirundinis	Swallow Louse Fly	Mouche des hirondelles	Ласточковая кровососка
Stephanitis piri		Tigre du poirier	Грушевая кружевница
– rhododendri	Rhododendron Bug	– – rhododendron	Рододендроновый клоп
Steppensattelschrecke	Katydid (N. A.)	Ephippigère des vignes	
Stielaugenfliegen	Stalk-eyed Flies	Diopsides	
Stilettfliegen	Stiletto Flies	Thérévidés	Ктыревидки
Stinkfliege		Mouche rouge du bois	Рыжая древесная муха
Stomoxys calcitrans	Stable Fly	– des étables	Жигалка
Stratiomyidae	Soldier Flies	Stratiomyidés	Львинки
Streifenwanze		Punaise d'Italie	Итальянский щитник или Полосатый клоп
Streifenzikade		Cigale à abdomen	Полосатая цикадка
Strepsiptera	Twisted-winged Insects	Strepsitères	Веерокрылки
Stromaphis quercus		Puceron du chêne	Дубовая тля
Stumpffühlerläuse		Poux à tentacle cônes	Короткоусиковые пухоеды
Stutzkäfer	Hister Beetles	Histéridés	Карапузики
Südliche Großschabe	Australian Cockroach	Blatte d'Australie	
Sumpffliegen	Shore Flies	Ephydridés	
Sumpfschnake		Tipule des marais	Вредная долгоножка или Льняная долгоножка
Supella supellectilium	Brown-banded Cockroach	Blatte des meubles	
Symphyta	Sawflies	Symphytes	Сидячебрюхие перепончатокрылые
Syrphidae	Hover Flies	Syrphidés	Журчалки
Syrphidea		–	Сирфы
Tabakthrips	Onion Thrips	Thrips de l'oignon et du tabac	Табачный трипс
Tabanidae	Horse-flies	Taons	Слепни
Tabanus	– –	–	Слепни
– bovinus	Large Horse Fly	Taon des bœufs	Бычий слепень
Tachinen	Parasite Flies	Larvivoridés	Тахины
Tachycines asynamorus	Greenhouse Camel-cricket	Sauterelle grillon de serre	Оранжерейный кузнечик
Taeniothrips dianthi		Thrips d'œillet	Гвоздичный трипс
– implex	Gladiolus Thrips	– du gladiole	Гладиолусовый трипс
Taghafte	Brown Lacewings	Hémérobidés	Стрекозки
Tagpfauenauge	Peacock	Paon de jour	Дневной павлиний глаз
Taillenwespen	Apocrites	Apocrites	
Tannenläuse	Adelgids	Puceron des sapins	Хермесы
Tannentrieblaus	Balsam Twig Aphid	– du sapin	Пихтовая тля
Tanzfliegen	Dance Flies	Empididés	Толкунчики
Taubenfederlinge	Pigeon-lice	Poux de colombes	Голубиные пероеды
Taubenschwänzchen	Humming-bird Hawk-moth	Moro-sphinx	Языкан
Taufliegen	Small Fruit Flies	Drosophilidés	Дрозофилы
Taumelkäfer	Whirling Beetles	Gyrins	Вертячки
Teichläufer	Water-measurers	Hydrométridés	Водомерки
Tendipedidae	Non-biting Midges	Tendipédidés	Звонцы или Комары-дергуны
Tenebrio molitor	Mealworm	Ténébrion meunier	Мучной хрущак
Tenebrionidae	Ground Beetles (N. A.)	Ténébrionidés	Чернотелки
Tenthredinidae	Sawflies	Tenthrédinidés	Настоящие пилильщики
Tenthredinoidea	Sawflies	–	Пилильщики
Teppichkäfer	Carpet Beetle	Anthrène de la scrophulaire	Ковровый кожеед
Terebrantes	Parasitical Hymenoptera	Parasites	
Terebrantia	Boring Thrips	Térébrants	Яйцекладные трипсы
Termiten	Termites	Termites, Isoptères	Термиты
Termitenfliegen	Termite Flies	Mouches des termitières	
Termitidae	Termites	Termitides	
Termitinae	–	Termes	
Termitoxenia	Termite Flies	Mouches des termitières	
Tetramorium caespitum	Erratic Ants	Fourmi des prés	
Tetrigidae	Grouse Locusts	Tetrigides	Тетригиды
Tettigonia viridissima	Great Green Bush-cricket	Grande sauterelle verte	Обыкновенный зеленый кузнечик
Tettigonidae	Bush-crickets	Tettigonides	Обыкновенные кузнечики
Tettigonioidea	–	–	Настоящие кузнечиковые
Teufelsblume		Mante de diable	Чертов цветок
Thaumetopoea pityyocampa	Pine-feeding Processionary Caterpillar	Processionnaire du pin	Пиниевый походный шелкопряд
– processionea		– – chêne	Дубовый походный шелкопряд
Thaumetopoeidae	Processionary Caterpillars	Processionnaires	Походные шелкопряды

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Theclinae	Hair-streaks	Théclines	Ктыревидки
Therevidae	Stiletto Flies	Thérévidés	Узкоголовый трипс
Thrips angusticeps	Cabbage Thrips	Thrips à tête étroite	Табачный трипс
– *tabaci*	Onion Thrips	Thrips de l'oignon et du tabac	
Thripse	Thrips	Thrips	Бахромчатокрылые
Thysanopteria	–	–	Бахромчатокрылые
Thysanura	Bristle-tails	Thysanoures	Щетинохвостки
Tierläuse	Animal Lice	Poux des animaux	Животные вши
Tinea pellionella	Case-making Clothes Moth	Teigne des fourrures	Шубная моль
Tineidae	Clothes Moths	Teignes	Моли
Tineola biseliella	Common Clothes Moth	Mite des vêtements	Мебельная моль или Платяная моль
Tingidae	Lacebugs, Tingids	Tingidés	Кружевницы
Tiphia	Rolling Wasps	Tiphides	
Tiphiidae	Tiphiid Wasps	–	Тифии
Tipula maxima	Giant Crane Fly	Tipule géante	Большая долгоножка
– *oleracea*	Common Crane Fly	– du chou	Огородная долгоножка
– *paludosa*		– des marais	Вредная долгоножка или Льняная долгоножка
Tipulidae	Crane Flies	Tipulidés	Долгоножки
Tortricidae	Leaf Rollers	Tortricides	Листовертки
Tortrix viridana	Pea-green Oak Twist	Tordeuse du chêne	Дубовая листовертка
Totengräber	Sexton Beetles	Nécrophores	Могильщики
Totenkopfschwärmer	Death's-head Hawk	Sphinx tête du mort	Мертвая голова
Trägspinner	Tussock-moths	Lymantriides	Волнянки
Trauermantel	Camberwell Beauty	Morio	Траурница
Trauermücken		Sciaridés	Грибные комарики
Treiberameisen	Sausage Ants	Dorylinés	
Treibhausthrips	Greenhouse Thrips	Thrips des serres	Оранжерейный трипс
Trialeurodes vaporarium	– White Fly	Mouche blanche des serres	Тепличная белокрылка
Trichiosoma lucorum	Birch Sawfly	Trichosome géant	
Trichodectes canis	Chewing Dog-louse	Pou du chien	Собачий власоед
Trichodes		Trichodés	Пчеложуки
Trichophaga tapetzella	Tapestry Moth	Teigne des tapis	Ковровая моль
Trichoptera	Caddice Flies	Trichoptères	Ручейники
Trictenotomidae	Cellar Beetles	Trictenotomidés	
Tridactylidae	Pigmy Mole-crickets	Tridactylides	Триперстовые
Triphaena pronuba	Common Yellow Underwing	Hibou	
Trogium pulsatorium		Pou de fropper	Домовый сеноед
Troglophilus neglectus	Cave Cricket	Troglophile	
Troides	Bird Wings		
Trypetidae	Large Fruit Flies	Mouches des fruits	Птицекрылки
Tsetsefliegen	Tsetse Flies	– tsé-tsé	Пестрокрылки
Tubulifera	Tubuliferae	Tubulifères	Мухи це-це
Tumbufliege	African Tumbu Fly	Cordylobia africaine	Трубкохвостые трипсы
Tunga trans	Jigger	Chique	
Typhlocyba rosae	Rose Leafhopper	Cicadelle du rosier	Вредная блоха
Typhoeus	Three-horned Dor Beetles	Minotaure typhée	Розанная цикадка
Uferaas	Carrionfly	Polymitarcis vierge	Трехрогие навозники
Uferfliegen	Stoneflies	Plécoptères	Береговая поденка
Uferwanzen	Shore Bugs	Saldidés	Веснянки
Ulmenblasenlaus		Schizonèvre laineux	Береговые клопы
Ulmenblattkäfer		Galérucelle d'orme	Пузырная тля
Ungefleckte Ameisenjungfer		Fourmis lion	Ильмовая козявка
Uraniafalter		Uraniides	Муравьиный лев
Uraniidae		–	Урании
Urmotten		Micropterygidés	Урании
Urocerus gigas	Large Woodwasp	Sirex géant	Первичные моли
Urschwänze	Proturans	Protoures	Большой рогохвост
Urtümlichste Kleinschmetterlinge		Homoneures	Бессяжковые насекомые
			Равнокрылые бабочки или Низшие бабочки
Ur- und Seidenbienen	Colletid Bees	Colletidés	Шелковые пчелы
Vanessa atalanta	Red Admiral	Vulcain	Адмирал
– *cardui*	Painted Lady	Belle-dame	Репейница
Veliidae	Water-crickets	Véliidées	
Vespa crabro	Grint Hornet	Frelon	Шершень
Vespidae	Yellow Jackets	Vespides	Складчатокрылые осы
Vespinae	Hornets	–	Общественные осы
Vierflecklibelle	Four-spotted Libellula	Libellule à quatre taches	Пятнистая стрекоза
Viergürtlige Schmalbiene	Four-banded Mining Bee	Halicte des sillons à quatre bandes	
Viteus vitifolii	Vine Louse	Phylloxéra	Виноградная филоксера или Виноградная тля
Vogelfalter	Bird Wings		Птицекрылки
Volucella bombylans		Volucelle bourdon	Шмелевидная мохнатка

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Wachsmotte	Wax Moth (N. A.)	Taupe teigne des ruches	Восковая моль или Большая пчелиная огневка
Wadenstecher	Stable Fly	Mouche des étables	Жигалка
Waffenfliegen	Soldier Flies	Stratiomyidés	Львинки
Waldgrille	Wood Cricket	Grillon des bois	
Waldschaben	– Cockroaches	Blattes des bois	Лесные тараканы
Waldwespe	Tree Wasp	Guêpe sylvestre	Лесная оса
Wandelndes Blatt	Leaf-insect		Листотел
Wanderheuschrecken	Migratory Locusts	Sauterelles de passage	
Wanzen	Bugs	Hétéroptères	Клопы
Warzenbeißer	Wart-biter	Dectique verrucivore	Серый кузнечик
Wasserflorfliege	Alder Fly	Sialis de la vase	Обыкновенная вислокрылка
Wasser-Kugelspringer	Water Springtail	Sminthuride d'eau	
Wasserläufer	Water-striders, Pondskater's (N. A.)	Gerridés	Водомерки
Wasserskorpion	Water-scorpion	Népa roux	Водяной скорпион
Wasserwanzen	Water Bugs	Punaises d'eau	Водяные клопы
Wasserzikaden	Corixids	Corixidés	Гребляки
Wegwespen	Spider-wasps	Pompilidés	Дорожные осы
Weichkäfer	Soldier-beetles	Cantharidés	Мягкотелки
Weidenbohrer	Goat Moth	Cossus gâte-bois	Пахучий древоточец
Weidenholzgallmücke	Willow-shoot Hole	Moustique des saules	Ивовая галлица
Weidenlibelle		Leste vert	Зеленая лютка
Weidenrutengallmücke		Rhabdophage des saules	Ростковая ивовая галлица
Weidenschaumzikade		Cigale du saule	Ивовая пенница
Weinhähnchen	Flower Tree-cricket		Трубачик
Weiße Citrusfliege	Citrus White Fly	Mouche blanche des Aurantiacées	Цитрусовая мушка
– Fliegen	Mealy Wings	Aleurodinés	Белокрылки
– Gewächshausfliege	Greenhouse White Fly	Mouche blanche des serres	Тепличная белокрылка
Weißlinge	Whites	Piérides	Белянки
Weißlingstöter	Braconid Fly	Ichneumon	Капустничный апантелес
Werftkäfer	Timber Beetles (N. A.)	Lymexylonidés	Жуки-матросы
Wespe	Mason Wasp	Guêpe des murailles	Стенная оса
Wickler	Leaf Rollers	Tortricides	Листовертки
Widderchen	Burnets	Zygénides	Пестрянки
Wiener Nachtpfauenauge		Grand paon de nuit	Большой ночной павлиний глаз
Wiesenschnaken	Crane Flies	Tipulidés	Долгоножки
Windenschwärmer	Convolvulus Hawk	Sphinx du ciseron	Вьюнковый бражник
Winterhafte	Snow Scorpion Flies	Boréides	
Wintermücken	Winter Gnats	Trichocéridés	Зимние комары
Winterschnake	Winter Gnat	Trichocère hivernal	
Wollbienen	Wool Carder Bees	Abeille cotonnière	
Wollsackschildlaus	Cottony-cushion Scale	Cochenille australienne	Австралийский желобчатый червец
Wollschweber	Bee-flies	Bombylidés	Жужжалы
Würfelfalter	Duke of Burgundy	Lucine	Лесная пеструшка
Wurzelbohrer	Swifts	Hépialides	Тонкопряды
Wüstenschrecke	Desert Locust	Sauterelle pélerin	Пустынная саранча
Xenopsylla cheopsis	Tropical Ratflea		Южная крысиная блоха
Xeris spectrum		Xeris du pin	Черный рогохвост
Xiphydriidae		Xiphydriidés	Ксифидрии
Xylocopinae	Large Carpenter Bees	Abeille charpentière	Пчелы-древогнезды
Yponomeutidae	Small Ermines	Hyponomeutidés	Гориостаевые моли
Zahnspinner	Prominents	Notodontides	Хохлатки
Zangenschwänze	Three-pronged Bristle-tails	Japyx	
Zehrwespen	Proctotrupoids	Proctotrupoidés	
Zeuzera pyrina	Wood Leopard	Zeuzère du marronnier	Въедливая древесница
Zickzackspinner	Pebble Prominents	Notodontides	Хохлатки
Ziegenlaus	Goat Louse	Pou du chèvre	Козья вошь
Zikaden	Cicadas	Cigales	Цикадовые
Zikadenwespen		Dryinides	Дриины
Zimmermannsbock	Timberman		Домовый дровосек
Zipfelfalter	Hair-streaks	Théclines	
Zipfelkäfer		Malachidés	Малашки
Zitronenfalter	Brimstone	Citron	Крушинница
Zoroptera	Zoropterons	Poux de terre	
Zuckerkäfer	Passalid Beetles (N. A.)	Passalidés	Сахарные жуки
Zuckerrohrzünsler	Sugar-cane Borer	Pyrole de la canne à sucre	
Zuckmücken	Non-biting Midges	Tendipédidés	Звонцы или Комары-дергуны
Zungenfliegen	Tsetse-flies	Mouches tsé-tsé	Мухи це-це
Zünsler	Snout Moths	Pyralididés	Огневки
Zürgelbaumfalter		Échancré	Носатка

GERMAN NAME	ENGLISH NAME	FRENCH NAME	RUSSIAN NAME
Zweiflügler	Flies	Diptères	Двукрылые
Zwerghonigbiene		Abeille naine	Карликовая пчела
Zwergläuse		Puceron de Cooley	Филоксеры
Zwergmotten		Nepticulidés	Моли-малютки
Zwergohrwurm	Small Earwig	Perce-oreille nain, Forficule nain	Малая уховертка
Zwergrückenschwimmer	Lesser Water-boatmen	Pleidés	
Zwergwasserläufer	Sphagnum Bugs	Hébridés	
Zwergwespen	Tiny Wasps	Mymaridés	
Zwergzikade		Cigale à six taches	Шеститочечная цикадка
Zwetschgen-Napfschildlaus	European Fruit Lecanium	Cochenille du cornouiller	Акациевая ложнощитовка
Zwiebelfliegen	Lesser Bulb Fly	Mouches des oignons	Луковичные мухи
Zwiebelthrips	Onion Thrips	Thrips de l'oignon et du Tabac	Табачный трипс
Zygaena filipendulae	Six-spot Burnet	Zygène-de-la-filipendule	Таволговая пестрянка
Zygaenidae	Burnets	Zygénides	Пестрянки
Zygoptera	Damselflies	Zygoptères	Равнокрылые стрекозы

3. French—German—English—Russian

L'abréviation N.A., mise entre parenthèses, indique que les noms respectifs ne sont utilisés qu'en Amérique du Nord.

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Abeille à abdomen conique	Kegelbienen		Пчелы-остробрюхи
– charpentière	Holzbienen	Large Carpenter Bees	Пчелы-древогнезды
– cotonnière	Wollbienen	Wool Carder Bees	
– découpeuse des feuilles	Mauer-, Mörtel- und Blattschneiderbienen	Leafcutting Bees	Мегахилиды
– de l'Inde	Indische Biene	Honey Bee	Индийская медоносная пчела
– des murailles	Mauerbienen	Mason Bees	Стенные пчелы
– domestique	Echte Bienen, Honigbiene	Bumble Bees, Honey Bee	Настоящие пчелы, Обыкновенная медоносная пчела
– naine	Zwerghonigbiene		Карликовая пчела
Abeilles à pantalon	Hosenbiene	Hairylegged Mining Bees	Мохноножки
– parasites	Schmarotzerbienen	Homeless Bees	
– sans aiguillon	Stachellose Bienen	Stingless Bees	
Acridiens	Feldheuschrecken	Grasshoppers	Настоящие саранчовые
Aeschna à abdomen court	Mosaiklibellen	Hairy Dragonfly	Коромысло
– bleue	Blaugrüne Mosaikjungfer	Southern Aeshna	
Aedes cendré	Graue Waldschnake	Grey Mosquito	Серый комар-кусака
– commun	Gemeine Waldschnake	Common Mosquito	Обыкновенный комар-кусака
– tacheté	Gefleckte Waldschnake	Spotted Mosquito	Пятнистый комар-кусака
Agreste	Ockerbindiger Samtfalter	Grayling	Сатир семеле
Agrion joli	Fledermaus-Azurjungfer	Variable Coenagrion	
Agromyzidés	Minierfliegen	Leaf Miners	Минирующие мушки
Alcon	Arion-Bläuling	Large Blue	
Aleurodinés	Mottenschildläuse	White Flies	Алейродиды
Alleculidés	Pflanzenkäfer	Comb-claw Beetles	
Alysia dorée	Goldfliegen-Brackwespe	Golden Braconid Fly	
Anax empéreur	Königslibelle	Emperor Dragonfly	
Andrenidés	Sandbienen	Solitary Bees	Андрены
Anisoptères	Großlibellen	Dragonflies	Разнокрылые стрекозы
Anophèles	Fiebermücken	Mosquitoes	Малярийные комары
Anoplurés	Echte Läuse	Sucking Lice	Настоящие вши
Anthomyiinés	Blumenfliegen	Cabbage Root Fly	
Anthonome du pommier	Apfelblütenstecher	Apple Blossom Weevil	Яблонный цветоед
Anthonomes	Blütenstecher	Blossom Weevils	Цветоеды
Anthophores	Pelzbienen	Potter Flower Bees	Антофоры
Anthrène de la scrophulaire	Teppichkäfer	Carpet Beetle	Ковровый кожеед
– du cabinet	Kabinettkäfer	– Beetle	Кабинетные кожееды
Anthribidés	Breitrüßler	Fungus Weevils (N. A.)	Ложнослоники
Apatura	Schillerfalter	Purple Emperor	Апатуры
Aphididés	Röhrenläuse	Aphids	Настоящие тли
Aphidiidés	Blattlaus-Schlupfwespen	Ichneumons	Тлиные наездники
Aphodiinés	Dungkäfer	Dung Beetles	Пометокопатели
Apocrites	Taillenwespen	Apocrites	
Apodère du noisettier	Haselblattroller	Hazel Leaf Roller	Орешниковый трубковерт
Apoidés	Bienen	Bees	Пчелиные
Apollon	Apollofalter	Apollo	Аполлон
Aradidés	Rindenwanzen	Flat Bugs	Подкорники
Arctiidés	Bärenspinner	Tiger-moths	Медведицы

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Argus satiné	Dukatenfalter		Огненный червонец
Ascalaphidés	Schmetterlingshafte		Аскалафы
Asilidés	Jagdfliegen	Assasin Flies	Ктыри
Athale de la betterave	Runkelrüben-Blattwespe	Turnip	Рапсовый пилильщик
Attelabe du chêne	Eichenblattroller	Oak Leaf Roller	Дубовый трубковерт
Azuré	Argusbläuling	Silver-studded Blue	
Belle-dame	Distelfalter	Painted Lady	Репейница
Belostamatidés	Riesenwanzen	Giant Water Bugs	
Bérytidés	Stelzenwanzen	Stilt Bugs	
Bibion de St. Jean	Johannisfliege	St. John's Fly	
– St. Marc	Märzfliege	St. Mark's Fly	Черная мошка
– des jardins	Gartenhaarmücke	Garden March Fly	Садовая мошка
Bibionidés	Haarmücken	March-flies	Комары-толстоножки
Biorhiza du chêne	Eichen-Schwammgallwespe	Oak-apple Gallfly	Губчатая дубовая орехотворка
Blatte américaine	Amerikanische Großschabe	American Cockroach	Американский большой таракан
– d'Allemagne	Hausschabe	German Cockroach	Рыжий таракан
– d'Australie	Südliche Großschabe	Australian Cockroach	
– de serre	Gewächshausschabe	Surinam Cockroach	Суринамский таракан
– des Cuisines	Küchenschabe	Common Cockroach	Черный таракан
Blatte des meubles	Braunband- oder Möbelschabe	Brown-banded Cockroach	
Blattes	Schaben	Cockroaches	Таракановые
– des bois	Waldschaben	Wood Cockroaches	Лесные тараканы
– vagabonds	Großschaben	Cockroaches	
Blépharocéridés	Lidmücken	Net-winged Midges	Сетчатокрылки
Bois veiné	Kamelspinner	Pebble Prominent	
Bombardiers	Bombardierkäfer	Bombardier Beetles	Жужелицы-бомбардиры
Bombycides	Echte Spinner	Silk Moths	Настоящие шелкопряды
Bombylidés	Wollschweber	Bee-flies	Жужжалы
Bombyx atlas	Atlasspinner	Atlas Moth	
– disparate	Schwammspinner	Gipsy	Непарный шелкопряд
– du mûrier	Maulbeerspinner	Silk Moth	Тутовый шелкопряд
– feuilles	Glucken	Lackeys and Eggars	Коконопряды
Boréides	Winterhafte	Snow Scorpion Flies	
Bostryches	Kapuzinerkäfer	False Powder-post Beetles (N. A.)	
Bourdon de terre	Erdhummel	Bumble Bee	Земляной шмель
Brachophage du trèfle	Kleesamenwespe		Клеверный семеед
Brachycères	Fliegen	Short-horns	Мухи или Короткоусые двукрылые
Braconides	Brackwespen	Braconid Flies	Бракониды
Braulidés	Bienenläuse	Bee-»Lice«	Пчелиные паразиты
Bruches	Samenkäfer	Seed Beetles	Зерновки
Buprestes	Prachtkäfer	Metallic Wood-borers (N. A.)	Златки
Byrrhidés	Pillenkäfer	Pill Beetles	Пилюльщики
Calliphoridés	Schmeißfliegen	Blow Flies	
Caloptérygidés	Prachtlibellen	Demoiselles	Лютки
Caloptéryx	–	Demoiselles	Красотки
– brillant	Gebänderte Prachtlibelle	Banded Agrion	Блестящая красотка
Camponotus	Roßameise		Муравьи-древоточцы
Cantharidés	Weichkäfer	Soldier-beetles	Мягкотелки
Capricorines	Bockkäfer	Long-horned Beetles	Усачи или Дровосеки
Capsid du pommier	Apfelwanze	Apple Capsid Bug	Яблочный клоп
Carabidés	Laufkäfer	Carabids	Жужелицы
Carabiques	–	–	Жужелицы
Carte géographique	Landkärtchen		Весенняя пестрокрыльница
Cassidinés	Schildkäfer	Tortoise Beetles	Щитоноски
Cécidomyus	Gallmücken	Gall Midges	Галлицы
Cèphe du blé	Getreidehalmwespe	European Wheat Stem Sawfly	Хлебный пилильщик
Cephenomyes	Rachendasseln	Mouth Flies	Глоточные оводы
Céphides	Halmwespen	Stem Sawflies	Стеблевые пилильщики
Cercopidés	Schaumzikaden	Spittle Bugs, Frog-hoppers	Пенницы
Cetonines	Rosenkäfer	Roses Chafers	Бронзовки
Charançons	Rüsselkäfer	Weevils (N. A.)	Долгоносики
Chique	Sandfloh	Jigger	Вредная блоха
Chloropidés	Halmfliegen	Gout Flies	Злаковые мушки
Chlorops du blé et de l'onge	Gelbe Halmfliege	– Fly	Желтая зеленоглазка
Chrysidides	Goldwespen	Cuckoo Wasps	Блестянки
Chrysis enflammée	Feuergoldwespe	Fire Cuckoo Wasp	Обыкновенная блестянка
Chrysomélidés	Blattkäfer	Leaf Beetles	Листоеды
Chrysopides	Goldaugen	Green Lacewings	Златоглазки
Chrysops	Blindbremsen	Blinding Breeze Flies	Златоглазки
– commun	Goldauge	Green Lacewing	Простая златоглазка
Cicadelle du rosier	Rosenzikade	Rose Leafhopper	Розанная цикадка

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
– écumeuse	Gemeine Schaumzikade		Слюнявая пеница
Cicadidés	Singzikadenartige	Cicadas	Певчие цикадовые
Cicindèle des champs	Feld-Sandlaufkäfer	Field Tiger Beetles	Полевой скакун
Cicindèles	Sandlaufkäfer	Tiger Beetles	Скакуны
Cigale à abdomen	Streifenzikade		Полосатая цикадка
– à creilles	Ohrzikade		Ушастая цикадка
– à six taches	Zwergzikade		Шеститочечная цикадка
– à tache noire	Schwarzpunktzikade		Черноточечная цикадка
– de 17ans	Siebzehnjahr-Zikade	Periodical Cicadas, Seventeen year Locust	Цикада семнадцатилетка
– de montagne	Bergzikade		Горная цикада
– du frêne	Eschenzikade		Ясеневая цикада
– du saule	Weidenschaumzikade		Ивовая пеница
– sanguinolent	Blutzikade		Кровавая пеница
Cigales	Singzikaden, Zikaden	Cicadas, Harvest Flies	Певчие цикады, Цикадовые
Cigarier	Rebenstecher		Виноградный слоник
Cimbex du bouleau	Große Birkenblattwespe	Great Birch Sawfly	Березовый булавоус
Cimbicidés	Knopfhorn-Blattwespen	Cimbicid Sawflies	Булавоусы
Cimicidés	Bettwanzenverwandte	Bed Bugs	Постельные клопы
Citron	Zitronenfalter	Brimstone Butterfly	Крушинница
Clairons	Buntkäfer	Checkered Beetles	Пестряки
Clavigéridés	Keulenkäfer		Булавчики
Cleptides	Diebswespen		Блестянки
Clythiidés	Rollfliegen	Flat-footed Flies (N. A.)	
Clythres	Sackblattkäfer		Клитры
Coccidés	Schalenschildläuse	Soft Scales	Подушечницы или Ложнощитовки
Coccinelle à sept points	Siebenpunkt-Marienkäfer	Ladybird	Семиточечная коровка
Coccinellidés	Marienkäfer	Ladybirds	Божьи коровки
Cochenille	Cochenille-Laus	Cochineal Insect	Мексиканская конишель
– australienne	Wollsackschildlaus	Cottony-cushion Scale	Австралийский желобчатый червец
– de l'ortie	Nesselröhrenlaus		Крапивный червец
– de verticille du sapin	Fichtenquirlschildläuse		Еловая ложнощитовка
– des arbres fruitiers	Kommaschildlaus	Mussel Scale, Oystershell Scale	Запятовидная щитовка
– des véroles	Pockenschildläuse	Pit Scales	
– du chêne	Eichenpockenschildlaus		Дубовый червец
– du cornouiller	Zwetschgen-Napfschildlaus	European Fruit Lecanium	Акациевая ложнощитовка
Cochenilles	Schildläuse	Coccids, Mealy Bugs	Кокциды
– du chêne	Eichennapfläuse	Pseudogall Coccids	
Coléophoridés	Sackmotten	Case Bearers	
Coléoptère de Columbie	Kolumbianischer Nashornkäfer		Колумбийский жук-носорог
– du bouleau	Birkenblattroller	Birch Leaf Roller	Березовый слоник
Coléoptères	Käfer	Beetles	Жуки
– luisants	Leuchtschnellkäfer		Щелкуны-светляки
Coléoptérides	Deckflügler		Жесткокрылые
Colias	Gelblinge	Clouded Yellows	Желтушки
Collemboles	Springschwänze	Springtails	Ногохвостки или Вилохвостки
Colletidés	Seiden- und Urbienen	Colletid Bees	Шелковые пчелы
Conioptérygidés	Staubhafte	Dusty Wings	
Conocéphalidés	Kegelköpfe	Cone-heads	Конусоголовые кузнечики
Conocéphalus	Schwertschrecken	–	
– brun	Langflügelige Schwertschrecke	Long-winged Cone-head	
Conopidés	Dickkopffliegen	Thick-headed Flies	Толстоголовки
Coprins	Kotkäfer	Dung Beetles	Копры
Copris	Mondhornkäfer	– Beetles	Лунные копры
Cordulégastrides	Quelljungfern	Golden-ringed Dragonflies	
Cordylobia africaine	Tumbufliege	African Tumbu Fly	
Cordyluridés	Kotfliegen	Dung Flies	Колосковые мухи
Coréidés	Lederwanzen	Leaf-footed Bugs, Squash Bugs	Краевики
Corethrines	Büschelmücken	Lake Flies	Перистоусики
Corixidés	Wasserzikaden	Corixids	Гребляки
Cossides	Holzbohrer	Goat Moths	Древоточцы
Cossus gâte-bois	Weidenbohrer	– Moth	Пахучий древоточец
Crambides	Graszünsler	Grass Moths	
Criquet d'Egypte	Ägyptische Knarrschrecke	Tree Locust	Египетская саранча
– italien	Italienische Schönschrecke	Italian Locust	Обыкновенный прус или Итальянская саранча
– marocain	Marokkanische Wanderheuschrecke	Maroccain Grasshopper	Марокккская саранча
– nomade	Rote Wanderheuschrecke	Red Locust	
Cryptophagidés	Schimmelkäfer	Cryptophagid Beetles (N. A.)	
Cténophore obscur	Schwarze Kammschnake		Гребневая долгоножка

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Cul doré	Goldafter	Brown-tail	Златогузка
Cyclorhaphes	Deckelschlüpfer		Круглошовные мухи
Cynipides gallicoles	Eigentliche Gallwespen	Gall Wasps	Настоящие орехотворки
Cynipoides	Gallwespen i. e. S.	– –	
Cynips du chêne	Gemeine Eichengallwespe	Common Oak Gallfly	Обыкновенная дубовая орехотворка
– – figuier	Feigenwespen	Fig Insects	
Danaïdes	Danaiden		Данаиды
Dectique verrucivore	Warzenbeißer	Wart-biter	Серый кузнечик
Demi-deuil	Schachbrett	Marbled White	Шашечница
Demi-paon	Abendpfauenauge	Eyed Hawk	Глазчатый бражник
Demoiselle	Gemeine Seejungfer	Demoiselle Agrion	Обыкновенная лютка
Dendroctones	Riesenbastkäfer		Большие лубоеды
Dermaptères	Ohrwürmer	Earwigs	Кожистокрылые
Dermeste commun	Gemeiner Speckkäfer	Common Hide Beetle	Ветчинный кожеед
Dermestes	Speckkäfer	Hide Beetles	Кожееды
Dermestidés	–	Common Hide Beetle	Кожееды
Diaspididés	Deckelschildläuse	Armored Scales	Щитовки
Diastrophus de la ronce	Brombeergallwespe		Ежевичная орехотворка
Diopsides	Stielaugenfliegen	Stalk-eyed Flies	
Diploglossates	Doppelzüngler	Parasitic Earwigs	
Diplolepis du rosier	Gemeine Rosengallwespe	Mossy Rose Gall	Розанная орехотворка
Diploures	Doppelschwänze	Two-pronged Bristle-tails	Двухвостки
Diprion du pin	Gemeine Kiefernbuschhorn-Blattwespe	Pine Sawfly	Сосновый пилильщик
Diprionides	Buschhorn-Blattwespen	Conifer Sawflies	
Diptères	Zweiflügler	Flies	Двукрылые
Dolichopodidés	Langbeinfliegen	Long-legged Flies	
Dorilaidés	Augenfliegen	Big-headed Flies	
Dorylinés	Treiberameisen	Sausage Ants	Цикадоедки
Drosophilidés	Taufliegen	Small Fruit Flies	
Dryinides	Zikadenwespen		Дрозофилы
Dynastes hercule	Herkuleskäfer		Дриины
Dynastinés	Nashornkäfer	Rhinoceros Beetles	Жук-геркулес
Dytiscides	Schwimmkäfer	Carnivorous Water Beetles	Исполинские жуки
Dytisque bordé	Gelbrandkäfer	Great Water Beetle	Плавунцы
Ecaille martre	Brauner Bär	Garden Tiger	Окаймленный плавунец
Échancré	Schnauzenfalter, Zürgelbaum-falter		Бурая медведица
Écureuil	Buchenspinner	Lobster Moth	Носатки, Носатка
Empididés	Tanzfliegen	Dance-flies	Буковый вилохвост
Ephémère commune	Gemeine Eintagsfliege	Mayfly	Толкунчики
Ephémères	Eintagsfliegen	Mayflies	Обыкновенная поденка
Ephippigère des vignes	Steppensattelschrecke	Katydid (N. A.)	Поденки
Ephippigérides	Sattelschrecken	Katydids (N. A.)	
Ephydridés	Sumpffliegen	Shore Flies	
Erébia	Mohrenfalter	Alpines	
Erinniés	Holzfliegen		Глазки-чернушки
Eristale gluante	Schlammfliege	Drone Fly	Древесные мухи
Eucnémidés	Schienenkäfer	False Click Beetles (N. A.)	Ильница
Eumènes	Pillenwespen	Potter Wasp	
Euménines	Lehmwespen	– Wasps	Эвмены
Evaniides	Hungerwespen	Ensign Flies	Одиночные осы
Feuille morte du pin	Kiefernspinner	Pine Lappet	Эваниды
Fidonie du pin	Kiefernspanner	Bordered White	Сосновый кокономряд
Flambé	Segelfalter		Сосновая пяденица
Flavicolle	Gelbhalstermite	Yellow-necked Termite	Подалирий
Forficule auriculaire	Gemeiner Ohrwurm	Common Earwing	Желтошеий термит
– nain	Zwergohrwurm	Small Earwig	Обыкновенная уховертка
Forficulides	Eigentliche Ohrwürmer	Earwigs	Малая уховертка
Formicidés	Ameisen	Ants	Уховертки
Fourmi Amazon	Amazonenameise		Муравьи
– brune des prés	Braune Wiesenameise		Муравей-амазонка
– des prés	Rasenameise	Erratic Ants	Темнобурый луговой муравей
– des récoltes	Ernteameisen		
– fuligineuse	Glänzendschwarze Holzameise	Jet Ant	Муравьи-земледельцы
– moissonneuse	Getreideameisen	Grain Ants	Муравей-древоточец
– noire des prés	Schwarze Wiesenameise	Small Black Ant	Муравьи-жнецы
– rousse	Große Rote Waldameise	Wood Ant	Черный луговой муравей
– sanguine	Blutrote Raubameise	Blood-red Ant	Лесной рыжий муравей
– noire cendré	Schwarzgraue Hilfsameise		Кровавый муравей
Fourmis lion	Ungefleckte Ameisenjungfer		Черный муравей
Fourmis-lions	Ameisenlöwen	Ant Lions	Муравьиный лев
Frelon	Hornisse	Grint Hornet	Муравьиные львы
Fulgoride européen	Europäischer Laternenträger	European Lantern-fly	Шершень
			Обыкновенная светоноска

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Fulgoridés	Laternenträger	Lantern-flies	Светоноски
Galérucelle d'orme	Ulmenblattkäfer		Ильмовая козявка
Galeruque de l'aulne	Blauer Erlenblattkäfer		Ольховая козявка
Gamma	C-Falter	Comma	
Gastéruptionidés	Gichtwespen		Гастерупционииды
Gastrophiles	Magendasseln	Horse Bot Flies	Желудочные оводы
Géocorises	Landwanzen		Наземные клопы
Géométrides	Spanner	Geometers	Пяденицы
Géotrupes	Echte Mistkäfer	Dor Beetles	Настоящие навозные жуки
Gerridés	Wasserläufer	Water-striders, Pondskater's [N. A.]	Водомерки
Gomphides	Flußjungfern	Club-tail Dragonflies	
Grand Charançon du sapin	Fichtenrüßler	Large Pine Weevil	Большой сосновый долгоносик
– Hydrophile	Großer Kolbenwasserkäfer	Great Silver Water-beetle	Черный большой водолюб
– mars changeant	– Schillerfalter	Purple Emperor	Мерцательница
– paon de nuit	Großes Nachtpfauenauge		Большой ночной павлиний глаз
– porte-queue	Schwalbenschwanz	Common Swallowtail	Махаон
– Pritisphore du larix	Große Lärchenblattwespe	Larch Sawfly	Большой лиственичный пилильщик
– Sylvain	Großer Eisvogel	Great Viceroy	Тополевая ленточница
Grande lyde champêtre	Große Kiefernbestands-Gespinstblattwespe	– Pine Web-spinning Pine-Sawfly	Большой сосновый пилильщик-ткач
– sauterelle verte	Grünes Heupferd	– Green Bush-cricket	Обыкновенный зеленый кузнечик
Grillon des bois	Waldgrille	Wood-cricket	
– – champs	Feldgrille	Field-cricket	Полевой сверчок
– myrmécophile de l'Amérique	Amerikanische Ameisengrille	American Ant-loving Crickets	
– – – l'Europe	Europäische Ameisengrille	European Ant-loving Crickets	
Grillons myrmécophiles	Ameisengrillen	Ant-loving Crickets	
Gryllides	Grillen	Crickets	Сверчковые
Gryllon domestique	Hausgrille	House-cricket	Домовый сверчок
Gryllotalpides	Maulwurfsgrillen	Mole-crickets	Медведки
Guêpe de Saxe	Sächsische Wespe	Tree Wasp	Саксонская оса
– des murailles	Wespe	Mason Wasp	Стенная оса
– – orchidées	Orchideenwespe	Orchid Wasp	Орхидеевый семеед
– – sables	Sandwespe	Sand Wasp	Обыкновенный пескорой
– moyenne	Mittlere Wespe		Средняя оса
– rousse	Rote Wespe	Wasp	Рыжая оса
– sylvestre	Waldwespe	Tree Wasp	Лесная оса
Guêpes piqueuses	Stechwespen		Жалоносные перепончатокрылые
Gyrins	Taumelkäfer	Whirling Beetles	Вертячки
Hachette	Nagelfleck		Рыжий ночной павлиний глаз
			Кошачий глаз
Halicte des sillons à quatre bandes	Viergürtlige Schmalbiene	Four-banded Mining Bee	
Hannetons	Echte Maikäfer, Maikäfer	Cockchafers, May Beetles	Майские хрущи, Майские жуки
Hébridés	Zwergwasserläufer	Sphagnum Bugs	
Heléides	Gnitzen	Biting Midges	Мокрецы
Helophoridés	Furchenwasserkäfer	Turnip Mud Beetles	
Hémérobidés	Taghafte	Brown Lacewings	Стрекозки
Hémiptères	Schnabelkerfe	True Bugs	Настоящие полужесткокрылые
Hépiale de la fougère	Heidekraut-Wurzelbohrer	Gold Swift	Вересковый тонкопряд
– du houblon	Hopfenwurzelbohrer	Ghost Swift	Хмелевый тонкопряд
Hépialidés	Wurzelbohrer	Swifts	Тонкопряды
Hespérides	Dickkopffalter	Common Skippers	Толстоголовки
Heteroceridés	Sägekäfer	Hide Beetles	
Hétéroneures	Höhere Schmetterlinge		Разнокрылые бабочки
Hétéroptères	Wanzen	Bugs	Клопы
Hibou	Hausmutter	Common Yellow Underwing	
Hippoboscidés	Lausfliegen	Bird Flies	Кровососки
Histénidés	Stutzkäfer	Hister Beetles	Карапузики
Homoneures	Urtümlichste Kleinschmetterlinge		Равнокрылые бабочки или Низшие бабочки
Homoptères	Pflanzensauger	Clear-winged Bugs	Равнокрылые хоботные
Hoplocampe du poirier	Birnensägewespe		Грушевый пилильщик
– – pommier	Apfelsägewespe	European Apple Sawfly	Яблоневый плодовый пилильщик
– jaune du prunier	Gelbbraune Pflaumensägewespe		Желтый сливовый пилильщик
– noir du prunier	Schwarze Pflaumensägewespe		Сливовый пилильщик

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Hoplocampes	Sägewespen	Sawflies	
Hydrométridés	Teichläufer	Water-measurers	Водомерки
Hydrophiles	Eigentliche Wasserkäfer	Water Beetles	Водолюбы
Hygrobiidés	Schlammkäfer	Screech Beetles	
Hylaeus	Maskenbienen		Пчелы-лесовки
Hylotome de la rose	Rosen-Bürsthornwespe	Rose Sawfly	Розанный пилильщик
Hylotrupe	Hausbockkäfer	House Longhorn	Домовый усач
Hyménoptères	Hautflügler	Sawflies, Wasps	Перепончатокрылые
Hypoderme du bœuf	Rinderbiesfliege	Cattle Warble Fly	Бычий овод
– – cerf	Hirschdasselfliege		Олений овод
– – chevreuil	Rehdasselfliege	Deer Warble Fly	Косулий овод
Hypodermes	Hautdassel	Warble Flies	Кожные оводы
Hyponomeutidés	Gespinstmotten	Small Ermines	Горностаевые моли
Ichneumon	Weißlingstöter	Braconid Fly	Капустничный апантелес
– commun	Gemeine Schlupfwespe		Обыкновенный наездник
– reclus	Riesenschlupfwespe		Гороховый наездник
Ichneumonides	Eigentliche Schlupfwespen	Ichneumons	Настоящие наездники
Insectes	Insekten	Insects	Насекомые
Isoptères	Termiten	Termites	Термиты
Janus du poirier	Birnentriebwespe		Грушевый стеблевой пилильщик
Japyx	Zangenschwänze	Three-pronged Bristle-tails	
Jassidés	Jassiden	Leaf hoppers	
Lampyre noctiluque	Großer Leuchtkäfer	Common Glowworm	Большой светляк
Lampyridés	Leuchtkäfer	Glowworms	Светляки
Larvivoridés	Raupenfliegen	Parasite Flies	Ежемухи
Lathriidés	Moderkäfer	Mould Beetles	
Lécanines	Schalenschildläuse	Soft Scales	Подушечницы
Lécanium du noisettier	Haselschildlaus	Hazel Scale	
Lépidoptères	Schmetterlinge	Butterflies and Moths	Чешуекрылые или Бабочки
Lépismatidés	Fischchen	Firebrats	
Leste vert	Weidenlibelle		Зеленая лютка
Lettre grecque	Gammaeule	Common Silver Y Moth	Совка гамма
Libellules	Libellen	Dragonflies and Damselflies	Стрекозы
Libellule déprimé	Plattbauch	Broad-bodied Libellula	Плоская стрекоза
– à quatre taches	Vierflecklibelle	Four-spotted Libellula	Пятнистая стрекоза
Lichénées	Ordensbänder	Underwings	Ленточницы
Limoniidés	Stelzschnaken	Crane Flies	Долгоножки
Lipoptène du cerf	Hirschlausfliege	Deer Ked	Оленья кровососка
Liriopeidés	Faltenmücken	False Crane Flies	
Livrée	Ringelspinner	Common Lackey	Кольчатый коконопряд
Lucane cerf-volant	Hirschkäfer	Stag Beetles	Жук-олень
Lucanes	–	– –	Рогачи
Lucine	Würfelfalter	Duke of Burgundy	Лесная пеструшка
Lycènes	Feuerfalter	Coppers	
Lycénides	Bläulinge	Blues	Голубянки
Lycidés	Schnabelkäfer	Net-winged Beetles (N. A.)	
Lyctidés	Splintholzkäfer	Powder-post Beetles	
Lyde bleue	Stahlblaue Kiefernschonungs-Gespinstblattwespe	False Pine Webworm	
– champêtre	Kiefernkultur-Gespinstblattwespe	Web-spinning Pine-sawfly	Одиночный сосновый пилильщик-ткач
– de l'épicéa	Fichten-Gespinstblattwespe	Fir Web-spinning Sawfly	
– du pêcher	Steinobst-Gespinstblattwespe		Вишневый паутинный пилильщик
– – poirier	Gesellige Birnblattwespe	Common Pear Web-spinning Sawfly	Общественный грушевый пилильщик-ткач
– – rosier	Rosen-Gespinstblattwespe	Rose Web-spinning Sawfly	Розанный пилильщик-ткач
– étoilée du laryx	Lärchen-Gespinstblattwespe	Larch Web-spinning Sawfly	
Lygaeidés	Langwanzen	Ground Bugs	Тощеклопы
Lymantriides	Trägspinner	Tussock-moths	Волнянки
Lymexylonidés	Werftkäfer	Timber Beetles (N. A.)	Жуки-матросы
Machilide du littoral	Küstenspringer	Shore Bristle-tail	
Machilides	Felsenspringer	Machilids	Махилисы
Malachidés	Zipfelkäfer		Малашки
Mallophages	Kieferläuse	Chewing Lice	Пухоеды
Mante de diable	Teufelsblume		Чертов цветок
– prie-Dieu	Gottesanbeterin	European Mantis	Обыкновенный богомол
Mantides	Fangschrecken	Praying Mantids	Богомолы
Mantis de Darwin	Darwin-Termite		Дарвинов термит
Mariée	Rotes Ordensband	Red Underwing	Красная ленточница
Méconema	Eichenschrecke	Oak Bush-cricket	Дубовый кузнечик
Mécoptères	Schnabelfliegen	Scorpion Flies	Скорпионовые мухи
Mégachiles	Blattschneiderbienen	Leaf-cutting Bees	Пчелы-листорезы
Mégaloptères	Schlammfliegen	Snake Flies	Большекрылые

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Méligèthe bronzé	Rapsglanzkäfer	Pollen Beetle	Рапсовая блестянка
Méloés	Maiwürmer	Dil Beetles	Майские букашки
Méloïdés	Ölkäfer	Blister Beetles	Нарывники
Mélophage du mouton	Schafslausfliege	Sheep Ked	Овечья кровососка
Mélusine commun	Gemeine Kriebelmücke		Обыкновенная мошка
– de Laponie	Lappländische Kriebelmücke		Лапландская мошка
Mélusinides	Kriebelmücken		Мошки
Membracidés	Buckelzirpen		Горбатки
Mesoveliidées	Hüftwasserläufer		
Micropterygidés	Urmotten		Первичные моли
Minime à baudes jaunes	Eichenspinner	Oak Eggar	Дубовый коконопряд
Minotaure typhée	Dreihorn-Mistkäfer	Three-horned Dor Beetles	Трехрогие навозники
Miridés	Schmalwanzen	Plant Bugs	Клопы-слепняки
Mite des vêtements	Gewöhnliche Kleidermotte	Common Clothes Moth	Мебельная моль или Платяная моль
Monarque	Monarchfalter	Monarch (N. A.)	
Mordellidés	Stachelkäfer	Tumbling Flower Beetles (N. A.)	Шипоноски или Горбатки
Morio	Trauermantel	Camberwell Beauty	Траурница
Moro-sphinx	Taubenschwänzchen	Humming-bird Hawk-moth	Языкан
Morphos	Morphofalter	Morphos	
Mouche blanche des Aurantiacées	Weiße Citrusfliege	Citrus White Fly	Цитрусовая мушка
– – – serres	– Gewächshausfliege	Greenhouse White Fly	Тепличная белокрылка
– bleue de la viande	Blaue Schmeißfliege	Blue-bottle Fly	Синяя мясная муха
– de la betterave	Runkelrübenfliege		Свекловичная муха
– des asperges	Spargelfliege	Asparagus Fly	Спаржевая бурилка
– – bouses	Kotfliege	Yellow Dung Fly	
– – carottes	Möhrenfliege	Carrot Rust Fly	Морковная муха
– – cerises	Kirschfliege		Вишневая муха
– – étables	Wadenstecher	Stable Fly	Жигалка
– – fenêtres	Buckelige Fensterfliege	Window Fly	Оконная муха
– – greiners	Eulentachine	Cluster Fly	Совковая ежемуха
– – hirondelles	Schwalbenlausfliege	Swallow Louse Fly	Ласточковая кровососка
– – martinets	Mauersegler-Lausfliege	Swift Louse Fly	Стрижиная кровососка
– – oranges	Mittelmeerfruchtfliege	Mediterranean Fruit Fly	Средиземноморская плодовая муха
Mouche d'Hesse	Hessenfliege	Hessian Fly	Гессенская муха
– domestique	Große Stubenfliege	House Fly	Большая комнатная муха
– du cheval	Pferdelausfliege		Лошадиная кровососка или Паутка
– – fromage	Käsefliege	Cheese Skipper	Сырная муха
– grise de la viande	Graue Fleischfliege	Grey Flesh Fly	Серая мясоедка
– mineuse	Falkenlausfliege		Соколиная кровососка
– noire des Aurantiacées	Schwarze Citrusfliege	Citrus Black Fly	Темнокрылая белая мушка
– rouge du bois	Rostrote Holzfliege		Рыжая древесная муха
Mouches des fruits	Fruchtfliegen	Large Fruit Flies	Пестрокрылки
– – oignons	Zwiebelfliegen	Lesser Bulb Flies	Луковичные мухи
Mouches d'Espagne	Spanische Fliegen	Spanish Flies	Шпанские мухи
– des termitières	Termitenfliegen	Termite Flies	
Mouches tsé-tsé	Tsetsefliegen	Tsetse Flies	Мухи це-це
Moustique commun	Gemeine Stechmücke	European House Mosquito	Обыкновенный комар
– de la fièvre jaune	Gelbfiebermücke	Yellow Fever Mosquito	Желтолихорадный комар
– des saules	Weidenholzgallmücke	Willow-shoot Hole	Ивовая галлица
Moustiques	Stechmücken	Mosquitoes	Настоящие комары или Кровососущие комары
Muscidés	Echte Fliegen	House Flies	Настоящие мухи
Mutille d'Europe	Europäische Ameisenwespe	European Velvet-ant	Европейская немка
Mutillides	Ameisenwespen	Velvet-ants	Немки
Mycetophilidés	Pilzmücken	Fungus Gnats	Грибные комарики
Mylabris	Blasenkäfer	Blister Beetles	Нарывники
Mymaridés	Zwergwespen	Tiny Wasps	
Myrmécinés	Bulldoggenameisen	Bulldog Ants	
Myrtil	Großes Ochsenauge	Meadow-brown	Воловий глаз
Nabidés	Sichelwanzen	Damsel Bugs	
Nacrés	Perlmutterfalter	Fritillaris	Перламутровки
Naucoridés	Schwimmwanzen	Saucer Bugs	
Nécrophores	Totengräber	Sexton Beetles	Могильщики
Némate du groseillier	Gelbe Stachelbeer-Blattwespe	Black Currant Sawfly	Желтый крыжовниковый пилильщик
Nématocères	Mücken	Thread-horns	Комары
Némestrinidés	Netzfliegen		Неместриниды
Népa roux	Wasserskorpion	Water-scorpion	Водяной скорпион
Népidés	Skorpionswanzen	Water-scorpions	Водяные скорпионы
Nepticulidés	Zwergmotten		Моли-малютки
Neuroptéroïdés	Netzflüglerartige	Alder Flies	Сетчатокрыловые
Nitidulidés	Glanzkäfer	Sap-beetles	Блестянки

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
		Sharks	
Noctuelle d'armoise	Grauer Beifußmönch	Turnip Dart	Озимая совка
– des moissons	Saateule	Cabbage Moth	Капустная совка
– du chou	Kohleule	Noctuids	Совки или Ночницы
Noctuelles	Eulenfalter	Alder Dogger	Ольховая стрельчатка
Noctuide d'aune	Erleneule	Black Arches	Монашенка
Nonne	Nonne	Prominents	Хохлатки
Notodontides	Zahnspinner	Back-swimmers	Гладыши
Notonectidés	Rückenschwimmer	Fritillaries	Многоцветницы
Nymphalides	Fleckenfalter	Oedemerid Beetles (N. A.)	Узконадкрылки
Oedémérides	Scheinböcke	Band-winged Grasshoppers	Кобылки
Oedipodinés	Schnarrheuschrecken		Лошадиный овод
Œstre du cheval	Pferde-Nasendassel	Sheep Gadfly	Овечий овод
– – mouton	Schaf-Nasendassel	Bot Flies	Носоглоточные оводы
Œstres	Nasendasseln	– –	Оводы
Œstridés	Dasselfliegen	Dung Beetles	Калоеды
Onthophagus	Kotfresser	Many-plume Moth	Веерницы
Orméodidés	Geistchen		Прямокрылые
Orthoptères	Geradflügler	Frit Fly	Овсяная шведская мушка
Oscinie frit	Fritfliege	Ostomatid Beetles	
Ostomidés	Jagdkäfer	Leaf-rollers	Паутинные пилильщики
Pamphilides	Gespinst-Blattwespen	Scorpion Flies	Скорпионницы
Panorpides	Skorpionsfliegen	Peacock	Дневной павлиний глаз
Paon de jour	Tagpfauenauge	Swallowtail Family	Парусники или Кавалеры
Papilionidés	Ritterfalter	Swallowtails	
Papilios	Echte Schwalbenschwänze	Parasitical Hymenoptera	
Parasites	Legwespen	Passalid Beetles (N. A.)	Сахарные жуки
Passalidés	Zuckerkäfer	Earwig	Прибрежная уховертка
Perce-oreille des rivages	Sandohrwurm	Small Earwig	Малая уховертка
– nain	Zwergohrwurm		Альпийский аполлон
Petit Apollon	Alpen-Apollo	Emperor Moth	Малый ночной павлиний глаз
– paon de nuit	Kleines Nachtpfauenauge		
		Smaller Larch Sawfly	Малый лиственничный пилильщик
– pritisphore du milize	Kleine Lärchenblattwespe		
		Fir Sawfly	Малый еловый пилильщик
– – – pin	– Fichtenblattwespe	Lesser House Fly	Малая комнатная муха
Petite mouche domestique	Kleine Stubenfliege		Малый осиновый усач
– saperde du peuplier	Espenbockkäfer	Small Tortoiseshell	Крапивница
– tortue	Kleiner Fuchs	Pigmy Cockroaches	
Petites Blattes	Kleinschaben	Puss	Вилохвосты
Petites-queues-fourchues	Gabelschwänze	Peppered Moth	Березовая пяденица
Phalène du bouleau	Birkenspanner		Зимняя пяденица
Phalins défeuillantes	Frostspanner	Stick- and Leaf-insects	Привиденьевые
Phasmes	Gespenstschrecken	Bee-hunting Wasp	Пчелиный волк
Philanthe apivore	Bienenwolf	Papatasi Sandfly	
Phlébotome de Papatau	Papatacimücke	Sandflies	Москиты
Phlébotomines	Sandmücken i. e. S.	Moth Flies	Бабочницы
Phlébotonies	Schmetterlingsmücken	Coffin Flies	Горбатки
Phoridés	Buckelfliegen	Window Fly	
Phryne des fenêtres	Fenstermücke	Vine Louse	Виноградная филоксера или Виноградная тля
Phylloxéra	Reblaus		
		Ambush Bugs (N. A.)	
Phymatidés	Fangwanzen	Black-veined White	Боярышница
Piéride d'aubépine	Baumweißling	Small White	Репная белянка
– de rave	Kleiner Kohlweißling	Large Cabbage-white	Капустная белянка
– du chou	Großer Kohlweißling	Green-veined White	Горчичная белянка
– – navet	Rübenweißling	Whites	Белянки
Piérides	Weißlinge	Beetbugs	
Piésmides	Meldenwanzen	Lace-wings	Сетчатокрылые
Planipennes	Hafte	Ambrosia Beetles	
Platypodidés	Kernkäfer		Бобровые блохи
Platypsylles	Biberlaus	Blues	
Plébiines	Echte Bläulinge	Stoneflies	Веснянки
Plécoptères	Steinfliegen	Lesser Water-boatmen	
Pleidés	Zwergrückenschwimmer	Silverfish	Чешуйницы
Poisson d'argent	Silberfischchen		Французская бумажная оса
Poliste française	Französische Feldwespe	Many-combed Bugs (N. A.)	Клопы летучих мышей
Polycténidés	Kammwanzen	Carrionfly	Береговая поденка
Polymitarcis vierge	Uferaas	Spider-wasps	Дорожные осы
Pompilidés	Wegwespen	Common Willow Sawfly	Обыкновенный ивовый пилильщик
Pontanie commune	Gemeine Weidenblattgallen-Wespe		
		Crab Louse	Лобковая вошь
Pou de feutre	Schamlaus		Домовый сеноед
– – fropper	Gemeine Staublaus	Sucking Horse Louse	Лошадиная вошь
– – l'âne	Pferdelaus		Слоновая вошь
– d'éléphant	Elefantenlaus		Вошь морских слонов
– – marin	See-Elefanten-Laus		

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
– de l'homme	Kopf- und Kleiderlaus	Men-louse	Человеческая вошь
– – San José	San-José-Schildlaus	San Jose Scale	Калифорнийская щитовка
– – vêtement	Kleiderlaus	Body Louse	Платяная вошь
– – la tête	Kopflaus	Head Louse	Головная вошь
– devin	Bücherlaus	Book-louse	Книжная вошь
– du chat	Katzenhaarling	Cat-louse	Кошачий власоед
– – chèvre	Ziegenlaus	Goat Louse	Козья вошь
– – chien	Hundehaarling, Hundelaus	Chewing Dog-louse, Dog-louse	Собачий власоед, Собачья вошь
– – lion marin	Seelöwenlaus		Сивучовая вошь
– – mouton	Schafslaus	Sheep Louse	Овечья вошь
– – porc	Schweinelaus	Pig Louse	Свиная вошь
– – rat	Rattenlaus	Spined Rat Louse	Крысиная вошь
– – veau	Langköpfige Rinderlaus	Long-nosed Oxlouse, Blue Cattle Louse	Длинноголовая коровья вошь
Poux	Primatenläuse	Men-lice	Вши приматов
– à tentacle cônes	Stumpffühlerläuse		Короткоусиковые пухоеды
– – trompes	Rüsselläuse	Probeseis Lice	Хоботковые пухоеды
– aux tentacles minces	Dünnfühlerläuse		Тонкоусиковые пухоеды
– de colombes	Taubenfederlinge	Pigeon-lice	Голубиные пероеды
– – livres	Staubläuse	Book Lice	Сеноеды
– – terre	Bodenläuse	Zoropterons	
– des animaux	Tierläuse	Animal Lice	Животные вши
– – bœufs	Rinderhaarlinge	Cattle-lice	Коровий власоед
Processionnaire du chêne	Eichenprozessionsspinner		Дубовый походный шелкопряд
– – pin	Pinien-Prozessionsspinner	Pine-feeding Processionary Caterpillar	Пиниевый походный шелкопряд
Processionnaires	Prozessionsspinner	Processionary Caterpillars	Походные шелкопряды
Procris	Grünwidderchen	Foresters	
Proctotrupoidés	Zehrwespen	Proctotrupoids	
Protoures	Halbinsekten	Proturans	Бессяжковые насекомые
Pselaphidés	Palpenkäfer		Ощупники
Psilidés	Nacktfliegen	Rust Flies	Голотелки
Psocidés	Läuseverwandte	Psocids	Вшевидные
Psychides	Sackspinner	Bag-worm Moths (N. A.)	Мешочницы
Psylle du poirier	Birnblattsauger	Big Pear Psylla	Грушевая медяница
– – pommier	Apfelblattsauger	Apple Psylla	Яблонная медяница
Psyllines	Blattflöhe	Phyllids	Листоблошки или Медяницы
Ptérophores	Federmotten	Plumes	Пальцекрылки
Ptérygotes	Fluginsekten	Largely-winged Insects	Высшие насекомые или Крылатые насекомые
Ptiliidés	Federflügler		Перокрылки
Ptinidés	Diebskäfer	Spider Beetles	Притворяшки
Puce de l'homme	Menschenfloh	Human Flea	Человеческая блоха
– d'olivier	Ölbaumblattsauger		Оливковая медяница
– du chat	Katzenfloh	Cat Flea	Кошачья блоха
– – chien	Hundefloh	Dog Flea	Собачья блоха
– – glacier	Gletscherfloh		Глетчерная блоха или Снежная блоха
Puces	Flöhe	Fleas	Блошиные
Puce tacheté du poirier	Gefleckter Birnblattsauger		Пятнистая грушевая медяница
Puceron de Californie	Kalifornische Ahornspringlaus		Калифорнийская кленовая тля
– – Cooley	Zwergläuse		Филоксеры
– – la fève	Bohnenlaus	Black Bean Aphid	Свекловичная тля
– des sapins	Tannenläuse	Adelgids	Хермесы
– du chêne	Eichenrindenlaus		Дубовая тля
– – hêtre	Buchenzierlaus	Beech Aphid	Буковая тля
– – platane	Ahornspringlaus		Кленовая тля
– – sapin	Tannentrieblaus	Balsam Twig Aphid	Пихтовая тля
– laineux	Blutlaus	Woolly Apple Aphid	Кровяная тля
Pucerons	Blattläuse	Aphids	Тли
Puceron vert du pêcher	Pfirsichblattlaus	Peach-potatoe Aphid	Персиковая тля
Punaise bordée	Randwanze		Обыкновенный краевик
– de courge	Kürbiswanze	Squash Bug	Тыквенный клоп
– d'Italie	Streifenwanze		Итальянский щитник или Полосатый клоп
– d'hirondelle	Schwalbenwanze	Swallow Bug	Ласточковый клоп
– de la fourmi	Ameisenwanze		Муравьиный клоп
– des baies	Beerenwanze	Sloebug	Ягодный клоп
– – lits	Bettwanze	Bed Bug	Постельный клоп
– – potagers	Kohlwanze	Brassica Bug	Рапсовый щитник

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
– du blé	Getreidewanzen		Остроголовые клопы
– – meurtre	Mordwanzen		Хищнецы
– grise du Cotton	Dunkle Baumwollwanze	Cotton Stainer	
– linéaire	Stabwanze	Water Stick-insect	Ренатра
– masqué	Kotwanze	Fly Bug	Грязный хищнец
Punaises d'eau	Wasserwanzen	Water Bugs	Водяные клопы
– de terre	Landwanzen		Наземные клопы
– des fleurs	Blumenwanzen	Flower Bugs	Цветочные клопы
– à bouclier	Schildwanzen	Shield Bugs	Щитники
Punaise sans ailes	Feuerwanze	Firebug	Бескрылый красноклоп
– verte	Grüne Stinkwanze	Green Shieldbug	Зеленый древесный щитник
Pyrale des pommes	Apfelwickler	Piercer	Яблонная плодожорка
Pyralididés	Zünsler	Snout Moths	Огневки
Pyrole de la canne à sucre	Zuckerrohrzünsler	Sugar-cane Borer	
Pyrophores	Leuchtschnellkäfer		Щелкуны-светляки
Pyrrhocoridés	Feuerwanzen	Pyrrhocorid Bugs	Красноклопы
Raphide aux yeux d'un serpent	Schlangenäugige Kamelhalsfliege	Snake Fly	
Raphidiidés	Kamelhalsfliegen	– Flies	Верблюдки
Réduviidées	Raubwanzen	Assasin Bugs	Хищнецы
Rhabdophage des saules	Weidenrutengallmücke		Ростковая ивовая галлица
Rhagionidés	Schnepfenfliegen	Snipe-flies	Бекасоноски
Rhipiphoridés	Fächerkäfer		Веероносцы
Rhizophagidés	Plattkäfer	Flat Bark Beetles (N. A.)	Плоскотелки
Rhogogaster vert	Grüne Blattwespe	Green Sawfly	Большой зеленый пилильщик
Rhysodidés	Runzelkäfer		Ризоды
Rhyssa persuasive	Pfeifenräumer		Рисса
Saldidés	Uferwanzen	Shore Bugs	Береговые клопы
Saturniides	Augenspinner	Emperor Moths	Павлиноглазки
Satyrides	Augenfalter	Meadow Browns	Сатиры
Sauterelle de Sibérie	Sibirische Keulenschrecke	Siberian Grasshopper	Сибирская саранча
– grillon	Grillenschrecken	Cave and Camel-crickets	Ненастоящие кузнечиковые
– – de serre	Gewächshausschrecke	Greenhouse Camel-cricket	Оранжерейный кузнечик
– pélerin	Wüstenschrecke	Desert Locust	Пустынная саранча
Sauterelles	Schrecken	Saltatoria	Прыгающие прямокрылые
– à longues antennes	Langfühlerschrecken	Bush-crickets	Кузнечиковые и Сверчковые
– de palpes courtes	Kurzfühlerschrecken	Short-tentacled Grasshoppers	Саранчовые и Триперстовые
– – passage	Wanderheuschrecken	Migratory Locusts	
Scarabée à corselet large	Gestreifter Pillendreher		Полосатый скарабей
Scarabés	Blatthornkäfer, Pillendreher	Cockchafers, Dung Beetles	Пластинчатоусые, Скарабеи
Schizonèvre laineux	Ulmenblasenlaus		Пузырная тля
Sciaridés	Trauermücken		Грибные комарики
Scolia à front jaune	Gelbstirnige Dolchwespe	Yellow-fronted Digger Wasp	Желтолобая сколия
Scoliides	Dolchwespen	Digger Wasps	Сколии
Scolytes	Borkenkäfer	Scolytid Beetles	Заболонники
Semi-apollon	Schwarzer Apollo		Черный аполлон
Serropalpidés	Düsterkäfer	False Darkling Beetles (N. A.)	
Sésie du framboisier	Himbeer-Glasflügler		Малинная стеклянница
– – peuplier	Hornissenschwärmer	Poplar Hornet Clearwing	Большая тополевая стеклянница
Sésies	Glasflügler	Clairwings	Стеклянницы
Sialides	Wasserflorfliegen	Alder Flies	Вислокрылки
Sialis de la vase	Schlammfliege	– Fly	Обыкновенная вислокрылка
Silphidés	Aaskäfer	Carrion Beetles, Burying	Мертвоеды
Sirex commun	Gemeine Holzwespe	Polished Horntail	Обыкновенный сосновый рогохвост
– géant	Riesenholzwespe	Large Woodwasp	Большой рогохвост
Siricidés	Holzwespen	Horn-tails	Настоящие рогохвосты
Sminthure vert	Luzernefloh	Lucerne Flea	
Sminthuride d'eau	Wasser-Kugelspringer	Water Springtail	
Souci	Postillion	Clouded Yellow	
Soufré	Gemeiner Heufalter	Pale-clouded Yellow	Луговая желтушка
Sphécidés	Grabwespen	Thread-waisted Wasps	Роющие осы
Sphingides	Schwärmer	Hawk-moth	Бражники
Sphinx du ciseron	Windenschwärmer	Convolvulus Hawk	Вьюнковый бражник
– – peuplier	Pappelschwärmer	Poplar Hawk	Тополевый бражник
– – troène	Ligusterschwärmer	Privet Hawk	Сиреневый бражник
Sphinx-gazé	Hummelschwärmer	Broad Bordered Bee Hawk-moth	
Sphinx tête du mort	Totenkopfschwärmer	Death's-head Hawk	Мертвая голова

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Staphylins	Kurzflügler	Rove Beetles	Настоящие коротконадкрылые жуки
Stratiomyidés	Waffenfliegen	Soldier Flies	Львинки
Strepsitères	Fächerflügler	Twisted-winged Insects	Веерокрылки
Symphytes	Pflanzenwespen	Sawflies	Сидячебрюхие перепончатокрылые
Syrphidés	Schwebfliegen	Hover Flies	Журчалки
Tabac d'Espagne	Kaisermantel	Silver-washed Fritillary	Большая лесная перламутровка
Taon des bœufs	Rinderbremse	Large Horse Fly	Бычий слепень
– – pluies	Regenbremse		Дождевка
Taons	Bremsen	Horse-flies	Слепни
Taupe-grillon commun	Maulwurfsgrille	Mole-cricket	Обыкновенная медведка
– teigne des ruches	Wachsmotte	Wax Moth (N. A.)	Восковая моль или Большая пчелиная огневка
Taupins	Schnellkäfer	Click-beetles	Проволочники или Щелкуны
Teigne de la farine	Mehlmotte	Mediterranean Flour Moth	Мельничная огневка
– – – grappe	Einbindiger Traubenwickler		Виноградная вертунья
– du Colza	Kohlmotte	Diamond-back Moth	Капустная моль
– des fourrures	Pelzmotte	Case-making Clothes Moth	Шубная моль
– – tapis	Gemeine Tapetenmotte	Tapestry Moth	Ковровая моль
Teignes	Echte Motten	Clothes Moths	Моли
Tendipédidés	Zuckmücken	Non-biting Midges	Звонцы или Комары-дергуны
Ténébrion meunier	Mehlkäfer	Mealworm	Мучной хрущак
Ténébrionidés	Schwarzkäfer	Ground Beetles (N. A.)	Чернотелки
Tenthrède du bouleau	Breitfüßige Birkenblattwespe	Birch Sawfly	Северный березовый пилильщик
Tenthrédinidés	Blattwespen	Sawflies	Пилильщики
Tenthride du pin	Europäische Fichtenblattwespe	Spruce	Европейский еловый пилильщик
Térébrants	Bohr-Fransenflügler	Boring Thrips	Яйцекладные трипсы
Termes	Eigentliche Termiten	Termites	
Termite à cou jaune	Gelbhalstermite	Yellow-necked Termite	Желтошеий термит
– aux pieds jaunes	Gelbfüßige Termite	Eastern Subterranean Termite	Желтоногий термит
– militaire	Kriegertermite		Воинственный термит
– photophobe	Lichtscheue Termite		Темнобурый термит
Termites géantes	Riesentermiten	Giant Termites	
Termitides	Höhere Termiten	Termites	
Tetrigides	Dornschrecken	Grouse Locusts	Тетригиды
Tettigonides	Laubheuschrecken	Bush-crickets	Настоящие кузнечиковые
Théclines	Zipfelfalter	Hair-streaks	
Thérévidés	Stilettfliegen	Stiletto Flies	Ктыревидки
Thripide dracaene	Drazänenthrips	Dracaena Thrips	
Thrips	Fransenflügler	Thrips	Бахромчатокрылые
– à chasse	Jagdthripse	Predatory	
– d'arbres	Baumthripse		Древесные трипсы
– de l'oignon et du tabac	Tabakthrips	Onion Thrips	Табачный трипс
Thrips à tête étroite	Schmalkopfthrips	Cabbage Thrips	Узкоголовый трипс
– des serres	Treibhausthrips	Greenhouse Thrips	Оранжерейный трипс
– d'œillet	Nelkenthrips		Гвоздичный трипс
– du blé	Getreidethripse	Grain Thrips	Хлебные трипсы
– – gladiole	Gladiolenthrips	Gladiolus Thrips	Гладиолусовый трипс
Thysanoures	Borstenschwänze	Bristle-tails	Щетинохвостки
Tigre du poirier	Birnen-Netzwanze	Rhododendron Bug	Грушевая кружевница
– – rhododendron	Rhododendron-Netzwanze	Lacebugs, Tingids	Рододендроновый клоп
Tingidés	Netzwanzen	Rolling Wasps	Кружевницы
Tiphides	Rollwespen		Тифии
Tipule des marais	Sumpfschnake		Вредная долгоножка или Льняная долгоножка
– du chou	Graue Kohlschnake	Common Crane Fly	Огородная долгоножка
– géante	Riesenschnake	Giant Crane Fly	Большая долгоножка
Tipulidés	Wiesenschnaken	Crane Flies	Долгоножки
Tordeuse des pousses	Kieferntriebwickler	Gemmet Shoot	Сосновая плодожорка
– du chêne	Eichenwickler	Pea-green Oak Twist	Дубовая листовертка
Tortricides	Wickler	Leaf Rollers	Листовертки
Trapèze	Mondraupeneule	Dun-bar	
Trichocère hivernal	Winterschnake	Winter Gnat	
Trichocéridés	Wintermücken	Winter Gnats	Зимние комары
Trichodés	Immenkäfer		Пчеложуки
Trichoptères	Köcherfliegen	Caddice Flies	Ручейники
Trichosome géant	Große Pelzblattwespe	Birch Sawfly	
Trictenotomdiés	Autokratkäfer	Cellar Beetles	
Tridactylides	Dreifingerschrecken	Pigmy Mole-crickets	Триперстовые
Troglophile	Höhlenschrecke	Cave-Cricket	

FRENCH NAME	GERMAN NAME	ENGLISH NAME	RUSSIAN NAME
Tubulifères	Röhren-Fransenflügler	Tubuliferae	Трубкохвостые трипсы
Uraniides	Uraniafalter		Урании
Varié de gris	Kieferneule	Pine Beauty	Сосновая совка
Véliidées	Bachläufer	Water-crickets	
Ver blanc	Feldmaikäfer	White Grub	Западный майский хрущ
Vespides	Faltenwespen	Yellow Jackets	Складчатокрылые осы
Volucelle bourdon	Hummelschwebfliege		Шмелевидная мохнатка
Vrillettes	Klopfkäfer	Drugstore Beetles	Точильщики
Vulcain	Admiral	Red Admiral	Адмирал
Xeris du pin	Schwarze Kiefernholzwespe		Черный рогохвост
Xiphydriidés	Schwertwespen		Ксифидрии
Zérène mouchetée du groseillier	Harlekin	Common Magpie Moth	Крыжовниковая пяденица
Zeuzère du marronnier	Kastanienbohrer	Wood Leopard	Въедливая древесница
Zygène-de-la-filipendule	Blutströpfchen	Six-spot Burnet	Таволговая пестрянка
Zygénides	Widderchen	Burnets	Пестрянки
Zygoptères	Kleinlibellen	Damselflies	Равнокрылые стрекозы

4. Russian—German—English—French

N. A. при английских названиях означает, что эти названия употребляются только в Северной Америке.

RUSSIAN NAME	GERMAN NAME	ENGLISH NAME	FRENCH NAME
Австралийский желобчатый червец	Wollsackschildlaus	Cottony-cushion Scale	Cochenille australienne
Адмирал	Admiral	Red Admiral	Vulcain
Акациевая ложнощитовка	Zwetschgen-Napfschildlaus	European Fruit Lecanium	Cochenille du cornouiller
Алейродиды	Mottenschildläuse	White Flies	Aleurodinés
Альпийский аполлон	Alpen-Apollo		Petit Apollon
Американский большой таракан	Amerikanische Großschabe	American Cockroach	Blatte américaine
Андрены	Sandbienen	Solitary Bees	Andrenidés
Антофоры	Pelzbienen	Potter Flower Bees	Anthophores
Апатуры	Schillerfalter	Purple Emperor	Apaturas
Аполлон	Apollofalter	Apollo	Apollon
Аскалафы	Schmetterlingshafte		Ascalaphidés
Атты	Blattschneiderameisen	Leaf-cutting Ant	
Бабочки	Schmetterlinge	Butterflies and Moths	Lépidoptères
Бабочницы	Schmetterlingsmücken	Moth-flies	Phlébotonies
Бахромчатокрылые	Fransenflügler	Thrips	Thrips
Бекасоноски	Schnepfenfliegen	Snipe-flies	Rhagionidés
Белокрылки	Mattenschildläuse	White Flies	Aleurodinés
Белянки	Weißlinge	Whites	Piérides
Береговая поденка	Uferaas	Carrionfly	Polymitarcis vierge
Береговые клопы	Uferwanzen	Shore Bugs	Saldidés
Березовая пяденица	Birkenspanner	Peppered Moth	Phalène du bouleau
Березовый булавоус	Große Birkenblattwespe	Great Birch Sawfly	Cimbex du bouleau
Березовый слоник	Birkenblattroller	Birch Leaf Roller	Coléoptère du bouleau
Бескрылый красноклоп	Feuerwanze	Firebug	Punaise sans ailes
Бессяжковые насекомые	Halbinsekten	Proturans	Protoures
Блестянки	Diebswespen, Glanzkäfer, Goldwespen	Sap-beetles, Cuckoo Wasps	Cleptides, Nitidulidés, Chrysidides
Блестящая красотка	Gebänderte Prachtlibelle	Banded Agrion	Caloptéryx brillant
Блошиные	Flöhe	Fleas	Puces
Бобровые блохи	Biberlaus		Platypsylles
Богомолы	Fangschrecken	Praying Mantids	Mantides
Божьи коровки	Marienkäfer	Ladybirds	Coccinellidés, Coccinelles
Большая долгоножка	Riesenschnake	Giant Crane Fly	Tipule géante
Большая комнатная муха	Große Stubenfliege	House Fly	Mouche domestique
Большая лесная перламутровка	Kaisermantel	Silver-washed Fritillary	Tabac d'Espagne
Большая пчелиная огневка	Wachsmotte	Wax Moth [N. A.]	Taupe teigne des ruches
Большая тополевая гарпия	Gabelschwanz	Puss	
Большая тополевая стеклянница	Hornissenschwärmer	Poplar Hornet Clearwing	Sésie du peuplier
Большекрылые	Schlammfliegen	Snake Flies	Mégaloptères
Большие лубоеды	Riesenbastkäfer		Dendroctones
Большой зеленый пилильщик	Grüne Blattwespe	Green Sawfly	Rhogogaster vert
Большой лиственничный пилильщик	Große Lärchenblattwespe	Larch Sawfly	Grand Pritisphore du larix

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Большой ночной павлиний глаз	Großes Nachtpfauenauge		– paon de nuit
Большой рогохвост	Riesenholzwespe	Large Woodwasp	Sirex géant
Большой светляк	Großer Leuchtkäfer	Common Glowworm	Lampyre noctiluque
Большой сосновый долгоносик	Fichtenrüßler	Large Pine Weevil	Grand Charançon du sapin
Большой сосновый пилильщик-ткач	Große Kiefernbestands-Gespinstblattwespe	Great Pine Web-spinning Pine-sawfly	Grande lyde champêtre
Боярышница	Baumweißling	Black-veined White	Piéride d'aubépine
Бражники	Schwärmer	Hawk-moth	Sphingides
Бракониды	Brackwespen	Braconid Flies	Braconides
Бронзовки	Rosenkäfer	Rose-chafers	Cetonines
Буковая тля	Buchenzierlaus	Beech Aphid	Puceron du hêtre
Буковый вилохвост	Buchenspinner	Lobster Moth	Écureuil
Булавоусы	Knopfhorn-Blattwespen	Cimbicid Sawflies	Cimbicidés
Булавчики	Keulenkäfer		Clavigéridés
Бурая медведица	Brauner Bär	Garden Tiger	Ecaille martre
Бычий овод	Rinderbiesfliege	Cattle Warble Fly	Hypoderme du bœuf
Бычий слепень	Rinderbremse	Large Horse Fly	Taon des bœufs
Веерницы	Geistchen	Many-plume Moth	Orméodidés
Веерокрылки	Fächerflügler	Twisted-winged Insects	Strepsitères
Веероносцы	Fächerkäfer		Rhipiphoridés
Верблюдки	Kamelhalsfliegen	Snake Flies	Raphididés
Вересковый тонкопряд	Heidekraut-Wurzelbohrer	Gold Swift	Hépiale de la fougère
Вертячки	Taumelkäfer	Whirling Beetles	Gyrins
Весенняя пестрокрыльница	Landkärtchen		Carte géographique
Веснянки	Steinfliegen	Stoneflies	Plécoptères
Ветчинный кожеед	Gemeiner Speckkäfer	Common Hide Beetle	Dermeste commun
Вилохвостки	Springschwänze	Springtails	Collemboles
Вилохвосты	Gabelschwänze	Puss	Petites-queues-fourchues
Виноградная вертунья	Einbindiger Traubenwickler		Teigne de la grappe
Виноградная тля	Reblaus	Vine Louse	Phylloxéra
Виноградная филоксера	–	– –	–
Виноградный слоник	Rebenstecher		Cigarier
Вислокрылки	Wasserflorfliegen	Alder Flies	Sialides
Вишневая муха	Kirschfliege		Mouche des cerises
Вишневый паутинный пилильщик	Steinobst-Gespinstblattwespe		Lyde du pêcher
Водолюбы	Eigentliche Wasserkäfer	Water-beetles	Hydrophiles
Водомерки	Teichläufer, Wasserläufer	Water-measurers, Water-striders	Hydrométridés, Gerridés
Водяной скорпион	Wasserskorpion	Water-scorpion	Néa roux
Водяные клопы	Wasserwanzen	Water Bugs	Punaises d'eau
Водяные скорпионы	Skorpionswanzen	Water-scorpions	Népidés
Воинственный термит	Kriegertermite		Termite militaire
Волнянки	Trägspinner	Tussock-moths	Lymantriides
Воловий глаз	Großes Ochsenauge	Meadow-brown	Myrtil
Восковая моль	Wachsmotte	Wax Moth (N. A.)	Taupe teigne des ruches
Вошь морских слонов	See-Elefanten-Laus		Pou d'éléphant marin
Вредная блоха	Sandfloh	Jigger	Chique
Вредная долгоножка	Sumpfschnake		Tipule des marais
Вшевидные	Läuseverwandte	Psocids	Psocidés
Вши приматов	Primatenläuse	Men-lice	Poux
Высшие насекомые	Fluginsekten	Largely-winged Insects	Ptérygotes
Въедливая древесница	Kastanienbohrer	Wood Leopard	Zeuzère du marronnier
Вьюнковый бражник	Windenschwärmer	Convolvulus Hawk	Sphinx du ciseron
Галлицы	Gallmücken	Gall Midges	Cécidomyus
Гастерупциониды	Gichtwespen		Gastéruptionidés
Гвоздичный трипс	Nelkenthrips		Thrips d'œillet
Гессенская муха	Hessenfliege	Hessian Fly	Mouche d'Hesse
Гладиолусовый трипс	Gladiolenthrips	Gladiolus Thrips	Thrips du gladiole
Гладыши	Rückenschwimmer	Back-swimmers	Notonectidés
Глазки-чернушки	Mohrenfalter	Alpines	Erébia
Глазчатый бражник	Abendpfauenauge	Eyed Hawk	Demi-paon
Глетчерная блоха	Gletscherfloh		Puce du glacier
Глоточные оводы	Rachendasseln	Mouth Flies	Cephenomyes
Головная вошь	Kopflaus	Head Louse	Pou de la tête
Голотелки	Nacktfliegen	Rust Flies	Psilidés
Голубиные пероеды	Taubenfederlinge	Pigeon-lice	Poux de colombes
Голубокрылая кобылка	Blauflüglige Ödlandschrecke	Blue-winged Waste-land Grasshopper	
Голубянка икар	Hauhechel-Bläuling	Common Blue	
Голубянки	Bläulinge	Blues	Lycénides
Горбатки	Buckelfliegen, Buckelzirpen, Stachelkäfer	Coffin Flies, Tree-hoppers, Tumbling Flower Beetles (N. A.)	Phoridés, Membracidés, Mordellidés

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Горная цикада	Bergzikade		Cigale de montagne
Горностаевые моли	Gespinstmotten	Small Ermines	Hyponomeutidés
Гороховый наездник	Riesenschlupfwespe		Ichneumon reclus
Горчичная белянка	Rübenweißling	Green-veined White	Piéride du navet
Гребляки	Wasserzikaden	Corixids	Corixidés
Гребневая долгоножка	Schwarze Kammschnake		Cténophore obscur
Грибные комарики	Pilzmücken, Trauermücken	Fungus Gnats	Mycetophilidés, Sciaridés
Грушевая кружевница	Birnen-Netzwanze		Tigre du poirier
Грушевая медяница	Birnblattsauger	Big Pear Psylla	Psylle du poirier
Грушевый пилильщик	Birnensägewespe		Hoplocampe du poirier
Грушевый стеблевой пилильщик	Birnentriebwespe		Janus du poirier
Грязный хищнец	Kotwanze	Fly Bug	Punaise masqué
Губчатая дубовая орехотворка	Eichen-Schwammgallwespe	Oak-apple Gallfly	Biorhiza du chêne
Данаиды	Danaiden		Danaïdes
Дарвинов термит	Darwin-Termite		Mantis de Darwin
Двукрылые	Zweiflügler	Flies	Diptères
Двухвостки	Doppelschwänze	Two-pronged Bristle-tails	Diploures
Длинноголовая коровья вошь	Langköpfige Rinderlaus	Long-nosed Oxlouse, Blue Cattle Louse	Pou du veau
Длинноусые двукрылые	Mücken	Thread-horns	Nématocères
Дневной павлиний глаз	Tagpfauenauge	Peacock	Paon de jour
Долгоносики	Rüsselkäfer	Weevils (N. A.)	Charançons
Долготелы	Langkopfkäfer	Brentid Beetles (N. A.)	
Дождевка	Regenbremse		Taon des pluies
Долгоножки	Stelzschnaken, Wiesenschnaken	Crane Flies	Limoniidés, Tipulidés
Домовый дровосек	Zimmermannsbock	Timberman	
Домовый сверчок	Hausgrille	House-cricket	Gryllon domestique
Домовый сеноед	Gemeine Staublaus		Pou de fropper
Домовый усач	Hausbockkäfer	House Longhorn	Hylotrupe
Дорожные осы	Wegwespen	Spider-wasps	Pompilidés
Древесные мухи	Holzfliegen		Erinniés
Древесные трипсы	Baumthripse		Thrips d'arbres
Древоточцы	Holzbohrer	Goat Moths	Cossides
Дриины	Zikadenwespen		Dryinides
Дровосеки	Bockkäfer	Long-hornes Beetles	Capricorines
Дрозофилы	Taufliegen	Small Fruit Flies	Drosophilidés
Дубовая листовертка	Eichenwickler	Pea-green Oak Twist	Tordeuse du chêne
Дубовая тля	Eichenrindenlaus		Puceron du chêne
Дубовый коконопряд	Eichenspinner	Oak Eggar	Minime à baudes jaunes
Дубовый кузнечик	Eichenschrecke	Oak Bush-cricket	Méconema
Дубовый походный шелкопряд	Eichenprozessionsspinner		Processionnaire du chêne
Дубовый трубковерт	Eichenblattroller	Oak Leaf Roller	Attelabe du chêne
Дубовый червец	Eichenpockenschildlaus		Cochenille du chêne
Европейская немка	Europäische Ameisenwespe	European Velvet-ant	Mutille d'Europe
Европейский еловый пилильщик	Fichtenblattwespe	Spruce	Tenthride du pin
Египетская саранча	Ägyptische Knarrschrecke	Tree Locust	Criquet d'Egypte
Ежевичная орехотворка	Brombeergallwespe		Diastrophus de la ronce
Ежемухи	Raupenfliegen	Parasite Flies	Larvivoridés
Еловая ложнощитовка	Fichtenquirlschildläuse		Cochenille de verticille du
Жалоносные перепончатокрылые	Stechwespen		Guêpes piqueuses
Желтая зеленоглазка	Gelbe Halmfliege	Gout Fly	Chlorops du blé et de l'ong
Желтолихорадный комар	Gelbfiebermücke	Yellow Fever Mosquito	Moustique de la fièvre jaun
Желтолобая сколия	Gelbstirnige Dolchwespe	Yellow-fronted Digger Wasp	Scolia à front jaune
Желтоногий термит	Gelbfüßige Termite	Eastern subterranean Termite	Termite aux pieds jaunes
Желтошеий термит	Gelbhalstermite	Yellow-necked Termite	– à cou jaune, Flavicolle
Желтушки	Gelblinge	Clouded Yellows	Colias
Желтый крыжовниковый пилильщик	Gelbe Stachelbeer-Blattwespe	Black Currant Sawfly	Némate du groseillier
Желтый сливовый пилильщик	Gelbbraune Pflaumensägewespe		Hoplocampe jaune du pruni
Желудочные оводы	Magendasseln	Horse Bot Flies	Gastrophiles
Жесткокрылые	Deckflügler	Beetles	Coléoptérides
Животные вши	Tierläuse	Animal Lice	Poux des animaux
Жигалка	Wadenstecher	Stable Fly	Mouche des étables
Жужелицы	Laufkäfer	Carabids	Carabidés, Carabiques
Жужелицы-бомбардиры	Bombardierkäfer	Bombardier Beetles	Bombardiers
Жужжалы	Wollschweber	Bee-Flies	Bombylidés
Жук-геркулес	Herkuleskäfer		Dynastes hercule
Жук-голиаф	Goliathkäfer	Goliath Beetle	
Жуки	Hirschkäfer	Stag Beetles	Lucane cerf-volant
Жуки-матросы	Käfer	Beetles	Coléoptères

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Журчалки	Werftkäfer	Timber Beetles (N. A.)	Lymexylonidés
Жуки-олени	Schwebfliegen	Hover Flies	Syrphidés
Заболонники	Borkenkäfer	Scolytid Beetles	Scolytes
Западный майский хрущ	Feldmaikäfer	White Grub	Ver blanc
Запятовидная щитовка	Kommaschildlaus	Mussel Scale, Oystershell Scale	Cochenille des arbres fruitiers
Зеленая лютка	Weidenlibelle		Leste vert
Зеленый древесный щитник	Grüne Stinkwanze	Green Shieldbug	Punaise verte
Земляной шмель	Erdhummel	Bumble Bee	Bourdon de terre
Зерновки	Samenkäfer	Seed Beetles	Bruches
Звонцы	Zuckmücken	Non-biting Midges	Tendipédidés
Зимние комары	Wintermücken	Winter Gnats	Trichocéridés
Зимняя пяденица	Frostspanner		Phalins défeuillantes
Злаковые мушки	Halmfliegen	Gout Flies	Chloropidés
Златки	Prachtkäfer	Metallic Wood-borers (N. A.)	Buprestes
Златоглазки	Blindbremsen, Goldaugen	Blinding Breeze Flies, Green Lacewings	Chrysops, Chrysopides
Златогузка	Goldafter	Brown-tail	Cul doré
Ивовая галлица	Weidenholzgallmücke	Willow-shoot Hole	Moustique des saules
Ивовая пенница	Weidenschaumzikade		Cigale du saule
Ильмовая козявка	Ulmenblattkäfer		Galérucelle d'orme
Ильница	Schlammfliege	Drone Fly	Eristale gluante
Индийская медоносная пчела	Indische Biene	Honey Bee	Abeille de l'Inde
Исполинская пчела	Riesenhonigbiene	Honey Bee	
Исполинские жуки	Nashornkäfer	Rhinoceros Beetles	Dynastinés
Итальянская саранча	Italienische Schönschrecke	Italian Locust	Criquet italien
Итальянский щитник	Streifenwanze		Punaise d'Italie
Кабинетные кожееды	Kabinettkäfer, Museumskäfer	Carpet Beetle, Museum Beetle	Anthrène du cabinet
Кавалеры	Ritterfalter	Swallowtail Family	Papilionidé
Калифорнийская кленовая тля	Kalifornische Ahornspringlaus		Puceron de Californie
Калифорнийская щитовка	San-José-Schildlaus	San Jose Scale	Pou de San José
Калоеды	Kotfresser	Dung Beetles	Onthophagus
Капустная белянка	Großer Kohlweißling	Large Cabbage-white	Piéride du chou
Капустная моль	Kohlmotte	Diamond-back Moth	Teigne du Colza
Капустная совка	Kohleule	Cabbage Moth	Noctuelle du chou
Капустничный апантелес	Weißlingstöter	Braconid Fly	Ichneumon
Карапузики	Stutzkäfer	Hister Beetles	Histénidés
Карликовая пчела	Zwerghonigbiene		Abeille naine
Кистехвост	Bürstenbinder	Scarce Vapourer	Brachophage du trèfle
Клеверный семеед	Kleesamenwespe		Puceron du platane
Кленовая тля	Ahornspringlaus		Clythres
Клитры	Sackblattkäfer		Hétéroptères
Клопы	Wanzen	Bugs	Polycténidés
Клопы летучих мышей	Kammwanzen	Many-combed Bugs (N. A.)	Miridés
Клопы-слепняки	Schmalwanzen	Plant Bugs	Pou devin
Книжная вошь	Bücherlaus	Book-louse	Oedipodinés
Кобылки	Schnarrheuschrecken	Band-winged Grasshoppers	Teigne des tapis
Ковровая моль	Gemeine Tapetenmotte	Tapestry Moth	Anthrène de la scrophulaire
Ковровый кожеед	Teppichkäfer	Carpet Beetle	Dermestes
Кожееды	Speckkäfer	Hide Beetles	Dermaptères
Кожистокрылые	Ohrwürmer	Earwigs	Hypodermes
Кожные оводы	Hautdassel	Warble Flies	Pou du chèvre
Козья вошь	Ziegenlaus	Goat Louse	Bombyx feuilles
Коконопряды	Glucken	Lackeys and Eggars	Cochenilles
Кокциды	Schildläuse	Coccids, Mealy Bugs	
Колорадский картофельный жук	Kartoffelkäfer	Colorado Beetles	
Колосковые мухи	Kotfliegen	Dung Flies	Cordyluridés
Колумбийский жук-носорог	Kolumbianischer Nashornkäfer		Coléoptère de Columbie
Кольчатый коконопряд	Ringelspinner	Common Lackey Moth	Livrée
Комары	Mücken	Thread-horns	Nématocères
Комары-дергуны	Zuckmücken	Non-biting Midges	Tendipédidés
Комары-толстоножки	Haarmücken	March-flies	Bibionidés
Конусоголовые кузнечики	Kegelköpfe	Cone Heads	Conocéphalidés
Копры	Kotkäfer	Dung Beetles	Coprins
Коровий власоед	Rinderhaarlinge	Cattle-lice	Poux des bœufs
Коромысло	Mosaiklibellen	Hairy Dragonfly	Aeschna à abdomen court
Коротконадкрылые жуки	Staphylinidenartige	Rove Beetles	
Короткоусиковые пухоеды	Stumpffühlerläuse		Poux à tentacle cônes
Короткоусые двукрылые	Fliegen	Short-horns	Brachycères
Косулий овод	Rehdasselfliege	Deer Warble Fly	Hypoderme du chevreuil
Кошачий власоед	Katzenhaarling	Cat-louse	Pou du chat

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Кошачий глаз	Nagelfleck		Hachette
Кошачья блоха	Katzenfloh	Cat Flea	Puce du chat
Краевики	Lederwanzen	Leaf-footed Bugs, Squash Bugs	Coréidés
Красная ленточница	Rotes Ordensband	Red Underwing	Mariée
Красноклопы	Feuerwanzen	Pyrrhocorid Bugs	Pyrrhocoridés
Краснокрылая кобылка	Rotflüglige Ödlandschrecke	German Grasshopper	
Красотки	Prachtlibellen	Demoiselles	Caloptéryx
Крапивница	Kleiner Fuchs	Small Tortoiseshell	Petite tortue
Крапивный червец	Nesselröhrenlaus		Cochenille de l'ortie
Кровавая пенница	Blutzikade		Cigale sanguinolent
Кровавый муравей	Blutrote Raubameise	Blood-red Ant	Fourmi sanguine
Кровососки	Lausfliegen	Bird Flies	Hippoboscidés
Кровососущие комары	Stechmücken	Mosquitoes	Moustiques
Кровяная тля	Blutlaus	Woolly Apple Aphid	Puceron laineux
Кровяные тли	Blutläuse	– Aphids	
Круглошовные мухи	Deckelschlüpfer		Cyclorhaphes
Кружевницы	Netzwanzen	Lacebugs, Tingids	Tingidés
Крушинница	Zitronenfalter	Brimstone	Citron
Крыжовниковая пяденица	Harlekin	Common Magpie Moth	Zérène mouchetée du groseillier
Крылатые насекомые	Fluginsekten	Largely-winged Insects	Ptérygotes
Крысиная вошь	Rattenlaus	Spined Rat Louse	Pou du rat
Ксифидрии	Schwertwespen		Xiphydriidés
Ктыревидки	Stilettfliegen	Stiletto Flies	Thérévidés
Ктыри	Jagdfliegen	Assasin Flies	Asilidés
Кузнечиковые и Сверчковые	Langfühlerschrecken	Bush-crickets	Sauterelles à longues antennes
Лапландская мошка	Lappländische Kriebelmücke		Mélusine de Laponie
Ласточковая кровососка	Schwalbenlausfliege	Swallow Louse Fly	Mouche des hirondelles
Ласточковый клоп	Schwalbenwanze	– Bug	Punaise d'hirondelle
Ленточницы	Ordensbänder	Underwings	Lichénées
Лесная оса	Waldwespe	Tree Wasp	Guêpe sylvestre
Лесная пеструшка	Würfelfalter	Duke of Burgundy	Lucine
Лесной рыжий муравей	Große Rote Waldameise	Wood Ant	Fourmi rousse
Лесные тараканы	Waldschaben	– Cockroaches	Blattes des bois
Лиственные жужелицы	Gespenstlaufkäfer	Violin Beetles	
Листоблошки	Blattflöhe	Phyllids	Psyllines
Листовертки	Wickler	Leaf Rollers	Tortricides
Листоеды	Blattkäfer	– Beetles	Chrysomélidés
Листотел	Wandelndes Blatt	Leaf-insect	
Лобковая вошь	Schamlaus	Crab Louse	Pou de feutre
Ложнослоники	Breitrüßler	Fungus Weevils (N. A.)	Anthribidés
Ложнощитовки	Schalenschildläuse	Soft Scales	Lécanines
Лошадиная вошь	Pferdelaus	Sucking Horse Louse	Pou de l'âne
Лошадиная кровососка	Pferdelausfliege		Mouche du cheval
Лошадиный овод	Pferde-Nasendassel		Œstre du cheval
Луговая желтушка	Gemeiner Heufalter	Pale Clouded Yellow	Soufré
Луковичные мухи	Zwiebelfliegen	Lesser Bulb Fly	Mouches des oignons
Лунные копры	Mondhornkäfer	Dung Beetles	Copris
Львинки	Waffenfliegen	Soldier Flies	Stratiomyidés
Льняная долгоножка	Sumpfschnake		Tipule des marais
Лютки	Prachtlibellen	Demoiselles	Caloptérygidés
Майские букашки	Maiwürmer	Dil Beetles	Méloés
Майские жуки	Maikäfer	May Beetles	Hannetons
Майские хрущи	Echte Maikäfer	Cockchafers	–
Малая комнатная муха	Kleine Stubenfliege	Lesser House Fly	Petite mouche domestique
Малая уховертка	Zwergohrwurm	Small Earwig	Perce-oreille nain, Forficule nain
Малашки	Zipfelkäfer		Malachidés
Малинная стеклянница	Himbeer-Glasflügler		Sésie du framboisier
Малый еловый пилильщик	Kleine Fichtenblattwespe	Fir Sawfly	Petit Pritisphore du pin
Малый лиственничный пилильщик	Kleine Lärchenblattwespe	Smaller Larch Sawfly	Petit pritisphore du milize
Малый ночной павлиний глаз	Kleines Nachtpfauenauge	Emperor Moth	– paon de nuit
Малый осиновый усач	Espenbockkäfer		Petite saperde du peuplier
Малярийные комары	Fiebermücken	Mosquitoes	Anophèles
Марокканская саранча	Marokkanische Wanderheuschrecke	Maroccan Grasshopper	Criquet marocain
Махаон	Schwalbenschwanz	Common Swallowtail	Grand porte-queue
Махилисы	Felsenspringer	Machilids	Machilidés
Мебельная моль	Gewöhnliche Kleidermotte	Common Clothes Moth	Mite des vêtements
Мегахилиды	Mauer-, Mörtel- und Blattschneiderbienen	Leafcutting Bees	Abeille découpeuse des feuilles
Медведицы	Bärenspinner	Tiger-moths	Arctiidés
Медведки	Maulwurfsgrillen	Mole-crickets	Gryllotalpides
Медяницы	Blattflöhe	Phyllids	Psyllines
Мексиканская конишель	Cochenille-Laus	Cochineal Insect	Cochenille

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Мельничная огневка	Mehlmotte	Mediterranean Flour Moth	Teigne de la farine
Мертвая голова	Totenkopfschwärmer	Death's-head Hawk	Sphinx tête du mort
Мертвоеды	Aaskäfer	Carrion Beetles, Burying Beetles	Silphidés
Мерцательница	Großer Schillerfalter	Purple Emperor	Grand mars changeant
Мешочницы	Sackspinner	Bag-worm Moths (N. A.)	Psychides
Минирующие мушки	Minierfliegen	Leaf Miners	Agromyzidés
Многоцветницы	Fleckenfalter	Fritillaries	Nymphalides
Могильщики	Totengräber	Sexton Beetles	Nécrophores
Мокрецы	Gnitzen	Biting Midges	Heléides
Моли	Echte Motten	Clothes Moths	Teignes
Моли-малютки	Zwergmotten		Nepticulidés
Монашенка	Nonne	Black Arches	Nonne
Морковная муха	Möhrenfliege	Carrot Rust Fly	Mouche des carottes
Москиты	Sandmücken i. e. S.	Sandflies	Phlébotomines
Мохноножки	Hosenbiene	Hairylegged Mining Bees	Abeilles à pantalon
Мошки	Kriebelmücken	Black Flies	Mélusinides
Муравей-амазонка	Amazonenameise		Fourmi Amazon
Муравей-древоточец	Glänzendschwarze Holzameise	Jet Ant	– fuligineuse
Муравьи	Ameisen	Ants	Formicidés
Муравьи-древоточцы	Roßameise		Camponotus
Муравьи-жнецы	Getreideameisen	Grain Ants	Fourmi moissonneuse
Муравьи-земледельцы	Ernteameisen		– des récoltes
Муравьиные львы	Ameisenlöwen	Ant Lions	Fourmis-lions
Муравьиный клоп	Ameisenwanze		Punaise de la fourmi
Муравьиный лев	Ungefleckte Ameisenjungfer		Fourmis lion
Мухи	Fliegen, Schnabelhaftverwandte	Short-horns, Scorpion Flies	Brachycères, Mécoptères
Мухи це-це	Tsetsefliegen	Tsetse Flies	Mouches tsé-tsé
Мучной хрущак	Mehlkäfer	Mealworm	Ténébrion meunier
Мягкотелки	Weichkäfer	Soldier-beetles	Cantharidés
Навозники	Blatthornkäfer		Cockchafers
Наземные клопы	Landwanzen		Punaises de terre, Géocorises
Нарывники	Blasenkäfer, Ölkäfer	Blister Beetles	Mylabris, Méloidés
Насекомые	Insekten	Insects	Insectes
Настоящие белянки	Echte Weißlinge	Whites	Piérides
Настоящие вши	Echte Läuse	Sucking Lice	Anoplurés
Настоящие комары	Stechmücken	Mosquitoes	Moustiques
Настоящие коротко-надкрылые жуки	Kurzflügler	Rove Beetles	Staphylins
Настоящие кузнечиковые	Laubheuschrecken	Bush-crickets	Tettigonidés
Настоящие мухи	Echte Fliegen	Mouse Flies	Muscidés
Настоящие навозники	Mistkäfer	Dor Beetles	
Настоящие навозные жуки	Echte Mistkäfer	– –	Géotrupes
Настоящие наездники	Eigentliche Schlupfwespen	Ichneumons	Ichneumonides
Настоящие орехотворки	– Gallwespen	Gall Wasps	Cynipides gallicoles
Настоящие пилильщики	– Blattwespen	Sawflies	Tenthrédinidés
Настоящие полужестко-крылые	Schnabelkerfe	True Bugs	Hémiptères
Настоящие пчелы	Echte Bienen	Bumble Bees	Abeille domestique
Настоящие рогохвосты	Holzwespen	Horn-tails	Siricidés
Настоящие саранчовые	Feldheuschrecken	Grasshoppers	Acridiens
Настоящие тли	Röhrenläuse	Aphids	Aphididés
Настоящие шелкопряды	Echte Spinner	Silk Moths	Bombycides
Неместриниды	Netzfliegen		Némestrinidés
Немки	Ameisenwespen	Velvet-ants	Mutillides
Ненастоящие кузнечиковые	Grillenschrecken	Cave and Camel-crickets	Sauterelle grillon
Непарный шелкопряд	Schwammspinner	Gipsy	Bombyx disparate
Низшие бабочки	Urtümlichste Kleinschmetterlinge		Homoneures
Ногохвостки	Springschwänze	Springtails	Collemboles
Носатка	Zürgelbaumfalter		Échancré
Носоглоточные оводы	Nasendasseln	Bot Flies	Œstres
Ночницы	Eulenfalter	Noctuids	Noctuelles
Общественные осы	Echte Wespen	Hornets	Vespides
Общественный грушевый пилильщик-ткач	Gesellige Birnblattwespe	Common Web-spinning Sawfly	Lyde du poirier
Обыкновенная блестянка	Feuergoldwespe	Fire Cuckoo Wasp	Chrysis enflammée
Обыкновенная висло-крылка	Schlammfliege	Alder Fly	Sialis de la vase
Обыкновенная горбатка	Dornzikade	Devil-hopper	
Обыкновенная дубовая орехотворка	Gemeine Eichengallwespe	Common Oak Gallfly	Cynips du chêne
Обыкновенная лютка	Gemeine Seejungfer	Demoiselle Agrion	Demoiselle
Обыкновенная медведка	Maulwurfsgrille	Mole-cricket	Taupe-gryllon commun
Обыкновенная медоносная пчела	Honigbiene	Honey Bee	Abeille domestique

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Обыкновенная мошка	Gemeine Kriebelmücke		Mélusine commun
Обыкновенная поденка	– Eintagsfliege	Mayfly	Ephémère commune
Обыкновенная светоноска	Europäischer Laternenträger	European Lantern-fly	Fulgoride européen
Обыкновенная уховертка	Gemeiner Ohrwurm	Common Earwing	Forficule auriculaire
Обыкновенные кузнечики	Heupferde	Bush-crickets	Tettigonides
Обыкновенный богомол	Gottesanbeterin	European Mantis	Mante prie-Dieu
Обыкновенный зеленый кузнечик	Grünes Heupferd	Great Green Bush-cricket	Grande sauterelle verte
Обыкновенный ивовый пилильщик	Gemeine Weidenblattgallen-Wespe	Common Willow Sawfly	Pontanie commune
Обыкновенный комар	– Stechmücke	European House Mosquito	Moustique commun
Обыкновенный комар-кусака	– Waldschnake		Aedes commun
Обыкновенный краевик	Randwanze		Punaise bordée
Обыкновенный наездник	Gemeine Schlupfwespe		Ichneumon commun
Обыкновенный пескорой	Sandwespe	Sand Wasp	Guêpe des sables
Обыкновенный прус	Italienische Schönschrecke	Italian Locust	Criquet italien
Обыкновенный сосновый рогохвост	Gemeine Holzwespe	Polished Horntail	Sirex commun
Овечий овод	Schaf-Nasendassel	Sheep Gadfly	Œstre du mouton
Овечья вошь	Schafslaus	– Louse	Pou du mouton
Овечья кровососка	Schafslausfliege	– Ked	Mélophage du mouton
Оводы	Dasselfliegen	Bot Flies	Œstridés
Овсяная шведская мушка	Fritfliege	Frit Fly	Oscinie frit
Огневки	Zünsler	Snout Moths	Pyralididés
Огненный червонец	Dukatenfalter		Argus satiné
Огородная долгоножка	Graue Kohlschnake	Common Crane Fly	Tipule du chou
Одиночные осы	Lehmwespen	Potter Wasps	Euménines
Одиночный сосновый пилильщик-ткач	Kiefernkultur-Gespinstblatt-wespe	Web-spinning Pine-sawfly	Lyde champêtre
Озимая совка	Saateule	Turnip Dart	Noctuelle des moissons
Окаймленный плавунец	Gelbrandkäfer	Great Water Beetle	Dytisque bordé
Оконная муха	Buckelige Fensterfliege	Window Fly	Mouche des fenêtres
Олений овод	Hirschdasselfliege		Hypoderme du cerf
Оленья кровососка	Hirschlausfliege	Deer Ked	Lipoptène du cerf
Оливковая медяница	Ölbaumblattsauger		Puce d'olivier
Ольховая козявка	Blauer Erlenblattkäfer		Galeruque de l'aulne
Ольховая стрельчатка	Erleneule	Alder Dogger	Noctuide d'aune
Оранжерейный кузнечик	Gewächshausschrecke	Greenhouse Camel-cricket	Sauterelle grillon de serre
Оранжерейный трипс	Treibhausthrips	– Thrips	Thrips des serres
Ореховый долгоносик	Haselnußbohrer	Nut Weevil	
Орешниковый трубковерт	Haselblattroller	Hazel Leaf Roller	Apodère du noisettier
Орхидеевый семеед	Orchideenwespe	Orchid Wasp	Guêpe des orchidées
Остроголовые клопы	Getreidewanzen		Punaise du blé
Ощупники	Palpenkäfer		Pselaphidés
Павлиноглазки	Augenspinner	Emperor Moths	Saturniides
Пальцекрылки	Federmotten	Plumes	Ptérophores
Парусники	Ritterfalter	Swallowtail Family	Papilionidés
Паутинные пилильщики	Pferdelausfliege		Mouche du cheval
Паутка	Gespinst-Blattwespen	Leaf-roller	Pamphilides
Пахучий древоточец	Weidenbohrer	Goat Moth	Cossus gâte-bois
Пахучий красотел	Puppenräuber	Caterpillar Hunter	
Певчие цикады	Singzikaden	Cicadas, Harvest Flies	Cigales
Пенницы	Schaumzikaden	Spittle Bugs, Frog-hoppers	Cercopidés
Первичные моли	Urmotten		Microptérygidés
Перепончатокрылые	Hautflügler	Sawflies, Wasps	Hyménoptères
Перистоусики	Büschelmücken	Lake Flies	Corethrines
Перламутровки	Perlmutterfalter	Fritillaris	Nacrés
Перокрылки	Federflügler		Ptiliidés
Персиковая тля	Pfirsichblattlaus	Peach-potatoe Aphid	Puceron vert du pêcher
Пестрокрылки	Fruchtfliegen	Large Fruit Flies	Mouches des fruits
Пестряки	Buntkäfer	Checkered Beetles	Clairons
Пестрянки	Widderchen	Burnets	Zygénides
Пилильщики	Blattwespen	Sawflies	Tenthrédinidés
Пилильщики-ткачи	Gespinst-Blattwespen	Leaf-rollers	Pamphilides
Пилюльщики	Pillenkäfer	Pill Beetles	Byrrhidés
Пиниевый походный шелкопряд	Pinien-Prozessionsspinner	Pine-feeding Processionary Caterpillar	Processionnaire du pin
Пиофилиды	Käsefliegen	Cheese Skippers	Mouches du fromage
Пихтовая тля	Tannentrieblaus	Balsam Twig Aphid	Puceron du sapin
Плавунцы	Gelbrandkäfer, Schwimmkäfer	Great Water Beetles, Carnivorous Water Beetles	Dytiscidés
Пластинчатоусые	Blatthornkäfer	Cockchafers	Scarabés
Платяная вошь	Kleiderlaus	Body Louse	Pou de vêtement
Платяная моль	Gewöhnliche Kleidermotte	Common Clothes Moth	Mite des vêtements
Плоская стрекоза	Plattbauch	Broad-bodied Libellula	Libellule déprimée

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Плоскотелки	Plattkäfer	Flat Bark Beetles (N. A.)	Rhizophagidés
Площица	Schamlaus	Crab Louse	Pou de feutre
Подалирий	Segelfalter		Flambé
Поденки	Eintagsfliegen	Mayflies	Ephémères
Подкожные оводы	Biesfliegen i. e. S., Hautdassel	Warble Flies	Hypodermes
Подкорники	Rindenwanzen	Flat Bugs	Aradidés
Подушечницы	Schalenschildläuse	Soft Scales	Lécanines, Cocoidés
Полевой сверчок	Feldgrille	Field-cricket	Grillon des champs
Полевой скакун	Feld-Sandlaufkäfer	Field Tiger Beetles	Cicindèle des champs
Полосатая цикадка	Streifenzikade		Cigale à abdomen
Полосатый клоп	Streifenwanze		Punaise d'Italie
Полосатый скарабей	Gestreifter Pillendreher		Scarabée à corselet large
Пометокопатели	Dungkäfer	Dung Beetles	Aphodiinés
Постельные клопы	Bettwanzenverwandte	Bed Bugs	Cimicidés
Постельный клоп	Bettwanze	– Bug	Punaise des lits
Походные шелкопряды	Prozessionsspinner	Processionary Caterpillars	Processionnaires
Прибрежная уховертка	Sandohrwurm	Earwig	Perce-oreille des rivages
Привиденьевые	Gespenstschrecken	Stick- and Leaf-insects	Phasmes
Притворяшки	Diebskäfer	Spider Beetles	Ptinidés
Проволочники	Schnellkäfer	Click-beetles	Taupins
Простая златоглазка	Goldauge	Green Lacewing	Chrysops commun
Прусак	Hausschabe	German Cockroach	Blatte d'Allemagne
Прыгающие прямокрылые	Schrecken	Saltatoria	Sauterelles
Прямокрылые	Geradflügler		Orthoptères
Птицекрылки	Vogelfalter	Bird Wings	
Пузырная тля	Ulmenblasenlaus		Schizonèvre laineux
Пустынная саранча	Wüstenschrecke	Desert Locust	Sauterelle pélerin
Пухоеды	Kieferläuse	Chewing Lice	Mallophages
Пчелиные	Bienen	Bees	Apoidés
Пчелиные паразиты	Bienenläuse	Bee-»Lice«	Braulidés
Пчелиный волк	Bienenwolf	Bees Wool	Philanthe apivore
Пчеложуки	Immenkäfer		Trichodés
Пчелы-древогнезды	Holzbienenverwandte	Large Carpenter Bees	Abeilles charpentières
Пчелы-лесовки	Maskenbienen		Hylaeus
Пчелы-листорезы	Blattschneiderbienen	Leaf-cutting Bees	Mégachiles
Пчелы-остробрюхи	Kegelbienen		Abeille à abdomen conique
Пяденицы	Spanner	Geometers	Géométrides
Пятнистая грушевая медяница	Gefleckter Birnblattsauger		Puce tacheté du poirier
Пятнистая стрекоза	Vierflecklibelle	Four-spotted Libellula	Libellule à quatre taches
Пятнистый комар-кусака	Gefleckte Waldschnake		Aedes tacheté
Равнокрылые бабочки	Urtümlichste Kleinschmetterlinge		Homoneures
Равнокрылые стрекозы	Kleinlibellen	Damselflies	Zygoptères
Равнокрылые хоботные	Pflanzensauger	Clear-winged Bugs	Homoptères
Разнокрылые бабочки	Höhere Schmetterlinge		Hétéroneures
Разнокрылые стрекозы	Großlibellen	Dragonflies	Anisoptères
Рапсовая блестянка	Rapsglanzkäfer	Pollen Beetle	Méligèthe bronzé
Рапсовый пилильщик	Runkelrüben-Blattwespe	Turnip	Athale de la betterave
Рапсовый щитник	Kohlwanze	Brassica Bug	Punaise des potagers
Ренатра	Stabwanze	Water Stick-insect	– linéaire
Репейница	Distelfalter	Painted Lady	Belle-dame
Репная белянка	Kleiner Kohlweißling	Small White	Piéride de rave
Ризоды	Runzelkäfer		Rhysodidés
Рисса	Pfeifenräumer		Rhyssa persuasive
Рогачи	Hirschkäfer	Stag Beetles	Lucanes
Рододендроновый клоп	Rhododendron-Netzwanze	Rhododendron Bug	Tigre du rhododendron
Розанная орехотворка	Gemeine Rosengallwespe	Mossy Rose Gall	Diplolepis du rosier
Розанная цикадка	Rosenzikade	Rose Leafhopper.	Cicadelle du rosier
Розанный пилильщик	Rosen-Bürsthornwespe	– Sawfly	Hylotome de la rose
Розанный пилильщик-ткач	Rosen-Gespinstblattwespe	– Web-spinning Sawfly	Lyde du rosier
Ростковая ивовая галлица	Weidenrutengallmücke		Rhabdophage des saules
Роющие осы	Grabwespen	Thread-waisted Wasps	Sphécidés
Ручейники	Köcherfliegen	Caddice Flies	Trichoptères
Рыжая древесная муха	Rostrote Holzfliege		Mouche rouge du bois
Рыжая оса	Rote Wespe	Wasp	Guêpe rousse
Рыжий ночной павлиний глаз	Nagelfleck		Hachette
Рыжий таракан	Hausschabe	German Cockroach	Blatte d'Allemagne
Садовая мошка	Gartenhaarmücke	Garden March Fly	Bibion des jardins
Саксонская оса	Sächsische Wespe	Tree Wasp	Guêpe de Saxe
Саранчовые и Триперстовые	Kurzfühlerschrecken	Short-tentacled Grasshoppers	Sauterelles de palpes courtes
Сатир семеле	Ockerbindiger Samtfalter	Grayling	Agreste

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Сатиры	Augenfalter	Meadow Browns	Satyrides
Сахарные жуки	Zuckerkäfer	Passalid Beetles (N. A.)	Passalidés
Свекловичная муха	Runkelrübenfliege		Mouche de la betterave
Свекловичная тля	Bohnenlaus	Black Bean Aphid	Puceron de la fève
Сверчковые	Grillen, Langfühlerschrecken	Crickets, Bush-crickets	Gryllides, Sauterelles à Congues antennes
Светляки	Leuchtkäfer	Glowworms	Lampyridés
Светоноски	Laternenträger	Lantern-flies	Fulgoridés
Свиная вошь	Schweinelaus	Pig Louse	Pou du porc
Священный навозник	Heiliger Pillendreher	Sacred Scarab	
Северный березовый пилильщик	Breitfüßige Birkenblattwespe	Birch Sawfly	Tenthrède du bouleau
Семиточечная коровка	Siebenpunkt-Marienkäfer	Ladybird	Coccinelle à sept points
Сенницы	Heufalter	Ringlets	
Сеноеды	Staubläuse	Book Lice	Poux de livres
Серая мясоедка	Graue Fleischfliege	Grey Flesh Fly	Mouche grise de la viande
Серый комар-кусака	– Waldschnake		Aedes cendré
Серый кузнечик	Warzenbeißer	Wart-biter	Dectique verrucivore
Сетчатокрылки	Lidmücken	Net-winged Midges	Blépharocéridés
Сетчатокрыловые	Netzflüglerartige	Alder Flies	Neuroptéroïdés
Сетчатокрылые	Hafte	Lace-wings	Planipennes
Сибирская саранча	Sibirische Keulenschrecke	Siberian Grasshopper	Sauterelle de Sibérie
Сивучовая вошь	Seelöwenlaus		Pou du lion marin
Сидячебрюхие перепончатокрылые	Pflanzenwespen	Sawflies	Symphytes
Синяя мясная муха	Blaue Schmeißfliege	Blue-bottle Fly	Mouche bleue de la viande
Сиреневый бражник	Ligusterschwärmer	Privet Hawk	Sphinx du troène
Скакуны	Sandlaufkäfer	Tiger Beetles	Cicindèles
Скарабеи	Pillendreher	Dung Beetles	Scarabées
Складчатокрылые осы	Faltenwespen	Yellow Jackets	Vespides
Сколии	Dolchwespen	Digger Wasps	Scoliides
Скорпионницы	Skorpionsfliegen	Scorpion Flies	Panorpides
Скорпионовые мухи	Schnabelfliegen	– –	Mécoptères
Слепни	Bremsen, Pferde- und Rinderbremsen	Horse-flies	Taons
Сливовый пилильщик	Schwarze Pflaumensägewespe		Hoplocampe noir du prunier
Слоновая вошь	Elefantenlaus		Pou d'éléphant
Слюнявая пеница	Gemeine Schaumzikade		Cicadelle écumeuse
Снежная блоха	Gletscherfloh		Puce du glacier
Собачий власоед	Hundehaarling	Chewing Dog-louse	Pou du chien
Собачья блоха	Hundefloh	Dog Flea	Puce du chien
Собачья вошь	Hundelaus	– Louse	Pou du chien
Совка гамма	Gammaeule	Common Silver Y Moth	Lettre grecque
Совки	Eulenfalter	Noctuids	Noctuelles
Совковая ежемуха	Eulentachine	Cluster Fly	Mouche des greiners – mineuse
Соколиная кровососка	Falkenlausfliege		Tordeuse des pousses
Сосновая плодожорка	Kiefernspanner	Gemmet Shoot	Fidonie du pin
Сосновая пяденица	Kiefernspanner	Bordered White	Varié de gris
Сосновая совка	Kieferneule	Pine Beauty	Feuille morte du pin
Сосновый коконопряд	Kiefernspinner	– Lappet	Diprion du pin
Сосновый пилильщик	Gemeine Kiefernbuschhorn-Blattwespe	– Sawfly	
Спаржевая бурилка	Spargelfliege	Asparagus Fly	Mouche des asperges
Средиземноморская плодовая муха	Mittelmeerfruchtfliege	Mediterranean Fruit Fly	– – oranges
Средняя оса	Mittlere Wespe		Guêpe moyenne
Стеблевидка	Mittelmeer-Stabschrecke	Mediterranean Stick-insect	
Стеблевые пилильщики	Halmwespen	Stem Sawflies	Céphides
Стеблевые сверчки	Baumgrillen	Tree-crickets	
Стеклянницы	Glasflügler	Clairwings	Sésies
Стенная оса	Wespe	Mason Wasp	Guêpe des murailles
Стенные пчелы	Mauerbienen	– Bees	Abeilles des murailles
Стрекозки	Taghafte	Brown Lacewings	Hémérobidés
Стрекозы	Libellen	Dragonflies	Libellules
Стрижиная кровососка	Mauersegler-Lausfliege	Swift Louse Fly	Mouche des martinets
Суринамский таракан	Gewächshausschabe	Surinam Cockroach	Blatte de serre
Сырная муха	Käsefliege	Cheese skipper	Mouche du fromage
Табачный трипс	Tabakthrips	Onion Thrips	Thrips de l'oignon et du tabac
Таволговая пестрянка	Blutströpfchen	Six-spot Burnet	Zygène-de-la-filipendule
Таракановые	Schaben	Cockroaches	Blattes
Тахины	Raupenfliegen	Parasite Flies	Larvivoridés
Темнобурый луговой муравей	Braune Wiesenameise		Fourmi brune des prés
Темнобурый термит	Lichtscheue Termite		Termite photophobe

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Темнокрылая белая мушка	Schwarze Citrusfliege	Citrus Black Fly	Mouche noire des Aurantiacées
Тепличная белокрылка	Weiße Gewächshausfliege	Greenhouse White Fly	– blanche des serres
Термиты	Termiten	Termites	Isoptères
Тетригиды	Dornschrecken	Grouse Locusts	Tetrigides
Тифии	Rollwespen	Tiphiid Wasps	Tiphides
Тли	Blattläuse	Aphids	Pucerons
Тлиные наездники	Blattlaus-Schlupfwespen	Ichneumons	Aphidiidés
Толкунчики	Dickkopffalter	Skippers	Hespérides
Толстоголовки	Tanzfliegen	Dance-flies	Empididés
Толстоголовки	Dickkopffliegen	Thick-headed Flies	Conopidés
Тонкопряды	Wurzelbohrer	Swifts	Hépialidés
Тонкоусиковые пухоеды	Dünnfühlerläuse		Poux aux tentacles minces
Тополевая ленточница	Großer Eisvogel	Great Viceroy	Grand Sylvain
Тополевый бражник	Pappelschwärmer	Poplar Hawk	Sphinx du peuplier
Тополевый листоед	Pappelblattkäfer	Red Poplar Leaf Beetle	
Точильщики	Klopfkäfer	Drugstore Beetles	Vrillettes
Тощеклопы	Langwanzen	Ground Bugs	Lygaeidés
Траурница	Trauermantel	Camberwell Beauty	Morio
Трескучая кобылка	Rotflüglige Schnarrschrecke	Red-winged Grasshopper	
Трехрогие навозники	Dreihorn-Mistkäfer	Three-horned Dor Beetles	Minotaure typhée
Триперстовые	Dreifingerschrecken, Kurzfühlerschrecken	Pigmy Mole-crickets, Short-tentacled Grasshoppers	Tridactylides, Sauterelles de palpes courtes
Трубачик	Weinhähnchen	Flower Tree-cricket	
Трубкохвостые трипсы	Röhren-Fransenflügler	Tubuliferae	Tubulifères
Тутовый шелкопряд	Maulbeerspinner	Silk Moth	Bombyx du mûrier
Тыквенный клоп	Kürbiswanze	Squash Bug	Punaise de courge
Узкоголовый трипс	Schmalkopfthrips	Cabbage Thrips	Thrips à tête étroite
Узконадкрылки	Scheinböcke	Oedemerid Beetles (N. A.)	Oedéméridés
Урании	Uraniafalter		Uraniides
Усачи	Bockkäfer	Long-horned Beetles	Capricorines
Уховертки	Eigentliche Ohrwürmer	Earwigs	Forficulides
Ушастая цикадка	Ohrzikade		Cigale à oreilles
Филоксеры	Zwergläuse		Puceron de Cooley
Форы	Buckelfliegen-Verwandte	Coffin Flies	
Французская бумажная оса	Französische Feldwespe		Poliste française
Хермесы	Tannenläuse	Adelgids	Puceron des sapins
Хищнецы	Mordwanzen, Raubwanzen	Assasin Bugs	Punaise du meurtre, Réduvidées
Хлебные трипсы	Getreidethripse	Grain Thrips	Thrips du blé
Хлебный пилильщик	Getreidehalmwespe	European Wheat Stem Sawfly	Cèphe du blé
Хмелевый тонкопряд	Hopfenwurzelbohrer	Ghost Swift	Hépiale du houblon
Хоботковые пухоеды	Rüsselläuse	Proboseis Lice	Poux à trompes
Хохлатки	Zahnspinner, Zickzackspinner	Prominents, Pebble Prominents	Notodontides
Цветоеды	Blütenstecher	Blossom Weevils	Anthonomes
Цветочные клопы	Blumenwanzen	Flower Bugs	Punaises des fleurs
Цикада семнадцатилетка	Siebzehnjahr-Zikade	Periodical Cicadas, Seventeen year Locust	Cigale de 17 ans
Цикадовые	Zikaden	Cicadas	Cigales
Цикадоедки	Augenfliegen	Big-headed Flies	Dorilaidés
Цитрусовая мушка	Weiße Citrusfliege	Citrus White Fly	Mouche blanche des Aurantiacées
Человеческая блоха	Menschenfloh	Human Flea	Puce de l'homme
Человеческая вошь	Kopf- und Kleiderlaus	Men-louse	Pou de l'homme
Черная мошка	Märzfliege	St. Mark's Fly	Bibion de St.-Marc
Чернотелки	Schwarzkäfer	Ground Beetles (N .A.)	Ténébrionidés
Черноточечная цикадка	Schwarzpunktzikade		Cigale à tache noire
Черный аполлон	Schwarzer Apollo		Semi-apollon
Черный большой водолюб	Großer Kolbenwasserkäfer	Great Silver Water-beetle	Grand Hydrophile
Черный луговой муравей	Schwarze Wiesenameise	Small Black Ant	Fourmi noire des prés
Черный муравей	Schwarzgraue Hilfsameise		– noire cendrée
Черный рогохвост	Schwarze Kiefernholzwespe		Xeris du pin
Черный таракан	Küchenschabe	Common Cockroach	Blatte des Cuisines
Чертов цветок	Teufelsblume		Mante de diable
Чешуекрылые	Schmetterlinge	Butterflies and Moths	Lépidoptères
Чешуйницы	Silberfischchen	Silverfish	Poisson d'argent
Шаровки	Spinnenfliegen	Fat Flies	
Шашечница	Schachbrett	Marbled White	Demi-deuil
Шелковые пчелы	Seidenbienen, Urbienen	Colletid Bees	Colletidés
Шершень	Hornisse	Grint Hornet	Frelon
Шеститочечная цикадка	Zwergzikade		cigale à six taches
Шипоноски	Stachelkäfer	Tumbling Flower Beetles (N. A.)	Mordellidés
Шмелевидная мохнатка	Hummelschwebfliege		Volucelle bourdon
Шпанские мухи	Spanische Fliegen	Spanish Flies	Mouches d'Espagne
Шубная моль	Pelzmotte	Case-making Clothes Moth	Teigne des fourrures

RUSSIAN NAME	GERMAN NAME	ENGLISH NAME	FRENCH NAME
Щелкуны	Schnellkäfer	Click-beetles	Taupins
Щелкуны-светляки	Leuchtschnellkäfer		Coléoptères luisants, Pyrophores
Щетинохвостки	Borstenschwänze	Bristle-tails	Thysanoures
Щитники	Schildwanzen	Shield Bugs	Punaises à bouclier
Щитовки	Deckelschildläuse	Armored Scales	Diaspididés
Щитоноски	Schildkäfer	Tortoise Beetles	Cassidinés
Эваниды	Hungerwespen	Ensign Flies	Evaniides
Эвмены	Pillenwespen	Potter Wasp	Eumènes
Эмбии	Fersenspinner	Embiids	
Южная крысиная блоха	Indischer Rattenfloh	Tropical Ratflea	
Яблонная медяница	Apfelblattsauger	Apple Psylla	Psylle du pommier
Яблонная плодожорка	Apfelwickler	Piorcer	Pyrale des pommes
Яблонный плодовый пилильщик	Apfelsägewespe	European Apple Sawfly	Hoplocampe du pommier
Яблонный цветоед	Apfelblütenstecher	Apple Blossom Weevil	Anthonome du pommier
Ягодный клоп	Apfelwanze	– Capsid Bug	Capsid du pommier
Ягодный цветоед	Beerenwanze	Sloebug	Punaise des baies
Язык-ан	Beerenstecher	Strawberry Blossom Weevil	
Яйцекладные трипсы	Taubenschwänzchen	Humming-bird Hawk-moth	Moro-sphinx
Ясеневая цикада	Bohr-Fransenflügler	Boring Thrips	Térébrants
	Eschenzikade		Cigale du frêne

Conversion Tables of Metric to U.S. and British Systems

U.S. Customary to Metric		*Metric to U.S. Customary*	
	Length		
To convert	*Multiply by*	*To convert*	*Multiply by*
in. to mm.	25.4	mm. to in.	0.039
in. to cm.	2.54	cm. to in.	0.394
ft. to m.	0.305	m. to ft.	3.281
yd. to m.	0.914	m. to yd.	1.094
mi. to km.	1.609	km. to mi.	0.621
	Area		
sq. in. to sq. cm.	6.452	sq. cm. to sq. in.	0.155
sq. ft. to sq. mi.	0.093	sq. m. to sq. ft.	10.764
sq. yd. to sq. m.	0.836	sq. m. to sq. yd.	1.196
sq. mi. to ha.	258.999	ha. to sq. mi.	0.004
	Volume		
cu. in. to cc.	16.387	cc. to cu. in.	0.061
cu. ft. to cu. m.	0.028	cu. m. to cu. ft.	35.315
cu. yd. to cu. m.	0.765	cu. m. to cu. yd.	1.308
	Capacity (liquid)		
fl. oz. to liter	0.03	liter to fl. oz.	33.815
qt. to liter	0.946	liter to qt.	1.057
gal. to liter	3.785	liter to gal.	0.264
	Mass (weight)		
oz. avdp. to g.	28.35	g. to oz. avdp.	0.035
lb. avdp. to kg.	0.454	kg. to lb. avdp.	2.205
ton to t.	0.907	t. to ton	1.102
l. t. to t.	1.016	t. to l. t.	0.984

Abbreviations

U.S. Customary

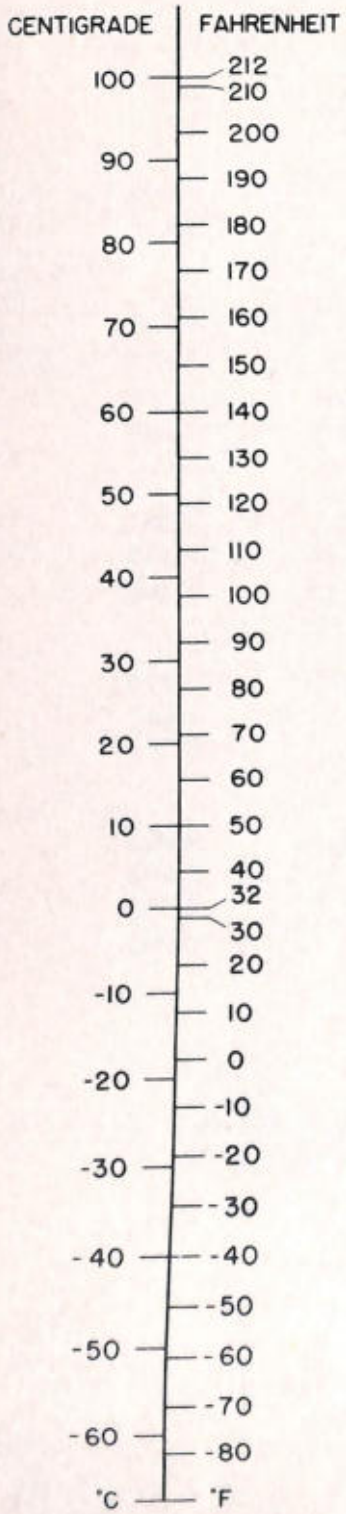
avdp.—avoirdupois
ft.—foot, feet
gal.—gallon(s)
in.—inch(es)
lb.—pound(s)
l. t.—long ton(s)
mi.—mile(s)
oz.—ounce(s)
qt.—quart(s)
sq.—square
yd.—yard(s)

Metric

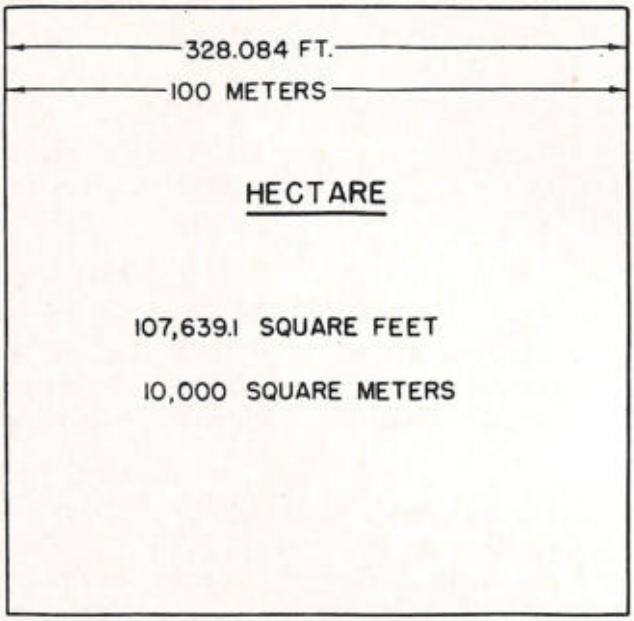
cc.—cubic centimeter(s)
cm.—centimeter(s)
cu.—cubic
g.—gram(s)
ha.—hectare(s)
kg.—kilogram(s)
m.—meter(s)
mm.—millimeter(s)
t.—metric ton(s)

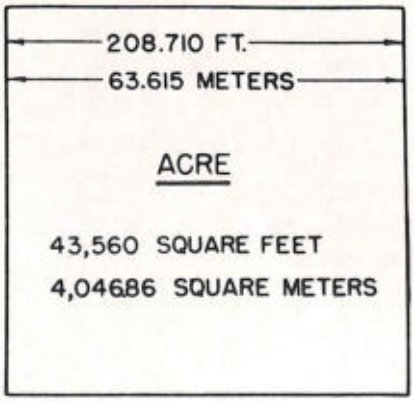
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TEMPERATURE



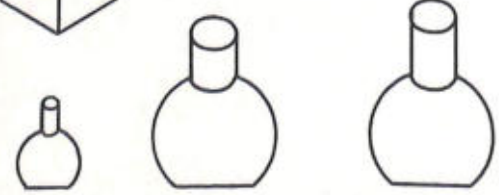
AREA







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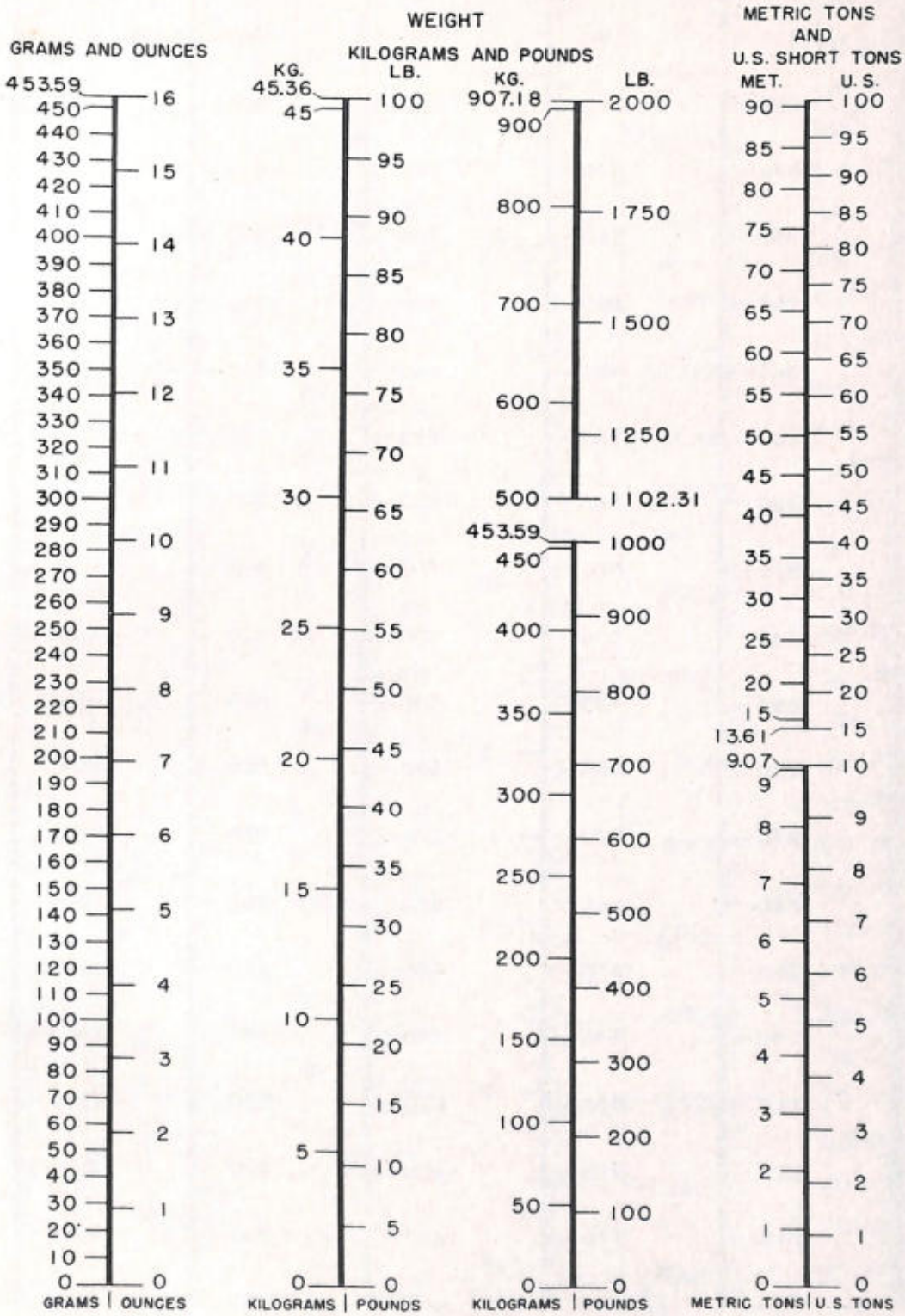


29.573 CC.
1 FL. OZ.

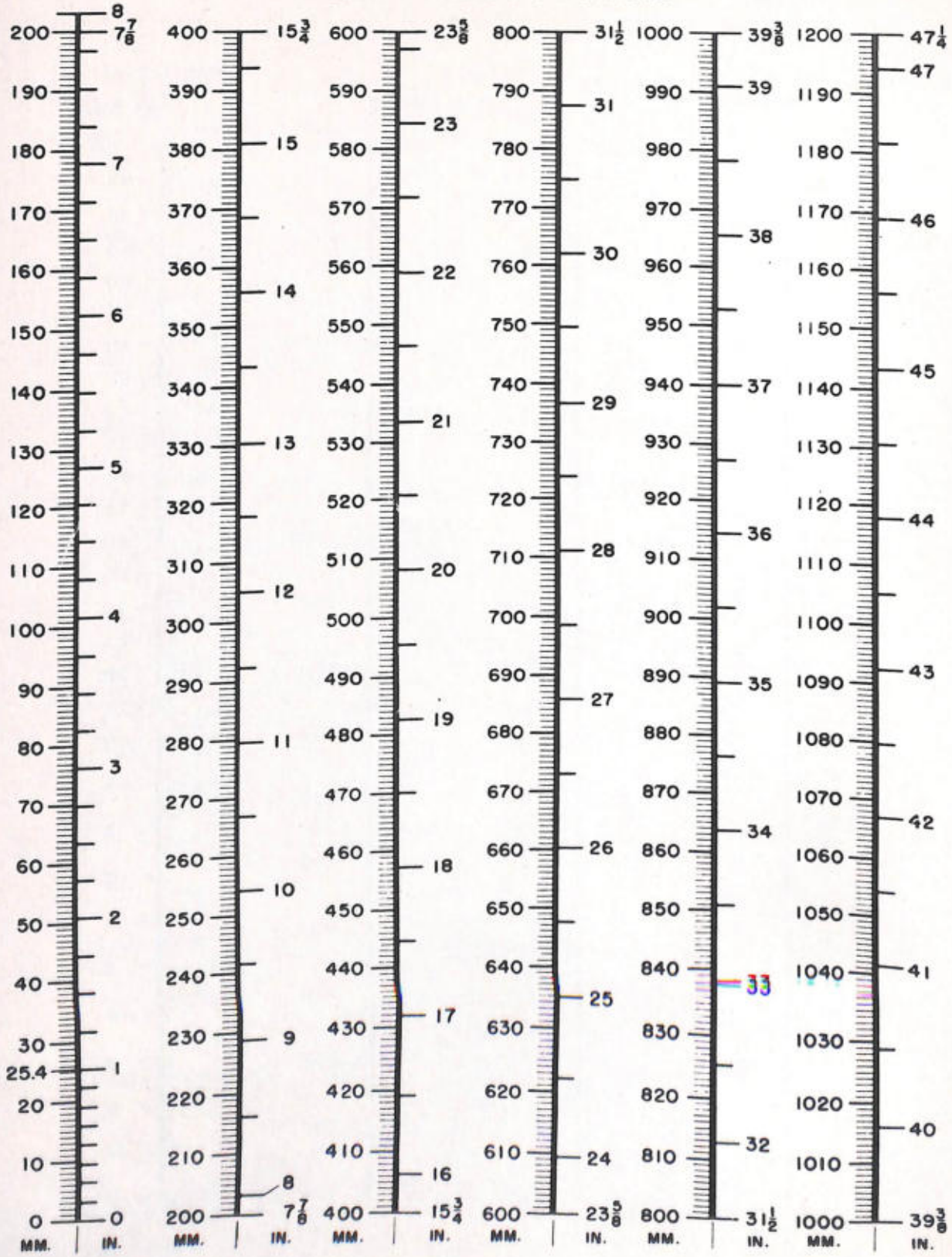
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1 QUART
32 FL. OZ.

1 LITER
1,000 CC.
1.057 QT.

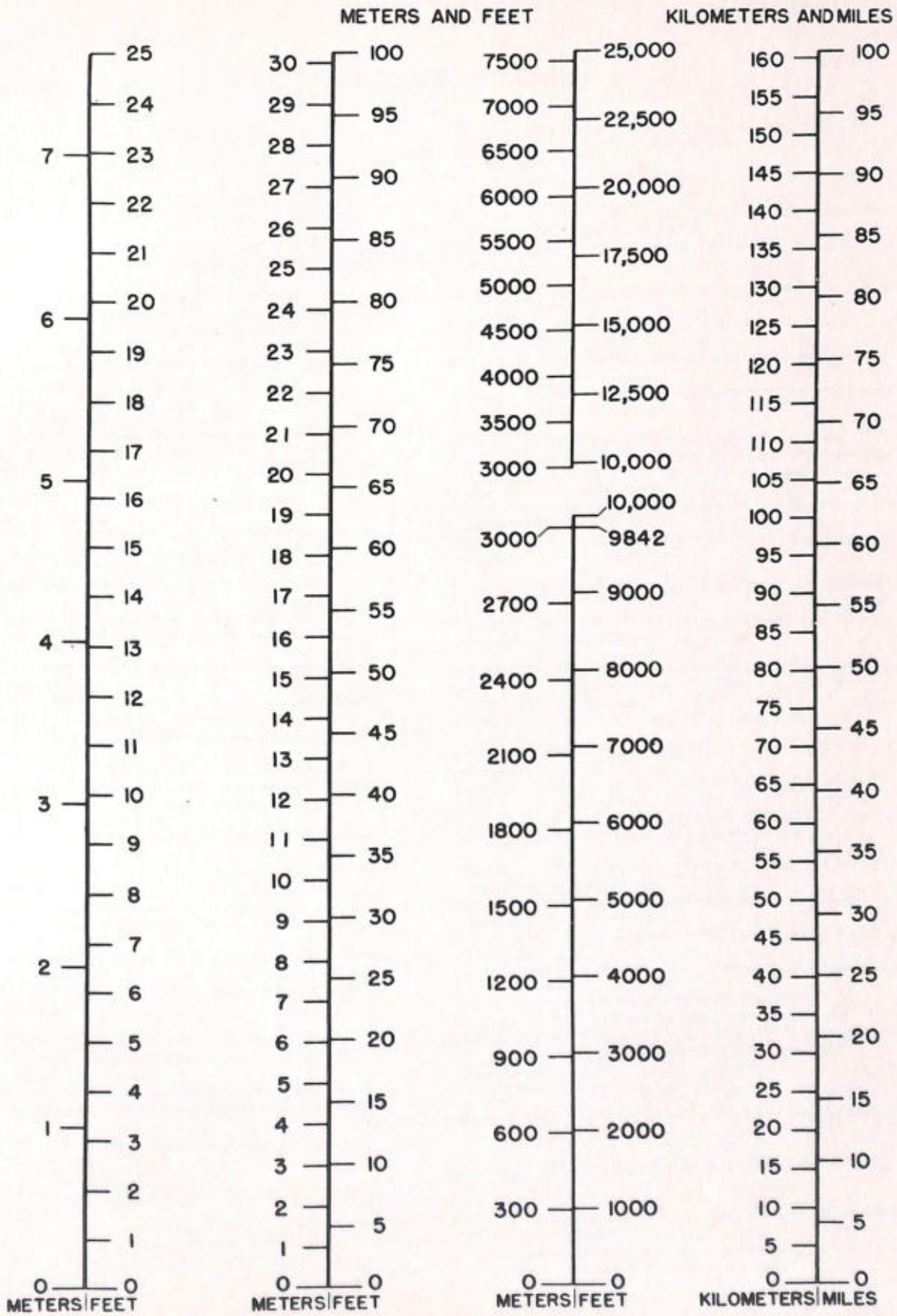
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GRAMS AND OUNCES
453.59
450
440
430
420
410
400
390
380
370
360
350
340
330
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310
300
290
280
270
260
250
240
230
220
210
200
190
180
170
160
150
140
130
120
110
100
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80
70
60
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40
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20
10
0
16
15
14
13
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11
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8
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4
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GRAMS
OUNCES
KILOGRAMS AND POUNDS
KG.
45.36
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35
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5
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LB.
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KILOGRAMS
POUNDS
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907.18
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KILOGRAMS
POUNDS
METRIC TONS AND U.S. SHORT TONS
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U.S.
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METRIC TONS
U.S TONS

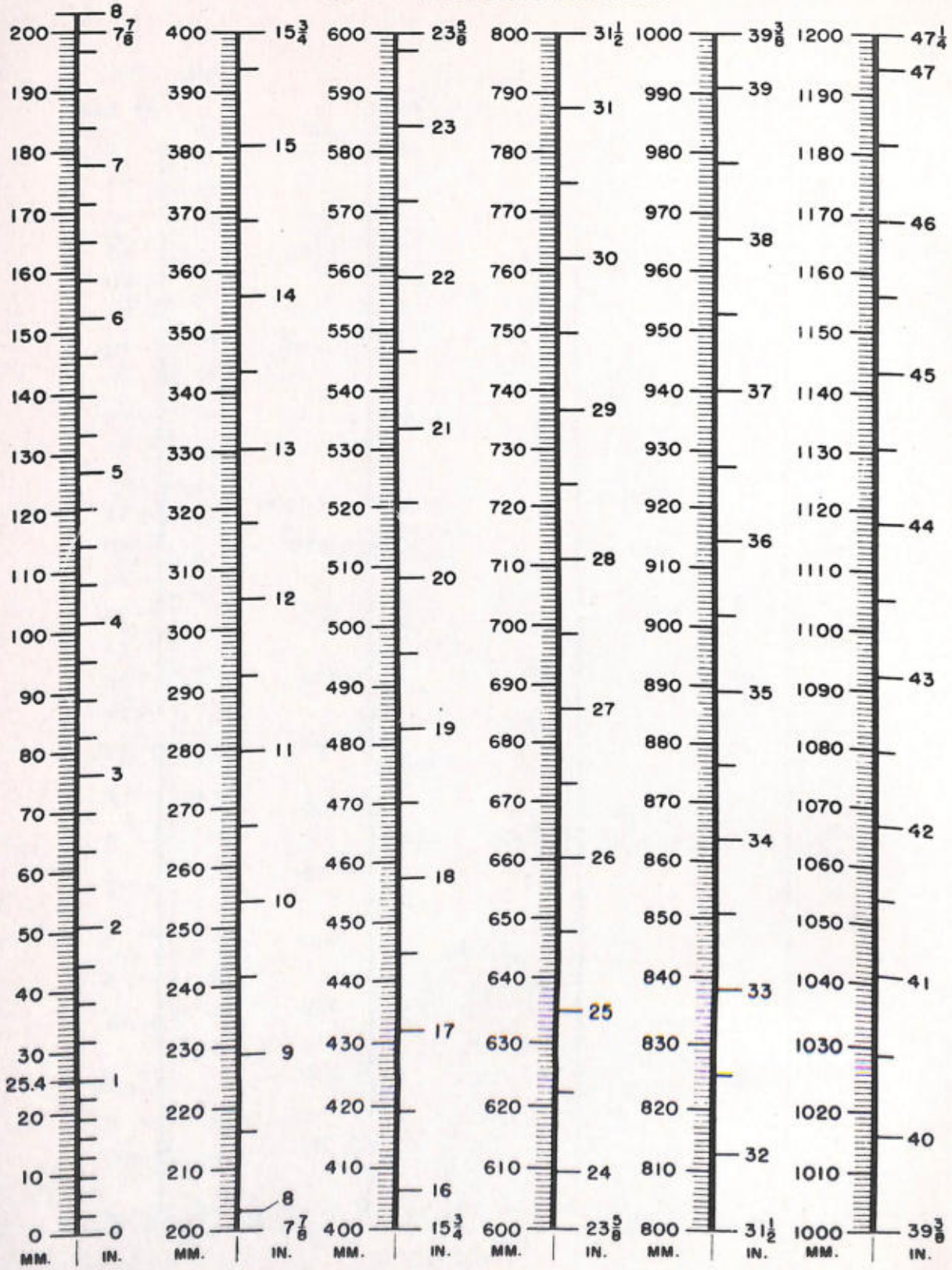
LENGTH: MILLIMETERS AND INCHES

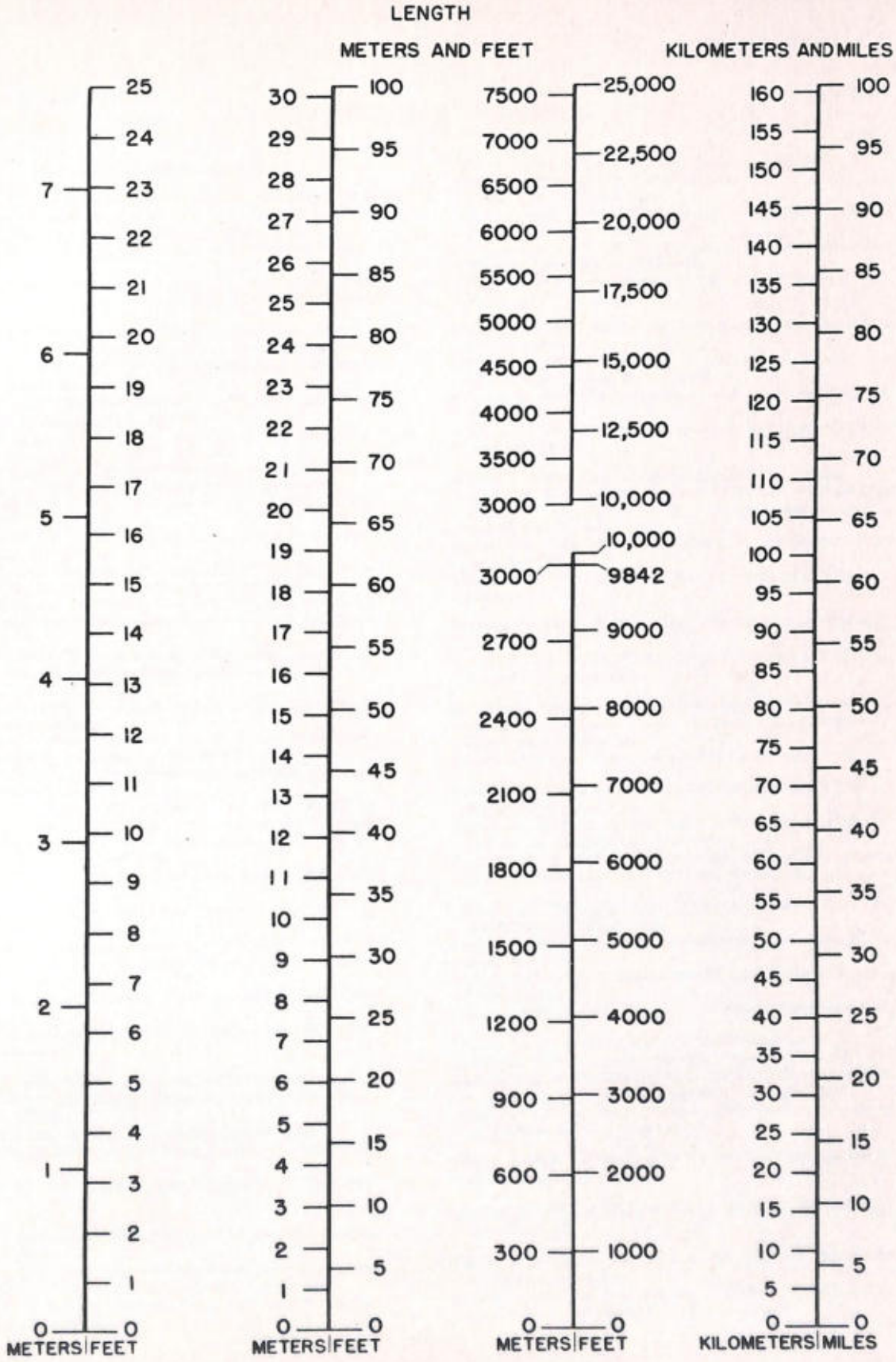


LENGTH


METERS AND FEET
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METERS
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0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
METERS
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0 1000 2000 3000 4000 5000 6000 7000 8000 9000 9842 10,000 12,500 15,000 17,500 20,000 22,500 25,000
METERS
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0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
KILOMETERS
MILES

LENGTH: MILLIMETERS AND INCHES




LENGTH
METERS AND FEET
KILOMETERS AND MILES
0 0
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25 25
METERS FEET
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40 40
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55 55
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85 85
90 90
95 95
100 100
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900 3000
1200 4000
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1800 6000
2100 7000
2400 8000
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5500 22,500
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7500 25,000
METERS FEET
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KILOMETERS MILES

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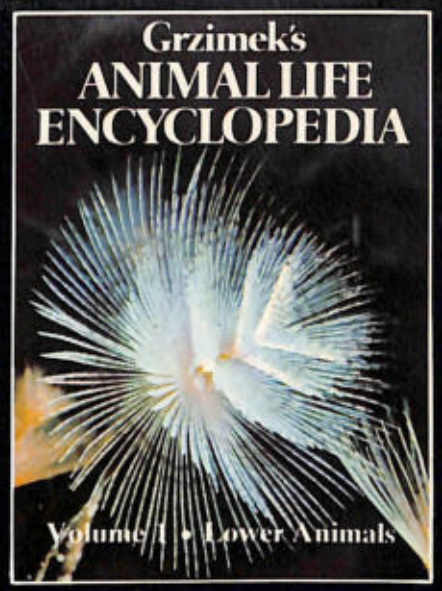
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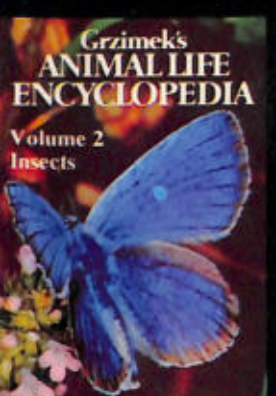
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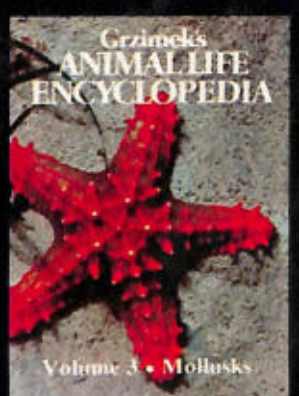
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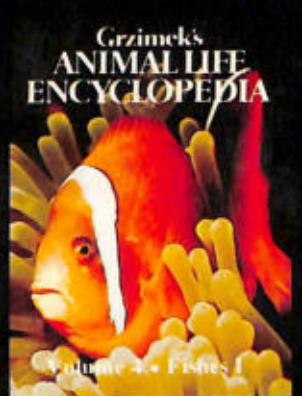
C, °C	Celsius, degrees centigrade
ff	following (pages)
L	total length
I.U.C.N.	Intern. Union for Conserv. of Nature and Natural Resources
BH	body height
HRL	head-rump length (from nose to base of tail or end of body)
TL	tail length
♂	male
♂♂	males
♀	female
♀♀	females
†	extinct
$\frac{2 \cdot 1 \cdot 3 \cdot 2}{2 \cdot 1 \cdot 3 \cdot 3}$	dental formula, explanation in Volume X
▻	following (opposite page) color plate
▻▻	color plate or double color plate on the page following the next
▻▻▻	third color plate or double color plate (etc.)
∅ ϕ	endangered species and subspecies
cc	cubic centimeters
mph	miles per hour
sp., spp.	species (singular, plural)

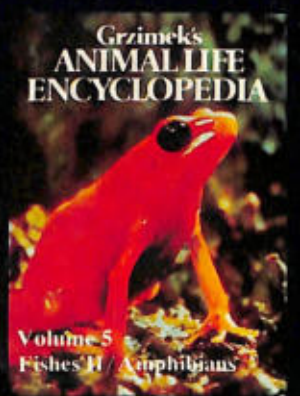
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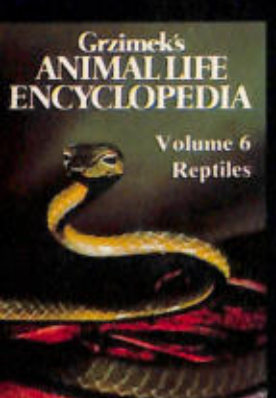


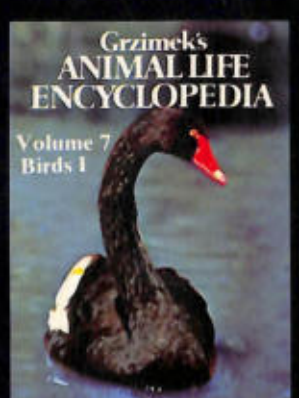


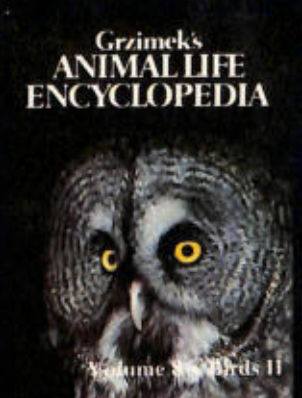


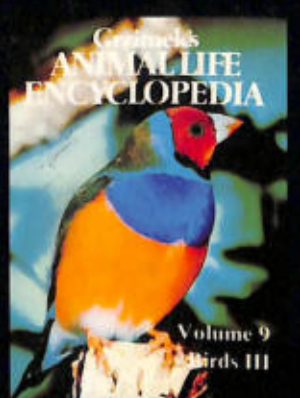


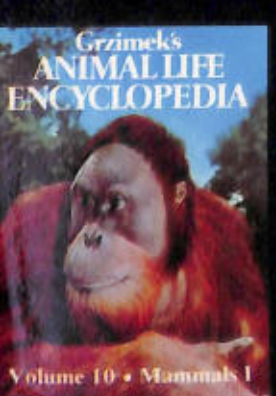


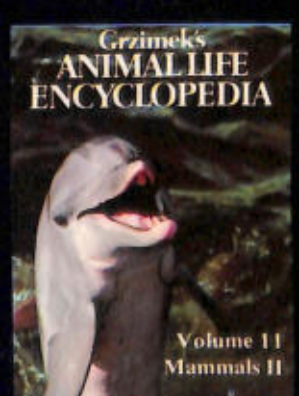


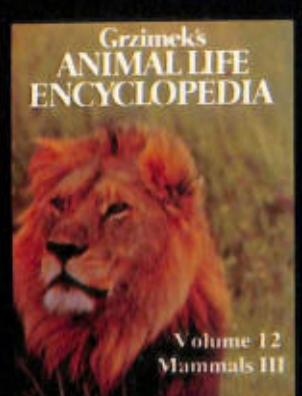


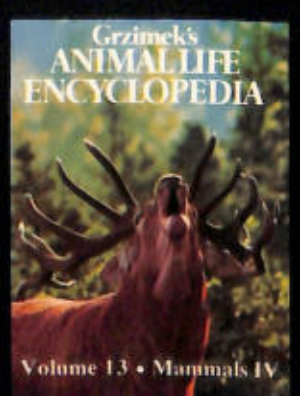


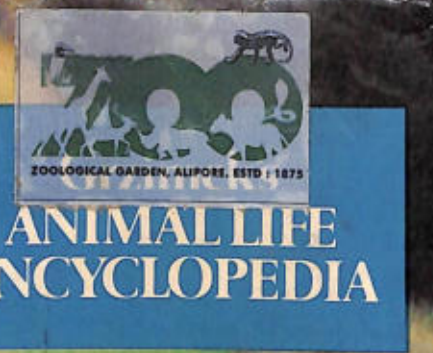












2

Insects

Proturans
Springtails
Two-pronged bristle tails
Bristle tails
Large-winged insects

