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No. 12

# SCIENTIFIC MEMOIRS

BY

OFFICERS OF THE MEDICAL AND SANITARY DEPARTMENTS

OF THE

GOVERNMENT OF INDIA.

---

ON THE MORPHOLOGY, TERATOLOGY AND DICLINISM OF THE FLOWERS  
OF CANNABIS.

BY

MAJOR D. PRAIN, M.B., I.M.S.

*(Indian Medical Service.)*

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BY THE SANITARY COMMISSIONER WITH THE GOVERNMENT  
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ON THE MORPHOLOGY, TERATOLOGY AND DICLINISM OF THE  
FLOWERS OF CANNABIS.

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SECTION I.—Introduction.

THE structure of the flower, fruit, and seed of *Cannabis* has long occupied the attention of botanists. The subject has received much patient organographic and histological study, and more than one theory has been advanced as to the correlation of parts in the flower of the two sexes and the nature of the organs that compose them. Most of the difficulties of structure and relationship have, as the result of these investigations, been satisfactorily cleared up, but as regards particularly, the morphological nature of the pistil and the ovule in *Cannabis*, the authors of the most recent, as it is the most exhaustive and accurate treatise on the subject,<sup>1</sup> have, after carefully discussing the theories hitherto advanced and comparing them with the actual facts of histology and organogeny, been compelled to reject them all and to declare that the question is baffling and insoluble.<sup>2</sup> All they are able to suggest is that in the female flower of *Cannabis* we possibly have to deal with an organ that is something apart, a *quid sui generis* that does not comply with the characters by which typical organs are conventionally distinguished.<sup>3</sup>

This indecisive result seems, since it was published, to have been accepted as the last word on the subject. It does not, however, appear to the writer that the time for abandoning the attempt to solve this problem has yet come. Though the position has proved unassailable by direct attack, and the use of histological and organogenic methods, even in hands so able as those of Payer and of Briosi and Tognini, has led to no definite conclusion, it is still permissible to enquire whether a systematic examination of such teratological phenomena as occur in *Cannabis* may not throw light on the problem or assist in its solution. This line of enquiry has not hitherto been definitely taken up; the present paper is the result of an attempt to utilise it.

The abnormalities that occur in the flowers and inflorescences of *Cannabis* are not, however, readily appreciable unless the normal arrangement be clearly

<sup>1</sup> Briosi and Tognini; *Intorno all' anatomia della Canapa*; Milan, (i) 1894; (ii) 1896.

<sup>2</sup> E se a mo' di conclusione dovessimo dir chiaro il pensier nostro intorno a questa disquisizione sulla natura assile o fogliare dell' ovulo, come intorno alla precedente della costituzione dell' ovario da uno o da due carpelli, dovremmo confessare che a noi sembrano questioni in parte insolubili e anche frustranee.

<sup>3</sup> L'organo è quello che si mostra, cioè un *quid sui generis*, un ente intermedio, nè fucto nè foglia, al quale non si adattano le nostre distinzioni artificiali, d'organi tipi, create della mente umana, ma non da natura.

understood. A brief sketch is therefore here given of the usual configuration and disposition of parts; this is followed by a *resumé* of the abnormal conditions hitherto observed or reported; the facts having been stated, their bearing on the problems under discussion is then considered: the nature of the ovary and origin of the ovule are dealt with first; the character and manifestation of the diclinism are then examined.

Since 1893, when the writer was deputed by Government to enquire into the cultivation and use of Gánjá in Bengal, the subject of *Cannabis* has interested him, and has occupied his attention at intervals. It is difficult to say in what direction the interest is greatest; whether it centres in the form of the plant that held, from the earliest times, in the estimation of the northern peoples outside the pale of the Egyptian, Assyrian and Mediterranean civilisations, the place that, as a fibre-plant, flax held among the races which these civilisations influenced; or whether it resides in the form of the plant which produces the potent narcotic that, though unknown to the Arabs till they conquered Persia, has since then spread to most lands and races influenced by the Arab faith. In either case the study of *Cannabis* offers a series of problems of agricultural, commercial, chemical and physiological interest, and leads into many historical, ethnological and linguistic bye-paths. The obscurity of its original habitat; the strange effects and peculiar character of its narcotic resin; the mystery that surrounds the problem of its sexuality; the dubiety that exists as regards its floral structure, all conspire to sustain the interest that has been taken by so many writers in the subject of *Cannabis*.

In the section dealing with the normal structure of the flowers of *Cannabis*, subordinate passages have been added which attempt to trace the gradual evolution of our existing knowledge. This has more than a direct interest; it illustrates how features that, if not obvious, are nevertheless readily apparent when looked for, may long escape the notice of the closest observers; it emphasises the value of direct observation as compared with the uncritical adoption of the observations of previous workers; it inspires a hope that one's own imperfect observations may yet prove stepping stones to those who follow.

A considerable number of the teratological facts here recorded were noted in 1893 while the writer was engaged in the enquiry into Gánjá already alluded to. At the request of friends the drawings were exhibited and remarked on before the Linnean Society of London on November 15th, 1894<sup>1</sup>; the invitation to publish a paper was declined because the deductions that seemed to follow from the conditions observed, which are those contained in this paper, did not then appear altogether conclusive; and because it was hoped that in the already quoted work by Briosi and Tognini, the appearance of which was at the time expected, the same ground might be covered. That valuable treatise, however, deals only incidentally with teratological considerations and does not systematically employ them in the discussion of the particular problems which it leaves unsolved. The writer has hoped, since Briosi and Tognini's *Intorno all' anatomia della Canapa* appeared, that some European botanist with more leisure than is at his disposal, would deal exhaustively with the teratology of hemp. He has himself, during the interval, revisited the area to which the cultivation of *Cannabis* is in Bengal restricted, and has grown plants experimentally in the Royal Botanic Garden at Shibpur. In this way he has been able to test and confirm the majority of his original observations of 1893 and in certain directions to supplement them. Now, finding that no one has been led to take up the subject independently, he offers here the information at his disposal.

<sup>1</sup> *Proceedings of the Linnean Society of London*: April 1896, p. 3.

## SECTION II.—Normal Structure of the Flowers of *Cannabis*.

*Male Flower*.—In *Cannabis* the flowers are normally strictly dioecious so that those of the two sexes must be separately described. The male flower (PLATE 1, figs. 4-6), consists of a perianth of five free, regularly quincuncially imbricated, somewhat unequal, oblong-lanceolate, pale-green, herbaceous segments. Opposite each segment is a shortly stalked stamen; the filament is slender and rather shorter than the pendulous anther; the anther is oblong, slightly narrowed upward, 2-celled and, when mature, opens longitudinally (PLATE 1, figs. 5-10). There is no trace, in a male flower of the normal type, where perianth-segments and stamens are each whorled, of a rudimentary pistil within the staminal circle.

Mention has been made of hermaphrodite flowers in *Cannabis* by Autenrieth,<sup>1</sup> Gasparrini,<sup>2</sup> and Masters.<sup>3</sup> Masters gives no details and does not state whether the abnormal flowers occurred on plants of male or of female type. Gasparrini likewise does not say clearly whether his hermaphrodite flowers were on plants of male or of female type; in any case his examples indicate, as will be shown further on, a monœcious rather than a hermaphrodite condition. Autenrieth's interesting observations were made on male plants which he had pruned; he found the new shoots giving, instead of male flowers, flowers in which the sexes were mixed. Here again, if the writer's interpretation of the facts be justified, the condition is not a hermaphrodite but a monœcious one, the existence of which in *Cannabis* was first noted by Nees.<sup>4</sup>

The question has received the especial attention of Briosi and Tognini<sup>5</sup> and there is no indication, from the histological side, that a carpellary whorl within the staminal whorl has been suppressed. The co-existence of stamens and carpels, as shown in the drawings both of Autenrieth and of Gasparrini, is either *in the same spiral*, or is collateral, that is to say, *in the same whorl*.

*Male Inflorescence*.—The individual male florets are short-stalked and drooping, and are aggregated in small paniculate cymes shorter than their leaves, mostly on special floral branches (PLATE 1, figs. 1 and 2), though throughout the greater part of the stem we find, at the base of these floral branches, in the axils of the free stipules of their subtending leaves, a pair of these paniculate cymes. These basal cymes, as a rule, are larger than any of those that follow along the floral branch, and one of the two usually considerably exceeds the other in size. The cymes along the floral branch also conform to this arrangement; they are in pairs, almost always unequal, in the axils of the stipules belonging to the more or less reduced leaves that mark its nodes. But none of these leaves or bracts, subsequent to the main-leaf in whose axil the floral branch arises, subtend leafy branches; the place of a branch has been found by Briosi and Tognini to be

<sup>1</sup> *De discrimine sexuali*: Tubingen, 1821; p. 6, t. 2.

<sup>2</sup> *Ricerche sulla embriogenia della Canapa*: Naples, 1862; p. 23, t. 3.

<sup>3</sup> *Vegetable Teratology*: London, 1869, p. 197.

<sup>4</sup> *Beschreibung officineller Pflanzen*: Düsseldorf, 1829; disp. 6.

<sup>5</sup> *Intorno all' anatomia della Canapa*: Milan, 1894; i. p. 84.

taken by a third panicle usually smaller than the lateral ones, often reduced to a simple cyme or a single flower; in Indian plants the writer has only once or twice met with a single flower, in most cases the axil is altogether empty (PLATE 1, fig. 1). Moreover, it is, in India, very usual to find that the *lowest* pairs of stipular panicles, that is to say, the pairs of panicles which should occur at the bases of the floral branches *lowest down* on the stem, are either entirely absent or are replaced by pairs of solitary female flowers (PLATE 1, fig. 2). Though simulating a panicle, the male inflorescence is not in reality a spiral of racemes but a spiral succession of cyme-systems in which the axis is defined and gives out two branches, the lower smaller than the higher, which latter repeats the process (PLATE 1, fig. 3).

The presence of a female flower, instead of a panicle of cymes, in the axil of a stipule at the base of a stem-branch in a male plant was first noticed by Autenrieth<sup>1</sup> though the flower referred to by him happened not to be a normal female but a pseudo-hermaphrodite one, and the fact that it replaced a whole panicle, not merely a single flower, does not seem to have impressed him.

In India the phenomenon is of very common occurrence; as a rule the leaves and branches low down on the stem are opposite or sub-opposite and, as a rule, too, the lowest branches are decidedly extra-axillary, a character in which the solitary female flowers which are basal to the lowest male floral branches follow them, though these indicate their relationship to the stipules as definitely as the upraised branches do their relationship to the leaves; these female flowers are very often abortive and are sometimes only represented by a partially developed enveloping bract.

A remarkable but well-known feature of hemp-cultivation, as practised in Bengal, is the care and success with which all male plants are eliminated, long before they flower. The object is to prevent undue fertilization of the female plants, which yield the Gánjá resin that it is the cultivator's object to obtain. The process of weeding out the males, which is conducted by a special expert—the *parukdar* or *poddar*—has been described by Kerr.<sup>2</sup> When the writer first visited the Gánjá mahals in 1893 it was impossible to test the accuracy of Kerr's statements, the season being so far advanced that the elimination of males had already been effected; it was, therefore, impossible to understand Kerr's allusion to certain "filaments or stipules," mentioned by him as the *poddar's* guides. The hemp districts were, therefore, re-visited, a few years later, at the proper season, in order to ascertain precisely what was meant. It was interesting to find then that the "filaments or stipules" in question were the often abortive, solitary female flowers that so frequently, in the Indian male hemp plant, take the place that theoretically should be occupied by the lowest pairs of paniculate male inflorescences.

The nature of the male inflorescence has been studied by Wylder,<sup>3</sup> Eichler,<sup>4</sup> and Briosi and Tognini.<sup>5</sup> The accounts that these authors give differ less in reality than would

<sup>1</sup> *De discrimine sexuali*, p. 7, t. 2, fig. 18.

<sup>2</sup> *Report on the cultivation of and trade in Gánjá in Bengal*: Calcutta 1877, p. 18.—The process, it need hardly be remarked, is empirical; the cultivators reverse the sexes and term the rejected plants, as being the less valuable kind, *females*; the nobler and more useful ones, which they retain, are, for them, the *males*. They know that pollen-bearing plants do in some way affect the value of the Gánjá crop and therefore remove them. But of the precise significance of what is done, neither the cultivators nor the *poddars* are aware.

<sup>3</sup> *Flora* (1844), p. 735, t. 3, f. 1, and *Flora* (1851), p. 434.

<sup>4</sup> *Bluthen-diagramme*: Berlin, 1878; ii. p. 60.

<sup>5</sup> *Intorno all' anatomia della Canapa*, i. 93.

at first appear; of the three accounts that by the Italian authors accords best with the natural conditions as seen in India. In any case it is certain, (1) that we have to deal with a continuous succession of definitions of the axis; (2) that of the two lateral branches associated with each such definition only one continues the process; also (3) that, except at the commencement and at the close, the definition and the concomitant branching do not occur in the same plane or at the same node. It is this last circumstance that is the confusing factor, and that has been the cause of whatever dubiety has existed.

*Female Inflorescence.*—The female inflorescence is subtended like the male by a leaf with two free basal stipules (PLATE 2, fig. 1). The axil of each stipule here, however, in place of containing a complex cymose inflorescence, contains a single exstipulate boat-shaped involving flower-bract; within each bract lies a solitary female flower (PLATE 2, figs. 4-9). The inner margins of the bracts overlap the outer (PLATE 2, figs. 5, 6) and the free margins look towards each other. A single nerve enters the base of each bract, but almost at once gives off two branches, rather stronger than the central continuation of the nerve (PLATE 2, fig. 8; PLATE 4, fig. 6); these in turn each emit a sub-horizontal zig-zag branch from which are given off 3 or 4 nerves more or less parallel to the primary nerves. In the axil of the stipulate leaf and between the two basal flowers, is situated an apparently indefinite spiral spicate series of pairs of female flowers quite like the basal pair, though not infrequently, especially near the ends of these branchlets, the leaf (or bract) with its stipules is abortive, and instead of a pair of flowers only one involving bract with its contained flower occurs; occasionally too, at the very tip, the flower may be present without any involving bract. Under ordinary circumstances these pseudo-spikes contain from 4-7 such pairs of female flowers, but often towards the apex of the stem and of its main-branches only the basal pairs of female flowers are to be found, the small spikelets being suppressed; on the other hand, towards the base of the stem, the spikelets are often replaced by leafy branchlets. The arrangement of the systems is shown schematically in PLATE 2, figs. 2, 3; the arrangement of a single basal pair is shown in PLATE 2, fig. 6.

The nature of the female inflorescence has been studied by Wylder,<sup>1</sup> by B. Clarke,<sup>2</sup> by Eichler<sup>3</sup> and by Briosi and Tognini.<sup>4</sup> The two former do not give very clear accounts, the two latter do.

The involving bract, the perianth of many of the older botanists, varies considerably in shape. In uncultivated Indian plants and in cultivated European ones it is usually acute or even acuminate; in cultivated Indian plants it is generally truncate at the apex (PLATE 2, figs. 4, 5; 7, 8; 14). Nees,<sup>5</sup> and in this he is followed by Reichenbach,<sup>6</sup> shows it as

<sup>1</sup> *Flora* (1844), p. 739, t. 3, f. 2; *Flora* (1851), p. 434; and *Flora* (1865), p. 318.

<sup>2</sup> *Ann. & Mag. Nat. Hist.* Ser. 2, xi. (1853), p. 459.

<sup>3</sup> *Bluthen-diagramme*, ii. 60.

<sup>4</sup> *Intorno all' anatomia della Canapa*, i. 93.

<sup>5</sup> *Gen. Plant. Flor. Germ. Monochlam.*: Berlin, 1835; t. 30.

<sup>6</sup> *lc. Flor. Germ.*: Leipzig, 1850; t. 655.

5-nerved; it is not impossible that in this there was a subjective tendency to consider it the equivalent of the 5 free sepals of the male flower; the disposition of the main-nerves, however, is against the view and, taken by itself, proves either too much or too little; there are at least 11 nerves to be made out altogether, but if merely the *strong* nerves are considered there are only three, whereof the two lateral are distinctly stronger than the central one—a feature much more marked in certain abnormal flowers (PLATE 4, fig. 6) than in normal ones. It may have been this feature that induced Baillon<sup>1</sup> to consider the involving bract, which he terms a bracteole, as equivalent to two connate stipules. This theory, however, is effectively refuted, as is that of the earlier writers, by the fact, pointed out by Briosi and Tognini,<sup>2</sup> that the whole of the nerves of the involving bract are branches of a single vein which only breaks up to innerve the organ *after* it has entered it. The first author to consider this organ a bract (*bracteola urceolata*), and not a perianth, was Schleiden,<sup>3</sup> though it must have been on theoretical grounds that he based his conclusion, not on his having discovered the existence of the true perianth.<sup>4</sup>

The orientation of these bracts has been somewhat differently interpreted. At times a pair are shown with their free margins looking towards the leafy axis in parallel planes—tangential to axis and at right angles to the plane of the leaf to which they belong; at times they are shown with their free margins looking towards each other—tangential to axis and parallel with the plane of the leaf to which they belong. The changes in position caused by the peculiar development of the female flower do ultimately lead to the second condition being simulated. The primary orientation has, however, as might be expected, reference not to the leaf to which the involving bract belongs, but to its stipules; it is in the axils of the stipules that these involving bracts lie, so that the axes of their centres and free margins are in planes at right angles to the planes of the stipules. The organic centres of a stipule, of its contained bract, and of the leafy axis are very nearly in the same straight line (PLATE 2, fig. 6; PLATE 3, fig. 1), and therefore in a plane radial to the leafy axis.

*Female Flower.*—The female flower proper, within the involving bract, is composed of a thinly membranous, gamophyllous, hyaline perianth with an entire and very nearly horizontal margin, closely embracing for rather more than half its height, but quite free from, the ovoid ovary (PLATE 2, figs. 6, 9-12). There is never any normal andrœcium within the perianth and between it and the gynœcium. The gynœcium itself consists of a unilocular ovary (PLATE 2, figs. 6; 9-12), crowned by two filiform deciduous styles, of which the posterior and internal is always slightly larger than the other (PLATE 2, figs. 4-7; 9), with hirsute (subplumose) stigmas along their opposing faces and, towards the apex, round their periphery (PLATE 2, fig. 13); they are usually quite free but sometimes become slightly united below. Within the ovary there is a solitary ovule, pendulous from the apex of the loculus, attached by a short funiculus just behind the point of attachment of the posterior internal style; the testa is olive-green, except for an orange-coloured patch round the funicle. The ovule is uncinatè, curved on

<sup>1</sup> *Hist. des Plantes*: Paris, 1875; 6, 159.

<sup>2</sup> *Intorno all' anatomia della Canapa*, i. 37, t. 7, figs. 5, 6.

<sup>3</sup> *Principles of Scientific Botany*; Eng. transl. by E. Lankester: London, 1849; p. 332.

<sup>4</sup> In a valuable manuscript collection of drawings by Schleiden, preserved in the British (Natural History) Museum, at vol. v., p. 45, *Cannabis* is dealt with. In these drawings there is no indication that Schleiden had detected the true perianth.

itself so that the micropyle comes just beneath the style-bases and close up to the hilum. (PLATE 2, figs. 11, 12; 17-21). The embryo, curved in agreement with the shape of the ovule, assumes a pseudo-incumbent position; the radicle, pointing to the micropyle, occupies the anterior (external) portion of the chamber; the cotyledons, forming the bulk of the ovule, occupy the posterior (internal) part. It may therefore be termed obcampylotropous.

To the earlier writers, who recognised the involving bract as the perianth, the true perianth was unknown; even some who had formed a true conception of the nature of the involving bract were unacquainted with the perianth, which is not shown in the figures given by Hayne<sup>1</sup> or Autenrieth,<sup>2</sup> or in the already quoted figures by Nees and Reichenbach. The first discovery of the perianth appears to have been made by Payer<sup>3</sup> though it is evident that it was independently detected about the same time by B. Clarke.<sup>4</sup> Since then it has always appeared in figures and been mentioned in descriptions of *Cannabis*. Schnitzlein<sup>5</sup> says that in certain cases it is not to be detected; Bentham and Hooker<sup>6</sup> do the same. The writer must, however, say that it is always to be found, if looked for, in a normal flower; the only instances in which he has failed to detect it have been in the cases of solitary female flowers, towards the apices of normal female spikelets, where the involving bract was also absent; and at the apices of abnormal female spikelets in which the sexes were mixed.

According to Payer<sup>3</sup> the development of the perianth follows that of the involving bract and precedes that of the ovary; he also has it that the perianth consists of two leaflets which soon became connate; a posterior which appears before the other which is anterior<sup>7</sup> and next the involving bract. B. Clarke<sup>4</sup> also makes it out to be higher behind than in front and Schnitzlein<sup>5</sup> not only makes it higher behind but deeply cleft in front.<sup>8</sup> The development of the perianth, however, according to Briosi and Tognini,<sup>9</sup> begins after the development of the ovary has commenced; and, if there be at first a more rapid development behind than in front, it is certain that in Indian plants the margin is ultimately almost perfectly horizontal.

B. Clarke<sup>10</sup> speaks of the perianth as adherent to the ovary except as an abnormality and Masters<sup>11</sup> has consequently included those cases where it is free among his instances of solution of the calyx. What, however, really happens is that, as a rule, the perianth is closely applied to the ripe fruit and fits so tightly as to form practically an outer coat; it is so described by Briosi and Tognini<sup>12</sup> but is, as they explain, applied to, not organically united with the nutlet. But this is not always the case; sometimes the perianth slips

<sup>1</sup> *Arzneigewächse*: Berlin, 1822; vii t. 7.

<sup>2</sup> *De discrimine sexuali*, t. 1, t. 2.

<sup>3</sup> *Organogénie*: Paris, 1857; p. 275, t. 68.

<sup>4</sup> *Ann. & Mag. Nat. Hist.* Ser. 3, i. (1858) t. 6, f. 8.

<sup>5</sup> *Iconographia*: Bonn, 1870; ii, t. 95.

<sup>6</sup> *Genera Plantarum*: London, 1880; iii. 357.

<sup>7</sup> These positions are, according to his view, opposite the position of the two parts of the ovary; in the carpellary whorl, according to Payer, the anterior appears before the posterior.

<sup>8</sup> This would make the perianth theoretically equivalent to one axial appendage opposite to the involving bract. The condition described by Schnitzlein is that characteristic of the closely allied *Humulus*, but the writer has never found it confirmed in Indian *Cannabis* flowers.

<sup>9</sup> *Intorno all' anatomia della Canapa*, i. 50.

<sup>10</sup> *Ann. & Mag. Nat. Hist.* Ser. 3, i. (1858), p. 102.

<sup>11</sup> *Vegetable Teratology*, 81, 82.

<sup>12</sup> *Intorno all' anatomia della Canapa*, i. 66, tt. 10, 11.

down as the fruit develops and is to be observed as a shrivelled collarette at its base; at other times, though this is very unusual, it remains wider than the nutlet and does not slip down. This last condition probably corresponds to the instance alluded to as abnormal by B. Clarke and Masters. But, in the case of the flower, the perianth is normally perfectly free from the ovary.

There are normally no traces visible of fibro-vascular bundles in the perianth. In certain abnormal conditions, however, alluded to by B. Clarke,<sup>1</sup> and in others to be described below, a fibro-vascular system is developed.

Stamens may occur in abnormal female flowers but they then always either replace, or are collateral with, a carpel; so far they have not been found as a complete or even a partial whorl outside the pistil, though Briosi and Tognini record instances in which they have observed, within the perianth, outgrowths between it and the pistil that in the text they hesitatingly, and in the explanation of their figures they more definitely suggest may be staminodes. They record, however, the occurrence of similar outgrowths outside the perianth and between it and the involving bract.<sup>2</sup> This fact leads to a suspicion that, whatever those extra-perigonal excrescences may be, they can hardly be accepted as rudimentary stamens, and to a further suspicion that the intra-perigonal excrescences are really of the same character as the extra-perigonal ones. If the subsequent evidence from teratological phenomena be accepted, the situation of these intra-perigonal protuberances should be the best proof of their non-staminal character. Even if they had only occurred intra-perigonally, the theory that they represent the casual development of a partial disk is rather more tenable than the theory that they represent stamens.

Hayne figures the stigmas as clavate, but this condition is not met with normally. Autenrieth figures the styles as they normally appear, so does Nees; Reichenbach copies both Hayne and Nees. The styles fall off after fertilisation.

The orientation of the styles is shown in PLATE 2, fig. 6. The two are in the same plane; this plane, which ought perhaps organically to be at right angles to the plane of the stipule, the involving bract, and the ovule (PLATE 3, figs. 1-7), is, owing to the intimate union of the ovule with the middle line of the posterior (internal) ovarian wall, distorted so that the ovule comes to be in the same plane with the two styles, and deflected so that the planes of the two flowers intersect in the floral axis or thereabouts. As development proceeds, further deflection takes place and the final position appears to be in the same plane as the involving bract, between the free margins of which the posterior style at length protrudes and the posterior aspect of the fruit ultimately projects (PLATE 2, fig. 14). But whatever position the plane in which the styles lie may assume, that plane is the same as the plane occupied by the body of the ovule and its radicle, and whether the planes of the two flowers intersect in the floral axis, or be coincident and tangential to the leafy axis, or even, finally become radial to the leafy axis, the body of the ovule is towards the posterior (inner) aspect and just under the posterior (larger) style. Schnitzlein,<sup>3</sup> however, shows the plane of the styles at right angles to the plane of the ovule, making the former coincident with the plane of the stipule and the involving bract. Besides this deviation from actual conditions, Schnitzlein further shows the radicle as occupying the inner, the cotyledons the outer part of the ovarian chamber. This interpretation, which is quite unreal, has been copied by Cesati, Passerini and Gibelli.<sup>4</sup>

<sup>1</sup> *Ann. & Mag. Nat. Hist.* Ser. 3, i. 1885, p. 102; *New Arrangem. Phan. Pl.*, Introd. p. 4.

<sup>2</sup> *Intorno all' anatomia della Canapa*, i. 53; tt. 5, 16.

<sup>3</sup> *Iconographia* ii., t. 95.

<sup>4</sup> *Compendio*: Milan, 1874; p. 229, t. 33, fig. 1.

The ovule commences as a papilla on the top of the axis, not however at the organic apex but immediately behind this (PLATE 3, figs. 8-12). The apex of the posterior wall of the ovarian chamber, becoming intimately associated with the ovule, carries it upwards as it grows till at length the ovule reaches the top of the ovary, where it already is before the ovarian chamber is closed (PLATE 3, figs. 13-16). According to Payer<sup>1</sup> the formation of the ovular coverings, the primine and secundine, is coincident with its passage upwards, but according to Briosi and Tognini<sup>2</sup> the ovule has already assumed the pendulous position before either the primine or the secundine are developed (PLATE 3, fig. 17). The upward progress of the ovule being due to intercalary growth there is no obvious trace of a funicle adnate to the ovary, though there is a thickening which corresponds to the path of its progression along the middle line of the inner (posterior) carpellary wall. This thickening was first, though not quite accurately, shown by B. Clarke,<sup>3</sup> was again shown by Berg and Schmidt,<sup>4</sup> and more accurately still by Schnitzlein, who is copied by Cesati, Passerini and Gibelli (PLATE 2, fig. 16).

The shape of the ovule is fairly accurately shown by Autenrieth; according to Nees, Mirbel was the first author to describe it, owing to its uncinat shape, as campylotropous. Payer speaks of it as anatropous, as does Baillon<sup>5</sup> with reference to its development; further on in the same work, however, with reference to its shape, Baillon terms it campylotropous. But it is hardly correct to speak of the development as anatropous, seeing that the change of direction of the hilum is not due to any growth of the funicle inverting the seed, but is owing to the place of its insertion being carried bodily upwards by the growth of the carpellary wall; there is therefore some reason for the contention of Duchartre<sup>6</sup> and others that it is orthotropous; the uncinat shape, however, precludes the use of this term. But though the shape be uncinat it is not quite correct to speak of it as a campylotropous ovule, since in this case the micropyle does not alter its original direction by being carried down towards the hilum; it is the hilum that changes its original direction by being carried up towards the micropyle; hence the proposed use of the term obcampylotropous.

The embryo-sac is horse-shoe-shaped and is at first of fairly uniform diameter, but subsequently it becomes altered by the expansion of the cotyledons in the direction of the hilum. The conditions have been well shown by Gasparrini<sup>7</sup>; by Schnitzlein,<sup>8</sup> who is copied by Cesati<sup>9</sup>; and by Briosi and Tognini.<sup>10</sup> Schleiden, however, as his manuscript drawings show (PLATE 3, figs. 21-23; \*taken by permission from the British (Natural History) Museum Schleiden collection), had anticipated these authors. The embryo-sac is at first partially filled with endosperm, which surrounds the embryo; this, however, does not ultimately form albumen but is completely absorbed during the development of the embryo. This endosperm was first detected by Gasparrini<sup>7</sup>; its progress and fate have been explained by Briosi and Tognini.<sup>10</sup>

According to Payer the development of the various parts of the female flower is acropetal; this, however, according to Briosi and Tognini<sup>11</sup> is not the case: the organic apex

<sup>1</sup> *Organgénie*, p. 275, t. 60 (1857).

<sup>2</sup> *Intorno all' anatomia della Canapa*, i. t. 6, fig. 10.

<sup>3</sup> *Ann. & Mag. Nat. Hist. Ser. 2.* xi. 1853 pl. 15, fig. 24.

<sup>4</sup> *Offizinellen Gewächse*, f. 19 b.

<sup>5</sup> *Hist. des Plantes*, vi. p. 160 (anatropous); p. 215 (campylotropous).

<sup>6</sup> *Elementes de Botanique*, Paris, 1867.

<sup>7</sup> *Ricerche sulla embriogenia della Canapa*, tt. 1-3.

<sup>8</sup> *Iconographie*, ii. t. 95.

*Compendio*, t. 33.

<sup>10</sup> *Intorno all' anatomia della Canapa*, i. t. 14.

<sup>11</sup> *Intorno all' anatomia della Canapa*, i. p. 50.

of the axis of a flower-bud is at first quite indistinguishable from the organic apex of a leaf-bud. Soon, however, the apex in a flower-bud gives rise to the ovule; this (PLATE 3, fig. 8) is followed shortly by the development of the involving bract (PLATE 3, fig. 9); then by the appearance of the ovarian parietes (PLATE 3, fig. 10); last of all by the appearance of the perianth (PLATE 3, figs. 11-14) between the involving bract and the ovary.

*The Fruit.*—The ripe fruit is a true nut with a hard crustaceous shell, enclosed below in a leathery husk (PLATE 2, fig. 14) and completely filled by a fleshy kernel. Seen from the side it has an oval outline with a subacute apex, the point whence the styles have fallen; seen from below it is rounded towards the inner (posterior) side, slightly ridged or crested towards the outer (anterior) side (PLATE 2, fig. 15), the ridge corresponding to the position within of the radicle. The base shows a circular scar marking the point of attachment to the stem. In colour the nut is greenish grey, somewhat mottled.

The nut is what is popularly known as the "seed" of hemp, used (for the sake, however, of the contained seed), sometimes as food, especially for birds, and largely for the purpose of expressing a fixed oil employed in various arts. Hayne<sup>1</sup> termed the fruit an achene, a term permissible, if the theory that the ovary is composed of one carpel be maintained, though it hardly complies with the technical definition of an achene because the style does not remain partially adherent. Harz<sup>2</sup> appears to be the first to term it a nut, apparently, however, only on the ground that it has a hard pericarp. Taking a nut technically to mean a one-seeded fruit, enveloped in a husk, with a hard shell composed of more carpels than one, we must in using the term accept the theory of a bicarpellary ovary. The husk is the partially shrivelled involving bract. The mottling outside is due to the remains of the closely applied perianth. The crustaceous character of the shell is due to the presence of a layer of irregularly columnar cells in the endocarp, developed everywhere except opposite the funiculus of the seed, where a small circular plug of minute rounded cells occupies the spot which corresponds to the placenta or original point of contact of the ovule with the ovarian wall.

*The Seed.*—The body of the kernel of the nut, which is the ripened seed, is composed mainly of the plano-convex cotyledons, embracing between them a considerable plumule. The upper or anterior, and somewhat smaller cotyledon is rather closely approximated to the semicylindric radicle which is thus pseudo-incumbent; an invagination of the testa separates the two. The body of the seed is close to the posterior, the radicle to the anterior wall of the seed (PLATE 2, figs. 17-21.)

The testa covering the body of the seed is sage-green, that covering the radicle is darker, almost olive-green; round the chalaza there is a circular patch of orange-brown colour. Within the green testa there is a white coat, of less uniform thickness, covering the whole of the embryo from the micropyle to the margin of the orange-brown chalazal patch, with which it is organically united. This white coat is the albumen of the seed, derived from the body of the ovule

<sup>1</sup> *Arzneigewächse*, viii. t. 35.

<sup>2</sup> *Landwirthschaftliche Samenkunde*: Berlin, 1885; p. 94.

external to the embryo-sac; it forms a thin layer round the outer aspect of the cotyledons and a somewhat thicker covering to the radicle; between the radicle and the anterior cotyledon it forms a fairly thick pad indented from above by the fold to which the upper surface of the testa is there reduced.

Round the body of the seed the testa is tightly applied to the albumen; round the radicle on the other hand it is looser and extends in two wing-like folds outwards and backwards from the edges of the radicle so as almost to touch by their free margins the body of the seed (PLATE 2, fig. 19). The testa is firm and crustaceous owing to compression of the subepidermal cells of the outer covering of the ovule.

The features characteristic of the albumen and embryo are readily studied with a hand-lens magnifying 6-8 diameters, and are, moreover, quite recognisable even without making a section of the seed, if the seed examined has been carefully removed from the shell *without injury to the testa* (this with a little trouble is easily effected), and then *boiled*. With ordinary care in using the needles the testa may first be removed from the seed; then, a slit having been made in the covering of albumen *along its convexity*, the embryo can be pressed downwards and inwards clear of the albumen which, except for the rent through which the embryo has been extruded, remains entire, retains its natural shape, and is capable of examination.

The relationship of the radicle to the anterior cotyledon is best seen when a vertical section of the seed (PLATE 2, fig. 18) is examined; it is, however, also well seen when a horizontal section above the middle is studied. The first author to speak of the radicle as incumbent is Baillon<sup>1</sup>; the expression is not applicable because, so far from being incumbent on this cotyledon, the radicle is separated from it by an invagination of testa and a thickish pad of albumen. The use of this inappropriate term which has, however, been adopted both by Bentham and Hooker<sup>2</sup> and by Engler,<sup>3</sup> should be given up.

The darker colour of the testa over the radicle, its paler colour elsewhere, is perhaps due to the greater distention of this covering over the body of the seed, where the cotyledons are so largely developed, than over the less developed radicle. To the same cause is perhaps due the winged character of the testa at the sides of the radicle; the explanation may, however, be that the stimulus to growth resulting from the pressure of the cotyledons over the greater part of the periphery extends also to that portion of the testa overlying the radicle, so that more testa is produced than the radicle and the albumen which surrounds it are capable of filling. This arrangement appears to have been overlooked by most writers; possibly it is not so marked in seeds of European Hemp: it is very characteristic of Indian Hemp seeds.

The orange-brown chalazal patch is of considerable interest as being the ultimate form assumed by the expanded discoid apex of the funiculus to which the body of the ovule is attached and from which the coats of the ovule arise. Its margin is therefore the point of origin both of the green covering of the embryo (the testa) and of the white covering (the albumen). It is described by Berg,<sup>4</sup> though here as in so many other matters Schleiden appears from his manuscript drawings to have been the first to observe the condition.

As regards the albumen we find on studying a vertical section of the seed (PLATE 2,

<sup>1</sup> *Histoire des Plantes*, vi. 216.

<sup>2</sup> *Genera Plantarum*, iii. 357.

<sup>3</sup> *Natürlichen Pflanzenfamilien*; Leipzig; 1894; iii. 1. 97.

<sup>4</sup> *Anatomisches Atlas*; Berlin 1865; p. 86.

fig. 18) that it lies as a thick pad in the sinus between the radicle and the smaller cotyledon, indented in its turn by the vertical invagination to which the upper surface of the testa is practically reduced. But such a section further shows that the peripheral pressure exerted by the growing cotyledons has not, as in many campylotropous seeds, been sufficient to obliterate completely the cushion of albumen on which they impinge; a sheet of albumen, much attenuated it is true but still readily discernible, separates the larger cotyledon from the overlying testa. In a longitudinal section of the seed we further observe that the plumule does not extend upwards beyond the middle, while the invagination of the testa does not pass below that level. Consequently in a horizontal section below the middle we find that the albumen has a figure-of-eight shape, the smaller loop embracing the radicle, the larger enclosing the cotyledons with the plumule between them, while a single layer of testa surrounds the whole (PLATE 2, fig. 20). In a horizontal section above the middle we find, on the other hand, that the albumen is in two rings separated by the invaginated testa, which is now figure-of-eight shaped; the cotyledons within the larger ring of albumen have now no plumule between them (PLATE 2, fig. 21).

The presence of albumen was first pointed out by Bentham and Hooker.<sup>1</sup> Most of the early authors have, however, seen and figured it though, not knowing what it was, they have not figured it very exactly and in many instances, with the actual tissue before them, have followed Agardh<sup>2</sup> in denying its existence. The latest author of outstanding authority to do this was Baillon<sup>3</sup>; the only authors, prior to Bentham and Hooker, who have attempted to explain the tissue, which no one can well fail to see, were Le Maout and Decaisne,<sup>4</sup> who supposed it to be an albuminoid thickening of the endopleura. While Bentham and Hooker are the first to recognise its existence, the account they give of it is not quite exact for they describe it as unilateral, and plentiful round the radicle. It is plentiful round the radicle and it is most abundant on the upper side between the radicle and the cotyledons, but it is not strictly unilateral; it forms a complete covering to the embryo. Their not quite accurate expression has, however, been adopted both by Engler<sup>5</sup> and by the writer<sup>6</sup>; this error should be avoided by future authors. An almost accurate description of the conditions present was given by Harz<sup>7</sup> who, however, recognises, as the remains of the body of the nucleus only 3 or 4 layers of small cells underneath the testa, and describes the bulk of the albumen as endosperm. These layers of cells seen by Harz, who has been followed in regard to the statement and the deduction from it, by Macchiati,<sup>8</sup> are supposed by Briosi and Tognini to be possibly the tegmen of the seed. Judging from the figures they may be tegmen, or they may be only the outer much compressed layers of the albumen. Whether the tissue that Harz and Macchiati take to be perisperm is part of the covering of the seed or part of the remains of the body of the ovule, there is no doubt that these botanists err in describing the bulk of the albumen as endosperm. Had this been the case the albumen would not necessarily have ended at the margin of the chalazal disk; it would probably not have persisted along the convexity of the larger cotyledon and it would possibly have filled more completely the available testa round the radicle. In any case, whether it ended at the margin of the chalaza or not, it would not have been organically

<sup>1</sup> *Genera Plantarum* iii. p. 357.

<sup>2</sup> *Theoria Systematis Plantarum*: Lund, 1858; p. 256.

<sup>3</sup> *Hist. des Plantes*, vi, p. 215.

<sup>4</sup> *Traité de Botanique*; Paris, 1868; p. 508.

<sup>5</sup> *Natürlichen Pflanzenfamilien*, iii. 1. 97.

<sup>6</sup> *Bengal Plants*; Calcutta, 1903; ii. 960.

<sup>7</sup> *Landwirthschaftliche Samenkunde*, ii. p. 890.

<sup>8</sup> *Sulla sessualità, etc., della Canapa*: Modena, 1889; p. 13.

continuous with the tissue of the chalazal patch. This, coupled with the fact that the endosperm is entirely used up in the development of the embryo, proves that all the albumen present in the seed must be derived from the body of the ovule and must therefore be perisperm and perisperm only.

The manifest inequality of the two cotyledons is more visible when the embryo is removed from its envelope of albumen (PLATE 2, fig. 21); the larger posterior cotyledon is regularly plano-convex, the smaller anterior one is subtruncate at the apex and slightly grooved vertically along its convex surface. The differences between the two cotyledons are doubtless the result of accommodation, under pressure of growth, to the confined space they occupy. Fibro-vascular bundles pass up the centre of the radicle and diverge fanwise in the cotyledons; within each, as a rule, fifteen delicate stands can be made out, three of the fifteen being slightly stronger than the others (PLATE 2, figs. 19, 20).

### SECTION III.—Abnormalities in the Flowers of Cannabis.

*Pathological Abnormalities.*—In Gánjá fields in Northern Bengal it is very usual to meet with cultivated female plants attacked by an insect pest not unlike the familiar 'Red spider.' Plants so affected become wholly or partially blighted. The effects of this blight on the leaves do not here concern us; the effects produced on the flowers interest us considerably. The ovary in the affected flowers, in place of developing a crustaceous shell, which in uncultivated plants is shorter and in cultivated ones is not much longer than the involving bract, becomes converted into a thinly leathery bladder twice as long as the involving bract (PLATE 4, fig. 1). This abnormal capsule is always finely pubescent outside, is crowned by persistent styles, and is surrounded at the base by a considerably thickened, subherbaceous, persistent perianth (PLATE 4, fig. 2). On being laid open, one of these malformed fruits is found to contain an undeveloped ovule depending from the organic apex (PLATE 4, fig. 3).

The pubescence and the continuance of vegetative functions in the cells of the styles, as well as the thickening of the perianth, are probably the consequence of irritative growth induced by the stimulation caused by the pest. The main direct interest of this pathological condition lies in the confirmation it affords of the accuracy of the statement that normally the perianth has a horizontal or sub-horizontal margin, and the contradiction it offers to the view that the perianth of *Cannabis*, like that of *Humulus*, is, or ought to be, split in front.

*Teratological Conditions.*—The chief interest of the pathological condition described above is not, however, an intrinsic one, but lies rather in the fact that these diseased ovaries provide a link between the normal female flower and fruit and a teratological condition that is of frequent occurrence in quite healthy and otherwise quite normal plants.

*Non-sexual Abnormalities.*—The sport in question is characterised by a proliferation of the carpels into organs less or more like foliage leaflets,—a phylloidy of the pistil comparable to that with which we are familiar in certain double roses

and in double cherries. Here we find in some cases two leafy carpels that, by reason of complete union of their opposed margins, give rise to a closed cavity no longer, however, as in the normal female flower, sessile, but very distinctly stipitate (PLATE 4, figs. 4-16). Attached to the margin of the posterior leaf of the pair we find an ovule remarkably like that which occurs in the flowers already described as irritated by disease. The midrib of the leaf to which the ovule is attached is distinctly thicker throughout than that of the opposite one (PLATE 4, fig. 7). In other cases, still with closed cavities, we find that the ovule does not reach the apex of the leaf to which it belongs (PLATE 4, figs. 9, 10) or is quite free from it except for a slight union of funicle and midrib at the base (PLATE 4, fig. 11). In still other cases we find the ovule and its funicle replaced by an axial leafy shoot (PLATE 4, fig. 12). In these cases it was observed that the shorter the funicle the stouter it had become, and that beyond the point of attachment a normal midrib innervated the posterior leaf.

Among the flowers with closed carpellary cavities occur others where the cavities remain open and the carpellary leaves, larger than in the preceding cases, gape at the mouth and include at the base of the tube a symmetrically placed terminal leaf-bud (PLATE 4, figs. 13-15). In yet other instances the gaping sac is replaced by two free leaflets, supported on an extension of the axis beyond the involving bract and perianth, which further projects between them as a leafy branch (PLATE 4, fig. 16).

Associated with all these abnormal conditions we find considerable modification of the perianth. This is no longer a thin, hyaline, membranous cup; it becomes herbaceous and develops a distinct fibro-vascular system of 5 rather stout straight nerves with, between these, 5 more slender nerves that branch anastomotically. The margin of the perianth becomes hirsute and is minutely 10-denticulate (PLATE 4, fig. 8).

The predominance of the primary branches of the main nerve of the involving bract over its mesial continuation is more marked in these abnormal flowers than in normal ones (PLATE 4, fig. 6). Moreover, the greater the deviation of the ovule from its normal position the longer is the stipe on which the modified ovary is borne. It is to be remarked further that, while the conditions shown in PLATE 4, figs. 7, 9, 10 and 11 are very common, they are representative and not exhaustive; all shades of intermediate states prevail. On the other hand, the condition shown in PLATE 4, fig. 12, is very rare and has only been met with on three or four occasions. But while in the case of carpellary leaves forming closed cavities leafy shoots replacing modified ovules *have* actually been met with, the converse has not been the case; no ovules, but only leafy shoots, have so far been met with in cases where the carpellary leaves formed an open sac or were free.

The interesting conditions manifested in this sport, the bearing of which on doubtful questions will be discussed further on, do not appear to have been recorded, so far, in European hemp plants. The sport was not at all uncommon in the Bengal hemp fields in 1893.

The vascular condition of the perianth associated with this sport does not accord with

an abnormality mentioned by B. Clarke,<sup>1</sup> where, in a monstrous flower with 3 stigmas, the perianth had three faintly marked but distinct green ribs.

*Functional Abnormalities: Khásiá Hemp.*—An abnormality of *Cannabis* that appears to be mainly of a functional character, the associated organic deviations from the normal condition being relative and trivial, is of common occurrence in the hemp fields of Bengal. While it is impossible to find anywhere in fields in the Gánjá mahals instances of male plants,<sup>2</sup> and while care is taken by the cultivators to prune away any stray twigs on female plants that may have male flowers, there is in every hemp field a variable but always fairly considerable number of female plants which are termed *Khásiá*; these plants, though quite valueless, the cultivators do not attempt to remove. The plants of *Khásiá* hemp are marked by a total absence of the narcotic resin for the production of which the crop is grown; they are female plants that flower quite as copiously as normal females do, but, though to all appearance organically perfect, they never set any seeds. The appearance of a *Khásiá* flower (PLATE 5, fig. 1) is that of a normal female flower with the difference that the glandular hairs scattered among the non-glandular ones are not discernible owing to their cells not forming any resinous material. If functionally defective there is no impairment of vegetative powers; these *Khásiá* plants are more bushy, and their leaves are of a darker green than is the case with normal plants.

Nothing quite corresponding to this curious condition has been reported from other regions where *Cannabis* is grown for its narcotic properties. It has been fully discussed by Kerr<sup>3</sup> and by the writer,<sup>4</sup> who examined carefully many hundreds of plants in 1893 and found in every case that the ovary enclosed an apparently perfect ovule though there never was the slightest trace of fecundation having been effected. The phenomenon is not apparently a case of non-pollination, because the styles and stigmas wither and drop off precisely as do those of plants in which seeds are formed.

The name applied to these plants does not really refer so much to the sex as to the fact that no resin is produced. Its exact meaning is "hermaphrodite" in the popular, not the scientific sense of that word, but it may be fairly accurately translated "eunuch," "caapon," or "gelding." The cultivator, thinking especially of the resin-producing property, terms the plant that yields gánjá *mardá* (male); the worse than useless staminate plant which, if left in the field would, as the cultivator knows by experience, cause all the gánjá yielding plants to set seeds and so destroy his gánjá crop, he terms *mádi* (female); the useless but harmless non-functional female which, because it has no resin, he terms *Khásiá*, he neither removes from his field while the crop stands nor reaps when the gánjá plants are cut. The reason these plants are not removed is that, though they can be easily detected at a fairly early stage from their more robust growth and more vivid

<sup>1</sup> *Ann. & Mag. Nat. Hist.* Ser. 3, i, p. 102; *New Arrangem. Phan. Plants*, Introd. p. 4. In the first passage "2 or 3 green ribs," in the second "3 green ribs" are mentioned; the two citations may of course refer to two different instances of the abnormality.

<sup>2</sup> C. B. Clarke in H. C. Kerr; *Report on the Cultivation of, and Trade in, Gánjá in Bengal*, p. 8; Prain; *Report on the Cultivation and Use of Gánjá*, p. 4.

<sup>3</sup> *Report on the Cultivation of, and Trade in, Gánjá in Bengal*, p. 9.

<sup>4</sup> *Report on the Cultivation and Use of Gánjá*, p. 2.

green colour, this differentiation cannot be certainly effected sufficiently early to admit of their being replaced by transplanting other individuals from the seed-beds. This being the case, and because, if they are of no use they nevertheless do not induce excessive formation of seed in the normal plants, they are left standing. With the male plants, which they term the female,<sup>1</sup> it is very different. As already explained, the greatest care is taken to detect and eradicate these before they flower at all, and a daily search is subsequently made for anything in the shape of a monoecious condition. As many as 20 fields were searched by the writer, plant by plant, in 1893 without a single abnormally monoecious plant being found. In another field which, owing to some irregularity in complying with excise regulations, had early in the season passed out of the owner's care and had consequently not received the two latest and, it might be imagined, most important visits from the *poddar*, only one plant was found where there were a few male flowers among the female. This field should have carried 2,500 plants; allowing for losses due to inattention to weeding and to irrigation it still contained over 1,800 plants. But while the absence of males from the fields is so striking and complete, it is impossible to find any normal plant without healthy fruits by the time that the Gánjá is ripe for the sickle. The explanation of this is not difficult, because though the males are so carefully removed from the fields, no attention is given to the surplus stock of plants in the seed-beds where the males and females both flower freely and, owing to the plants being comparatively starved, do so much earlier than the plants that grow in the fields or that come up as casuals about homesteads and along roadsides. Moreover, though the males among the plants near dwellings are sometimes pulled up, this is not always done, and the males that come up in hedges are rarely interfered with. A certain amount of pollination in a field is thus inevitable in an anemophilous species like *Cannabis*, and the formation of some fruit is easily accounted for without its being necessary to postulate parthenogenesis, although that has been, on apparently good grounds, claimed by Spallanzani as possible.<sup>2</sup> With the *Khásiá* plants it is very different; they never set seeds at all.<sup>3</sup> It is not impossible that these plants are a consequence of impregnation by imperfect pollen such as is sometimes met with in abnormal flowers; seeds may have been set and these seeds were not only capable of germination but capable of producing outwardly normal plants, which, however, are incapable of further reproduction. On the other hand, it has to be noted that *Khásiá* plants have never been found either in seed-beds or in waste places, and the explanation of the condition may be that the conditions under which the plants are grown in fields are somewhat abnormal. They are subjected to the highest cultivation possible, stimulated by manures and irrigation; it may therefore only be that their vegetative functions are so overstimulated, that the sexual functions remain dormant.

*Monœcious Conditions.*—It is by no means unusual for monoecious conditions to occur in dioecious plants and in *Cannabis* such conditions are frequent. A

<sup>1</sup> This misapplication of the sexual names prevailed as generally in Europe 300 years ago as it does in India now; Dalechamps (*Hist. Gen. Plant.* p. 497 [1587]) is among the last of the systematic herbalists to describe the seed-bearing sex as *Cannabis mas*, the sex with flowers *inutiles et vanescentes* being for him *Cannabis femina*. In common speech the same error prevails still among country people, male hemp in Germany being known as *Fimmel*, female as *Müschel*; in England the male is, or was, *Fimble Hemp*, the female was *Carle Hemp*. While, however, all the peoples speaking Romance or Teuton tongues, thus, like the Indo-Persians, reverse the sexes, in Russia, the late Dr. Batalin informed the writer, the common people, like the inhabitants of China and Japan, term the seed-bearing plant female, the staminate one male.

<sup>2</sup> *Dissertationi di fisica animale e vegetale*: Modena, 1780; ii, p. 279.

<sup>3</sup> We have thus to deal with the fact that *Cannabis*, if allowed to form seeds, will not yield a full crop of the Gánjá resin; the resin is formed but is reabsorbed during the ripening of the seeds. On the other hand, unless the plant is capable of forming seed, it does not produce the resin.

whole branch or a part of a branch in a male plant may bear female flowers ; a branch or part of a branch in a female plant may bear male flowers.

*Male plants with female flowers : Sheória Hemp.*—Plants of male habit and appearance have been recorded in which the lower portion of each branch, sometimes up to half its length, had nothing but male flowers in close fascicles, the upper part bearing nothing but females ; at the same time the ends of the main-stems were female. The converse condition, where in plants of male type the lower one-third to one-half of each floral branch bears nothing but female flowers, the upper portion nothing but males, is so well-known in India that such plants receive a special name, *Sheória*. In extreme cases, which are, however, rare, *Sheória* plants may have none but female flowers (PLATE 5, fig. 7). The whole plant, in spite of this, has all the characteristics and habit of a normal male. These *Sheória* plants only exhibit, in a more exaggerated form, the condition already described as very common, where the pair of inflorescences at the bases of the lowest floral branches of male plants are replaced by a pair of perfect or imperfect female flowers (PLATE 1, fig. 2). The condition is often accompanied by abnormalities in the flower, as apart from the inflorescence, which will be dealt with in another paragraph.

*Female plants with male flowers.*—A plant of female habit and appearance has also once been recorded in which only male flowers occurred, united in a dense inflorescence. In India it is not uncommon to find an otherwise female plant with a single branch, or more than one branch, which bears only male cymes ; this condition recalls what one would expect if it were possible to graft a male flowering branch on a female plant. This condition, though quite usual in plants in seed-beds, is never to be seen in fields, such male branches being carefully removed by the cultivator. At times, however, the manifestation of male influence is less marked and we find that only the basal pair of female flowers of a female inflorescence are replaced by cymose panicles of male flowers, sometimes on both sides, at others only on one side. This phenomenon, whether unilateral or bilateral, has always, so far, been found associated with complete suppression of the axillary spikelet of female flowers normally developed between the basal pair. The abnormality is, however, apparently rare ; it has been found by the writer only six times, five of the instances being unilateral, only one of them being 2-lateral.

*Mória Hemp.*—On the other hand a very common abnormality in India is to find the axillary spikelet which occurs between the basal pair of female flowers developing stamens. The occurrence, which will be described in fuller detail in a subsequent paragraph, is so usual that plants which exhibit it receive in India a special name, *Mória* (PLATE 5, figs. 2-6).

The first definite allusion to *Cannabis* plants of male type bearing female flowers is that by Autenrieth<sup>1</sup> who observes, moreover, that according to his experience, the later the

<sup>1</sup> *De discrimine sexuali*, p. 6 ; t. ii, figs. 17, 18.

flowering of male plants the more they approximate to female *Cannabis* plants in appearance. The first writer to speak of monoecious conditions in hemp is Nees<sup>1</sup> who says that though *Cannabis* is a dioecious species, individual plants occur with both male and female organs in separate flowers. Many other writers refer casually or particularly to instances of this monoecious condition.<sup>2</sup> Kanitz has recorded such<sup>3</sup>; Heyer mentions their occurrence as interesting variations of unknown origin<sup>4</sup>; Masters includes *Cannabis* in his list of dioecious plants in which the presence of flowers of both sexes on one plant is common,<sup>5</sup> without going into any detail. We have, however, more special references by Spallanzani,<sup>6</sup> Bernhardt,<sup>6</sup> B. Clarke,<sup>7</sup> Braun<sup>8</sup> and Holuby<sup>9</sup> to the presence of male flowers in plants of female type; besides Autenrieth,<sup>10</sup> Gasparrini<sup>11</sup> and Holuby<sup>9</sup> record the presence of female flowers in plants of male type.

According to Spallanzani, Bernhardt, Autenrieth, and Gasparrini this tendency for plants of one sex to produce flowers of the opposite sex is often the result of mutilation, or is the effect of growth under unusual or adverse conditions; Autenrieth indeed explains that the phenomenon can be induced by experimental mutilation. The writer's experience is that variations, though occurring also in the fields, are much more usual among the stunted, uncared for plants of seed-beds. In plants growing by road-sides or in hedges they are much less common even than in plants grown in fields.

The most detailed accounts are those of Braun and Holuby. The condition described by the former is one, Braun says, 'to understand which the reader must imagine all the tips of the shoots of a male plant cut off and female shoots substituted.' This condition, which is of considerable interest as being the condition usually reported in the allied genus *Humulus* when that plant is abnormally monoecious, has never been met with by the writer in Indian *Cannabis* plants. The converse condition, which in India is common, was apparently first observed by the Danish Missionaries at Tranquebar in 1778. Holuby, who says that monoecious *Cannabis* plants are well known in the Slovak provinces of Hungary as *Svereka* (wild) or *nárrisches* (fatuous) hemp and adds that they play a part in certain superstitious customs at Slovak weddings, describes the conditions observed by him collectively as *Cannabis sativa* var. *monoica*. But his 'variety' is itself very variable and he has given four subvariations; *a*, with unisexual flowers, very variable, now male, now female flowers predominating—this corresponds to the conditions when male floral branches may occur on female plants and *vice versa*; *β*, with conspicuous female flowers in long lax panicles—corresponding to the Indian *Shebria* hemp; *γ*, compressed-flowered females, with single horizontal projecting branches below, longer than the quite short pyramidal inflorescence—a condition that does not quite deserve to be included in any VAR. *monoica*, though it indicates the tendency that some female plants have to assume, partially, the male habit; and *δ*, a form, only once seen, with male flowers only, but with these united in close inflorescences as if they were females—this too is technically out of place in VAR. *monoica*; it is, however, extremely interesting because it apparently corresponds to the Indian *Mória* hemp, differing only in being general, instead of local on the plant. This general condition has never been

<sup>1</sup> *Beschreibung officineller Pflanzen*; disp. 6.

<sup>2</sup> *Erdélyi Museum*, 1874, p. 159.

<sup>3</sup> *Bericht. Landwirthsch. Inst. Univ. Halle*, v, (1883).

<sup>4</sup> *Vegetable Teratology*, p. 194.

<sup>5</sup> *Dissertazioni di fisica animale e vegetale*, ii, p. 279.

<sup>6</sup> Cited by Macchiati: *Sulla sessualità, etc., della Canapa*, p. 4.

<sup>7</sup> *New Arrangement of Phanerogamous Plants*; Introd. p. 4 (1866).

<sup>8</sup> *Sitzungsber. der Gesellsch. Naturforsch. Freunde*, Berlin, 19th November 1872: *Bot. Zeitung* 1873.

<sup>9</sup> *Oesterreichs Botanische Zeitschrift*, xxviii, p. 367 (1878).

<sup>10</sup> *De discrimine sexuali*, p. 7.

<sup>11</sup> *Ricerche sulla embriogenia della Canapa*, p. 23.

seen by the writer ; a much less complete state of the same phenomenon where, throughout a plant of female type, only the basal flowers were normal females and *alī* the female flowers on all the intervening axillary spikelets were replaced by stamens, has only been met with twice. This last is the closest approximation to Holuby's interesting instance that has been noted in Indian hemp fields.

*Abnormal Flowers.*—Abnormalities in the flower as opposed to abnormalities in the inflorescence are of less common occurrence. Moreover, in the cases of abnormal male flowers hitherto recorded we find no transitions to female flowers ; what we do find are forms that shade gradually into the abnormal spicate mixed inflorescences of the *Mória* plants already alluded to. If the figures given are examined (PLATE 5, figs. 2-6) it will be observed that the condition is one of extreme variability. But amid a considerable number of variations, of which the figures given are only representative instances, the following general features can be made out. The basal pair of female flowers are normal and the abnormality is confined to the axillary spike on which, owing to the suppression of the foliar bract with its attendant stipules, the flowers are reduced to a spiral of bracteoles, corresponding to the involving bracts of normal female flowers. These bracteoles are sessile and the lowest is sometimes empty (PLATE 5, g. 4). The lowest two or three, if the lowest is not empty, contain normal and perfect female flowers, the three or four next above are replaced by solitary stamens, the uppermost, or perhaps the two uppermost stamens may even be without bracteoles (PLATE 5, figs. 2, 4). The end of the spikelet is always crowned by a female floret which never has a subtending bracteole and never has a perianth ; usually too it is more or less deformed, generally with only one style and stigma and very often incompletely closed (PLATE 5, figs. 2, 4, 5, 6) ; the ovule, which is usually present, and, as a rule, appears to be quite normal, projects through the hiatus thus left (PLATE 5, fig. 3). Close to and apparently collateral with this imperfect terminal ovary we may find a mere papilla (PLATE 5, fig. 4) a rudimentary carpel crowned by a rudimentary style (PLATE 5, fig. 5), a complete 2-styled ovary (PLATE 5, fig. 6), or at times a stamen (PLATE 5, figs. 2, 3, 16, 17). The stamens, which represent the flowers of the upper part of the spikelet, though usually, are not always arranged in a spiral ; a quite common arrangement is a spiral disposition of the female flowers towards the base of the spikelet, the upper 1-anthered flowers, from suppression of internodes, being arranged in a horizontal plane and therefore axillary to the bracteoles of an imbricated whorl (PLATE 5, figs. 5, 6), in all respects comparable with the parts of a normal male flower (PLATE 1, figs. 4-6). In two cases, as already mentioned, all the flowers of the spikelet except the terminal imperfect female flower, were represented by solitary stamens, each in the axil of one of a spiral series of bracteoles, corresponding in origin to female involving bracts, but in appearance exactly simulating male sepals.

In male flowers in India the writer has met with no abnormalities, but in Europe very interesting examples have been recorded and figured by Autenrieth<sup>1</sup> and Gasparrini.<sup>2</sup> The former has not clearly described the condition met with but his figures<sup>1</sup> are sufficiently instructive. He shows in one figure what looks like a normal male flower with a whorl of sepals, followed by a whorl of stamens, within which lies a cluster of female flowers. But the companion figure of the same instance, in which the perianth remains *in situ*, but from which the stamens have been removed, shows several female flowers, not in a cluster but in a spiral towards the upper part of a central axis, in the axils of bracteoles corresponding to involving bracts (PLATE 5, fig. 15). The condition appears to be, in fact, the exact converse of a condition that is repeatedly met with in the inflorescence of a female plant of *Mória* type.

The instances observed by Gasparrini, though very different from that of Autenrieth, are not less interesting. He found—and has figured one example of—male flowers where the five perianth-segments (these he has omitted from the figure) were normal, but where the stamens, in place of being in a whorl, were disposed spirally on a central axis terminated by a more or less developed, more or less deformed ovary, free or adnate to the next adjacent stamen; the deformity, as a rule, was limited to the ovule (PLATE 5, fig. 14). This condition is therefore precisely that met with in the upper part of the abnormal female spikelets of *Mória* hemp (PLATE 5, figs. 5, 6) and is very similar to that in the spikelets where only stamens are developed.

In female flowers of normal female plants the abnormalities observed have been quite few and very slight, the most striking being the occasional absence of the external (anterior) style and stigma. In female flowers of plants of the *Sheória* type, on the other hand, deformity is very common and remarkably variable. The greatest, and at the same time the commonest, abnormality, is to find in the axil of an involving bract, which is itself pedicelled in place of sessile, an organ that resembles nothing so much as a mere prolongation of the pedicel crowned by a solitary stigma. There is no trace of a true perianth; from the position assumed by the stigma it corresponds to the posterior (internal) style of a normal flower (PLATE 5, fig. 8). The next most common abnormality is a staminody of the pistil. Here an otherwise perfect female flower with a perfect ovule and ultimately a perfect seed, enclosed in a complete true perianth, is surmounted by only one posterior (internal) style; the anterior (external) style is replaced by a filament supporting a perfect anther, which is sometimes bent downwards and forwards so as to be organically united with the exterior aspect of the ovarian wall (PLATE 5, figs. 9, 10).

<sup>1</sup> *De discrimine sexuali*, pp. 28, 29; tab. i, figs. 9, 10.

<sup>2</sup> *Ricerche sulla embriogenia della Canape*, pp. 23, tab. iii, fig. 8.



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A rare abnormality, of which only two instances have so far been observed by the writer, is for the male influence to be so strong, or the female so weak, as to stop short at the formation, within the involving bract, of a normal female perianth, not, however, sessile but at the end of a short prolongation of the sub-bracteal pedicel; inside the perianth are two stamens of which the anterior has a filament and is perfect, the posterior a monstrous non-polliniferous sessile anther with a broad connective, so incompletely developed that each of its cells remains 2-chambered (PLATE 5, figs. 11-13).

Autenrieth considered the instances in which he found a prolongation of the axis with spirally disposed ovaries, inside a whorl of sepals and stamens, to be examples of hermaphroditism. The conclusion at first sight is not unnatural. But further reflection shows that it must be erroneous since the ovaries he figures are really separate and complete female flowers, and whether the sepals and stamens below be considered to constitute a male flower or not, there is no question that the central axis represents precisely the converse of such an inflorescence as one meets with in female plants of *Mória* type. This being the case the question that arises is whether, in the whorl of sepals and stamens, constituting what we are accustomed to consider a male *Cannabis* flower, we do not have an instance of a compressed inflorescence rather than a true flower; something, in fact, comparable with the inflorescence of an *Euphorbia*.

The instance recorded by Gasparrini, where the conditions usual in *Mória* inflorescences, instead of being reversed, are almost exactly repeated, strongly bears out this suggestion; here, however, from the other point of view, the claim that we have to deal with a hermaphrodite flower is stronger and, but for Autenrieth's instructive example, the question might have remained an open one.

Besides these, however, another claim has been made for the occurrence of hermaphrodite flowers in *Cannabis*, the writer making it being Masters,<sup>1</sup> the greatest living authority on teratology. It is, however, as Penzig<sup>2</sup> remarks, unfortunate that no detail has been published of the precise conditions present in Masters' specimens, and it is not certain whether he had before him flowers approximating to the *Mória* type, flowers approximating to the *Sheória* type, or something quite unlike either and really hermaphrodite.

Some of the conditions noted by the writer as occurring in abnormal female flowers of plants of the *Sheória* type have already been recorded by Autenrieth,<sup>3</sup> notably that in which the flower is replaced by a solitary style; and one of the most interesting of Autenrieth's figures (tab. ii, fig. 21) represents what is very like an exact parallel of the condition shown at the apex of a *Mória* inflorescence (PLATE 5, fig. 3; fig. 16). Unfortunately Autenrieth does not appear to have been aware of the existence of the true perianth, as it is not shown in this or in any of the other figures that he gives of female hemp flowers. None of the writer's examples of *Sheória* flowers quite accord with this of Autenrieth's, the nearest approximation being that shown in PLATE 5, figs. 9, 10. In one or two of the cases where the fruit had developed a ripe seed, the shrivelled remains of an attached anther, on the side of the nut next the radicle, showed that there had been a staminody of the pistil. In these cases sclerenchymatic hardening of the pericarp did not take place along the anterior (external) face opposite the radicle, this part of the wall of the nut remaining soft and flexible.

<sup>1</sup> *Vegetable Teratology*, p. 197.

<sup>2</sup> *Pflanzen-teratologie*, ii. : Genua, 1894.

<sup>3</sup> *De discrimine sexuali*, p. 7, t. ii.

Autenrieth and Gasparrini both figure very interesting examples of stamens with the connective prolonged upward as a style and stigma, or of a carpel reduced to the connective of an anther (PLATE 5, figs. 18-20). The writer has not met with this phenomenon in India.

Staminody of the pistil, such as is here described, is a well-known phenomenon. It is recorded by Masters<sup>1</sup>; parallel conditions to those described here have been noted by Baillon as occurring in *Ricinus*, and have been pointed out to the writer by Professor Trail as occurring in the white-flowered form of *Passiflora coerulea*. Except, however, for Autenrieth's instance, which has been overlooked or misunderstood by subsequent writers, the condition has not before been recorded in *Cannabis*.

*Summary of Teratological Phenomena.*—It has already been explained that the citation of *Cannabis* as an instance of a plant sometimes showing solution of calyx can only be continued in a very modified sense. On the other hand, however, *Cannabis* may now be added to the list of genera cited in teratological works as exemplifying solution of carpels, and this whether the monocarpellary or bicarpellary theory of ovarian structure be adopted (PLATE 5, figs. 3-6); staminody of pistils (PLATE 5, figs. 9-13 and possibly fig. 3); phyllody of carpels (PLATE 4, figs. 4-7, 9-16); and phyllody of ovule (PLATE 4, figs. 12, 15, 16).

*Abnormal Embryos.*—In *Cannabis* the seed, which has normally two cotyledons, is not infrequently found with three; the posterior larger cotyledon is often replaced by two.

The occurrence of a third cotyledon was first noticed by B. Clarke<sup>2</sup>; since then it has been recorded by Struve,<sup>3</sup> by Bode,<sup>4</sup> by Winkler<sup>5</sup> and by Macchiati.<sup>6</sup> The condition is easily detected because normally the first two foliage leaves are opposite or very nearly so; not infrequently a seedling shows a whorl of three foliage leaves instead of a pair, and when such a seedling is carefully examined the seed is found, in almost every case, to have had three cotyledons. It is rare to find a considerable sowing with no instance of this; the largest number ever met with by the author at one time was seven 3-cotyledonary seeds in a sample sowing of 100 seeds. It has, however, to be explained that the 100 seeds in question were all shaken out of the same bundle of "round Gánjá;" those who know how Gánjá is prepared will realize that probably all these seeds were produced by one plant; possibly therefore the unusual number merely indicated a tendency inherited from a parent plant in which it was strongly marked.

An instance is recorded in which the two cotyledons were of equal size, and another in which they were connate; these conditions, and that recorded by Bode where 4 cotyledons occurred, have not so far been met with in Indian hemp.

<sup>1</sup> *Vegetable Teratology*, p. 301.

<sup>2</sup> *New Arrangement of Phanerogamous Plants*; Intro., p. 4.

<sup>3</sup> Struve. The writer has noted in his MSS. of 1894, that the observation was recorded by Curt Struve in 1875, but he cannot now refer to the particular publication.

<sup>4</sup> *Pflanzenabnormitäten (Sitzungsber. Bot. Verein. Brandenburg, 28th March 1879)*, p. 57. Bode has also found four cotyledons in one seed.

<sup>5</sup> *Die Keimblätter der deutsch. Dicotyl. (Verhand. Brandenb., xxv., p. 37 [1885])*.

<sup>6</sup> *Sulla sessualità, etc., della Canapa*, p. 10.

#### SECTION IV.—Nature of the ovary and origin of the ovule in Cannabis.

*Discussion of contending theories.*—The nature of the female ovary has, as already explained, given rise to several theories. Some authors hold that primarily the ovary is monocarpellary, others that primarily it is 2-carpellary, but most who hold the second view admit that one of the carpels becomes abortive; all agree that the solitary carpel, or the persistent carpel if there be originally two, is anterior. Still others hold that the ovary is not properly referable to the leaf-type of organs, but is a *quid sui generis*, neither truly appendicular nor truly axial. The nature of the ovule has also been equally in dispute, some of the theories postulating for it an epicarpellary, others a hypocarpellary or truly axial origin. It is necessary to examine these theories in detail before offering a substitute.

The first author, so far as the writer can find, who has attempted to elaborate a theory on the subject is B. Clarke.<sup>1</sup> "The two stigmas," according to this author, "are anterior and posterior to the central point of the axil." This observation is very accurate; as already explained, the primary planes of orientation of the styles of the two flowers in the axils of a pair of stipules intersect in the floral axis that occupies the axil of the leaf or bract to which their stipules belong (PLATE 2, fig. 6). "The seed is pendulous, with a superior radicle, which is always on the external side of the ovary directly away from the axil laterally, the cotyledons being on the axillary side." This also is quite accurate. "In its early stages the ovule appears to be pendulous from the apex of the cell, but in the ripened seed the attachment inclines distinctly to the posterior side, though less so than in *Humulus*." As a matter of fact the small plug of less differentiated tissue in the carpellary wall that corresponds to the attachment of the ovule is just posterior to the apex of the cell—the point of origin of the posterior style—at all stages of growth subsequent to the closure of the ovarian chamber; in the ovule, as in the seed, it is the micropyle and not the chalaza that is immediately under the organic apex of the ovarian chamber. The point is not, however, important since it does not invalidate, indeed it rather strengthens, Clarke's theory. "On the internal side of the ovary, that is, next the central point of the axil, a thickened rib, somewhat grooved, extends from the attachment of the ovule to its base, which considering also the position of the radicle and its cotyledons is doubtless the placenta; this rib appears as if consisting of two columns, whereas the rib on the opposite or external side of the ovary is single and acuminate and each of them is opposite a stigma. The structure of the ovary therefore is the same as that of *Elatostemma* and *Morus* and taken in connection with the cotyledons and radicle, leaves no doubt that the fertile carpel is always anterior." The two ribs here described by Clarke are indeed present and are easily seen, and the posterior rib is, as he states, thicker than the anterior; but this posterior rib is certainly, so far as the writer's observations extend, never grooved and is undoubtedly never 2-columnar (PLATE 2, fig. 16). This thickened posterior rib therefore does not in reality bear out Clarke's theory that we have here a placenta composed of the two united margins of a single carpellary leaf with, at the upper end of this placenta, an ovule of foliar origin arising from it. In any case the placenta, so far as the histology, as apart from the organogeny, of the ovary shows, is not linear, but consists of a tiny circular patch

<sup>1</sup> *Ann. & Mag. Nat. Hist.* Ser. 2, vol. xi, p. 439 (1853).

of less differentiated tissue. Apart, however, from this, Clarke's theory fails to explain why there are two styles, and particularly why the posterior one, where by his interpretation there is no carpel at all, should be longer and stronger than the anterior, which belong to the only carpel that he admits. Clarke's careful attempt, from organographic considerations alone, to interpret the structure of the ovary and the origin of the ovule, cannot therefore be accepted as successfully explaining all the conditions.

The next important attempt to explain the structure of the ovary in *Cannabis* we owe to Payer.<sup>1</sup> This author states that the ovary commences as two carpels, at first distinct, but afterwards united at the base and forming two styles. At the base of each carpel there is a depression; of these, the posterior soon becomes entirely obliterated while the anterior becomes enlarged and forms the solitary loculus of the ovary. The ovule he claims as internal and axial. When the ovule appears, the loculus is not very deep and the ovule does not quite fill the cavity; it is thereafter carried up by intercalary growth to the apex of the loculus, the primine and the secundine being developed during its transit. Comparing the *Cannabineæ* with the *Tremandreeæ*, Payer says that as regards the ovary they differ only in this, that whereas in the *Tremandreeæ* there are two carpels, both lateral to the axis, and each forming a loculus, in the *Cannabineæ* only one of the carpels, the anterior, is lateral to the axis and forms a loculus; the posterior remains as a rudimentary structure at the apex of the axis and does not form a loculus.

This must mean, if it means anything, either that the axis continues to grow upward carrying on its apex the ovule and, just behind the ovule, the internal style; or, if the apex of the axis remains stationary, that the anterior carpellary loculus progressively deepens so that its base gradually leaves the two styles and the solitary ovule behind. In either case the posterior aspect of the ovarian wall—the part corresponding to B. Clarke's 'placenta'—should be of axial origin.

However, from what Briosi and Tognini<sup>2</sup> have shown, Payer's theory does not accord so well with reality as do his drawings. He speaks of two carpels as appearing before the ovule; he shows a small central swelling round which a circular cushion of tissue develops, from the margins of which subsequently arise the two out-growths—one behind, the other in front—that become ultimately the larger posterior and smaller anterior styles. The cavity of the loculus too remains open at the top till a comparatively late stage, a fact that is confirmed in the drawings of Briosi and Tognini; this is quite at variance with Payer's theory, which postulates the union of his two carpels before the growth of the posterior one becomes aborted—presumably therefore before the amplification of the loculus formed by the depression at the base of the anterior carpel has much more than commenced. The Italian botanists also find that the ovarian chamber is closed and the solitary ovule has reached its final position just behind the apex of the loculus, before the ovular integuments appear, whereas Payer's figures make the appearance of these integuments antecedent to the closing of the ovarian chamber and contemporaneous with a passage upward of the ovule along the posterior wall of the ovary. But, if the posterior side of the ovarian wall is of axial nature, there can be no such passage up that wall. The ovule was at the posterior side of the apex to begin with, and must have continued to be there all along, whether the axis grew upwards by intercalary growth or the anterior carpel became hollowed out downwards.

Payer's theory succeeds in explaining the origin of a posterior as well as an anterior style, and to this extent is more satisfactory than that of Clarke. But it does not explain why the style belonging to the abortive posterior carpel should be larger than that of

<sup>1</sup> *Traité d'organogénie comparée de la fleur*, p. 281 (1857).

<sup>2</sup> *Intorno all'anatomia della Canapa*, ii. p. 57.

the developed anterior one, and the thicker rib on the posterior carpellary wall is not much better explained by supposing it to be axial than it is by supposing it to be placental. On the whole therefore Payer's attempt to explain, on organogenic grounds, the structure of the ovary and the nature of the ovule is not more satisfactory than Clarke's organographic one.

Doell<sup>1</sup> appears to be the next writer to express a definite opinion on the subject. He advances the theory, already put forward by B. Clarke, that in *Cannabineæ* we have normally a solitary carpel in the ovary. He explains the second style, which B. Clarke does not deal with at all, as an excrescence on the ventral suture of the carpel. But though this view was at one time endorsed by Celakowsky,<sup>2</sup> it has only to be stated in order to realise its insufficiency; Clarke's reticence on the point is by comparison almost commendable.

Schnitzlein,<sup>3</sup> whose drawings have been referred to already, makes a quite different attempt to explain the two styles by showing them at right angles to the axis of the cavity formed by the single carpel, which is coincident with the long axis of the embryo. If this had accorded with organographic facts it might have accounted for the existence of the two styles as belonging to one carpel, though it would still have failed to explain why one of the styles should be larger than its neighbour. The carpel, according to Schnitzlein, is internal not external. But the whole drawing is out of accord with actual fact; the styles and the long axis of the embryo are in the same, not in intersecting planes; moreover, Schnitzlein has shown the radicle where the cotyledons ought to be, and *vice versa*.

Celakowsky soon abandoned the view of B. Clarke as modified by Doell, and adopted that of Payer, for in his magistral works on this subject<sup>4</sup> his views as regards the structure of the ovary are mainly those of Payer repeated in another form, and are, as he himself practically admits, based on the results obtained by Payer in the classic *Organogénie*.

'The apex of the floral axis is clothed with foliar tissue belonging primarily to two separate carpels, of which the inner is practically abortive, being pushed to one side by the outer which develops more strongly, and ultimately is represented by the portion of the ovarian wall overlying the chalaza and by the posterior internal style.' Thus put, all the objections to the original theory stand unanswered; in particular the view here expressed is irreconcilable with the fact that the posterior style, which should belong to an abortive carpel, is nevertheless the stronger of the two.

Celakowsky's view regarding the ovule, though at first sight diametrically opposed to Payer's, since Payer holds that the origin of the ovule is axial while Celakowsky insists that it is of foliar origin, is nevertheless merely Payer's view modified to accord with Celakowsky's thoughtful hypothesis. 'The growing point of the floral axis is displaced by the greater development of the anterior carpel to the lateral posterior position it actually occupies. This growing point, however, includes nothing belonging to the axis; it is of foliar nature; the stele has no true apex, at any rate no bare apex; this subtends, is blended with, and is lost in the substance of the apical tissue.' Whatever may be the case in other plants there is nothing in the structure of *Cannabis* that affords the slightest

<sup>1</sup> *Flora des Grossherzogthums Baden*; Karlsruhe, 1857-62.

<sup>2</sup> Ueber die morphologische Bedeutung der Samenknospen (*Flora* 1874, p. 274).

<sup>3</sup> *Iconographia*, ii. p. 95 (1870).

<sup>4</sup> Ueber Placenten und Hemmungsbildungen der Carpellen. Prag. 1875: *Vergleichende Darstellung der Placenten in den Fruchtknoten der Phanerogamen*. Prag. 1876.

foundation for the theory propounded by Celakowsky, and adopted by Schaeffer<sup>1</sup> and others as to the origin of the ovule from a hypothetical tissue of foliar nature which intervenes between the ovule and the apex of the axis. To the writer the whole hypothesis appears unnecessary; in *Cannabis* it is certainly baseless.

So far, therefore, neither the organographic considerations of B. Clarke, the organogenic researches of Payer, nor the subjective conceptions of Celakowsky have satisfactorily explained the nature of the ovary and the origin of the ovule of *Cannabis*. To Briosi and Tognin<sup>2</sup> we are indebted for a careful attempt to attack the problem from the histological side. To attain their object they studied a series of progressive horizontal sections of the base of a female flower from the level of its insertion upwards.

In the very short pedicel are to be found four vascular traces, of which one is anterior, one is posterior, and two are lateral (PLATE 3, figs. 1, 2). Of these the anterior— $\alpha$ , and the posterior— $\delta$ , are very nearly in the plane which is common to the centre of the stipule in whose axil the flower is situated and to the centre of the leafy axis. The anterior— $\alpha$ , is the smallest of the four, the posterior— $\delta$ , the largest; the lateral— $\beta, \gamma$ , are opposite each other and of equal size but are rather nearer the anterior than the posterior trace. Rather higher up (PLATE 3, fig. 3), one finds the anterior smallest trace— $\alpha$ , entering the base of the involving bract; the three remaining traces are much as before except that the internal lateral— $\gamma$ , and the posterior— $\delta$ , now slightly approach each other. Still higher up (PLATE 3, fig. 4), the bract is now free from the axis and the anterior trace— $\alpha$ , which innerves it, has given off the two strong subhorizontal zig-zag branches already described (PLATE 2, fig. 8). The pedicel is now assuming an oval outline as it approaches the base of the ovary and has now only three traces, the lateral— $\beta, \gamma$ , and the posterior— $\delta$ . The external lateral— $\beta$ , is now being pulled round towards the external end of the long axis of the pedicel; the internal lateral— $\gamma$ , and the posterior— $\delta$ , approach the internal end.

A stage higher up shows the base of the ovary and the involving bract above the level of the subhorizontal branches of the bract (PLATE 3, fig. 5). In the base of the ovary we find that the external lateral trace— $\beta$ , gives off two subhorizontal branches which run side by side towards the periphery at the anterior side of the ovary; the internal lateral trace— $\gamma$ , also sends out two subhorizontal branches which run round the base of the ovary, each of the two branches giving off a slender offset which passes backward towards the periphery at the posterior side of the ovary, coalescing as a trace— $x$ , before they get so far; the posterior trace— $\delta$ , is now closer than ever to the internal lateral trace— $\gamma$ , and is enclosed within the loop made by its external subhorizontal branch. Yet higher up and just before the base of the ovarian chamber is reached (PLATE 3, fig. 6), we find that the two subhorizontal branches of the external lateral trace— $\beta$ , run up close together as the two juxtaposed fibro-vascular bundles of the anterior carpellary rib, to the base of the anterior styte; the two subhorizontal branches of the internal trace— $\gamma$ , have given off a number of vertical traces which innerve the greater part of the carpellary wall, all of it indeed except the narrow vertical strip next the involving bract which is innerved by the two vertical strands into which the external lateral trace— $\beta$  has been divided; finally, the posterior trace— $\delta$ , which began as the strongest of the four original traces, is altered by the twisting and interweaving of its histological constituents into a small swelling opposite the centre of the base of the posterior carpellary wall, passes from thence backward towards the periphery of the ovary at the posterior side, becomes there closely associated with but

<sup>1</sup> *Flora*, lxxiii. p. 62 (1890).

<sup>2</sup> *Intorno all' anatomia della Canapa*, i. p. 53, t. xviii, figs. 1-7.

is not joined by the secondary trace— $x$ , derived from the subhorizontal branches of the internal lateral trace— $\gamma$ , and forms the bulk of the fibro-vascular bundle which runs up the posterior wall of the carpel to the base of the posterior style. No fibro-vascular bundles enter either of the styles.

This configuration has, as already explained, appeared to Briosi and Cognini to satisfactorily dispose of the theories of B. Clarke, Payer and Celakowsky. As to this there can be no doubt. They, however, believe that the conditions they have so clearly described do not throw any light on the question as to whether the ovary is monocarpellary or 2-carpellary, or as to whether the ovule is axial or foliar, though they appear to incline towards the view that the ovule is axial and that in the carpel of hemp we have to deal with an intermediate form or a transitional stage, as yet incompletely differentiated and therefore neither referable to axis nor to leaf. Such a conclusion is not very satisfactory; it is, moreover, in the writer's opinion not altogether necessary. It is true that it effectively refutes the theories of Clarke, Payer, and Celakowsky but it does not seem to be out of harmony with the theory, based on teratological considerations, that the writer explained to the members of the *Linnean Society* in November 1894, and that is explained again in the next paragraph.

*Proposed alternative theory.*—The true nature of the gynœcium in *Cannabis* appears to be as follows. There are two united sessile carpels, each crowned by a deciduous style. One carpel is posterior, internal, next the floral axis; the other, facing this, is anterior, external. The posterior, internal, is the larger of the two and is crowned by the larger of the two styles; from its connection with the ovule it may be termed the fertile carpel, the anterior, external, is narrower than the posterior, and has a smaller style; the two, united by their margins throughout together form a one-celled ovary containing a solitary ovule. From its earliest stage the ovule is lateral to the organic apex, between which and the posterior carpel it lies in the position of a bud in the axil of this posterior carpel. The ovule, however, originates slightly before the ovary, and when the latter appears the two become from the first organically united, so that, as the posterior wall of the ovary grows upwards, it carries with it the attached ovule. Subsequently, on the margins of the united carpels, at opposite points corresponding to the apices of their midribs, are developed the two styles; these, uniting at their bases, close the open sac formed by the carpellary cup, and explain the position of the small circular placenta immediately behind and below the base of the posterior style. This slightly posterior position explains the curvature of the ovule; the micropyle must curve upwards to reach the bases of the styles and, as these are at the organic apex of the chamber, the radicle has consequently to turn upwards on the side away from the point of attachment of the ovule.

This statement of the conditions explains all the organographic requirements. The thicker rib on the posterior wall is due to a coalescence of the midrib of what is the larger carpel with the funiculus of the ovule; the thinner rib in front is the duplex midrib of the narrower sterile carpel. The larger posterior carpel is surmounted naturally by the larger style. Preceding theories have satisfied the demands of the ribs, but no other theory will account for the larger posterior style. The statement further accords with the organogenic

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facts detailed by Payer and augmented and emended by Briosi and Tognini. It also, the writer believes, is in strict accordance with the histological details given by these authors. The two carpels are innervated by the two opposite lateral traces in the pedicel (PLATE 3, figs. 1-7.  $\beta$ ,  $\gamma$ .), the external, lateral trace innervating the anterior, external, sterile carpel, the internal lateral innervating the posterior, internal, fertile carpel. It is noteworthy how closely the nervature of the two carpels accords with the nervature of the involving bract which is innervated by the companion anterior trace (PLATE 3, figs. 1-6,  $\alpha$ ). All three, immediately after entering their respective leaves, give off two strong subhorizontal branches. In the case of the involving bract we have seen (PLATE 2, fig. 8; PLATE 4, fig. 6) that even the first of the secondary branches from these subhorizontal primary branches are stronger than the central prolongation of the trace. In the case of the narrow anterior carpel we see that these two branches occur without any accompanying central prolongation; in the case of the posterior carpel we find an intermediate condition, since the central prolongation of the trace, though absent as in the other carpel, is nevertheless replaced by the union of two minor branches, one from each of the subhorizontal branches, to form a central nerve  $x$ . Finally, the remaining primary axial trace, the posterior and the largest of the four (PLATE 3, figs. 1-7,  $\delta$ ) ends at the base of the ovarian chamber in a specialized swelling at a point corresponding, not to the apex of the axis but to the axil of the posterior carpel, in which position we have seen that the ovule at first appears; from this position the specialized strand passes backwards subhorizontally towards the periphery, to a position corresponding with the point of coalescence of the rudimentary ovule with the rudimentary posterior carpel.

The only further requirement is that the theory now stated should accord with teratological phenomena. A consideration of the cases of phyllody of the pistil detailed in the section devoted to abnormalities in *Cannabis* (PLATE 4, figs. 4-16) shows not only that this is the case, but that no other theory will satisfactorily account for the conditions. The conditions exhibited here seem almost to afford a reverse confirmation of the conditions figured by Payer, as opposed to the actual conditions in the developing ovary, but while Payer's figures, if accurate, would certainly explain them, they are still quite intelligible, under actual conditions, as a reversion, under the influence of abnormal foliar development of its associated carpel, of the ovule at different stages of *carpellary* growth to the *modus* of a leafbud. An examination of the cases of staminody of the pistil detailed in the same section (PLATE 5, figs. 9-13; possibly also fig. 3) shows that the posterior carpel is still the fertile one even if the ovary be unclosed, only the anterior being replaced by a stamen; if both carpels are replaced by stamens, the posterior is represented by an imperfect stamen outwardly almost as much resembling an abnormal carpel as it does an abnormal anther.

## SECTION V.—Character of the Diclinism in *Cannabis*.

*Male and female inflorescences contrasted.*—When the male and the female inflorescences of *Cannabis* are contrasted it is seen that the apparent remarkable diversity between the two disappears and that, as a matter of fact, their ground-plan is identical. The difference indeed lies only in this that whereas in the male there is a weak development or abortion in the axils of the leafy bracts on a floral branch, with a strong development—a cymose panicle of male flowers—in the axils of their concomitant stipules, in the female there is a strong development—a

pseudo-spicate system of female flowers—in the axils of the leafy bracts, and a weak development—a solitary involving bract with its contained female flower—in the axils of the concomitant stipules (PLATE 1, figs. 1, 3; and PLATE 2, figs. 1-3).

*Alternation between male inflorescence and female flower.*—The contents of the stipular axils, which are the primary objects of contrast, are thus, in the males a cymose system of male flowers, and in the females a single involving bract with a solitary female flower. This is brought out even more strongly in the case of abnormally monœcious plants. We have seen (PLATE 1, fig. 2) how manifest the alternation between cymose male panicle and solitary female flower is, in the case of the contents of the axils of the basal stipules in the lowest floral branches of otherwise normal males; and have encountered the converse opposition in the case of the contents of the axils of the basal stipules in otherwise normal female inflorescences. The contrast is even more marked in the case of *Sheória* hemp (PLATE 5, fig. 7). In *Cannabis* therefore, whether in normal or in abnormal conditions, that this, whether in the same or in different individuals, the change of *modus* from male to female does not result in an alternation of male flower and female flower, but in an alternation of male inflorescence and female flower, The absence of a female whorl in the male flower, so long at least as the stamens are situated in the same plane, and the absence of a male whorl in the female flower, are in keeping with this observation.

*Alternation between male flower and female inflorescence.*—If, however, the change of *modus* attending the substitution of male for female be interpreted aright as involving an alternation between female flower and male inflorescence, the converse change of *modus*, attending the substitution of female for male, should involve a corresponding alternation between male flower and female inflorescence. The evidence that this is the case seems very definite. In the abnormal male flower recorded by Autenrieth, within which was produced an axis bearing a spiral of female flowers with their subtending involving bracts; in those recorded by Gasparrini where a normal whorl of sepals subtends a spiral of stamens on an axis tipped by a female flower; and in all the intermediate conditions exhibited by the abnormal female spikelets of *Mória* hemp (PLATE 5, figs. 2-6), we have abundant evidence that the male flower and the female axillary spikelet are homologous throughout. But if the male flower and the female inflorescence be equivalent their component parts must likewise be equivalent, and the contrast cannot in this case be between flower and flower, but between the male stamen with its co-ordinate sepal on the one hand, and the female ovary with its co-ordinate involving bract on the other. These *Mória* spikelets show clearly that this is the only contrast possible. The bearing of this on the structure of the male flower is therefore clear, its bearing on the

structure of the female flower has now to be developed; the only point to be noted before we proceed to do so is that, since the sepals of the male flower correspond to the involving bracts of the female spikelet, no contrast is permissible between male perianth and female perianth, the latter being an organ quite unrepresented in the male flowers.

*Channels of Diclinism.*—In plants of *Mória* hemp it is usual to find, closely applied to the often open monocarpellary ovary which constitutes the terminal female flower of the spikelet, a single stamen, sometimes sessile, at other times stalked (PLATE 5, figs. 2, 3; 16, 17). The two look as if they were in the same horizontal plane and belonged to the same whorl (we know that at any rate they belong to the same spiral), but the absence of a perianth, which is a characteristic of the terminal female flowers of these spikelets, whether complete or incomplete, renders the condition equivocal. The case is, however, different when a study is made of the abnormal flowers so common in *Sheória* hemp (PLATE 5, figs. 9-13). From these we learn that within the involving bract there are two points of growth, one external, nearest to the involving bract, and another internal, nearest to the floral axis. Of these two channels of growth only the posterior internal is essentially that in which the female influence shows itself; the anterior external is essentially the channel in which the male influence is manifested. In plants where the female *modus* is the dominant one, growth takes place along both lines though most markedly in the posterior channel, and the two are subsequently surrounded by a special covering, the perianth. In the axil of the phyllome which marks the posterior channel of growth appears an ovule that becomes intimately associated with that phyllome, and the opposed anterior phyllome, by a process of growth corresponding to pistillody of the androecium, instead of becoming a stamen, has the filament developed as a sterile carpel which completes the ovarian cavity, and has the anther developed as a style. The presence of the ovule thus not only serves to stimulate its own, the posterior, phyllome to grow into a carpel but similarly stimulates the anterior phyllome. When, on the other hand, the male *modus* is the dominant one and there is no ovule present to stimulate its growth, the posterior phyllome does not develop at all, the anterior only develops; it grows now as a stamen and the production of a perianth is not induced. Occasionally, even in this channel of growth, there is a manifestation of female influence, to the extent of inducing the formation of anthers whose connectives are prolonged as styles; and occasionally in the posterior channel there is a manifestation of male influence, since the fertile carpel may be replaced by a deformed anther. But these exceptions may be taken as proving the rule, which the majority of those teratological phenomena appears to establish, that the diclinism of *Cannabis* asserts itself in two channels of growth which are collateral and not successive.

*Nature of the Diclinism.*—The nature of this diclinism, like almost every other point in connection with *Cannabis*, has been disputed, some contending that it is inherent or primitive, others that it is abortive or derivative. The teratological facts discussed above—and, since deviations from diclinism must in a normally dioecious plant belong to the category of teratological phenomena, it is only from the teratological side that the problem is to be satisfactorily discussed—leave us in no doubt as to which view is correct. The diclinism here is in the highest degree inherent, and is the result of a dichogamy that is essential, not accidental; the alternation in the sexual *modus* in the first place manifests itself in what are morphologically the same organs, and in the second place precludes any comparison between the collection of organs that goes to form a male flower and the collection of organs that constitutes a female flower.

Delpino,<sup>1</sup> to whom we owe the distinction between primitive and secondary diclinism, places *Cannabis* among diclinous plants of the former category, in which the unisexuality is inherent, primitive and necessary. Macchiati,<sup>2</sup> on the other hand, believes that *Cannabis* is a diclinous plant of the second category; that it is constructed on a bisexual type, becoming unisexual female by atrophy of the andrœcium, unisexual male by atrophy of the gynœcium.

As the male and female flowers cannot be contrasted, either as regards structure or as regards sexual *modus*, Macchiati's statement, which embodies the general belief, is obviously without foundation and Delpino's view is amply substantiated.

## SECTION VI. Summary of results.

*The Problems.*—Of the many unsolved problems relating to *Cannabis* only those have been here attacked on which a study of abnormalities in the flower and in the inflorescence is calculated to throw light. The chief of these relate to the nature of the ovary, whether composed of one carpellary leaf or of two, or indeed whether composed of an organ or organs that may be referred to the leaf-type at all; and to the origin of the ovule, whether axial or foliar. As a correlated question the character of the diclinism exhibited by *Cannabis* has had to be considered.

The monocarpellary theories hitherto held have postulated the existence of only an anterior carpel in the female ovary; the bicarpellary theories have postulated the existence of both an anterior and a posterior carpel, of which only the anterior is developed, the posterior remaining abortive. The latest view suggests that the pistil may be an organ of intermediate character, a *quid sui generis* neither foliar nor axial. The theories as to the foliar origin of the ovule have involved either an interpretation of the placenta that is opposed to histological characters, or the hypothetical existence of an intracarpellary organ of foliar nature, intervening between axis and ovule, that does not actually occur.

<sup>1</sup> *La Distribuzione dei sessi nelle piante*: Milan, 1867.

<sup>2</sup> *Sulla sessualità, etc., della Canapa*, p. 1.

*The Results.*—The instances of phyllody of the gynoecium, detailed in section 3, show that the pistil is composed of two carpels, both of leaf-type, and both capable, under abnormal influences, of becoming leaves. But, of these two, it is the posterior, not the anterior carpel that is fertile; moreover, in an abnormal, but still a closed ovary neither of the two becomes abortive; the anterior, though sterile and smaller than the posterior, nevertheless forms an organic part of the pistil and, by union with the posterior, completes the ovarian chamber. This is also precisely what occurs normally, and this interpretation, as is shown in section 4, fulfils all the requirements of organography, which no theory hitherto proposed does; accords with all known organogenic facts; and finally, interprets satisfactorily all known histological characters.

The instances of phyllody of the ovule, detailed in section 3, show that the ovule is truly axial, not, however, terminal but axillary to the posterior carpellary phyllome with which it becomes from the first organically united and by which it is carried by intercalary growth to the apex of the loculus. This interpretation, as is shown in section 4, again satisfies all the demands of organography, organogeny and histology.

The character of the diclinism is shown, from an examination of the facts detailed in section 3, to be primitive and essential, not, as has been generally contended, accidental and derivative; the condition is further shown to be manifested in channels of growth that are collateral and not successive; moreover, its phases do not, as is usual, involve a change of *modus* within comparable flowers of male sex and of female sex. The flowers are, alike as regards structure and development, incapable of comparison either as a whole or in detail; the change of sexual *modus* involves a contrast and an alternation, which are habitual and normal, between the female flower and the male inflorescence; and a corresponding contrast and alternation, which are casual and abnormal, between the female inflorescence and the male flower.



D. Prain del.

CANNABIS SATIVA Linn. ♂

K. D. Chandra lith.

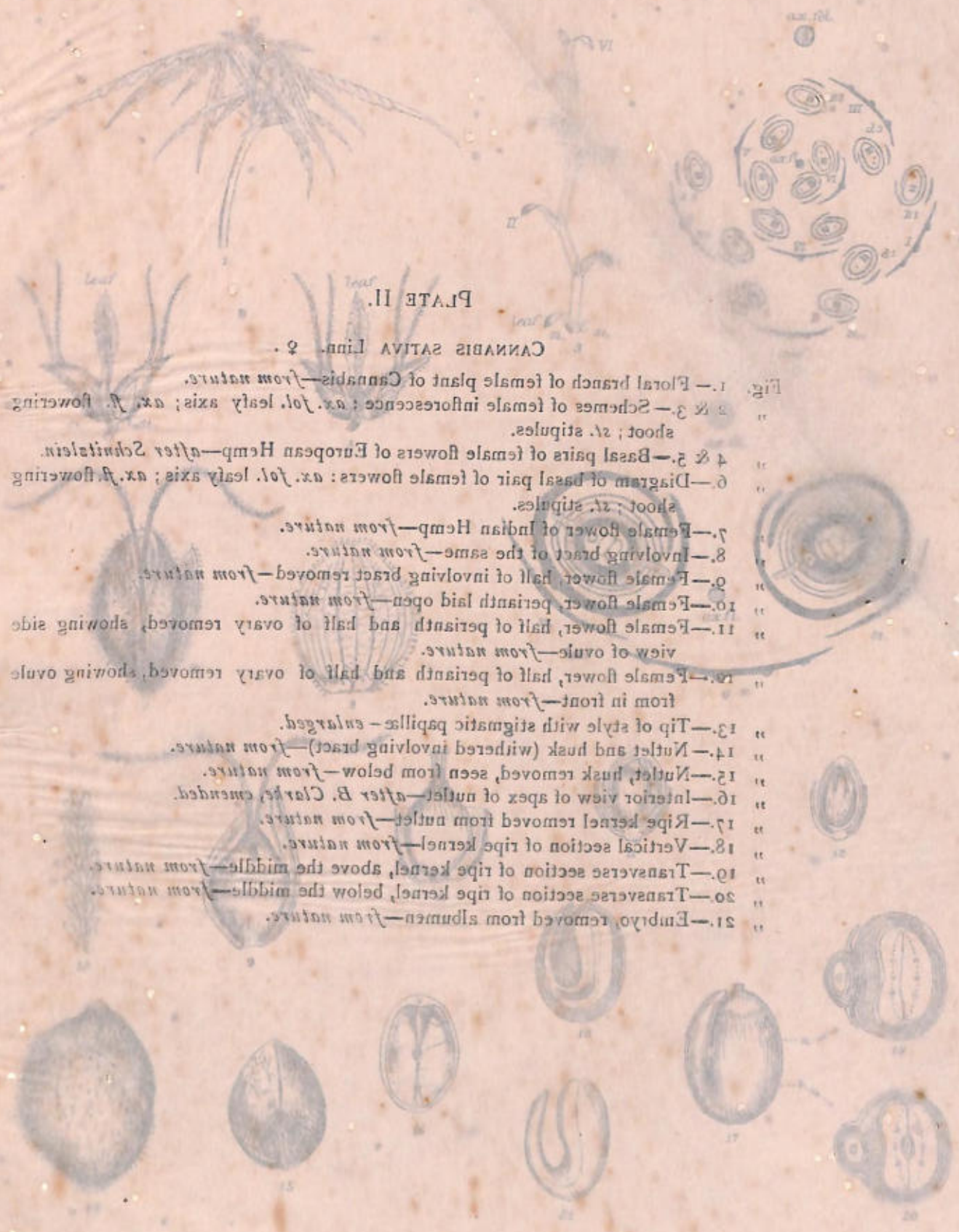
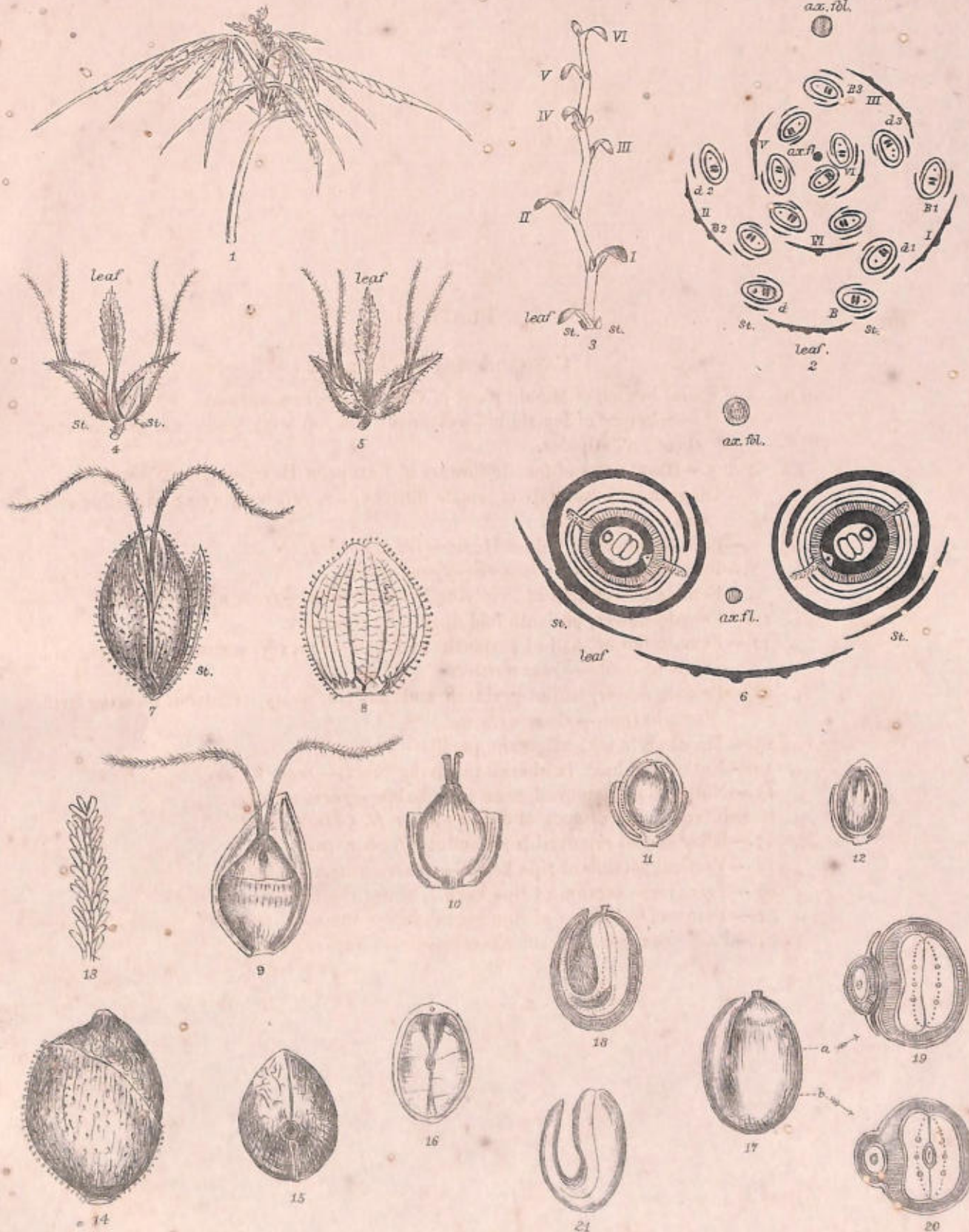


Fig. 1.—Floral branch of female plant of Cannabis—from nature.  
 2 & 3.—Schemes of female inflorescence: ax. fol. leafy axis; ax. fl. flowering  
 shoot; st. stipules.  
 4 & 5.—Basal pairs of female flowers of European Hemp—after Schmitzlein.  
 6.—Diagram of basal pair of female flowers: ax. fol. leafy axis; ax. fl. flowering  
 shoot; st. stipules.  
 7.—Female flower of Indian Hemp—from nature.  
 8.—Involving bract of the same—from nature.  
 9.—Female flower, half of involving bract removed—from nature.  
 10.—Female flower, perianth laid open—from nature.  
 11.—Female flower, half of perianth and half of ovary removed, showing side  
 view of ovule—from nature.  
 12.—Female flower, half of perianth and half of ovary removed, showing ovule  
 from in front—from nature.  
 13.—Tip of style with stigmatic papillae—enlarged.  
 14.—Nucleus and husk (withered involving bract)—from nature.  
 15.—Nucleus, husk removed, seen from below—from nature.  
 16.—Interior view of apex of nucleus—after B. Clark, condensed.  
 17.—Ripe nucleus removed from nucleus—from nature.  
 18.—Vertical section of ripe nucleus—from nature.  
 19.—Transverse section of ripe nucleus, above the middle—from nature.  
 20.—Transverse section of ripe nucleus, below the middle—from nature.  
 21.—Embryo removed from albumen—from nature.

PLATE II.

CANNABIS SATIVA Linn. ♀.

- Fig. 1.—Floral branch of female plant of Cannabis—*from nature*.  
" 2 & 3.—Schemes of female inflorescence: *ax. fol.* leafy axis; *ax. fl.* flowering shoot; *st.* stipules.  
" 4 & 5.—Basal pairs of female flowers of European Hemp—*after Schnitzlein*.  
" 6.—Diagram of basal pair of female flowers: *ax. fol.* leafy axis; *ax. fl.* flowering shoot; *st.* stipules.  
" 7.—Female flower of Indian Hemp—*from nature*.  
" 8.—Involving bract of the same—*from nature*.  
" 9.—Female flower, half of involving bract removed—*from nature*.  
" 10.—Female flower, perianth laid open—*from nature*.  
" 11.—Female flower, half of perianth and half of ovary removed, showing side view of ovule—*from nature*.  
" 12.—Female flower, half of perianth and half of ovary removed, showing ovule from in front—*from nature*.  
" 13.—Tip of style with stigmatic papillæ—*enlarged*.  
" 14.—Nutlet and husk (withered involving bract)—*from nature*.  
" 15.—Nutlet, husk removed, seen from below—*from nature*.  
" 16.—Interior view of apex of nutlet—*after B. Clarke, emended*.  
" 17.—Ripe kernel removed from nutlet—*from nature*.  
" 18.—Vertical section of ripe kernel—*from nature*.  
" 19.—Transverse section of ripe kernel, above the middle—*from nature*.  
" 20.—Transverse section of ripe kernel, below the middle—*from nature*.  
" 21.—Embryo, removed from albumen—*from nature*.



D. Prain del.

CANNABIS SATIVA Linn. ♀

K. P. Dass lith.

### PLATE III.

#### ORGANOGENY OF *CANNABIS* ♀.

- Fig. 1-6.—Successive transverse sections through pedicel and lower part of ovary of female flower of *Cannabis* to show position and destiny of the fibro-vascular traces. (*st.*, stipule; *br. inv.*, involving bract; *α* trace innervating the involving bract; *β*, trace innervating the anterior, external, sterile carpel; *γ*, trace innervating the posterior, internal fertile carpel; *δ*, trace innervating funiculus of ovule; *x*, secondary trace derived from *γ*—after *Briosi and Tognini*.)
- „ 7.—Vertical section through pedicel and base of ovary, showing the foregoing traces, *β*, *γ*, *δ* and *x*—after *Briosi and Tognini*.
- „ 8.—Apex of female inflorescence, showing earliest stages of development of female flowers; *ov.*, ovules; *st.* bracts, corresponding to stipules; *br. inv.*, involving bract; *ax. fl.*, floral axis—after *Briosi and Tognini*.
- „ 9.—Slightly more advanced stage of development of a female flower; *ov.* ovule; *st.*, stipular bract; *br. inv.*, involving bract—after *Briosi and Tognini*.
- „ 10.—Young female flower; *ov.*, ovule; *car.*, ovary; *per.*, perianth; *br. inv.* involving bract—after *Briosi and Tognini*.
- „ 11.—Vertical section (diagrammatic) of young female flower, at an early stage before the axillary position of the axial ovule is marked—after *Briosi and Tognini*.
- „ 12.—Vertical section (diagrammatic) of young female flower, to show the position of the ovule as axillary to the posterior carpellary phyllome—after *Briosi and Tognini*.
- „ 13.—Young female flower, ovarian parietes hiding the ovule but the cavity not yet closed—after *Briosi and Tognini*.
- „ 14.—More advanced stage of young female flower, the opening contracted but still unclosed—after *Briosi and Tognini*.
- „ 15.—Further stage of female flower, the styles forming but not yet united at their bases,—after *Briosi and Tognini*.
- „ 16.—Still further stage of female flower, the cavity closed by union of the bases of the styles, but the line of union still visible as a faint cicatrix—after *Briosi and Tognini*.
- „ 17.—Longitudinal section (diagrammatic) of recently closed ovary, showing obcampylotropous ovule still destitute of ovular integuments—after *Briosi and Tognini*.
- „ 18-20.—Vertical section (diagrammatic) of young flower of female *Cannabis*, to show development of ovule integuments—after *Briosi and Tognini*.
- „ 21.—Young unfertilized ovary—after *Schleiden*, and from nature.
- „ 22.—Vertical section of young unfertilized ovary—after *Schleiden*, and from nature.
- „ 23.—Vertical section of young ovary, to show commencement of development of embryo—after *Schleiden*, and from nature.

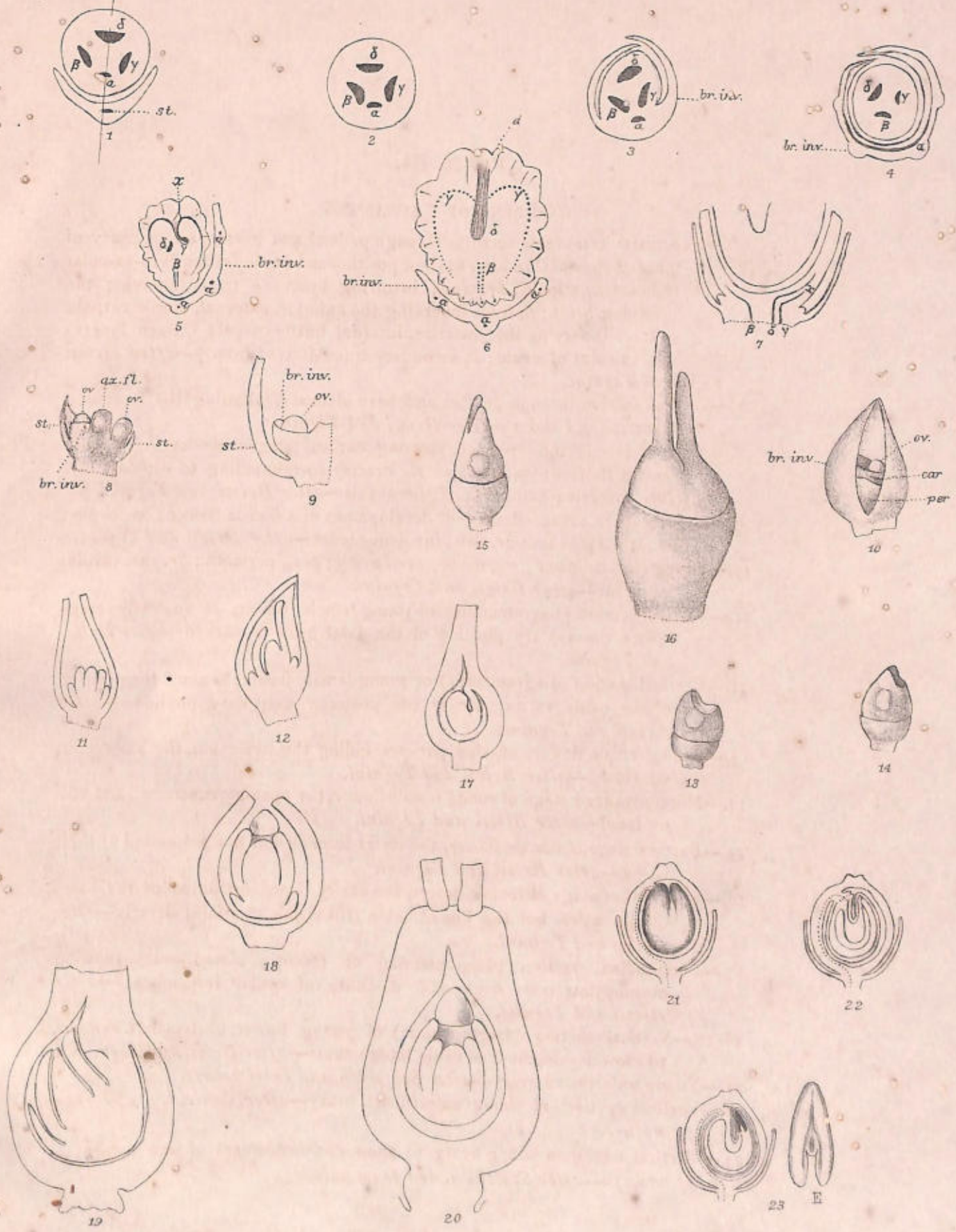
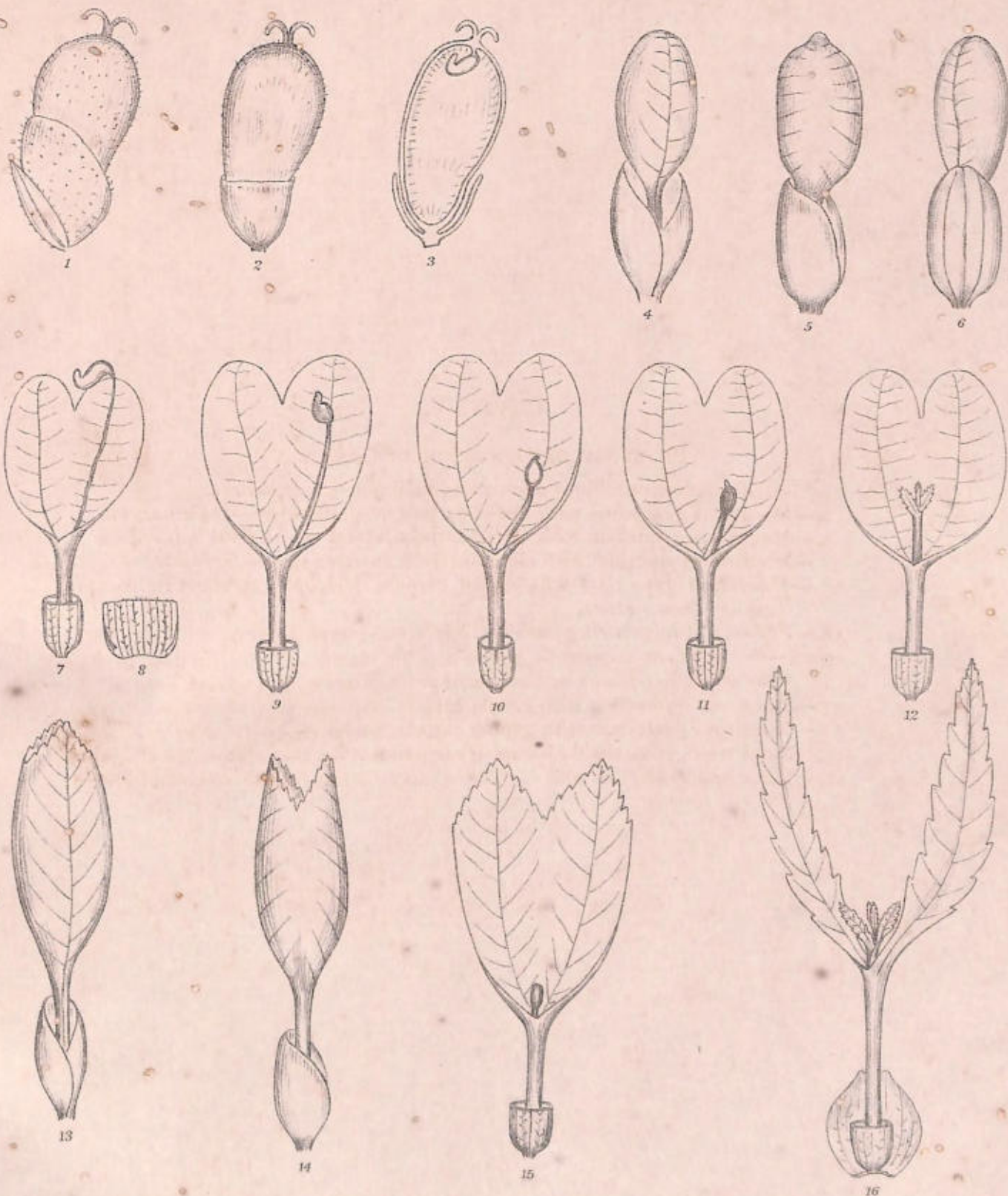


PLATE IV.

PHYLLODY OF GYNÆCIUM IN *CANNABIS*.

- Fig. 1-3.—Pathological conditions due to Insect Blight—*from nature*.  
" 4.—Monstrous gynæcium with closed carpels, posterior view—*from nature*.  
" 5.—Monstrous gynæcium with closed carpels, lateral view—*from nature*.  
" 6.—Monstrous gynæcium with closed carpels, anterior view—*from nature*.  
" 7.—Monstrous gynæcium with closed carpels, laid open to show rudimentary ovule—*from nature*.  
" 8.—Perianth of monstrous gynæcium, laid open—*from nature*.  
" 9-12.—A series of monstrous gynæcia with closed carpels, laid open to show variations in position and nature of rudimentary ovules—*from nature*.  
" 13.—Monstrous gynæcium with gaping carpels, posterior view—*from nature*.  
" 14.—Monstrous gynæcium with gaping carpels, lateral view—*from nature*.  
" 15.—Monstrous gynæcium with gaping carpels, laid open—*from nature*.  
" 16.—Monstrous gynæcium with carpels replaced by free leaflets—*from nature*.



D. Frain del.

PHYLLODY OF GYNOCIUM IN CANNABIS.

K. D. Chandra lith.

PLATE V.

KHÁSIÁ, MÓRIA AND SHEÓRIA CANNABIS.

- Fig. 1.—Flower from plant of Khásiá Hemp, abnormal female apparently organically perfect but functionally sterile—*from nature*.
- „ 2.—Inflorescence from plant of Mória Hemp, *i.e.*, *Cannabis* with male flowers on a female plant—*from nature*.
- „ 3.—Terminal flowers from Mória inflorescence—*from nature*.
- „ 4.—A second inflorescence from plant of Mória Hemp—*from nature*.
- „ 5.—A third inflorescence from plant of Mória Hemp—*from nature*.
- „ 6.—Terminal flowers from a fourth plant of Mória Hemp—*from nature*.
- „ 7.—Portion of inflorescence from plant of Sheória Hemp, *i.e.*, *Cannabis* with female flowers on a male plant—*from nature*.
- „ 8.—Flower of Sheória Hemp showing only an involving bract and stalked stigma—*from nature*.
- „ 9.—Flower of Sheória Hemp with anterior style replaced by an anther—*from nature*.
- „ 10.—Vertical section of Sheória Hemp with anterior style replaced by an anther—*from nature*.
- „ 11.—Pair of flowers of Sheória Hemp, one perfect, the other deformed, the anterior carpel and style replaced by a perfect stamen, the posterior carpel and style replaced by a monstrous 4-celled non-polliniferous sessile anther—*from nature*.
- „ 12.—The same abnormal flower, half the perianth removed—*from nature*.
- „ 13.—The abnormal monstrous sessile anther of the same flower, seen from behind—*from nature*.
- „ 14.—Male flower 'with sepals whorled' but with the 5 stamens spirally disposed on an elongated receptacle tipped by a slightly modified carpel—*after Gasparrini*.
- „ 15.—'Hermaphrodite' flower, occurring spontaneously, the anthers removed, so as to show scattered 'female organs'—*after Autenrieth*.
- „ 16.—'Hermaphrodite' flower with single style, the ovary adnate to an anther—*after Autenrieth*.
- „ 17.—Carpel in which the ovary, adherent to the base of an anther, is almost entirely abortive except that the styles are developed—*after Gasparrini*.
- „ 18.—Anther with connective prolonged as a short style—*after Autenrieth*.
- „ 19-20.—Two instances of carpels united, by means of the abortive ovary, which is reduced to a connective, to the face of an anther of which one locus is almost completely abortive, the other little developed—*after Gasparrini*.



D. Prain del.

KHÁSIÁ, MORIA AND SHEORIA CANNABIS.

K. P. Dass lith.

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ON THE MORPHOLOGY, TERATOLOGY AND DICLINISM OF THE FLOWERS  
OF CANNABIS.

BY

MAJOR D. PRAIN, M.B., I.M.S.

*(Indian Medical Service.)*

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