

On the Floral Mechanism of Welwitschia mirabilis (Hooker).

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Communicated by A. C. SEWARD, F.R.S.

(Received December 23, 1913,—Read February 5, 1914.)

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The present paper is the outcome of a suggestion of Prof. SEWARD that the details of the flowers of *Welwitschia* might be with advantage considered from the standpoint of methods which have been found serviceable in the case of the floral mechanisms of Angiosperms. The spirit material used in the investigation was also kindly supplied by Prof. SEWARD, and was part of some material collected by Prof. PEARSON in 1907.

As a plant of unique vegetative habit, producing flowers also unique among existing Gymnosperms, *Welwitschia* requires no introduction to the botanical student; and, since the time of its original description by HOOKER (1864), numerous observers have given an account of its special features, chiefly from anatomical or cytological points of view, the most important of these being PEARSON'S last contribution to the study of the process of fertilisation (PEARSON, 'Phil. Trans.,' B, 1908).

Similar material has been more recently exhaustively examined by SYKES (1910), and LIGNIER and TISON (1912); so that, though little more new information may be obtainable, it may be of general interest to consider the details from a new standpoint, and a concise revision of the facts of observation may be useful at this stage. The literature of the subject has been recently so fully catalogued by LIGNIER and TISON ('Ann. Sci. Nat., Bot., 1912, p. 180) that further references, except to classical well-known papers, are really uncalled for.

As the number of investigators of *Welwitschia* increases, so the amount of theoretical speculation also grows, and it becomes increasingly important to distinguish between actual details and facts which may be observed, and the often extremely erroneous conceptions which may have been founded on them, and to distinguish clearly the nature of the evidence, on which elaborate, and possibly very far fetched, hypotheses have been based.

It was from the outset intended that a special feature should be made of suitable (317.)

illustrations, and to this end sectional elevations have been planned to scale, for both staminate and ovulate flowers, in both median and transverse planes of the floral diagram, while similar elevations, to a uniform scale, have been constructed for a very complete set of developmental stages.

I. THE OVULATE CONES AND FLOWERS.

Welwitschia is strictly dioecious, and the ovulate "cones" are borne in considerable numbers (up to 23, PEARSON, 1908) on branched inflorescence systems which arise in indefinite series from pits in centrifugal shallow ridges from the crown of the plant, a ridge being fertile for a number of years (PEARSON, 1908). These ridges form zones beyond the foliage leaves, and are usually regarded as extra-axillary shoots which, owing to the failure of the foliage-leaf system, acquire a greatly exaggerated importance and serial formation. According to PEARSON (1908), "sub-foliar inflorescences," at first regarded as rare (HOOKER, 1864), are also common, and normal on acropetal ridges from a "floriferous meristematic zone," probably a type of callus-formation, and another secondary abnormality consequent on the lack of leaf-axils.

The *inflorescences* themselves present perfectly normal construction, as branching paniced systems developed in a regular decussate phyllotaxis, and ramifying to the third and fourth degree (as figured by HOOKER, 1864). Ramification is rendered irregular (1) by reduction of terminal buds to leaf scales only, or small terminal cones, leading to a dichasial habit in the ultimate ramifications, and (2) by irregular internodal extension, which spaces the cones apart on fairly long internodes. On the ultimate ramifications, where this internodal extension is omitted, the terminal and last lateral cones are closely clustered, giving a suggestion of dichasial triads or groups of five "more or less umbellate" (HOOKER, 1864). Ultimate reduction gives, as might be expected, a system reduced to a single terminal cone (PEARSON, 1908). Subtending bracts are present at all points of ramification as pointed, somewhat connate, tooth-like scales, of simple form; and the first leaves of lateral axes are in the transverse plane (prophylls).

Ramification, though reduced, and much more so than in the case of the staminate inflorescence, is thus perfectly normal from a morphological standpoint; that is to say, in this part of its organisation *Welwitschia* presents evidence of a capacity for working out a perfectly normal decussate phyllotaxis system, with mechanism of internodal extension and successive axillary ramification, which are characteristic features of higher plants: and it is sufficiently obvious that these features, being characters of the assimilating mechanism of plant shoots, have been inherited and retained in the inflorescence-system from a normally extending and ramifying vegetative plant of normal arboreal habit. Irregularities in inflorescence-construction, as the closing of the system by a small vegetative bud, with the extension from fertile bracts below it—a general feature of higher plants ("dichasial growth")—and irregular production of internodal extension, giving clusters of cones or spikelets

(*cf. Cyperus alternifolius*) are again features which can be understood, and may be regarded as reduction-stages, often the expression of xerophytic adaptation, in inflorescence-building.

The *ovulate cones*, when at the commencement of the pollination stage, which from a floral standpoint may be termed the functional condition, are beautiful examples of decussate construction, with closely imbricating scales. A good cone would be 40 mm. long by 20 mm. in diameter, and is somewhat pyriform; the four accurate orthostichies of scales rendering it slightly four-angled, especially in the upper region, where the four orthostichy lines are sharply defined and converge on the dome-like apex (Plate 9, fig. 1).

The cones begin to flower when about 30 mm. by 18 mm., and successive "flowers" function in normal acropetal sequence, with the result that a perfectly graded sequence of scales may be obtained from below upwards to the apex, which is closed by a tuft of a few sterile scales. The cone is thus sterile at both ends: the basal region, at this time often extending to just half the body of the cone, consists of stout, closely imbricating decussate scales, to the extent of about eight pairs, distinct in form from the connate scales of the inflorescence ramifications, or five to four, less commonly three, scales along each orthostichy line. At the extreme apex of the cone, the space between the last inarching fertile bracts is filled by a small sterile proliferation of the otherwise normal spindle-shaped axis, which bears one or two pairs of rudimentary members, while the end of the axis persists as a dome-shaped apex (fig. 2). The apex, as pointed out by PEARSON (1908), commonly develops an archesporial cell, and so closes the growth of the axis.

Owing to the perfectly regulated growth of the cone as a whole, successively younger stages of flowers are observed in acropetal series; so that a cone in which the lower fertile scales are becoming functional shows all stages to the first primordium in the vicinity of the apex. It appears possible, therefore, to regard these developmental stages as quite normal, since it is probable that most of the younger stages come to maturity. Thus PEARSON (1908) gives the number of functional flowers as 60 (*i.e.*, 15 in a row), and says that the end ones remain small and attached as relics to the axis, after the shedding of the cone-scales and seeds. HOOKER (1864) figures old red cones with stylar tubes protruding from 20 to 22 scales in each row up from the base. The cone figured shows 16 recognisable in one row, total 64, with archesporial cells to the lowest stage (figs. 2, 5). No growth-change takes place as the cones become functional, the scales remaining closely adpressed, and there is no internodal extension in the axis. The protrusion of the "stylar tube" does no more than lift the extreme edge of the subtending bract of each flower, so that there is nothing that can be classed as mechanism in the cone-structure. HOOKER (1864) was so struck by this fact that he assumed that pollination must take place when the cones were very small, no bigger than the staminate ones; the case of *Pinus* probably affording the suggestion.

From the analogy of other cone-mechanisms this retention of a closed condition in the functional stage must be regarded as secondary, and due to the *elimination* of an opening mechanism: since it is obvious that, as in other Gymnosperms, the pollen grains once fell directly on the nucellus or in its immediate vicinity. That such failure to open is the expression of xerophytic adaptation will be freely granted; and it may be noted that the essential parts of the ovule (embryo sac and nucellus apex) now remain buried beneath about three overlapping scales, each with strongly cuticularised epidermis and marked xerophytic structure, at a distance of 3–4 mm. from the exterior, and thus probably beyond the reach of injurious intense light. Such clisanthly is familiar in Angiosperms, in which under unfavourable conditions of growth the styles may protrude from unopened buds (*cf. Ænothera*), and be efficiently pollinated, when all the other growth-factors of the floral mechanism have failed.

Sectional Elevation constructed for a cone just commencing to flower ($\times 12$) gives a good idea of these features, as also of the relative rates of growth of the ovules, the basal embryo-sac region and the nucellar beak, and the relative rates of extension of (1) the “perianth” envelope, (2) the “stylar” tube, which ultimately projects like a stiff bristle for 4–5 mm. beyond the tip of the subtending bract. On the outer face of the cone these stiff bristle-like extensions follow the four orthostichy lines with considerable accuracy, continuing their previous growth-curve without any intentional deviation. Curves drawn through the apices of the different members afford a guide to the relative symmetrical correlations of rates of growth.

Neither the sterile scales at the base of the cone nor the fertile bracts are connate below, as in the case of the staminate cone; they remain simple scale-leaf members, which do little more than fill their normal room in the bud: *i.e.*, they extend to 180° in the decussate system, and just overlap where they make contact round the axis. In this way the imbrication lines follow very beautifully down the cone diagonally with the four orthostichies; while in section in the plane of an orthostichy the edges of the next upper pair of scales are just cut as they overlap for a distance about equal to the height of the nucellus in the ovule, thus affording much the same additional protective investment as in the case of the connate scales of the staminate cone. The portion of the scale exposed to the exterior is about one-seventh of its total length.

The simplicity of the organisation of the cone is as admirable as its efficiency from the standpoint of (1) xerophytic adaptation, (2) successional flowering, though the rate at which successive flowers become functional is still undescribed, as are also the general time-factors for the whole cone.

The term *carpellary* as applied to the construction is purely conventional from the analogy of the flowers of other diclinous Conifers, and merely implies that the construction produces the megasporangia, and is only one degree less objectionable than the expression “female-flower.” The term “ovulate” is possibly better than

“ovuliferous,” and, though not exactly co-ordinate with “staminate,” may be retained as the most generally convenient expression (COULTER and CHAMBERLAIN, ‘Morphology of Gymnosperms,’ 1911).

As the theoretical interpretation of the flower ranges from (1) an axillary ovule with two integuments (SYKES, 1910) to (2) a syncarpous ovary of four carpels with a single erect basal orthotropous ovule, invested by a perianth of one if not two or more whorls (a total of five whorls of a decussate system, P, (2+2); A, 2; G, (2+2) (LIGNIER and TISON, 1912)), a simple statement of the facts is necessary.

Considering a single flower in further detail :—

1. *The subtending bracts* are simple scale-leaf members, about 15 mm. by 15–12 mm., curved as they follow the contour of the cone, and closely resembling in form and thickness a finger-nail. By the pressure of the ovule in growth, a thin area is produced in the median line, so that in a region corresponding in area to the nucellus the scale becomes translucent, and a translucent median line is even left corresponding to the pressure of the style-tube. By this detail the fertile scales can be distinguished when detached from the sterile lower leaves of the cone.

These scales present several features of extreme interest, and though the parts usually rejected in cytological work, they are particularly to be recommended for class exercises.

(1) They are not at all connate, but free leaf-members of a normal phyllotaxis system, rendered thin by radial retardation in growth, but not by tangential extension; as already indicated they only extend to the slightest degree beyond their theoretical boundaries.

(2) The vascular system is visible to the unaided eye, as two beautifully sympodial systems, coming from two trace bundles each well clear of the median line, which ramify dichotomously in a manner which distinctly recalls the venation of *Ginkgo*. Ultimate ramifications may become slightly irregular, as in the case of the inflorescence-bracts and staminate-cone bracts (*cf.* LIGNIER and TISON, 1912); but there can be no doubt of the fact that these leaf-members are the nearest approach to the ancestral leaf-venation of the plant now available, since the huge foliage members are exceptionally specialised. The lack of a median vein has clearly nothing to do with pressure of the ovule: it is equally absent in the inflorescence-bracts and sterile scales; and in this respect it is interesting to compare the leaf-venation of *Welwitschia* with that of *Ginkgo*, *Pinus* and the Pteridosperms with double leaf-traces (fig. 4).

(3) Histologically these bracts are of greater interest as presenting a graded change from “shade-construction” in their lower shielded region, to a condition of most advanced xerophytic specialisation in their upper exposed portions.

Thus, in the lower region, the epidermal cells of the outer surface contain abundant chlorophyll and small starch grains, the bundles are simple, and the mesophyll cells are elongated along the length of the member. In the upper one-fourth of the leaf (about 5 mm. behind the tip) the epidermis of the exposed lower surface becomes large rounded

aqueous cells with a thick cuticle; sunk stomata, 150–300 per square millimetre, are present, and beneath the epidermis a distinct attempt at palisade elongation is observable. Among these cells massive, thick-walled sclerites ramify, and extend as an irregular layer underneath the epidermis. Beneath these a network of mucilage-cysts intervenes between the bundle terminations with their beautifully frondose fringes of transfusion-tracheides. (A tangential section of this region, treated with phloroglucin HCl, affords the most effective demonstration possible of what is meant by such “transfusion tracheides.”) On the inner (upper) surface of the member, the cuticle is less thick, but the cellulose walls of the epidermis more massive, and the zone of fibres consists of finely woven slender elements. About $\frac{1}{2}$ mm. from the edge sclerosis ceases, and these special features are lost as the leaf thins to the margin.

The special interest of the histology lies in the fact that between the two regions all transitional stages are present; and it is possible to trace the sliding growth, wavy course and thickening deposits of the sclerites within the limits of a single longitudinal section.

In the axils of these members arise singly, in the accurate median line, what are regarded as the ovuliferous or carpellary flowers, as definite stalked axillary formations: the whole cone being a bi-axial structure. Few will object to this obvious interpretation. Suggestions for a monaxial view have been put forward (SYKES, 1910); but a median section of the cone-apex shows that if this is not to be termed axillary ramification, there is no significance in the term as applied to the ordinary appearances seen in bud-sections of floral development in higher plants. All stages in development are to be traced at the apex of a “flowering” cone; and it is interesting to note that the overlap of the decussate scales is visible from almost their first appearance, and is but slightly advanced in subsequent stages; that is to say, nothing beyond what would be normally expected.

It may be taken as established, therefore, that the axillary product is to be regarded as a floral axis, however much it may be reduced. On the other hand, there is no special merit in trying to force the ovulate cone into strict morphological homology with the staminate one, since nothing is gained by doing so. If definite evidence can be obtained that it is quite a distinct formation, that evidence must be accepted. The bi-axial hypothesis holds because there is no real evidence against it, that is to say, it is the simplest statement of the facts of observation (*cf.* SYKES, 1910, p. 208). With regard to the floral axis itself, however, the facts are sufficiently simple and clear, if their interpretation has been often obscure and involved.

(1) Two small leaf-rudiments, transversely placed, have been described for a few cases in flowers at the base of the cone by LIGNIER and TISON (1912, p. 129), and these are regarded as leaves, and not mere protuberances of tissue filling gaps, because they have a bundle-supply; and, according to these observers, the vestigial bundles may be traced even when these leaves are wanting. There is always a fundamental objection to the recognition of “vestigial bundles” formed to supply

non-existing tissue; but, taking the observations at their full value, they imply a production of two transverse prophyll members, which might be normally expected to continue the phyllotaxis system. The progressive loss of such members and their vestigial retention in the lowermost flowers of an inflorescence system is a familiar feature of floral organisation in higher plants. The mere occurrence of such rudiments does not, however, in the least postulate that any further members of a decussate system are to be hypothecated, unless they can be actually proved to be present (LIGNIER and TYSON, 1912, Whorl II).

The rest of the flower consists of a terminal ovule. There can be no doubt about the fact that it is an ovule, being composed of a massive nucellus, with central megaspore and endosperm, and this is invested by two envelopes.

The outer envelope springs from the extreme base of the ovule, and is enormously extended tangentially to give rise to a wing-expansion, ultimately utilised in seed-dispersal. To all intents it is a simple outer integument (SYKES, 1910); but, following the use since the time of HOOKER (1864), it may be convenient to still designate it "*perianth*." In the functional flower it is a delicate wing, about 10 mm by 12 mm., following the general contour of the subtending bract, to which it is closely adpressed (fig. 3). It completely encloses the nucellus and base of the styler tube as an efficient investment, only a small aperture as a slit between tooth-like edges at the apex allowing the styler tube to pass through. Histologically it is remarkable for differentiation into—(1) an inner region of thin-walled aqueous tissue, on either side of the ovule, continued over the narrow diameter of the ovule as an aqueous epidermis only, and just covering the nucellar region; (2) a production of peculiar, wavy, wandering fibres, with cellulose walls, which ultimately contribute the greater part of the tough papery wing of the seed; (3) a membranous peripheral region of small, undifferentiated tissue, mainly epidermis only. Two teeth, diverging in the ripe seed as prominent horns,* obvious to the eye, apparently exaggerate the lobing of the aperture of the envelope; but such irregular teeth, more especially in the form of two lateral lobes, are in no way suggestive of definite perianth-members in the transverse plane of the diagram (*cf.* LIGNIER and TYSON, 1912, Whorl III). Two lateral bundles run up to the apex of this outer investment, just outside the aqueous inner zone, to supply the comparatively large mass of tangentially extended tissue in the most direct manner, and LIGNIER and TYSON (1912, p. 143) naturally regard them as confirmatory evidence of two component members, and, in fact, the homologue of two stamen-traces.† On the other hand, SYKES (1910) prefers to trace an analogy with the cupule of *Lagenostoma*!

* In the adult seed the cells in this region share in the general tendency to fibrous elongation, and the "lip" processes are thus extended as slender wisps of fibrous cells and may attain a length of 5 mm. (fig. 9).

† In the adult seed six bundles pass up the neck of the perianth-region. These have a symmetrical orientation, recalling that of the six filaments of the andrœcial whorl (fig. 9).

The inner envelope rises as a delicate tube from the level of the original megaspore; in the flowering stage, about half way up the endosperm. It is a mere slender tube, prolonged beyond the apex of the nucellus in the familiar "stylar" extension, like a slender hollow bristle, 0.25 mm. in diameter, with a fairly uniform circular bore, 0.1 mm. in diameter. Its wall is only five to six cells thick, and the lining epidermis presents a thick brown cuticularised wall around the cavity of the tube, which undoubtedly assists in mechanical support. This tube extends for an ultimate length of 10–12 mm., and protrudes in the flowering stage for 4–5 mm. beyond the tip of the subtending bract. It terminates in a distinct funnel-shaped expansion, not so definite, it is true, as the mushroom-shaped head of the integument of the staminate flower, but recognisably the same sort of thing, 0.3–0.45 mm. in diameter, with a ragged papillose fringe of segments. In spirit material of adult cones, the tips of the tubes are commonly broken off or damaged; they are better seen in examples which have not yet extruded beyond the bracts of the cone. The slender wall contains no visible vascular supply: though SYKES (1910), by continuing an imaginary line, suggests that some traces ought to belong to it, and LIGNIER and TISON (1912) have traced slender strands of undifferentiated tissue just into the base where it is slightly more massive, though without any indication whatever of the four hypothetical carpels. To this structure the term "integument" may still be applied (HOOKER, 1864): no evidence is so far forthcoming that it can be regarded as an "ovary-wall" (STRASBURGER, 1872; LIGNIER and TISON, 1911). The most reliable evidence concerning these structures should be obtained from developmental stages; and these are readily obtained without any difficulty from the axils of the uppermost scales of a functional cone.

Stages of development have been more or less illustrated by HOOKER (1864) and McNAB (1872) and others, but the main facts are still somewhat confused. Drawings of early stages are given (figs. 5–8) for sectional elevations of transparent buds seen from the anterior side; while sections of the cone-apex give median elevations for stages numbered in agreement with the tangential ones (fig. 5). It may be noted that observation of floral development is mainly a question of plotting curves: the time has passed when freehand drawings of primordia are of any real use. All such figures require to be (1) planned carefully to the same scale, so far as possible; (2) all curves to be followed with the greatest exactness; (3) the figures should be sufficiently large to express the ultimate detail due to cellular structure, and (4) the relative size of the cell-units should be indicated for comparison with that of the primordia. Figures in which the individual cells of the young meristems are 1 or 2 mm. in diameter are to be preferred. Such developmental figures indicate in a manner which can be measured, the marked tangential extension of the flower-bud from the earliest stage (figs. 5–6: 1–3.) Hence generalisations based on the manner in which primordia usually arise in centric phyllotaxis systems require to be carefully revised: ellipsoidal extension does not necessarily indicate two lateral primordia. In this case

the young buds are about three times as broad (tangentially) as they are deep (radially).

The outer envelope arises first as a fairly uniform collar on the definitely stalked primordium-axis (fig. 6: 2, 3, 4). This is generally agreed (HOOKER, 1864, PEARSON, 1908, LIGNIER and TISON, 1912), but with subsequent tangential growth it becomes more prominent laterally, and has been commonly regarded as indicating two lateral primordia. But there is no definite evidence of such primordia at all (fig. 6: 5-7). The edge of the tangentially extended collar, thicker at the ends than at the sides, where it is under pressure, becomes lobed as it extends into the free space in the axil of the subtending bract; and, lateral growth being exaggerated, it tends to further develop in this direction; but subsequent lobing is wholly irregular, a third lobe may even be as conspicuous (fig. 7: 8), and in later stages the irregular lobes converge over the cavity of the flower as a loose saccate envelope, through which the inner integument tube will be ultimately projected. The margins of this growth, and the so-called lateral lobes, have at no period the characteristic clean wave-outline or smooth curve of an appendage-primordium; and to interpret such irregular protuberances as indicative of leaf-members is going beyond the range of structural morphology. Evidence in favour of the constitution of this "perianth" from a whorl of a decussate series is then weakened by the facts of development. It is interesting to note that a similar free outgrowth of lateral lobes from the integument of *Pinus* into space left free on the flanks of an ovule packed in the axil of a cone-scale has been in the past similarly interpreted as indicative of two leaf-units (STRASBURGER). So far, then, there is no direct evidence whatever that the outer envelope may be regarded as based on two leaf-members. It is a simple tubular investment with an irregular edge, to which the term "perianth" may remain applied as an innocuous convention, and the use of the term "integument" may be avoided since it arises first in development.

Similar phenomena are characteristic to a less marked degree of the *inner envelope*, which arises later, but is less extended laterally. At first a uniform collar (fig. 6: 3, 4, 5), its margin also grows irregularly into wavy folds (fig. 7: 8, 9, 10); with sometimes a similar suggestion of two lateral lobes (fig. 7: 8), or at others several quite irregular projections which may be confined to a definite group of cells. There is no definite evidence whatever of two or four lobes symmetrically placed, or arising as clean-grown protuberances, which might be expected if the structure were composed of four carpels (LIGNIER and TISON, 1912, p. 154). In subsequent stages the irregular marginal growths become a definite fringe, in which individual marginal cells may grow out into long papillæ; this being particularly well seen in the case of buds 6 mm. long, in which the integument just protrudes beyond the outer envelope (fig. 2). Hypotheses built on the fact that lateral lobes of the compressed envelopes, both outer and inner, are indicative of component leaf members of a presumably decussate system, of which the median members have therefore been lost, are wholly speculative and serve no useful purpose. Nothing can be gained by trying to force all facts into a

decussate scheme, in order to homologise the staminate and ovulate flowers : in fact a much wider view of the possibilities of *Welwitschia* is gained when decussate construction is entirely eliminated as a non-essential detail.

The *archesporial cell* is indicated at an early date, usually being recognisable from the first. A similar archesporium in the apical growing point of the cone was found in all specimens examined, and may be taken as the rule (PEARSON, 1908).

The archesporium remains very definitely at a level just above the origin of the inner envelope. Subsequent intercalary growth in the region below it delimits two regions in the nucellus : (1) An upper *pyriform* portion enclosed by the integument, above the developing endosperm ; and (2) a basal region which contains most of the endosperm, and extends with its growth to an ovoid shape, as the body of the nucellus proper, the function of which is the nutrition of the endosperm. Extension of this basal region gives in median section the appearance of a long stalk ; in the tangential elevation this is seen to be due to the great development of the perianth wing-extension. The apex of the nucellus, squeezed into the orifice of the integument, takes on a definite mamilliform appearance (figs. 2, 4).

The vascular system has been elegantly worked out by LIGNIER and TISON (1912, p. 143) ; but the supply of the postulated five whorls is not particularly convincing. Figures of bundle-strands, in a comparatively very small structure, in which the exact significance of the tissues interpreted as "bundles" remains obscure and the dimensional relations of these cells to the adjacent parenchyma are not given, remain unsatisfactory. They afford no evidence of carpellary origins. On the other hand, when it is recognised that the plexus of small strands at the base of the nucellus has a relatively new and important function to perform in the provision of a water supply for a copious exudation of sugar solution from the nucellar tissue beyond the endosperm, it is difficult to regard them as vestigial and, presumably, functionless carpel traces, rather than a fairly symmetrical provision of conducting tissue as a direct adaptation for a definite and important function.*

A feature of special interest in the construction of the cone is the question of *pressure*. This requires to be carefully examined before being put forward glibly as a cause of decadence in floral structure. The main causes of floral reduction are want of food, especially water supply ; young growing tissues can always grow at the expense of older ones, and the assumption that members are flat because

* On the other hand, it may be noted that the vascular supply of the nucellar region persists on into the seed stage and is then well marked. In the adult seed the remains of the nucellus persist as a tough membranous sac, 10 mm. long, which may be readily dissected off the endosperm. On warming with H_2SO_4 and phloroglucin, the bundle system is clearly seen. From the main series of four strands at the base of the nucellus simple strands, without cross meshes, six to eight in number, without precise orientation or definite arrangement, pass up near the outer surface of the nucellus without reaching the free integument. It is difficult to imagine that it would be possible for such a functional gynoeceal region to lose all record of "vestigial carpellary bundles" (*cf.* LIGNIER and TISON, *loc. cit.*, p. 152), while they might be retained in the sterile much less differentiated ovule of the staminate flower.

they are under pressure is as much a psychological obsession as that spiral growth effects are always due to torsion. As already indicated, the ultimate lobation of the outer envelope, as also its great wing extension and the two transverse teeth exaggerated in the seed, are but the result of the free margins growing in the open crevice left between the scales as the growing ovules push them apart. In any aggregated mass of members, if growth be uniform throughout the mass, there need be no pressure at all, or all the contact pressures may be equally distributed. Pressures are only set up when one member grows faster than another; and such pressures require to be fully established before any theory can be based on them. In the case of *Welwitschia*, the pressure is set up not so much by the cone-scales against the flowers, as by the flowers growing at the expense of the cone-scales. The nucellus retains its circular section very fairly; the scales are forced apart and squeezed, and the effect of the ovule pressure is most obviously seen in the fact that if all the ovules press equally they would make accurate ridge-lines on the cone. But, by slipping over each other slightly, they make mutual adjustments, as seen in longitudinal section along the orthostichy lines, which cuts the superposed ovules differently. Hence the sectional elevation (fig. 2) is slightly diagramatised, and successive scales pushed slightly more open than they should be, so that the fitting of the parts is not absolutely accurate as in nature. That is to say, the greatest pressure is exerted along the orthostichy lines by the flowers pressing against their predecessors, in default of sufficient extension in the main axis. Actual measurements give a clear idea of the amount of deformation from circular section. In the functional stage the lower part of the nucellus, enclosing the endosperm at its broadest, is about 2.1 mm., tangentially, by 1.2 mm. in the radial direction, a very considerable flattening; the enclosed prothallus being 0.85 mm. by 0.65 mm. The upper region, being much smaller, tangentially, remains fairly circular, 1.15 mm. by 1.3 mm.; the pressure being taken by the lower portion. Similarly, the cavity of the perianth enclosing the stylar tube is 0.34 mm. by 0.35 mm., and the stylar tube itself practically circular at 0.1 mm. That is to say, it is the growth-pressure of the basal part of the nucellus which does the work of opening up the flat chink between the scales, into which the perianth-tube extends in the functional flower. In the earliest stages, the deformation of the bract and the pressure of the flower is followed in developmental figures (fig. 5); and the resultant chamber left between successive scales in fig. 2. In the case of the staminate flower, with ovule of much the same size, growing under closely similar conditions, between very similar scales, room is still found for the whole andrœcium and perianth members in the chink above and on the flanks of the ovule which takes the pressure; so that mere pressure in the bud will not account for the extensive reduction of the ovulate flower, which, as in the case of higher Angiosperms, reduces by obliterating all parts except those which have a present essential function. It is, in fact, the biologically important seed-dispersal wing of the perianth which

monopolises not only all the room in the cone but also the food supply, and thus appears as a secondary useful alternative for a production of useless vestigial organs.

It is also convenient at this stage to mark a distinction between a *cone* and a *strobilus*, the former implying a condensed xerophytic structure which aims at presenting the smallest transpiring surface for its volume, and hence approximates a spheroidal or ovoid form. That such ovoid cones are advantageous in the case of constructions developed inside bud-formations is sufficiently obvious, and is generally held as sufficient to account for the assumption of such a form. But development inside a closed protected bud-cavity is again only a form of xerophytic adaptation; so that both from this standpoint, and from that of exposing minimum surface, the cone comes back to a xerophytic adaptation in inflorescence-construction, derived from an indefinitely elongated strobilus (*cf. Alnus*, ♂ and ♀). To attain such a cone-construction form with a given decussate phyllotaxis is not easy; there are two alternatives: (1) either a few members only of approximately isodiametric surface facets are retained (*cf. Cupressus* cone), or (2) more members can be put in if these are enormously thinned down by growth-retardation in the longitudinal direction. The thin laminae of the cone-scales are not pressure-effects, but phenomena of growth regulated to a given aim. Correlation of growth in the main axis will still allow the ovules to expand fairly equally in radial and tangential directions. We thus get a working idea of the general phylogenetic sequence of events in the history of the plant. Given decussate phyllotaxis in the inflorescence-scheme (itself a structural feature derived from an assimilating shoot-system in which it constitutes a xerophytic modification, in that it admits of practically maximum superposition of leaf-members, and consequent minimum exposure to intense light which promotes excessive transpiration), further specialisation along the same path would lead to the condensed conoidal construction still retaining a full number of flowers. The flattening of the only apparently tangentially extended scales by excessive radial retardation follows; and the pressure of the growing ovules, no longer fully compensated by internodal extension of the main axis, opens up chinks between the scales into which the free ends of the floral members grow to fill up all available room. Hence the thin laminar extension of the perianth, which soon finds a new use from the standpoint of wind dispersal; and this, with consequent precocity of formation, usurps the place of all other useless parts. There is no reason why these may not have once included functionless stamens derived from a once hermaphrodite flower, although there is no direct proof available at the present time. These correlations are not merely fanciful: they afford a logical sequence for the deduction of the fact, sufficiently obvious, though requiring to be established, that the ancestral cone was a more elongated strobilus, in the axils of whose scales arose centric flowers and a centric nucellus invested by centric envelopes, without lateral extensions. Furthermore, in such a cone, the scales would at some time have been separated by internodal

extension, so that the pollen-grains fell between the scales directly on the nucellus; the micropyle being a mere collecting funnel to which a long tube was non-essential and non-existent. That is to say, it is sufficiently clear that at one time (1) the cone must have had an opening mechanism; (2) it was originally essentially strobiloid (even if we had not at hand the staminate cone, with about an equal number of less reduced flowers, since less xerophytically adapted owing to its transitory existence); (3) the outer envelope, originally centric, showed differentiation into at least internal aqueous tissue and an external zone of fibrous wavy cells, now no longer sclerosed, but originally affording a sclerosed investment to the seed, in the manner of a sclerotesta, or even more suggestive of the interwoven fibres which constitute the drupe-stones of such plants as *Hedera* and *Ilex*. The special peculiarity of the ovulate flower of *Welwitschia* really owes its existence to the loss of the opening mechanism. In response to extreme xerophytic conditions the cones became *cleisanthous*, and the integument extended to reach the surface, in a manner which recalls a stylar growth, though it can never afford any nutrition to pollen grains through the thick cuticularised lining wall. There is now nothing to show to what extent the outer envelope may have been originally a pollen-collecting integument, or what may have been the original mutual relations between the two envelopes. Developmental stages suggest that the outer is the survival, as a merely loose investing envelope, of what may have been once a gamophyllous leafy perianth; and though the evidence of two component leaves is at the present time negligible, it is possible for the gamophyllous zone to be retained when the actual free members have been lost. Thus a gamophyllous perianth of two median members, with feebly developed free lobes, is actually present in a phase of degradation in the staminate flower. With such a loose investment to the central nucellus, the micropyle was probably originally carried to its exterior by a "stylar" prolongation; since in development it at first always lags behind the perianth (fig. 2). The subsequent rapid acceleration of its rate of growth to form the present 10 mm. tube suggests that it is only the excessive elongation that is secondary. That is to say, given an elongated "stylar" micropyle for some such preceding cause, its present extreme extension is clearly a secondary modification, occurring late in development, and consequent on the assumption of the cleisanthous condition by the cone as a whole.

The fact remains that neither the cone nor the flower present any mechanism in terms of a special growth-factor beyond the gradual elongation and protrusion of the "stylar" tube. There is no ultimate internodal extension to open up the subtending scales, and the extruded tubes merely push back the slender tip of the bract in their passage. In this continued growth the tube again merely follows the course of the simple curve impressed on it in following the contour of the bract-scale, the result being that it only rises about 1 mm. free from the cone-surface, and displays no further structural modifications for insect pollination.

Biologically the essential point of interest centres in the *starch-storage* of the

young ovule. At a time when the stylar tube has not yet protruded, so that the flowers cannot be termed functional, starch accumulates abundantly in the cells of the nucellus, and especially in the pyriform terminal portion, which turns intense black with iodine solution, with the exception of the larger celled aqueous epidermis. Definite storage also obtains in the basal region and around the endosperm, while in the envelopes starch is curiously restricted to the thick-walled inner epidermis of the outer envelope, and to a less extent in the epidermis of the inner envelope and stylar tube. As we know from PEARSON (1907) that a very definite and copious exudation of sugar, as an "intensely sweet viscous drop," takes place from the stylar tube, and suffices to attract insects, more particularly a field bug, *Odontopus sexpunctulatus*, it is evident that this sugar is formed at the expense of the starch in the upper portion of the nucellus, and that the fluid rises 10 mm. in the tube to reach the exterior.

In this way we get a very clear idea as to the probable sequence of events in the transition of such a flower from a condition of anemophily to that of entomophily, assisted more particularly by conditions of desiccation as an antecedent to the successful visitation by secretion-seeking insects. The familiar drop-mechanism of the Gymnosperm takes sugar from the nucellus in increasing quantity, and this region is utilised as a nectary in the most direct manner possible. The whole of the sugar must come from the nucellus apex, so that the pyriform apical portion of the nucellus now functions primarily as a nectary, and may be distinguished from the very distinctly differentiated basal region which has so far been nourishing the endosperm. The cells of the outer envelope with thick outer walls cannot assist in the secretion, as their exudation would not reach the exterior of the cone, while the epidermis of the inner envelope and stylar tube is cuticularised, and thickened to such an extent that the outer wall is as thick as the lumen is wide, and shows no perforations. To what extent the active storage of starch in the nucellus apex has for its primary function the intensification of the drop-mechanism as a definite nectary, or whether it was primarily intended to feed the pollen-tubes, or again to what extent these functions may be correlated with the undoubtedly secondary function of feeding the cœnocytic cæca of the endosperm ("prothallial tubes" of PEARSON, 1908), may be left an open question. The point remains that the relation of the stylar tube to the secreting organ is sufficiently clear from the standpoint of the present floral organisation and its entomophilous condition. Although a slight depletion of starch is to be noticed in the cells immediately adjacent to the cœnocytic endosperm cæca before pollination, it is evident that only a very small amount is utilised for this purpose, and the same applies to the germinating pollen tubes. Successfully pollinated ovules apparently still present this excessive amount of starch, so that its ultimate function is that of feeding the embryos. Depletion of the cells at the apex of the nucellus, and their disorganisation, as in the case of *Pinus*, takes place obviously, and has been described by PEARSON (1908). On the other hand

the amount of sugar secreted must be considerable. According to PEARSON a drop of sweet fluid stands on the tip of the projecting micropyle as the exudation concentrates on evaporation; and the stylar tubes apparently exude for a considerable time, two or three days. As it is at first sight not very clear how pollen-grains can be collected in large quantities, the tubes being filled (PEARSON), and be drawn down a distance of 10 mm. to the nucellus, PEARSON (1908) suggests that the grains sink by their own weight, though the tubes are not vertical and the solution is apparently dense. It would appear that the secretion is poured out intermittently, for example every morning, to condense by evaporation during the heat of the day. In this way pollen-grains may be drawn back, and new dilute fluid rise over them each day over quite an extended period, more grains being collected with repeated diurnal insect visits, though wind-borne grains would be equally well retained. According to PEARSON (1908), excretion lasts from sunrise to sunset, or from 9.30 A.M., at any rate, as late as 3 P.M.

The presence of this highly plasmolytic concentrated sugar solution in the stylar tube now explains the necessity for the previously noted starch-storage, the thick walls and cuticle of the cells lining the canal as pseudo-xerophytic characters induced in tissue presumably bathed by a concentrated solution. It is clear (*contra* PEARSON, 1908) that such living cells can have no nutritive function. The excessive starch-storage of the nucellus thus bears a relation to the following functions:—

- (1) The provision of the exudation for a drop-mechanism.
- (2) The nutrition of germinating pollen-tubes.
- (3) The nutrition of endosperm cæca.
- (4) The nutrition of resulting embryos.
- (5) As the sugar passes out with the fluid of the original drop-mechanism, the more it evaporates and so tends to accumulate outside the micropyle, the more available does it become for low-grade insects which seek plant juices. The presence of abundant starch-storage thus provides the wherewithal for the assumption of a new function.

It is even possible that the peculiar fertilisation processes of *Welwitschia* owe their special modifications to the same excessive storage of nutriment and a necessary efficient water supply below the pyriform apex of the nucellus, with the result that the early stages of embryology are extra-endospermial, within the pyriform apex; the suspensors thus at first drawing their food supply from the nucellus instead of *viâ* the endosperm, as more normally obtains at a later phase.

The point is that it is the *pyriform apex* of the nucellus, as opposed to the basal intercalated region, which is the part essentially concerned in all these functions, and the region which now undoubtedly subserves the function of a nectary; the intense starch-storage affording the primary point of interest and importance. It will be shown later that the same pyriform region is present and exercises the same nectary function in the staminate flower.

The floral mechanism of the ovulate flower may thus be included under the special heads:—

(1) *The evolution of an extrusive micropylar extension* as a “stylar” tube, in a closed cone-construction, as a special xerophytic adaptation consequent on the cleisanthy of the cone-mechanism.

(2) *The intensification of the drop-mechanism* to subserve a nectary function in relation to insect visits.

(3) *Pigmentation effects*: According to PEARSON the young cones are green, but turn red after the style tubes are exerted; older cones turn yellow. The red colour is intensified at the angles of the cone, *i.e.*, along the bract “midribs,” as if to emphasise “honey guides” along the orthostichies (PEARSON, 1907).

(4) *Elimination of all parts not directly functional* and strictly utilitarian, as the expression of extreme reduction specialisation, by which the flower is reduced to a minimum expression, both morphologically and physiologically.

(5) *Time factors* for the duration of the secreting period, rate of successional flowering, etc., not yet recorded, beyond the statements already quoted from PEARSON.

II. THE STAMINATE CONES.

The *construction of the staminate inflorescence* repeats that of the ovulate system. The inflorescences have similar origin, and ramify also to the third and fourth degree as decussate systems. All end branches terminate in sterile buds or spikelet-like constructions which constitute the biaxial staminate cones or strobili. These are much smaller than the ovulate cones, the best noted being 30 mm. by 8 mm. only; more slender and spindle shaped, and commencing to produce functional blossoms when 20 mm. long. They produce a total of about 70 flowers, giving 18–19 in each vertical orthostichy line, along which as many as six may present extruded stamens; these are fairly uniformly spaced over the flowering surface, the anthers being nowhere more than 2 mm. apart. The inflorescence system differs in: (1) the smaller size of the end “cones,” and (2) in the relative greater length and more slender development of the internodal extensions; the resemblance to clusters of spikelets of a *Cyperus* form being still more pronounced. As these clusters are 5 (= 2+2+T) as often as 3 (= 2+T), the expression “dichasial cymes” should be avoided. (*Cf.* Photo; PEARSON, in ‘Nature,’ 1907, p. 536.)

At the base of each cone a few sterile scales may be found; less frequently the cone is fertile to the base, or the two prophylls alone are sterile. The apex shows rudimentary flowers, the uppermost of which, as in the case of the ovulate cone, probably never become functional. Full developmental stages are similarly to be found near the apex. Time factors for the duration of the cone and the extent to which it may continue to produce functional staminate flowers are not available (fig. 10).

The *subtending bracts* are markedly connate (4 mm. by 5 mm., and connate for 2 mm. up); they are smaller and less differentiated than in the case of the ovulate

cones; the vascular system is based on the same plan from two leaf-traces, but the dichotomy is less precise (*cf.* LIGNIER and TISON, 1912, p. 100). The general structure of the functional staminate flower is sufficiently simple and well known (HOOKER, 1864); but much theoretical discussion has involved considerable elaboration of details on often extremely vague and insufficient evidence.

From the widest general standpoint the flower may be regarded as an anthostrobilus construction in which well-defined regions, (1) perianth, (2) andrœcium, (3) gynœcium, are successively represented; and it may be added that, as among modern Angiosperms, these regions once elaborated may be specialised or reduced each wholly independently of the others. These three regions may be thus considered separately.

I. *The Envelope Members or Perianth.*—The term “perianth” was applied by HOOKER (1864) under the impression that four membranous leaf-members were present, arranged 2+2, in normal decussate series. Of these, two outer members, arranged in the transverse plane of the system, consist of membranous scales, flattened in the transverse plane, with broad winged or keeled midrib; they contain no vascular tissue and consist of epidermal layers enclosing a small amount of parenchyma and longitudinal sclerites. Theoretically they represent the lateral prophylls of the axillary system, and may be so termed (fig. 11). It is interesting to note that in some cases (HOOKER, 1864; LIGNIER and TISON, 1912) these members may be united below on the posterior side of the flower, and thus give a case directly parallel to the so-called “two-keeled prophyll” of many Monocotyledons, which similarly always arises from two primordia and represents two members.

Succeeding these, two median members (4 mm. by 3 mm.) are gamophyllous for a distance of 2.5 mm. to form a flat sac-like investment (gamophyllous perianth) with free rounded lobes which just reach the level of the staminal tube. In the bud these alone constitute the close investing envelope over the essential organs, and hence may be regarded as a true perianth, reduced in a decussate system to the minimum number of members (2) which will make contact round the axis. These members again contain no vascular tissue, but consist of little more than an epidermal system enclosing a single series of longitudinally extended sclerites. They afford the best possible material for the exhibition of these structures without cutting a section. The posterior lobe is more developed than the anterior, and overlaps in the bud all round its free margin, thus sealing the bud-chamber as an efficient protective investment, to which the term perianth may be therefore restricted (fig. 20).

II. *The andrœcium* is represented by a series of six stamens carried up on a massive staminal tube, which reaches the length of the subtending bract and projects the stamens beyond the surface of the cone. The tube is 4 mm. long, 2 mm. broad tangentially, and 0.8 mm. deep in the median plane. Six vascular bundles pass through it to supply the filaments of the anthers, and then terminate in a group of transfusion tracheides in the connective region. The filaments are about 1.3 mm. long, and are incurved and inarched in different degrees, as distinct posterior, lateral,

and anterior pairs. The posterior pair erect, and lie against the next upper scale, the anterior bend forward at almost a right angle to the preceding, the lateral inarch in the transverse plane. The anthers, about 1 mm. each way before dehiscence, shrink to half this size when discharged; they are borne on the ends of the filaments, are three-locular, and dehisce by three slit-pores on their upper surface. The dehiscence mechanism is indicated by banded cells of the whole epidermal surface. The pollen grains are oval, striately marked with several meridional ridges, and 0.055 mm. by 0.04 mm.

Special interest attaches to the interpretation of the androecium, since it was described by HOOKER in 1864, from the standpoint of the theoretical diagram, additional evidence, of doubtful value, having been adduced from (1) the facts of development (McNAB, 1872; STRASBURGER, 1872) and (2) the bundle supply (LIGNIER and TISON, 1912).

The most general account (HOOKER, 1864) simply states that the six stamens, being all alike, and similarly carried up on a tube extension, represent a single whorl of six members, placed symmetrically around the flower, with two transverse members, and no exactly median ones; this being the arrangement seen directly on looking at an open flower, or on cutting a section of the anthers as arranged in the bud, or a section of the staminal tube with its vascular bundles. This view states simple easily checked facts, and indicates that the androecium is *not conformable* with the preceding decussate perianth and prophyll system.

On clearing a flower with potash, it is easy to see that the bundles supplying the lateral stamens appear to come away from the central system at a level definitely lower than those supplying the other four, in fact, 0.18 mm. below them. Again, the lateral members were said to arise slightly earlier in development. On these facts the supposition was put forward that the androecium was to be regarded as a (2+4) type (STRASBURGER, 1872).

Another view, originating with McNAB (1872, p. 512), suggested that the six stamens were better regarded as two sets of three, or two single stamens with three branches bearing anthers; as a matter of fact, the branches do run up the sides of the staminal tube in widely spaced sets of three along the angular edges, and McNAB's figures, as also those of STRASBURGER, apparently so clearly support this view that it has been since generally accepted without question (PEARSON, 1908); while LIGNIER and TISON have endeavoured to support the view by exhaustive study of the vascular system of the adult flower, in order to make it fit in, as an androecium of two lateral stamens, with their views on the five-whorled decussate flower.

In dealing with this class of evidence it must be remembered—

(1) That the secondary supply of vascular tissue to members already in existence does not necessarily denote morphological origins; while the vascular supply of a secondary zone of growth (as a staminal tube) does not necessarily repeat that of the original free members.

(2) Time factors in development indicate relative rates of growth, and do not give absolute evidence of initiation unless the construction is symmetrical and centric.

(3) Nothing is gained by trying to force the andrœcium into a decussate system conformable with the perianth. There is no obligation whatever for so doing nor any advantage to be demonstrated by continuing the floral phyllotaxis system from the vegetative shoot into the sporophylls. As already noted, there is nothing particularly valuable about a decussate system; in fact, we obtain a much wider view of the flower of *Welwitschia* if strict decussation can be shown to be wanting. Its real history is undoubtedly much more complicated than such a simple standpoint would admit.

On the whole, the evidence of the six stamens being anything more than they at first appear, a single whorl of six equal members, does not seem in any way conclusive; it was founded on the developmental figures of McNAB and STRASBURGER, the mistake of which will be explained later; and, so far, the andrœcium may be accepted as a whorl of six stamens, tangentially extended in the specially flattened flower, and not conformable to the preceding perianth, but a separate construction, indicative of a special andrœcial region of the flower, with a certain individualisation of its own, but here found in the form of a certain almost minimum reduction phase, just as the true perianth is a minimum of two members.

The interpretation of floral morphology, as based on much of the older developmental work, is often extremely vague and unsatisfactory, and the suggestions above quoted would perhaps not be so unconvincing if there were not an accurate parallel already at hand and under common observation. Identically the same three interpretations have been applied to the reduced andrœcium of many members of the *Rhœadineæ*; whether as six stamens in a whorl (two lateral and four symmetrically placed) *Cleome spinosa*, 2 + 4 in the tetradynamous Crucifer, and two lateral sets of three, interpreted as branched lateral members, in *Corydalis*. As it is sufficiently clear that if the *Rhœadineæ* form one coherent group at all, the story of the andrœcium must run conformably throughout; it should be also sufficiently obvious that the indefinite andrœcium of *Papaver* and *Capparis* represents the full type of the group from which reduction has followed to progressive minimum phases of efficiency. It is interesting to note that a sufficient number of reduction stages are still in existence (*cf. Reseda, Polanisia, Cleome*), leading to the final tangentially extended types of the Crucifer and *Fumariaceæ*, in which lateral stamens of a group of six may have a slightly different bundle-supply, and even appear to arise earlier in development. It is fair to suppose that the case of *Welwitschia* is an exact morphological parallel, and to be regarded as a specialised tangentially extended reduction limit of a wholly indefinite whorl sequence (*cf. Reseda* and *Cycadeoidea*), which is in turn similarly a reduction expression of an indefinite sequence, the irregular construction version of a once accurate phyllotaxis mechanism which controlled the elaboration of a full strobilus of microsporophylls.

III. The *gynæcium* is at first sight equally simple; a central terminal pyriform nucellus-like mass (1.5 mm. by 1.2) is surrounded by a thin envelope (integument), only 3–4 cell-layers wide, and this is continued as a long, slightly kinked, “stylar” tube (2 mm.), which terminates at the level of the top of the staminal tube in a flat “stigmatic disc,” just 1 mm. across, and covered with remarkable thick-walled papillæ which give it the appearance of a basket of eggs on end. These terms introduced by HOOKER (1864) still remain expressive, whatever the strict homologies of the parts. No embryo-sac or archesporial cell has been ever seen in the nucellus: the vascular supply of the integument is extremely doubtful (*cf.* LIGNIER and TISON, 1912, p. 111); but beneath the mass of the nucellus, which has a rounded base and pyriform shape, there is a bundle-system which may be conveniently termed the perinucellary plexus.

Interpretation again varies between regarding this as (1) a sterile, single integumented terminal ovule, and (2) an ovary of two median carpels (McNAB, 1872), or of four carpels (two median and two transverse) with a basal, orthotropous, erect, naked ovule reduced to nucellus only. From the former standpoint the “stigmatic disc” is the remains of a pollen-collecting micropylar funnel; according to the latter it would be a true stigma, on which pollen-grains once presumably germinated; but if the evolution of a stigmatic surface on which pollen-grains can germinate outside the ovary cavity is an up-grade character in the evolution of an Angiosperm from the Gymnospermous condition, it would seem curious that the stigma should be retained in a functionless condition in the staminate flower, while the ovulate flower, which is the important one, still allowed pollen-grains free access to germinate on the surface of the nucellus. The balance of probability thus remains in favour of the former view: evidence for and against being based on (1) comparison with the functional ovule of the ovulate cone and its mode of development; (2) study of the vascular supply (SYKES, 1910; LIGNIER and TISON, 1912).

(1) In the former case it is important to note that the integument springs from the base of the ovule, and the nucellus is definitely pyriform in shape, with a rounded base and mamilliform beak tip. No definite vascular tissue enters the pyriform mass itself, which consists of uniform rounded parenchyma storing abundant starch; but there is a plexus just below it. This may be termed the perinucellary system (SYKES, 1910). It is a well defined short zone between the exit of the upper staminal traces and the insertion of the integument, a distance of not more than 0.45 mm., corresponding to little more than a dozen rows of small parenchymatous cells between the staminal bundle and the base of the pyriform nucellus. Comparison of the structure of the ovule in the ovulate flower, in which it is evident that the basal region, containing the greater part of the embryo-sac, is clearly differentiated from an upper pyriform starch-storing region, while the archesporium was originally situated just at the level of the insertion of the integument, so that the basal region is largely secondary and intercalary, would

seem to indicate that the pyriform ovule here is the exact homologue of the apical section of the ovule of the ovulate flower; that in shape, size, and histology it is practically identical. The integument with basal insertion is the homologue of the integument of the ovulate flower, and the "stylar tubes" are homologous, though the cavity of the tube is here negligible, since pollen-grains do not have to pass along it; the kink is due to pressure in a confined bud, and the flattened stigma head, at first sight a new departure, is only an enlarged funnel with closed aperture, the essential and special feature of which consists in the remarkable specialisation of the epidermal cells of the expanded lips. The large rounded papillose cells, the outer walls of which are strongly thickened and pitted, the lumen being almost obliterated in the papillæ, are certainly not secretory, but indicate a marked xerophytic structural adaptation, the papillæ being restricted to the disc surface, and the edges of the lips, so far as to exactly close over the aperture to the tube.

(2) The relation of the vascular supply has been investigated by SYKES (1910) and LIGNIER and TISON (1912). Apart from the six bundles of the stamens, which pass in on the sides of the central cylinder, and connect up in a simple and direct manner, with cross connections between, making a simple girdle around the andrœcial node, the supply of the perinucellary zone above was given by SYKES as a simple symmetrical construction, based on small bundles taken off from the traces of the anterior and posterior stamens; the lateral members being spaced too far away on the flanks of the flattened bud, and the object being clearly to provide a simple vascular system, as nearly circular as possible, in the centre of the flattened axis, to supply the nearly circular base of the nucellus; the bundle cylinder being about 0.6 mm. by 0.45 mm. (SYKES, 1910, p. 188). A much more elaborate system has been built up by LIGNIER and TISON (1912, p. 109), and a very elegant scheme figured, which still presents a simple symmetrical plan of bundle-supply to this region, but emphasises the presence of two median bundles, arising from the trace girdle of the stamens, which ramify again and connect laterally to give ultimately four (two median and two transverse) strands, which to these observers suggest the vestigial traces of four lost carpels of a syncarpous ovary wall!

It must be remembered that these last traces contain no differentiated vascular tissue, but remain in the "procambial stage" only. They are difficult to follow: the two median are said to just enter the base of the integument (*loc. cit.*, p. 111). Ovules of older flowers, cut at the level of the insertion of the integument, and cleared in Eau de Javelle, show simple small-celled parenchyma with loose intercellular spaces but no sign of such strands. The figures of LIGNIER and TISON, drawn apparently from microtomed sections in canada balsam, illustrate contracted cells, the only differentiation being a thicker wall in the drawing. Still, even if the two traces do in some instances actually enter the base of the integument, and it is

not denied that the lower portions of such bundles are in a position to do so if continued farther, this does not invalidate the value of the integument as an integument; while it certainly affords no proof of carpellary nature. There is not the slightest reason to suppose, in the general morphology of Angiosperms, that a syncarpous ovary-wall, itself a secondary intercalated growth-zone, which replaces the original carpels, should necessarily retain the midrib bundles of the carpels after these had been completely lost as distinct primordia. The new syncarpous structure might have had a new bundle-system of its own, just as a gamophyllous perianth, or gamopetalous corolla, does not necessarily continue the midrib bundles of the original free members. Also, it must be borne in mind that the total distance for which this plexus travels is very short and small in comparison with the size of the tissues composing it. Bundle-schemes constructed in fine lines, which give no clue to the relation of the component elements to the adjacent cells, may readily create a false impression; so that judgment may be suspended until cell drawings are available. The fact which does emerge from these differing published accounts is that the plexus is a fairly simple symmetrical bundle-meshwork confined to a definite region. Its function is sufficiently obvious: it supplies the pyriform nucellus with an evenly distributed water supply, as a girdle and four free strands symmetrically arranged; just as a very similar plexus does in the more extended ovule of the ovulate flower; and here again, when we know the importance of the function of the system, the assumed phylogenetic value of the scheme, as indicative of hypothetical carpels, appears not so much far fetched as completely beyond the range of the evidence.

On the other hand, a floral form in which the gynœcium, originally composed of free carpels, had not only passed on to a condition of complete syncarpy, but had even lost all outward sign of the original carpel members, and had subsequently reduced the gynœcium to a mere rudiment, and much more rudimentary in the functional flower than in the staminate one, would have no claim to be regarded as a Pro-Angiosperm, since the limit of reduction-specialisation in the highest Angiosperm phyla can do no more than this at the present time. Analogies with ovary-structure in *Peperomia*, *Juglans*, *Myrica*, *Polygonum*, *Loranthus*, etc., are no more satisfactory than they would be with the gynœcium of a Composite or Crucifer.

Returning to the recognition of the gynœcium of *Welwitschia* as composed of a single terminal ovule, with a single integument, the question still arises as to what has become of the megasporophyll demanded by the carpellary theory. To this the answer is quite definite: similar terminal ovules are found among quite a wide range of distinct types of Gymnosperms: from *Cordaites* to *Ginkgo*, *Cycadeoidea*, and *Taxus*. If the megasporophylls of Angiosperms, in which they phylogenetically close up to constitute an ovary chamber for purposes of protection from desiccation, may be wholly lost and replaced by new and improved syncarpous ovarian formations, and be even reduced to mere free stigmatic tips (Composites, *Geranium*, etc.), and these in

turn be replaced by commissural stigmas (*Cruciferae*, *Lilium*) and other secondary stigmatic regions, it is sufficiently obvious that under xerophytic stress, in highly specialised Gymnosperm phyla, the functionless megasporophyll would be rapidly reduced and would soon entirely vanish, leaving its limiting single residual ovule alone in its place. The fact that such loss of the megasporophyll had taken place in the Palæozoic age (*Cordaites*), in the Mesozoic (*Cycadeoidea*), as well as in modern Taxoids, shows that *Welwitschia* is not particularly exceptional in this respect.

Its special significance and value is that it presents a reduction of the gynœcium to the *absolute minimum* in a floral structure that also contains an andrœcium, and was once presumably hermaphrodite. In this it is unique. While the ovulate flower of *Taxus*, for example, presents a decussate perianth of free scales (2+2+2), an aril used for a dispersal function, an integument and a terminal nucellus, the ovulate flower of *Welwitschia* shows two prophylls, a perianth of possibly two members originally, used for a dispersal function, a pollen-collecting integument and a terminal nucellus; a stage one degree more reduced than that of *Taxus*, but on distinctly the same lines. Not that there need be the slightest affinity or relationship between these types: we are only dealing with general principles of reduction to a minimum in different lines of descent. An analogous reduction to a minimum in a diclinous Angiosperm may present in the limit a floral mechanism closely comparable at first sight (*cf. Juglans*, etc.), if we did not know from other evidence that it was fundamentally different.

Again, to those satisfied with the drawing of less fanciful homologies, it is interesting to compare the staminate anthostrobilus of *Welwitschia* with its *three reduced minimum expressions of three successive non-conformable regions, i.e.*—

- (1) A perianth of two connate segments,
- (2) An andrœcium of a transversely extended minimum of six members in one bilateral tube,
- (3) A gynœcium of one ovule,

with the well known restoration of the anthostrobilus of *Cycadeoidea* (WIELAND), in which the same three regions are represented by—

- (1) An indefinite spirally arranged perianth,
- (2) A radially symmetrical andrœcium of one tube zone with a less reduced number of microsporophylls,
- (3) A gynœcium of an indefinite number of ovules.

As a morphological construction this flower of *Welwitschia* presents a remarkable parallelism in reduction, on lines clearly identical with those of *Cycadeoidea*, but carried much farther; as might be expected when the flowers of *Welwitschia* are small and still in strobili, while those of the *Cycadeoidea* were large and solitary.

It must be noted once more that these features do not necessarily indicate any relationship whatever with the *Cycadeoidea*, any more than certain resemblances in the reduction of the andrœcium show affinity to the *Rhæadineæ*; the apparent

resemblances are only cases of parallelism in the construction system reduced under similar conditions of extreme xerophytic environment, as expressed by inefficient water supply and feeble nutrition, along corresponding lines, as the working out of certain general elementary principles of morphology.

Most of the earlier *stages of development* are to be found at the apical region of a single cone when commencing to flower, and these suffice to bring out several details of interest, and emphasise the preceding generalisations. The point is to see if possible where error may have crept in, and to state precisely the actual facts.

An apical region equal to 5 mm. contains all the essential early stages, or even a shorter piece of 3 mm. On removing such a portion, and picking off the bracts, about 12 pairs of flower-buds will be obtained, in graded sequence to the earliest primordia just behind the growing point. As in the case of the ovulate cones and their young flowers, the smallest of these are most readily investigated, owing to their flattened form and posterior flat side, by clearing them in potash and observing them from the anterior side, as in the manner adopted for the elevation of the adult flower in the tangential plane, and a series of figures (about 12 stages) can be readily drawn to scale to correspond. Similarly, also, sections cut in the longitudinal orthostichy plane of the cone give a sequence of graded flowers for comparison and measurement; but it is obvious that the fuller view of the flower as a whole is that in the tangential plane, or transverse plane of the floral diagram.

The apex shows a terminal dome-shaped growing point, about 40 cells limiting its periphery, and continuing the decussate construction, the young leaf-members being distinctly connate from the first. The primordia of the flowers are simple normal axillary protuberances (fig. 15 : 1). These soon elongate, and give rise to two lateral prophylls as normal leaf-rudiments (fig. 15, No. 2 bud, 0.23 mm. long). The young axis shows a definite tendency to extend in the tangential plane, and as in the ovulate flower may be nearly three times as broad as deep; and the ratio is fairly maintained. The next two members grow up in the median plane, as flat laminæ, like a bivalve shell, almost enclosing the growing apex. From the first the posterior segment grows at a rate greater than that of the anterior and soon overlaps it (fig. 15 : 3; bud 0.3 mm. long). Even at this stage, as soon as the perianth is well differentiated, the floral axis shows a sign of differentiation into two regions;—a lower andrœcial region wholly enclosed by the two perianth-members, and a terminal gynœcial cone (fig. 15 : 4; bud 0.3 mm.). The andrœcial region extends to a dome-shaped mass, flattened tangentially, on which the gynœcial region remains as a fairly circular terminal papilla; as the bud is nearly three times as broad as deep, the andrœcial region stands out laterally as two shoulder-like masses. Such a distinct differentiation of regions preceding the elaboration of further primordia is a definite and somewhat unusual state of things, found, for example, in complex floral constructions of Angiosperms (*cf.* Malvaceæ), and it serves to indicate directly that the construction as a whole is by no means a simple phyllotaxis formation (fig. 15 : 5; bud, 0.4 mm. long).

This andrœcial region was clearly figured by McNAB (1872, p. 512, figs. 3-4): he termed it the "primordial staminal cushions." STRASBURGER (1872, fig. xviii: 3, 3*b*) also mistook it for the commencement of the lateral stamens ahead of the others. With continued regular growth of prophylls and perianth-segments, differentiation of six low rounded primordia takes place on the andrœcial region, while a trace of a collar-growth begins around the gynœcial papilla (fig. 15: 6; bud, 0.53 mm. high). The six papillæ indicating the stamen-primordia appear simultaneously, and are of identical size and appearance in all early stages; but the two lateral members are lower down than the other four. In fact McNAB (1872) missed them altogether, as they would not be seen from above. There is no evidence that the lateral stamens are in any way different from the others or arise earlier; if they represented a normal outer whorl, they should be developed earlier and be always growing at a greater rate than the others. They establish normal contact relations, and the appearances seen are identical with those of six equal primordia as in the general case of Angiosperm floral development. That is to say, the six rounded primordia extend to just touch all round the ellipsoidal axis. The fact that the whorl droops as it were on the two sides is clearly the expression of fact that the floral axis is (1) tangentially extended, and (2) under considerable pressure, pinched as it were in its rounder median portion; the periphery of the mass has freer conditions of growth, and what should have been a circular whorl on a centric axis is arched over the contour of an ellipsoidal knob. When members (1) arise simultaneously, (2) make similar and normal lateral contacts, (3) grow at an identical rate, they must be regarded as morphologically identical, and equivalent to members of a symmetrical whorl. These are the criteria of such phyllotaxis-constructions; there are no others. The floral axis is here ellipsoidal in section instead of being centric, and the whorl droops laterally as it were around the shoulders of the andrœcial region; but there is nothing anomalous in this; a crested series obtains instead of the ring of the more usual centric system. The rounded apex with the two lateral stamens low down on its flanks now explains why the vascular bundles which will supply them are subsequently seen to be lower in the axis than the other four; the plane of the whorl is to be judged by taking a curved base of insertion and not a horizontal line. Another interesting feature is that, as the six primordia further differentiate, the rounded shoulders of the "primordial cushions" remain on either side of the gynœcial cone, giving the appearance of accessory protuberances, which at one time are so like the stamen-primordia and just the same size, that they may be readily mistaken for stamens (fig. 15: 6, and fig. 16: 7; bud 0.53 mm. high). This in fact is what happened. McNAB (1872) figures these apparent sets of three primordia on either side of the gynœcium, omitting the lower lateral stamens altogether. STRASBURGER (1872) missed the intermediate stages. This emphasises the value of serial figures, drawn to corresponding scale. By comparing the series 6-12 (figs. 15-19), it becomes obvious that the shoulders of the andrœcial region, or "primordial cushions" of McNAB, at first larger than the six primordia, then

the same size, gradually fall behind as the stamens grow, until they are left as papillæ, the representative of an elliptical collar around the base of the gynœcium (9–10, figs. 17 and 18). Ultimately (fig. 19: 12) it represents the region more particularly concerned in the extension of the staminal tube of which it continues to form the lateral shoulders. In all subsequent stages the six stamens continue to grow at equal rates, their contact relations are normal; posterior and anterior pairs of members making the same contact with each other in the median line as they do with the laterals (figs. 17 and 18: 8, 9, 10); and each differentiates normally, as in Angiosperm floral development, into an anther-head to which later a filament region is added (fig. 18: 10, 11). There is not the slightest evidence for regarding the andrœcium as represented by two members (the primordial cushions) producing three sori; or, for example, for calling it two lateral members each throwing off three pinnules which are antheriferous segments of a compound sporophyll. The simple statement that a segmented andrœcial region of the axis gives rise to one whorl of identically equal and normally constructed stamens most clearly expresses all the facts available. During the differentiation of the andrœcium, the prophylls extend, and soon nearly enclose the greater part of the bud: the posterior perianth-segment overlaps the anterior at the margin and tip; the collar of the gynœcial cone extends, and delimits a distinct stalked terminal ovule (fig. 17: 8, bud 0.68 mm. high; 9, bud 0.76 mm. high). The integument growing up to touch the closely investing perianth, and spreading out laterally in the free room left between the six stamens, soon becomes definitely tangentially extended, nearly twice as broad as deep (figs. 16–18: 11–12) and gives the appearance of two lips with a slit aperture between them. In this way McNAB (1872) initiated the idea of two carpels, taking the lips themselves as indicative of primordia; LIGNIER and TISON (1912, p. 112) have assumed the same idea, and “predominance of the radial carpels”; though it is not clear why the two angles would not have done just as well for transverse carpels (as in the theory of hypothetical transverse perianth members in the ovulate flower), but this would not have suited the bias of these observers in favour of a decussate construction.

Older buds merely show progressive differentiation of all the features already in existence; the prophylls meet over the apex; the perianth-members become more distinctly gamophyllous by an intercalated zone; the stamens develop three-lobed anthers and short curved filament regions—the two lateral stamens inflexing, and the other four facing each other introrsely in two pairs, as a simple way of fitting in six members on the sides and ends of an ellipse; the great development of the stigmatic disc at this time is not explained, but in this condition it may well represent the original pollen-collecting investment and funnel (fig. 18: 11; bud, 1.06 mm. high).

Buds beyond this stage are preferably sectioned. Sectional elevation constructed for a 1.5 mm. bud shows the further differentiation of the preceding factors. The pressure set up by the members growing within a closed bud-cavity, enclosed by

prophylls and perianth-members, is seen to account for (1) a slight curvature of the extending "stylar" region of the integument, while the "stigmatic disc" continues to mushroom against the perianth arch; (2) the inarching curvatures of the lateral stamens, and, to a less extent, of the median ones, with their introrse anthers pressing over those of the lateral stamens, as a result of these latter being a little lower to begin with. The dome-shaped androecial region is now flattening out, and a line drawn through the points of insertion of all the members clearly indicates the changes in the shape of the floral axis (fig. 18 : 11; fig. 19 : 12; bud, 1.5 mm. high). Such a bud indicates recognisably the construction of the adult flower, with the exception of active growth in the secondary zones of extension.

Special Mechanism.—Comparing these stages with the longitudinal section along the orthostichy line of the cone, which gives median sectional elevation of successive flowers, in such a sequence it is easy to follow the overlapping of the perianth-members, though the prophylls are not indicated, the growth of the staminal tube, and the remarkable extension of the stylar integument, while the apical nucellar region remains small. In the 1.5 mm. bud the stylar region begins to show a tendency to bend towards the posterior side; this being due to the fact that the posterior stamen, like the posterior perianth-segment, shows a slightly advanced rate of growth, as compared with the corresponding anterior members, with the result that the posterior pair of anthers push over those of the anterior stamens. This increased rate of growth of the posterior side of the flower has no reference to the shape of the bud as a whole, which, notwithstanding its position between the close-fitting cone-scales, remains remarkably symmetrical (fig. 16 : 12; fig. 19 : 12).

Little remains to be added to the growth-factors of the flower, and buds almost full grown thus present definite features of construction (fig. 20). The prophylls are overtaken by the other members, and no longer enclose the bud; the perianth-segments become relatively thinner, though maintaining their overlapping edges which seal the bud-chamber, the connate region (a gamophyllous zone of growth) increases to constitute the real protective investment of the bud; the stamens retain their relative arrangement, and the filaments only exaggerate the curvatures impressed on them in the young bud. Pollen is early developed in the anthers, and these latter complete their histological details. Great advance is seen in the staminal tube which closely invests the nucellus region of the ovule, now grown to a pyriform mass enclosed by a relatively thin integument; this is continued into a long tube now definitely kinked on the posterior side, but retaining the stigmatic head well pressed against the investing perianth. Four special growth-extensions may be noted: (1) gamophyllous zone of the perianth; (2) staminal tube; (3) staminal filaments; (4) "stylar" tube of integument.

Growth-curvatures are seen in: (1) the staminal filaments; (2) the stylar tube; these appear to be largely accidental features of growth, due in the former case to the fact that two lateral stamen-primordia were dropped below the horizontal level of

the others to begin with, and so tend to curl back from the bud-margin under the others; while in the latter case the curve of the style merely follows the line of least resistance inside the packed bud, and expresses the energy with which the "stigmatic disc" is pressed against the boundary of the bud (figs. 14 and 20).

The Stage of the "Next Bud."—In addition to these features of special mechanism, a new factor may be indicated in adult buds as they approach the zone of functional flowers. Buds 3-4 distant along the orthostichy line from the uppermost expanded flowers show the commencement of a remarkable starch-storage which follows definite lines and attains its maximum in the adult bud which is next to expand. The whole of the staminal tube, consisting of fairly isodiametric parenchymatous cells, takes on a dense storage of starch to the extent that even a thin section turns deep black with iodine solution. Storage also extends to the stamen-filaments, but there is no starch in the anther itself. Similarly another starch-storage commences in the nucellus of the ovule, beginning at the apical region, until the entire pyriform mass gives an equally black reaction in the adult bud. On the other hand there is no trace of storage in the perianth: only a trace in the integument, which in an iodine preparation is clearly marked as a white zone between the black staminal tube and the black nucellus. Starch-storage ceases at the plexus of vascular tissue, and there is a small amount present in the stalk-region of the flower; but there is no marked storage in a quantity which must indicate some special function. Starch in the integument is restricted to the inner epidermis, as also in the whole length of the styler tube and the superficial cells of the stigmatic disc. It is thus possible to distinguish between androecial starch and gynoecial starch.

The structure of the adult bud is thus a feature of special interest, and section of a series of such buds in which starch-storage is progressing shows the essential features of the mechanism: the buds at this stage are markedly symmetrical, as seen in longitudinal section of the cone (= median plane of the flowers); much more so than might be expected from the way they grow between the close-fitting scales of a strobilus; the subtending bracts closely imbricate, that of one flower extending to the middle of the next above; they are connate half-way up their length, and pressure of the growing nucellus has squeezed a thin spot (translucent) in their basal median region to correspond. The overlapping of the posterior perianth-segment, the introrse anthers on the inflexed filaments, and the kinked style are conspicuous, as also the great enlargement of the upper portion of the staminal tube, which apparently had as its original function the protection of the enclosed ovule, over which it exactly fits (fig. 14). Buds in this condition have an extreme length of 3.5-4 mm.

The Working Mechanism of the Flower.—In converting the adult bud into a functional blossom one factor alone is active, all other parts take a passive share in the proceeding. The essential feature is, briefly, the rapid extension of the staminal tube, which elongates sufficiently to thrust the stamens beyond the level of the tip of

the subtending bract. The bract is passive, its tip is simply lifted and tilted back. The perianth-members are also forced apart, and the staminal-tube edge is just brought to the level of their margin. The filaments spread out, according to the bias impressed on them in the bud stage; the posterior erect, fairly well along the surface of the next bract above; two anterior bend forwards horizontally almost at right angles to the preceding, while the two lateral inarch on the flanks. The stigmatic disc is pulled up and the styler tube tends to straighten out in the now narrow and slender staminal tube.

The active agency employed in this process is that of rapid cell-extension of the parenchyma of the staminal tube; these cells are now to be seen as long narrow elements instead of short, rounded, fairly isodiametric ones; while all trace of starch has vanished in the andrœcium of all open flowers with extruded stamens. That is to say, there can be no doubt that, since it has suddenly disappeared, the whole of the andrœcial starch has been utilised in this sudden growth-extension; and it is quite clear that this starch has no significance from the standpoint of a nectary (*cf.* COULTER and CHAMBERLAIN, 1911, p. 373).

While the function of the andrœcial starch-storage is so far evident, the gynœcial starch still remains in the functional flower, in which the nucellus section still shows up as a clear black mass with iodine solution. On cutting sections of the nucellus in flowers successively older down the orthostichy line, half a dozen of which continue to show extruded anthers, though mostly dead, with practically empty loculi, it is easy to show that depletion of starch takes place in older flowers, and the oldest may show not a trace of starch left, but a shrivelled empty mass of cells (HOOKER, 1864). Other flowers may show depletion of an apical region first, which apparently acts as a collecting organ in which conversion into sugar is completed, and the fluid is discharged from the tip of the nucellus. That is to say, the great storage of gynœcial starch is undoubtedly for a nectary function, and the secretion is discharged *viâ* the styler tube on the surface of the stigmatic disc. As in the case of the ovulate flower, it is abundantly clear that no useful secretion can take place from the outer epidermis of the integument, since it would never reach the exterior, and no secretion takes place from the cuticularised walls of the cells lining the tube, while no extensive secretion can take place from the curiously thickened papillose cells of the stigmatic disc, although they may contain numerous small starch granules. In fact, the significance of the slight starch-storage in the thick-walled epidermis lining the tube and the papillose cells of the stigmatic disc is probably to be again regarded as a response to the conditions to which they will be exposed when a strong solution of plasmolytic sugar is poured over them.*

* These curiously protected papillose cells may possibly be regarded as modified in connection with the visits of insects, which lick the rough surface which carries the exudation of the "styler" canal. It is also possible that such pseudo-xerophytic structure may be correlated with the overflow of strong

It would appear, therefore, that the protected, deeply placed, pyriform mass of the nucellus is the functional nectary corresponding to the similar pyriform starch-storing mass at the apex of the ovulate flower; the "stylar tube" is necessary to conduct the secretion, and the "stigmatic disc" constitutes a platform surface on which the exudation may collect, evaporate, and concentrate, thus becoming increasingly attractive to licking insects. The utility of the central disc is emphasised by the direction of the growth-curvatures of the filaments which inarch on this spot; while it may be also noted that the filaments do not rise more than 1 mm. beyond the surface of the cone-scales, the same height as the tips of the longer but low-lying tubes of the ovulate cone project. Also the relative dimensions of the adjacent functional flowers are such that the anthers are fairly uniformly and symmetrically spaced on the cone surface, this being particularly striking in uninjured specimens; four clear gangways, along which the secretion will be found, being left along the vertical orthostichy lines, while the flanking anthers of adjacent series are as near together as they are to the next anthers of their own flowers (fig. 10). That is to say, the spacing mechanism of adjacent flowers is fairly efficient; the convergence of the anthers of one flower over the "nectary" is also fairly efficient, and the exudation which, as in the ovulate cone, is thus discharged along the orthostichy lines, is presumably sufficiently copious, as indicated by the intensity of the starch-storage in the pyriform nucellus. PEARSON (1907) records that the surface of the staminate cone is sticky to the touch, and the pollen masses are sticky.

The flowers presumably function little more than one day each, or perhaps two, since the protrusion of the staminal tube must be rapid, and the anthers dehisce on exposure to dry air, and soon shed their pollen by the long slit pores, which open widely as the anthers dry and shrink to half their original diameter. Since all flowers in spirit material are either unopened buds or fully extended flowers, it is probable that the functional sequence resembles that of the Composite capitulum, a full contact cycle of the construction (in this case 2 + 2) coming on each morning.

Although time factors are still wanting, and detailed observation of the plant in its natural habitat necessarily somewhat scanty, it is possible to obtain a fair working conception of the way in which the flower has come to be associated with insect visits. On the assumption of dicliny the drop-mechanism of the functional ovule, which had been utilised by insects, is retained in the staminate flower in full working order, since insects which go to one flower for honey are likely to expect

plasmolytic sugar-solution, and this may even abstract water from the cell-contents of the massive stigma-head by exosmosis through the surface-pits.

But the question really involved is the extent to which this "stigma disc," with its insect-visited exudation, was similarly constructed and equally entomophilous in the original hermaphrodite flowers, at a period, that is to say, when it also acted as a pollen-collecting funnel. The fact that the edges of the disc are incurved in older withered flowers, and the papillose surfaces more or less approximated, suggests the possibility of a preceding mechanism for pollen-retention.

honey in the other (*cf.* the gynœcial nectary of the staminate flower of *Ilex*). At any rate the fact remains that only that portion of the ovule (the pyriform mass extending just to the level of insertion of the integument) is retained for this special function alone; it similarly stores starch, but, having no other use, it is rapidly and completely depleted in older flowers. The "stylar tube" is retained since the secretion from a deep-seated nucellus must be taken to the exterior, and this rapidly extending tube, pressed in early stages against a sealed perianth, takes on the kinking curvatures which are accidental, and possibly spreads out into the characteristic "disc." The remarkably exaggerated and early development of this region is not wholly explained by this hypothesis; an alternative view would be that it retains a phase of the micropylar tube, as it existed in the ancestral hermaphrodite flower, when its expanded head just filled the aperture of the staminal tube on exposure and so corked the aperture of the flower and helped to keep the deep-seated ovule from desiccation and exposure to the external air. In the modern ovulate cone with the assumption of the cleisanthous condition this becomes unnecessary, while the want of the old closed perianth enables the tube to follow on unchecked. At any rate it is clear that the "stigmatic disc" does not secrete, but, on the contrary, presents marked xerophytic adaptations to resist the excessive loss of water from its cells.

It is interesting to note that while the ovulate flower could not be said to present any definite adaptation for insect guests, since the starch-storage and drop-mechanism subserve other functions as well as that of a nectary, the retention of these factors in the sterile staminate flower, in which they would be otherwise quite useless, affords evidence of a definite adaptation in this flower at any rate. On the other hand, the present relations of the flowers to the spotted bug *Odontopus sexpunctulatus* do not appear to be much more than accidental; the insect touches both anthers and stylar tubes with its lower surface in crawling over the cone surfaces. As this bug has a proboscis $\frac{1}{2}$ inch long, and is quite capable of sinking it in the tissue of the cone, it is evident that this insect can tap the source of supply without troubling about the exudation. HOOKER (1864) records the manner in which the cones may be damaged by such boring and perforation. Further observations may fill in additional details, but the case for entomophily is established by the demonstration of a special adaptation as a nectary organ in the staminate flower, whether insect pollination at the present time is absolutely efficient or not.

III. THEORETICAL CONSIDERATIONS.

Summing up the general features of the construction of the flower, it is then fairly concluded:—

1. No one now seriously disputes that the dicliny is secondary; *i.e.*, the original condition of the flower was hermaphrodite. This was a perfectly legitimate deduction

(STRASBURGER), long before the discovery of the flower of *Cycadeoidea* made it fashionable. Again, the reason for the reduction was, as in general, a xerophytic floral adaptation, owing to there being insufficient water supply, which in the long run means enfeebled nutrition, for all the floral shoots to attain the maturity of seed-production. Such dicliny is, to a certain extent, merely a physiological repetition of the mechanism which led to the evolution of heterosporry.

2. Reduction phenomena are exhibited in—

- (α) Dicliny, or separation into flowers bearing transitory microsporophylls only, and more permanent seed-producing ovulate flowers.
- (β) In the diminished number of members produced, *i.e.*, a tendency to a minimum in member-production.
- (γ) An associated reduction of phyllotaxis-construction may also follow, giving systems of cycles with fewer members per cycle ; but since a practical limit had been already attained in the vegetative shoot, though it must not be supposed that floral shoots necessarily follow, the fact remains that these present a tendency to decussate construction, which is quite definite so far as the inflorescence-system is concerned ; though extending as far as the perianth, there is no evidence that it was ever continued into the sporophylls.
- (δ) On the other hand, in the condensation of the older strobili to cones with reduced surface, the number of flowers is not markedly reduced, but they then necessarily become “flattened,” as also do the subtending bracts.

3. Of the two flowers, the functional ovulate flower clearly retains least of the general ancestral characters, just as it has to stand the more exhaustive strain of seed-production. It is reduced to a minimum construction containing nothing which is not strictly necessary ; the two essential features being the elongated collecting tube, and the precocious development of the dispersal wing. The occasional presence of vestigial prophylls (LIGNIER and TISON) is a feature of interest in this respect ; whether the “perianth” be regarded as such (HOOKER), a second integument or “cupule” (SYKES), or a specialised andrœcium (LIGNIER and TISON), is really immaterial, since there is no definite evidence either way. On the other hand, given a gamophyllous perianth in the ancestral hermaphrodite flower (as suggested by the staminate construction), a deteriorated version might be expected to retain the gamophyllous zone after the loss of the free members ; this being the suggestion of developmental stages. The presence of two transverse bundles, or even a series of six, does not affect the question ; in the decadence of a gamophyllous region commissural bundles are as likely to be maintained as “midrib” bundles (this is the story of the gamopetalous corolla of Composites). For this reason the term “perianth” has been retained.

On the whole, therefore, ancestral characters are to be looked for in the more

transitory staminate cones and flowers, and here quite a number of points of interest are to be noted.

4. The staminate flower is clearly a simple anthostrobilus type, obviously differentiated into three primary regions of perianth, androecium, and gynoecium in normal succession. As might be expected in a specialised form, the three regions are non-conformable, each is independently specialised and independently reduced (*cf.* such floral types as *Papaver*, *Malva*, *Pæonia*).

5. The natural tendency in such a xerophytic type will be to a minimum construction in all three regions. In this case the plant itself has undoubtedly attained a remarkable phase of minimum construction, and one is possibly always safe in regarding *Welwitschia* as a xerophyte, that is to say, it is a xerophyte all the year round.

6. Such minimum construction clearly obtains—beyond the prophylls, which only fill lateral chinks, and are utilised as a covering to the bud in early stages during the development of the pollen—

(1) The *Perianth* is reduced to the ultimate minimum of the two members of one contact cycle of the decussate system (*cf.* calyx of *Papaver* in *Rhœadineæ*) A former function of the protection of the once included functional ovule in the opening cone is indicated by its gamophylly to a definite tubular or saccate investment, extending just above the level of the ovule. In the present closed condition of the cone (secondary cleisanthy) protection by the subtending bracts is efficient, and the perianth deteriorates to a membrane without vascular tissue. Its protective nature is still seen in an efficient closing of the bud-chamber throughout development.

(2) The *Androecium* presents a limiting term (though not the absolute minimum of two) curiously paralleled by that of Crucifers and some Capparids (*Cleome*) among the *Rhœadineæ*, in that, as in these types with a tangentially extending flower, six members give a minimum symmetrical arrangement, in which two lateral members are given free room, while median members in the plane of the gynoecium are avoided. That is to say, six has advantages over four or eight. Just as the six stamens of the Crucifer or *Cleome* suggest the ancestral more numerous series (*Polanisia*, *Reseda*) in a single whorl, and these in turn the multicycled type of *Papaver* and *Capparis*, clearly the relic of an indefinite construction originally repeating the Fibonacci systems of the vegetative shoots, so the six stamens of *Welwitschia*, in a true developmental whorl, postulate an originally greater number (*Cycadeoidea*), and through these afford the only direct indication of the fact that the ancestral *Welwitschia* presented normal Fibonacci systems before it became decussate.

(3) The *Gynoecium* in both flowers is clearly the ultimate limit of one free integumented ovule. There is no need to trace fancied homologies with the single basal ovule of *Polygonum* or *Juglans* among Angiosperms any more than with

uni-ovulate Composites or spikeletted *Cyperaceæ*. Such curious misconceptions of the fundamentals of plant morphology have only an historic value. Parallel examples of biological reduction to a minimum of one ovule per flower, or one flower one seed, are so general, that it is often forgotten that such a condition directly implies a previous multi-ovulate condition. Nowhere else in the vegetable kingdom do numerous ovules of this gymnospermous type occur except in the flower of the *Cycadeoidea*, so that it may be said that the gynœcium of *Cycadeoidea*, reduced to a limit of one ovule, would give a close approximation to the gynœcium of *Welwitschia* which has attained the minimum construction.

7. *A minimum construction does not, however, imply any phylogenetic relationship to other minimum types.* It is important not to confuse parallel biological features, due to similar response to similar xerophytic conditions, with indications of phylogenetic relationship. The flower of *Cycadeoidea* is also, it is true, a generalised anthrostrobilus, with perianth region, andrœcium, and gynœcium, each independently specialised and non-conformable in phyllotaxis construction. It also presents a much less tendency to minimum construction, each region is still practically "indefinite," though this is in agreement with the fact that the flowers of *Cycadeoidea* were large and solitary, while those of *Welwitschia* are small and enclosed in spikelets or strobiloid inflorescence constructions. On the other hand, special features of the floral mechanism are also in agreement. The peculiar staminal tube is much the same in both types, as a biological adaptation to subserve the investment and protection of the gynœcium during the period of expansion, probably as much as a shield from the action of intense light as from simple desiccation (*cf. Papilionaceæ* and *Pæonia Moutan*). Recapitulatory standpoints are always of interest in floral development, since there must be a reason for the way in which every factor of growth or time is initiated or comes into action; thus the original habit of the flower of *Welwitschia* is evidently best seen in the full-grown buds, since the extension-mechanism of the staminal tube is clearly secondary, and as in cleisanthous *Gramineæ*, correlated with the fact that the flowers are no longer exposed *in situ* by the divergence of the cone-scales. It is evident that the staminal tube originally functioned in the condition it has in these buds of exactly fitting over and shielding the central ovule, as that of *Cycadeoidea* did the entire gynœcial cone, and the staminal tube of the *Papilionaceæ* does at the present day (fig. 20).

8. Again, a minimum construction being established, this implies a non-minimum or indefinite ancestral condition. Thus the flower was: (1) hermaphrodite; (2) with indefinite parts in all three regions; also (3) open and expanded to the outer air in the axils of diverging subtending bracts, and therefore (4) in a more extended strobilus, much less laterally extended; *i.e.*, more nearly centric in construction, as is the general habit of non-specialised floral shoots.

9. In this condition a short micropylar tube, extending as far as the aperture of the gamophyllous perianth, a second investment outside the staminal tube, would

have sufficed for the drop-mechanism; the extended "stigmatic funnel" being possibly an original pollen-collecting device, or possibly filling the aperture of the staminal tube, and rendering protection of the enclosed ovule more efficient. To what extent insect guests were available at this time is not known, but such visitation is now seen to be a factor entirely dependent on the amount of secretion of the drop-mechanism; again a question of the amount of starch-storage in the pyriform nucellus, and the amount of water brought on by the perinucellary plexus. Which came first, the extreme xerophytic adaptations or the insect visits? Probably the former; the excess of sugar being possibly at first utilised in maintaining the fluid condition of the drop; and as this increased in volume and percentage of sugar on evaporation, it became increasingly attractive to insects also subjected to the same xerophytic environment and demanding water.

10. The essential peculiarity of the flower as we now have it comes in with the progressive cleisanthy of the cones, again a xerophytic response, implying a failure of the opening mechanism. In the ovulate cone this necessitates a progressive elongation of the stylar tube to reach the exterior, though possibly the continued extension of this tube for an apparently unnecessary distance of 5 mm. beyond the surface may be regarded as a special adaptation for insect visits, as it may function as a scraper, removing adherent pollen from the abdominal surfaces. In the case of the staminate cone the shooting-mechanism of the previously existing staminal tube solves the problem of the included flower in an entirely satisfactory manner, instead of elongating each filament independently as in the case of the free stamens of cleisanthous Gramineæ and Cyperaceæ.

11. The flowers of *Welwitschia* are thus of the greatest interest as presenting phases of dioecious, minimum-reduction versions of a generalised floral organisation known elsewhere only in Mesozoic Cycadeoideæ—from the widely spread relics of *Williamsonia*, etc., undoubtedly an extremely early and general type of floral construction, confusing to us at the present day owing to a still previous loss of foliaceous megasporophylls. On the other hand, since the carpellary theory holds for the Cycadeoideæ, in which frondose microsporophylls infallibly indicate once equally frondose megasporophylls, it may hold equally for *Welwitschia*, however remote it may appear at first sight.

12. In conclusion, these interesting Gymnospermous flowers present no indication whatever of any relation to the carpellary flowers of Angiosperms, in which, though even now a majority may have replaced the original megasporophylls by new ovary-formations not involving leaf-members, vestigial carpels usually remain to indicate the progression. The general resemblance is merely that of a parallel progression of physiological mechanism devoted to seed-production, on special non-assimilatory shoot-systems conventionally termed "flowers."

IV. DESCRIPTION OF PLATES.

PLATE 9.

- Fig. 1.—Ovulate cone, 40 × 21 mm. ; external view at the time of pollination of the lowermost flowers.
- Fig. 2.—Sectional elevation of the upper portion of a similar cone in the radial plane ; individual flowers cut in the median plane of the floral diagram ; progressive development from the apex to the lowest pollinated flower.
- Fig. 3.—Fertile scale of ovulate cone ; ovule in the axil of the subtending bract, viewed from the posterior side. Vascular bundles of the scale and internal structural lines dotted.
- Fig. 4.—The same scale with ovule in sectional elevation for the transverse plane of the floral diagram. Vascular bundles of the scale and ovule dotted ; structural lines in agreement with the preceding fig. 3.

PLATE 10.

- Fig. 5.—Ovulate cone. Development of the ovulate flowers in serial succession behind the apex of the cone. Elevation to scale in the radial plane of the cone (median plane of the individual flowers) ; essential stages in the origin of the perianth and integument.
- Fig. 6.—Corresponding stages of the young ovulate flowers, drawn to the same scale and numbered 1-7, for the transverse plane of the floral diagram in sectional elevation.
- Fig. 7.—Similar stages, to the same scale, numbered in series 8, 9, 10.
- Fig. 8.—Older stages to correspond 11 ; Nos. 3, 7, 10, 11 in this series represent the transverse elevations of the median elevations of fig. 5, numbered to correspond.

PLATE 11.

- Fig. 9.—Ripe seed (dry material), in median section, to correspond with the sectional elevation in transverse plane of ovulate flowers.
- Fig. 10.—Staminate cone-cluster as a terminal triad with continuing branch (indicated on one side only). The central cone in functional condition with four florets expanded in each orthostichy line.
- Fig. 11.—Elevation of functional staminate flower in the axil of subtending bract (dotted) ; external view on removal of the bract ; internal structures dotted.
- Fig. 12.—The same flower in sectional elevation for the transverse plane of the floral diagram ; missing parts dotted to correspond with preceding figure.

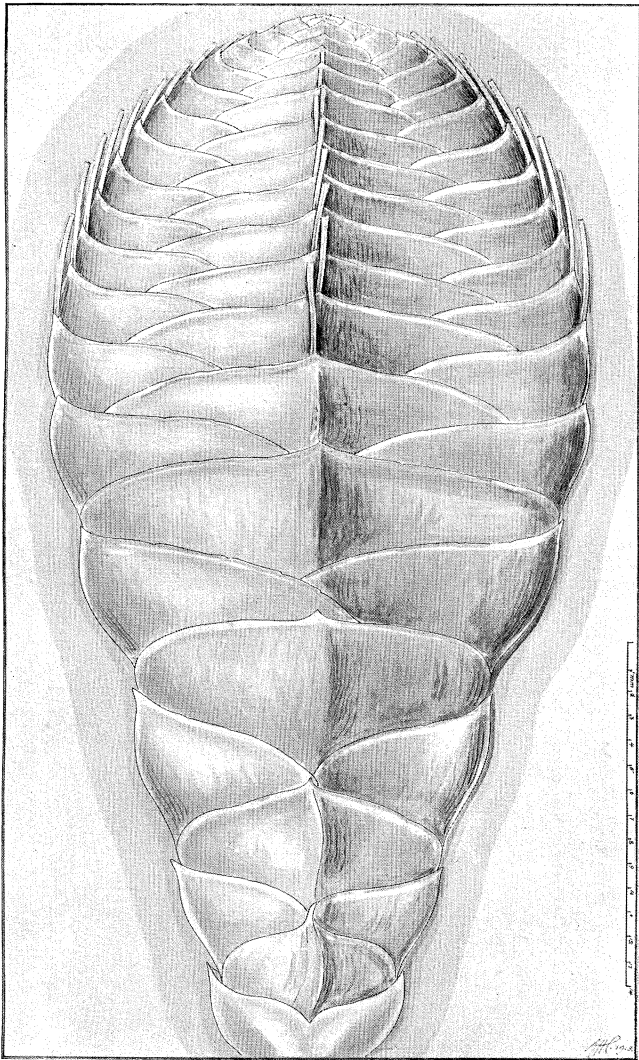


Fig. 1

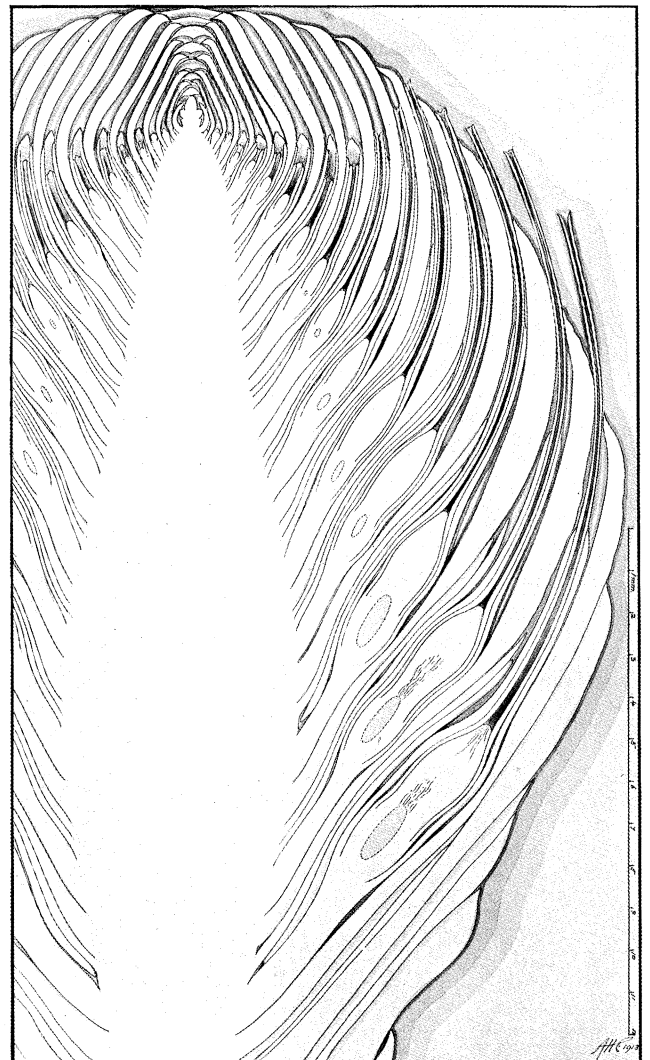


Fig. 2

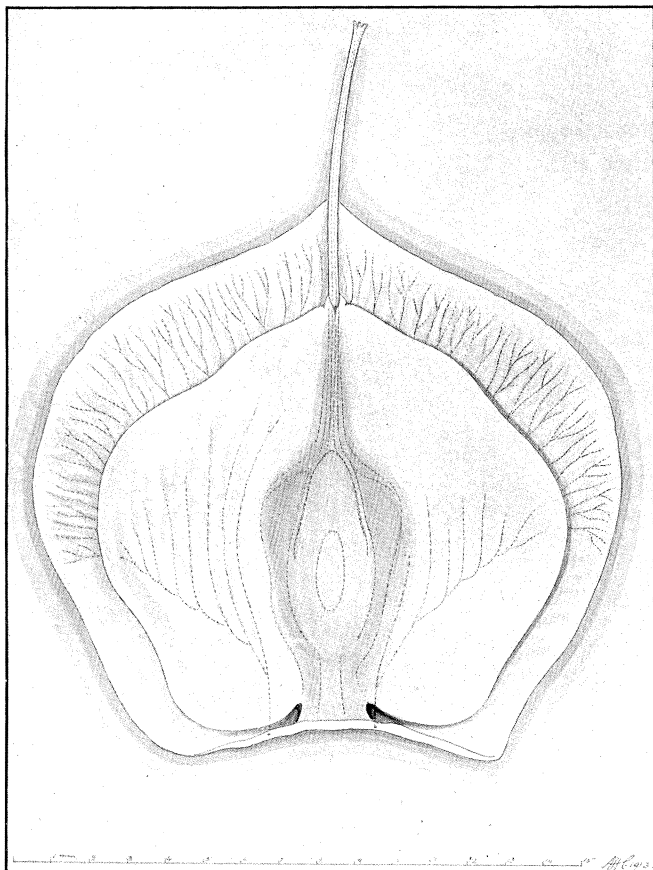


Fig. 3

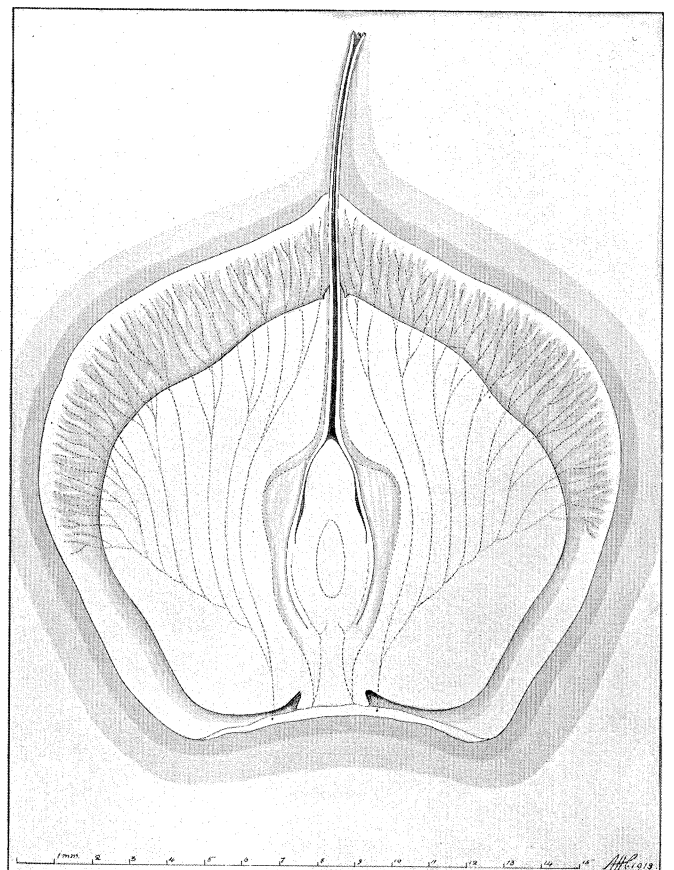


Fig. 4

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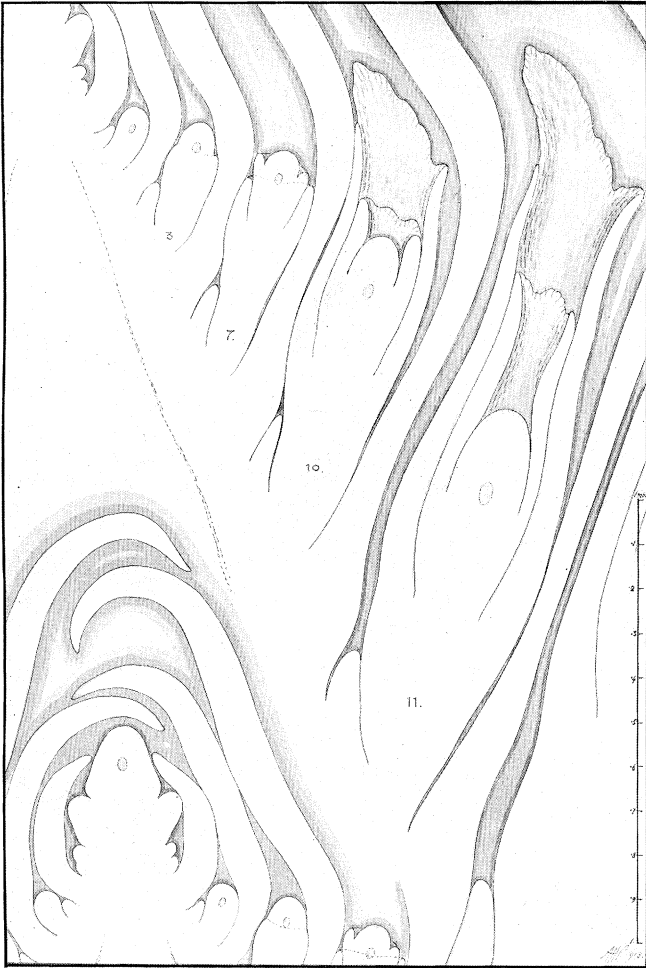


Fig. 5

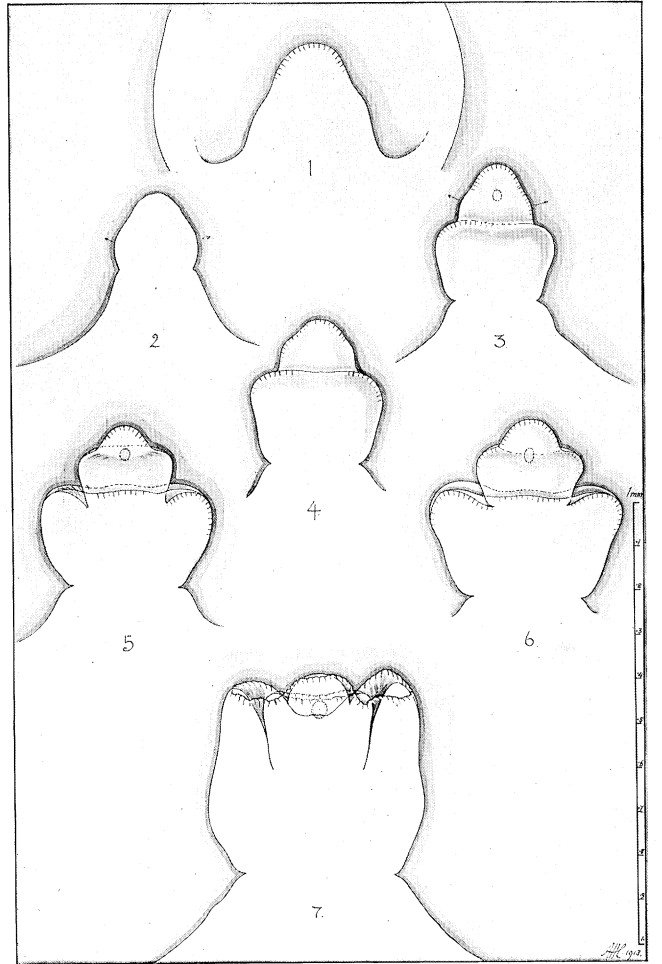


Fig. 6

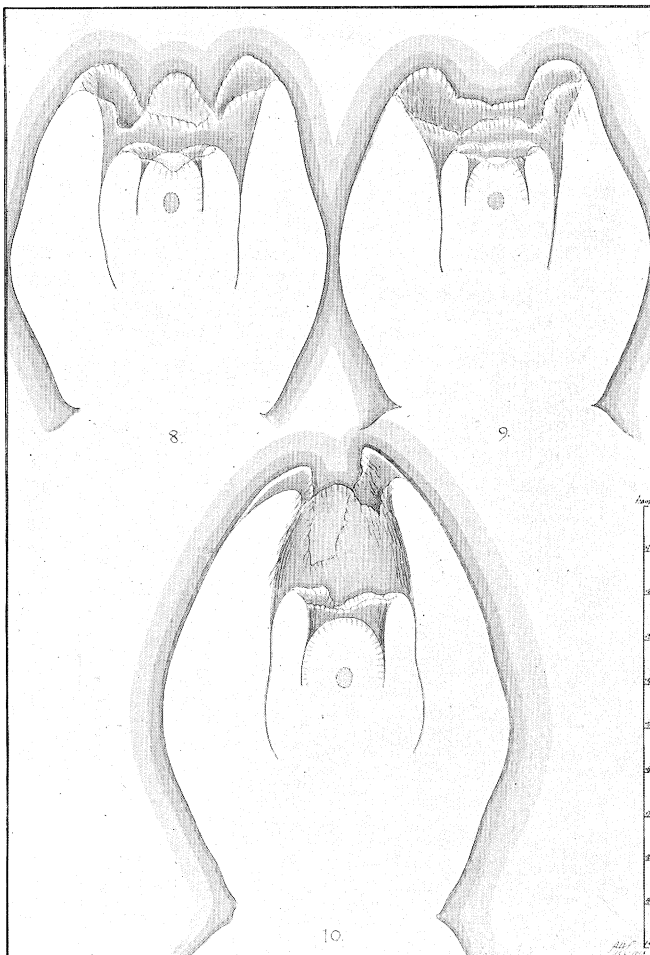


Fig. 7

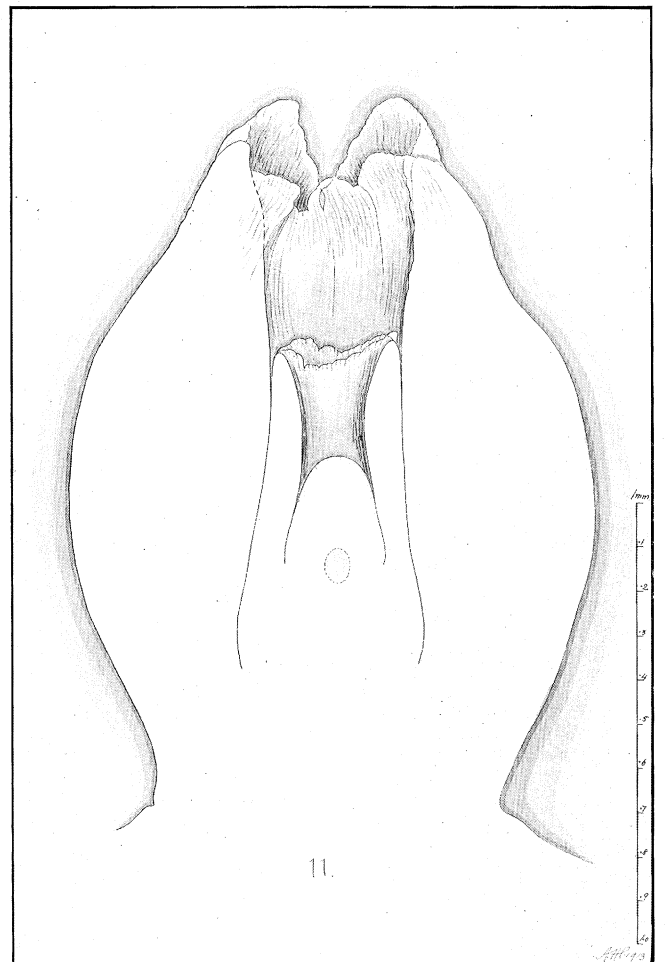


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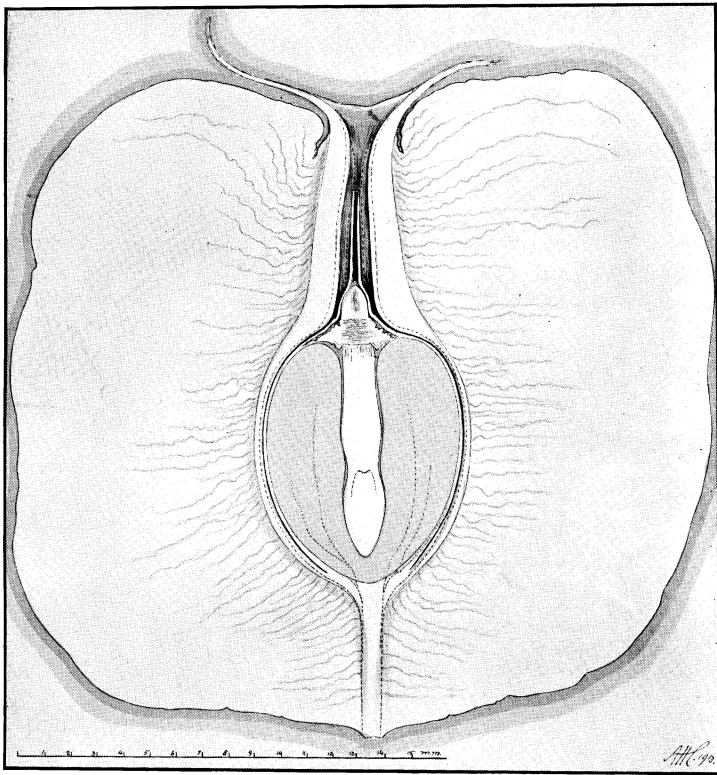


Fig. 9

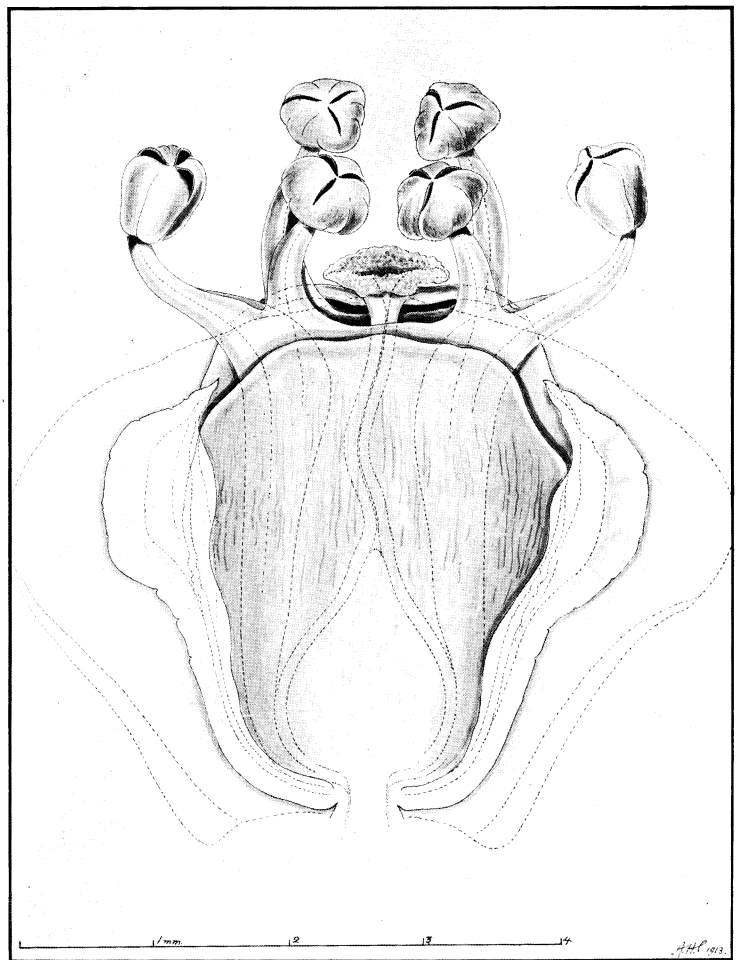


Fig. 11

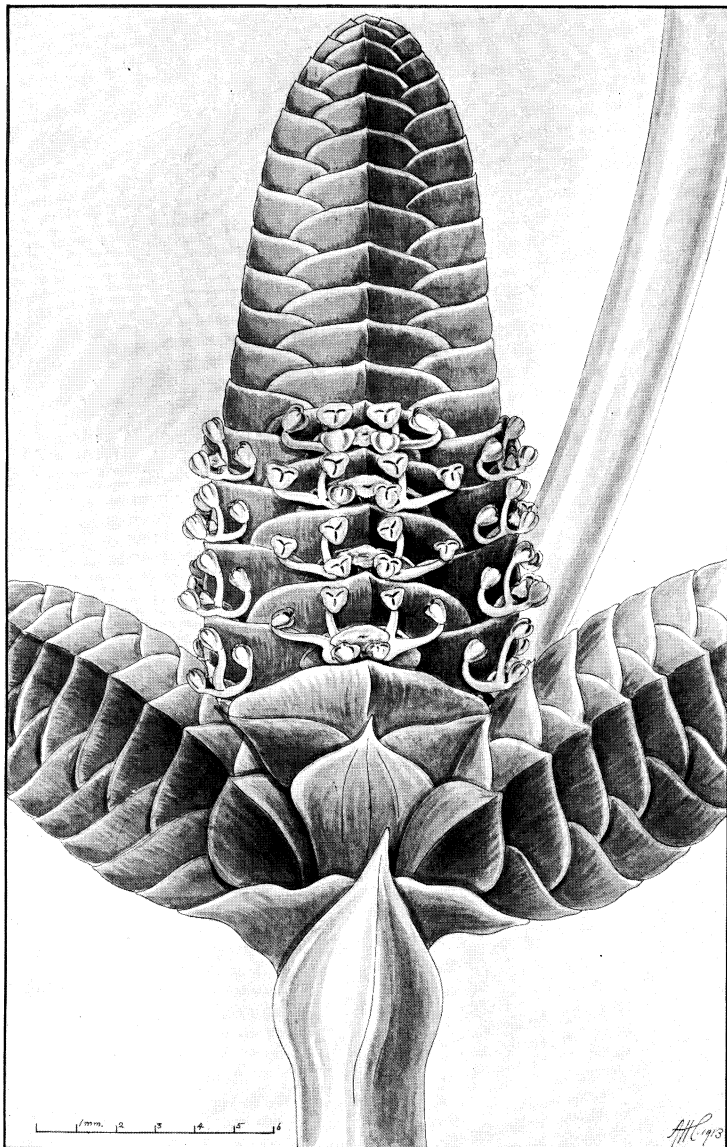


Fig. 10

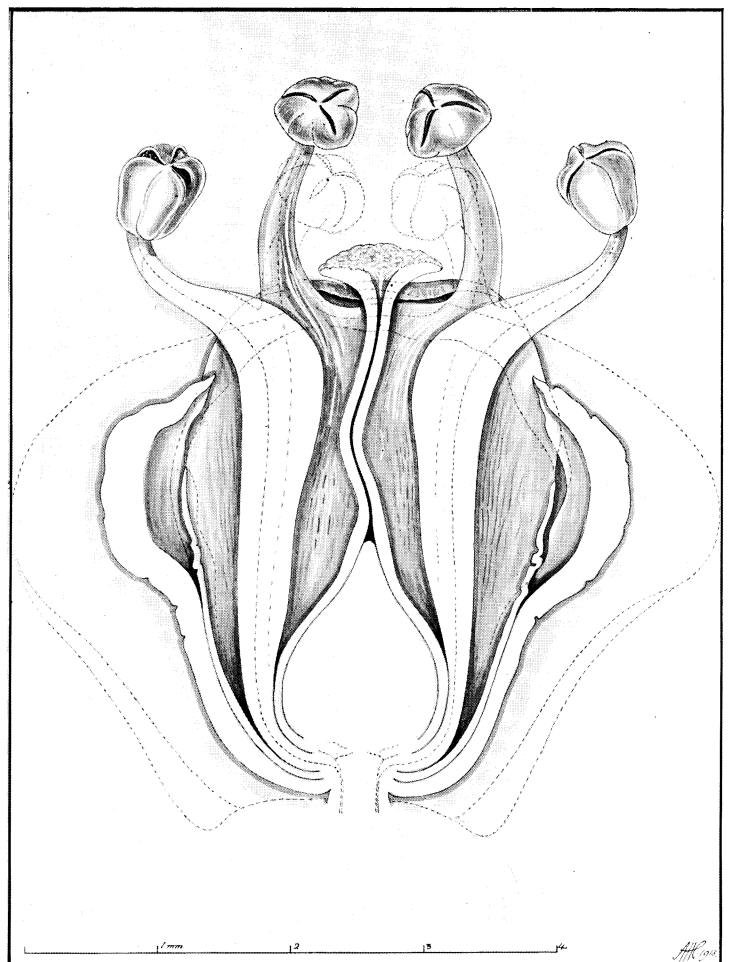


Fig. 12

Grout sc. et imp.



Fig. 13

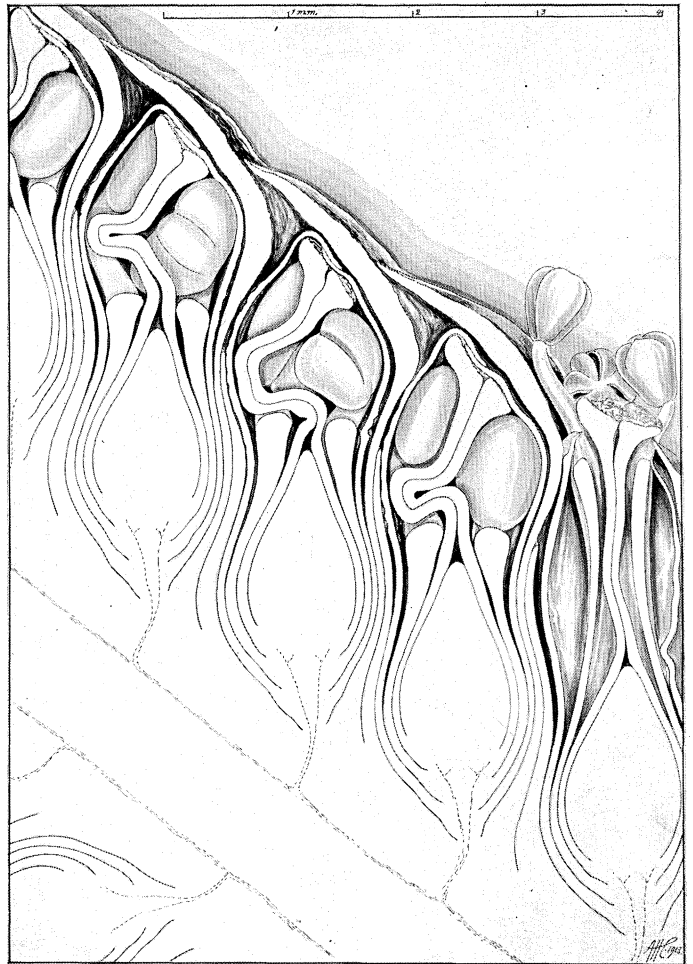


Fig. 14

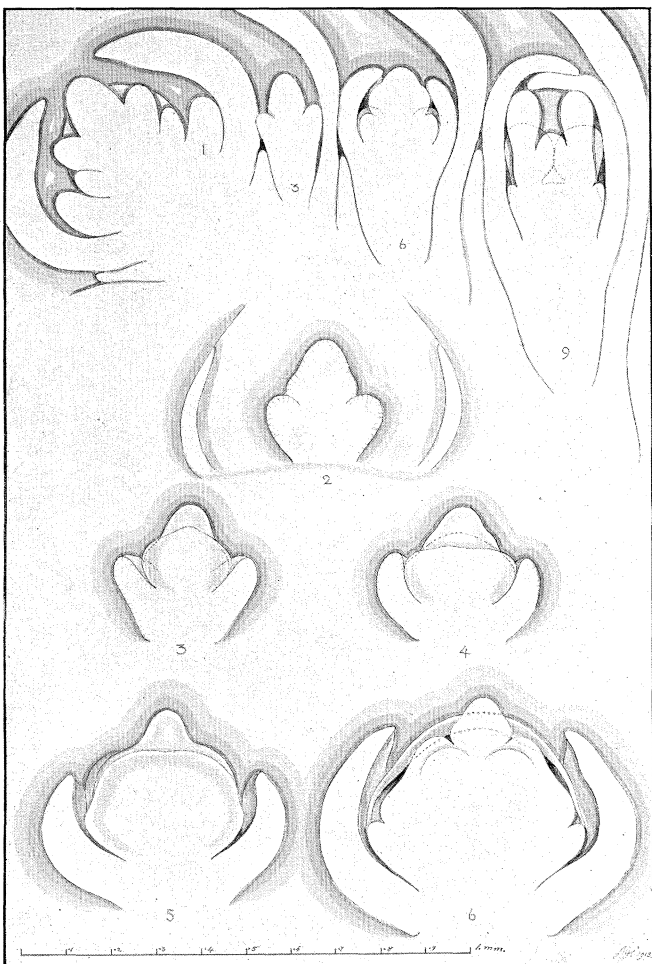


Fig. 15

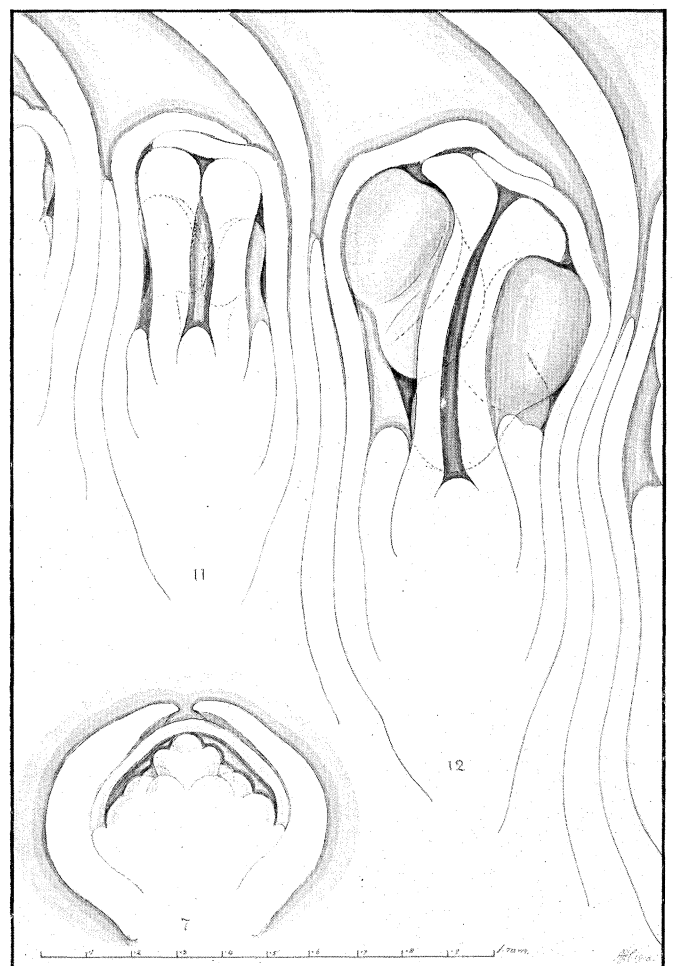


Fig. 16

Grout sc. et imp.

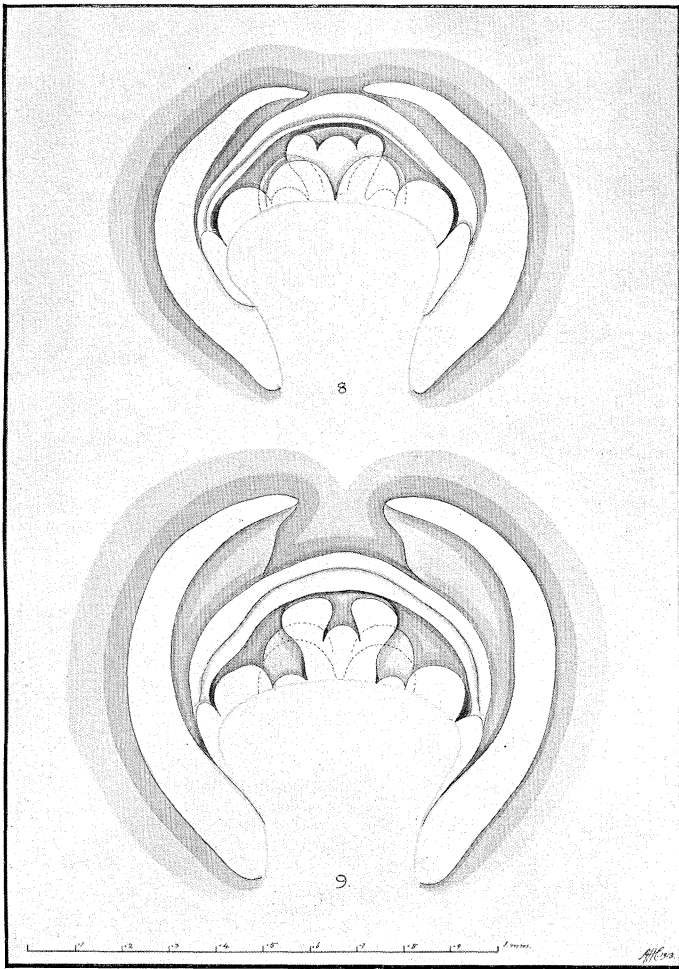


Fig. 17

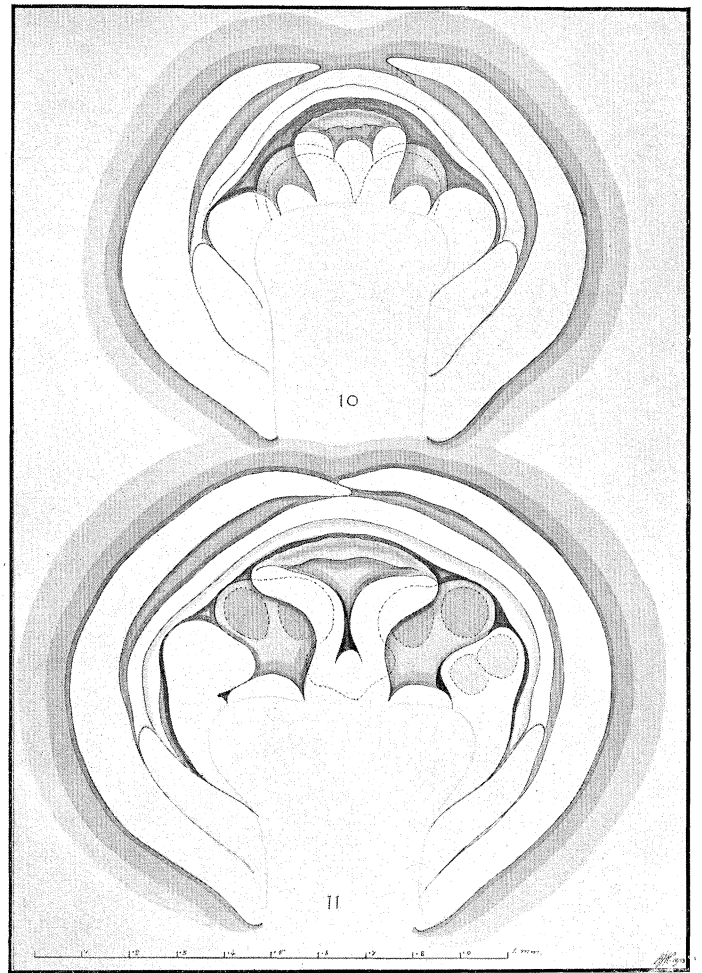


Fig. 18

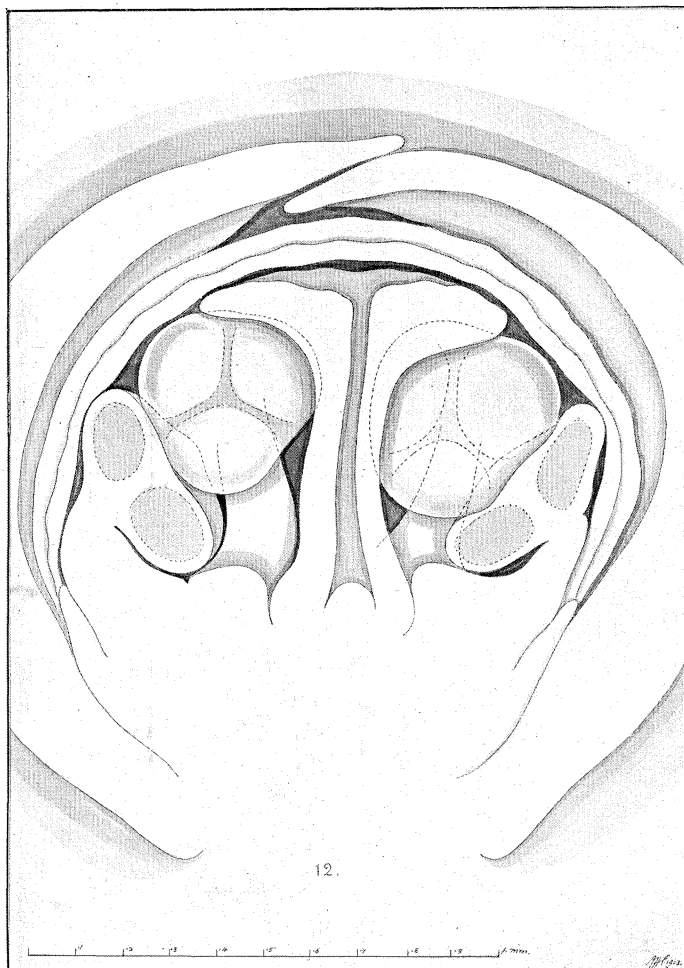


Fig. 19

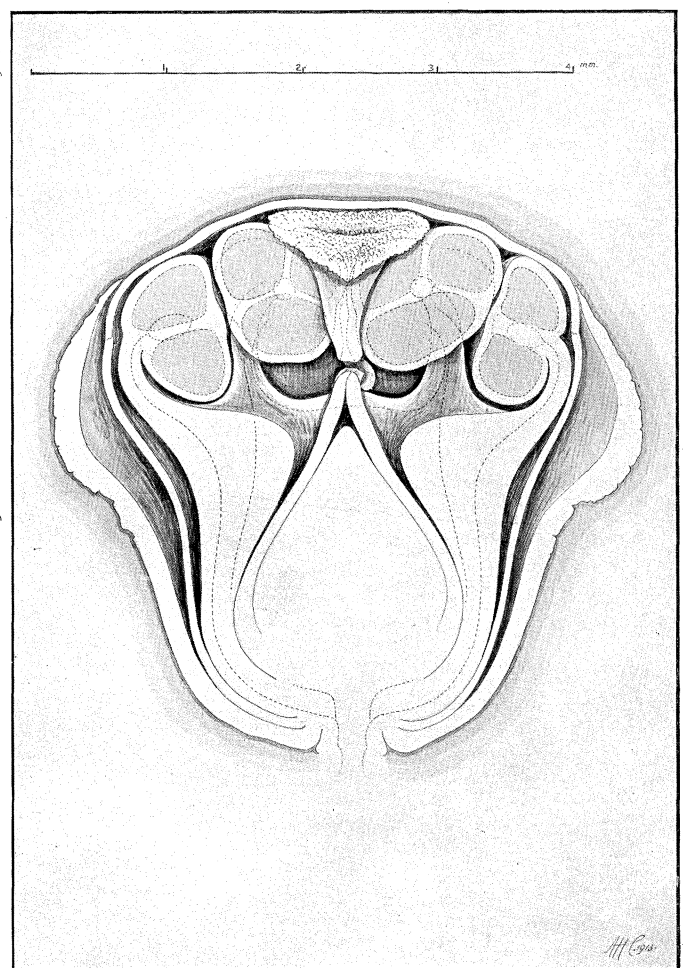


Fig. 20

Grout sc. et imp.

PLATE 12.

- Fig. 13.—Sectional elevation scheme for the median plane of the floral diagram for a series of four functional florets; constructed to the same scale as the preceding elevations.
- Fig. 14.—Corresponding sectional elevations of the three next buds in the same vertical series. (Stage of the adult bud.)
- Fig. 15.—Developmental stages of the staminate flower in series behind the apex of the staminate cone, being elevations in the median plane of the floral diagram for buds numbered 1, 3, 6, 9. Corresponding elevations in the transverse plane for buds numbered 2, 3, 4, 5, 6 (origin of prophylls, perianth-segments and the androecial region with first trace of stamen-primordia).
- Fig. 16.—Developmental stages in continuation of the preceding; median elevations 11 and 12; transverse elevation of 7, showing six equal stamen primordia making contact on the crested compressed androecial region.

PLATE 13.

- Fig. 17.—Continuation stages in transverse-plane elevations 8 and 9. Progressive and equal differentiation of six stamen-primordia.
- Fig. 18.—Continuation stages to correspond, for stages 10 and 11.
- Fig. 19.—Sectional elevation of older bud to correspond, stage 12, showing differentiation of "stigma" and "stylar tube," also the first trace of the staminal tube (figs. 15-19, all constructed to the same scale).
- Fig. 20.—Sectional elevation in transverse planes of adult bud, to correspond with elevations in fig. 14.
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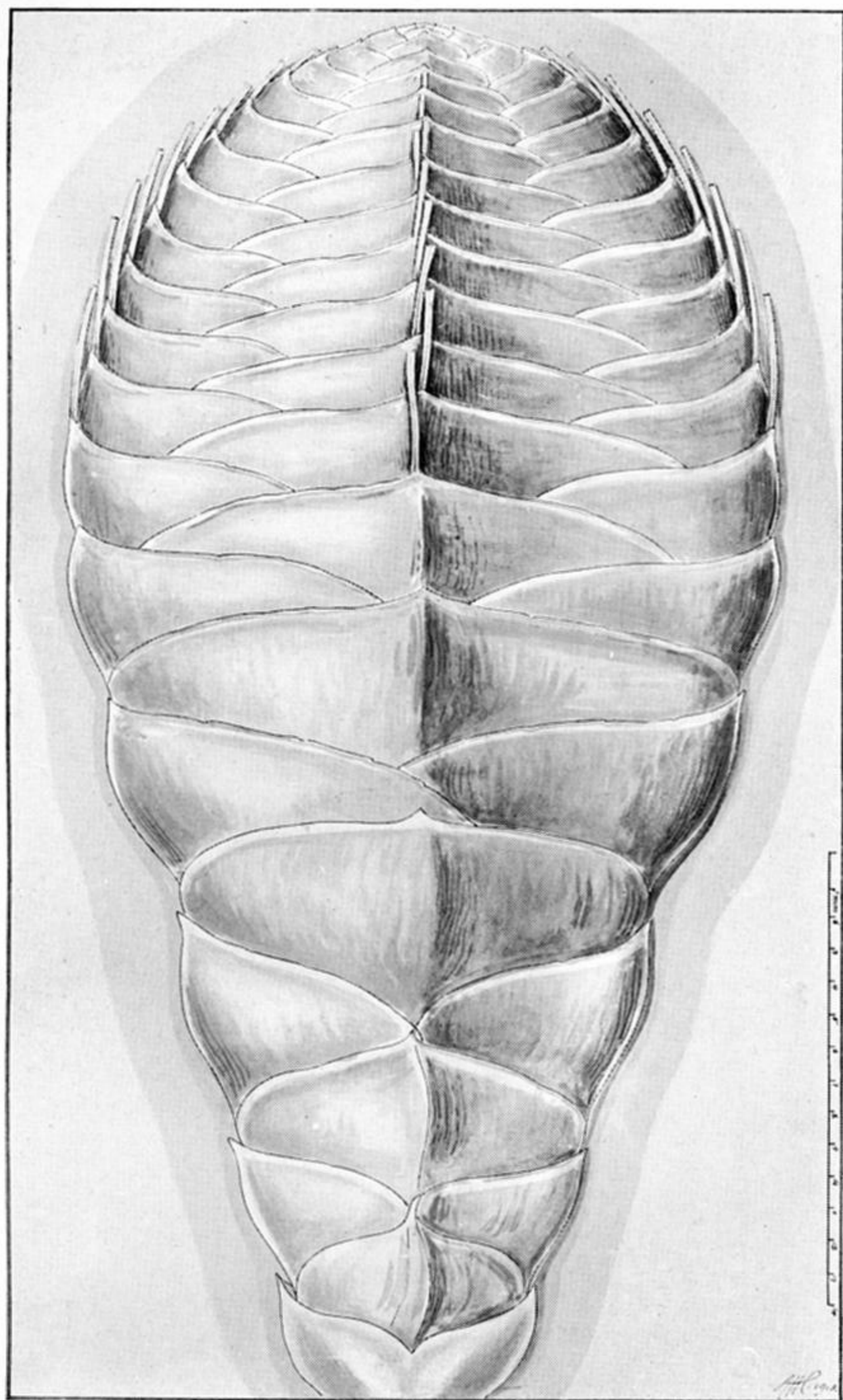


Fig. 1

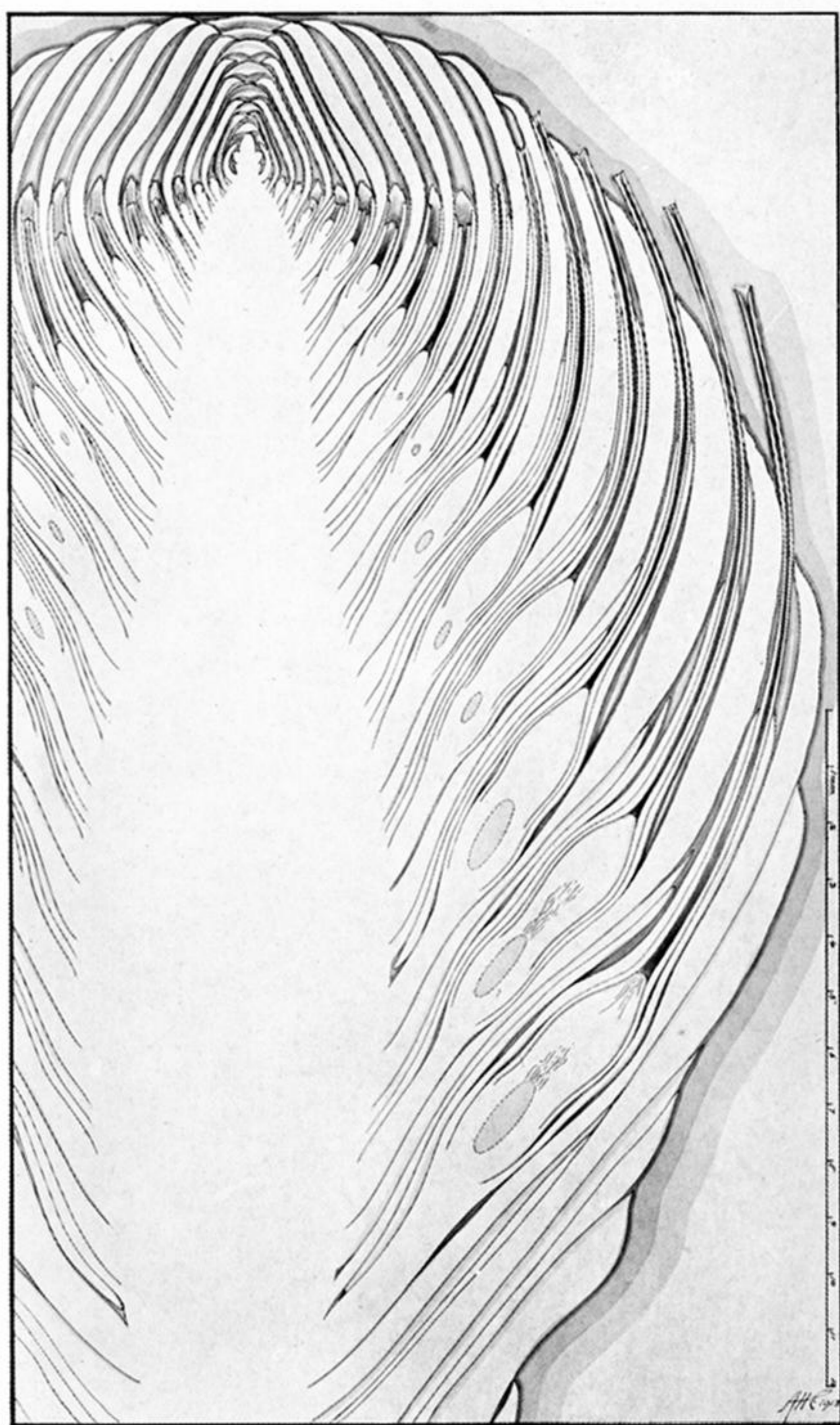


Fig. 2

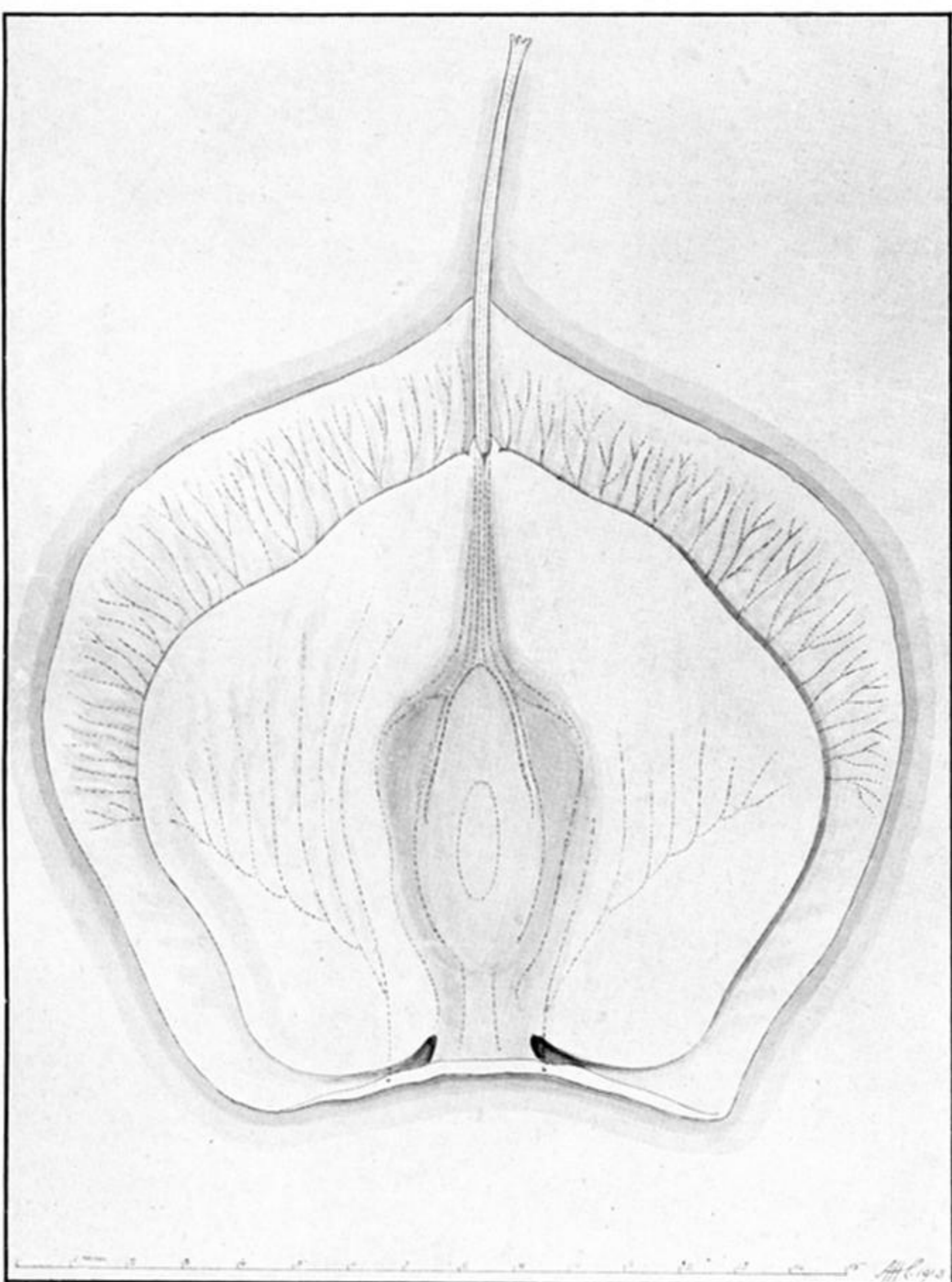


Fig. 3

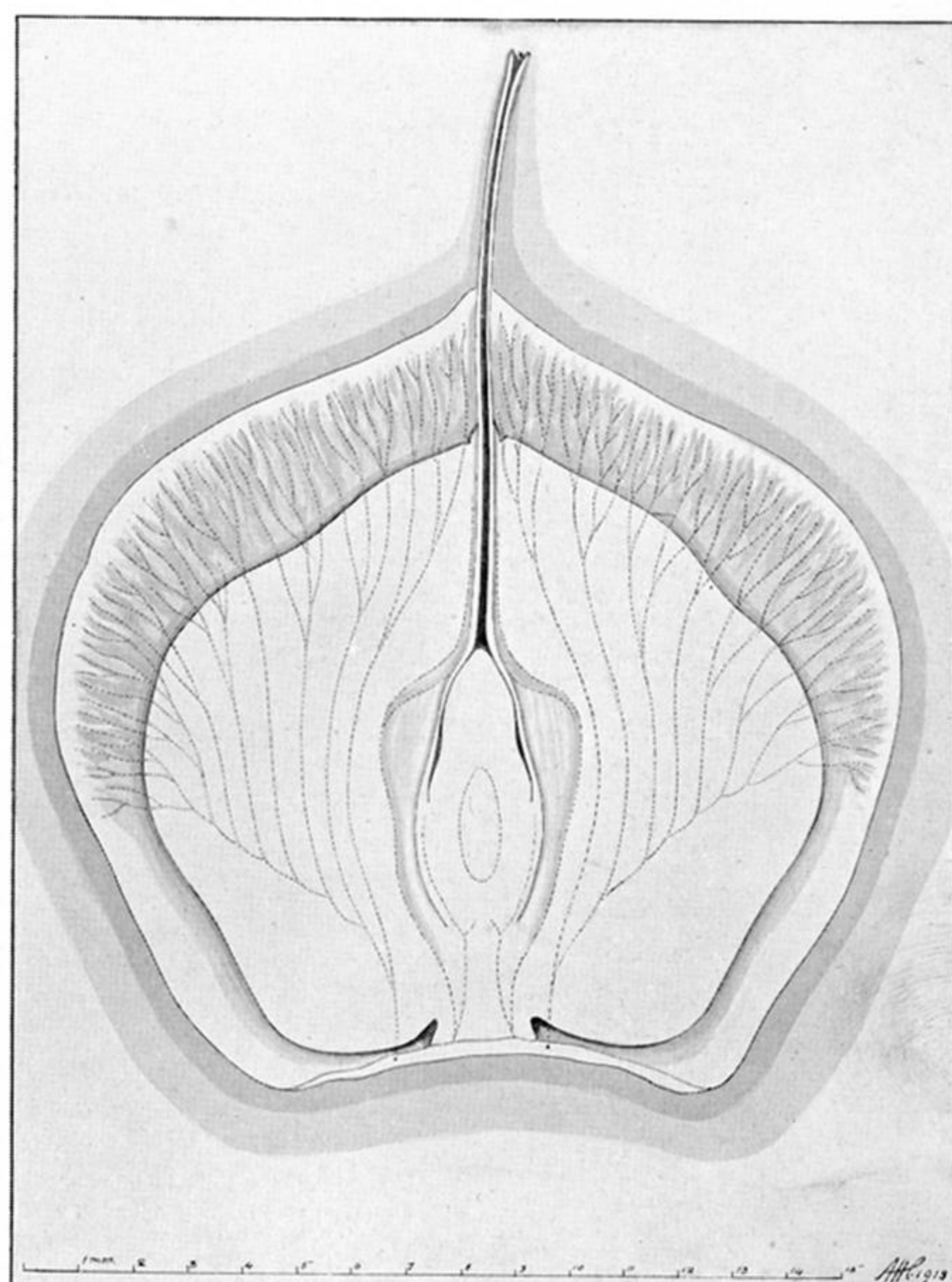


Fig. 4

PLATE 9.

Fig. 1.—Ovulate cone, 40×21 mm. ; external view at the time of pollination of the lowermost flowers.

Fig. 2.—Sectional elevation of the upper portion of a similar cone in the radial plane ; individual flowers cut in the median plane of the floral diagram ; progressive development from the apex to the lowest pollinated flower.

Fig. 3.—Fertile scale of ovulate cone ; ovule in the axil of the subtending bract, viewed from the posterior side. Vascular bundles of the scale and internal structural lines dotted.

Fig. 4.—The same scale with ovule in sectional elevation for the transverse plane of the floral diagram. Vascular bundles of the scale and ovule dotted ; structural lines in agreement with the preceding fig. 3.

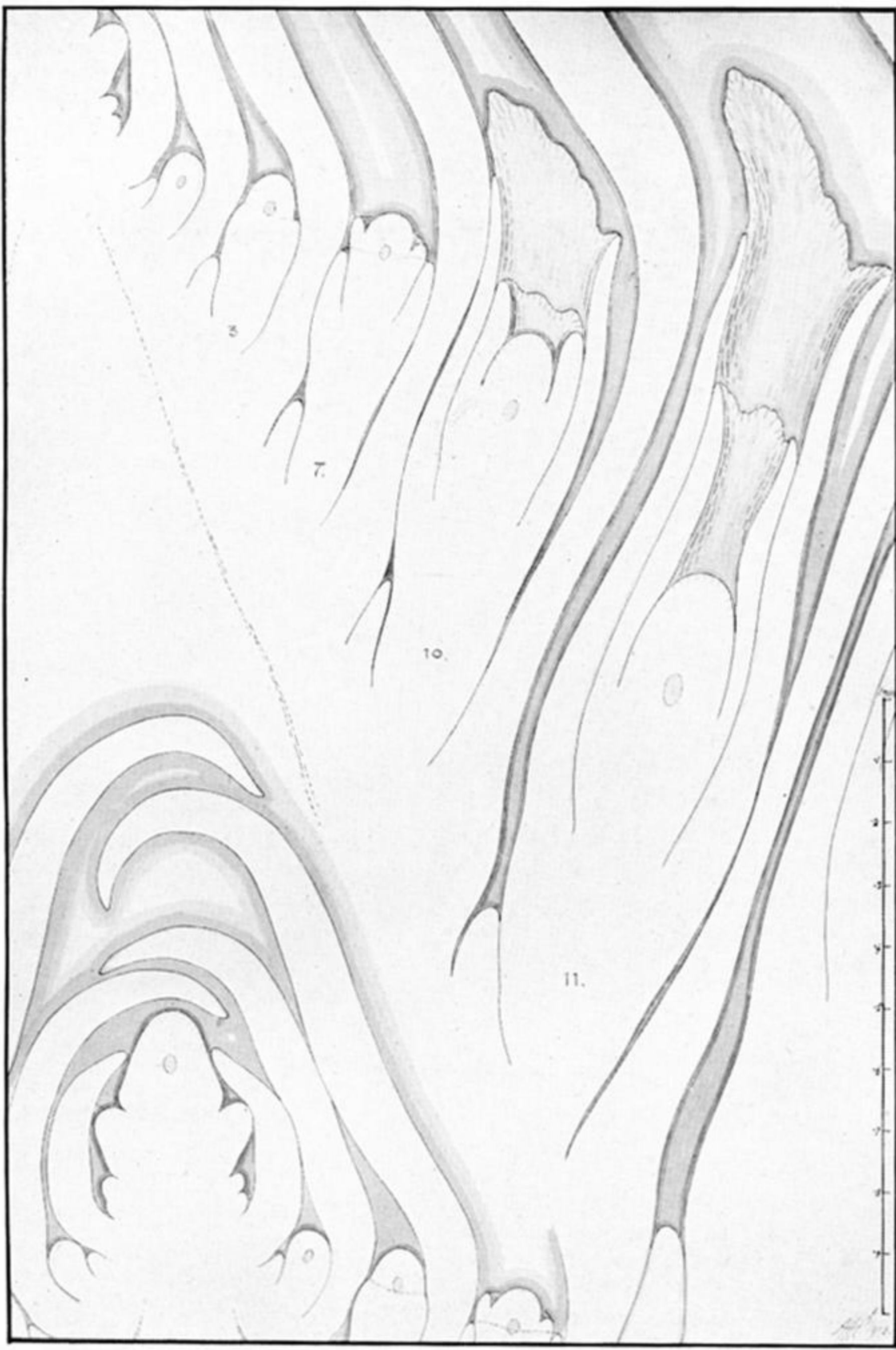


Fig. 5

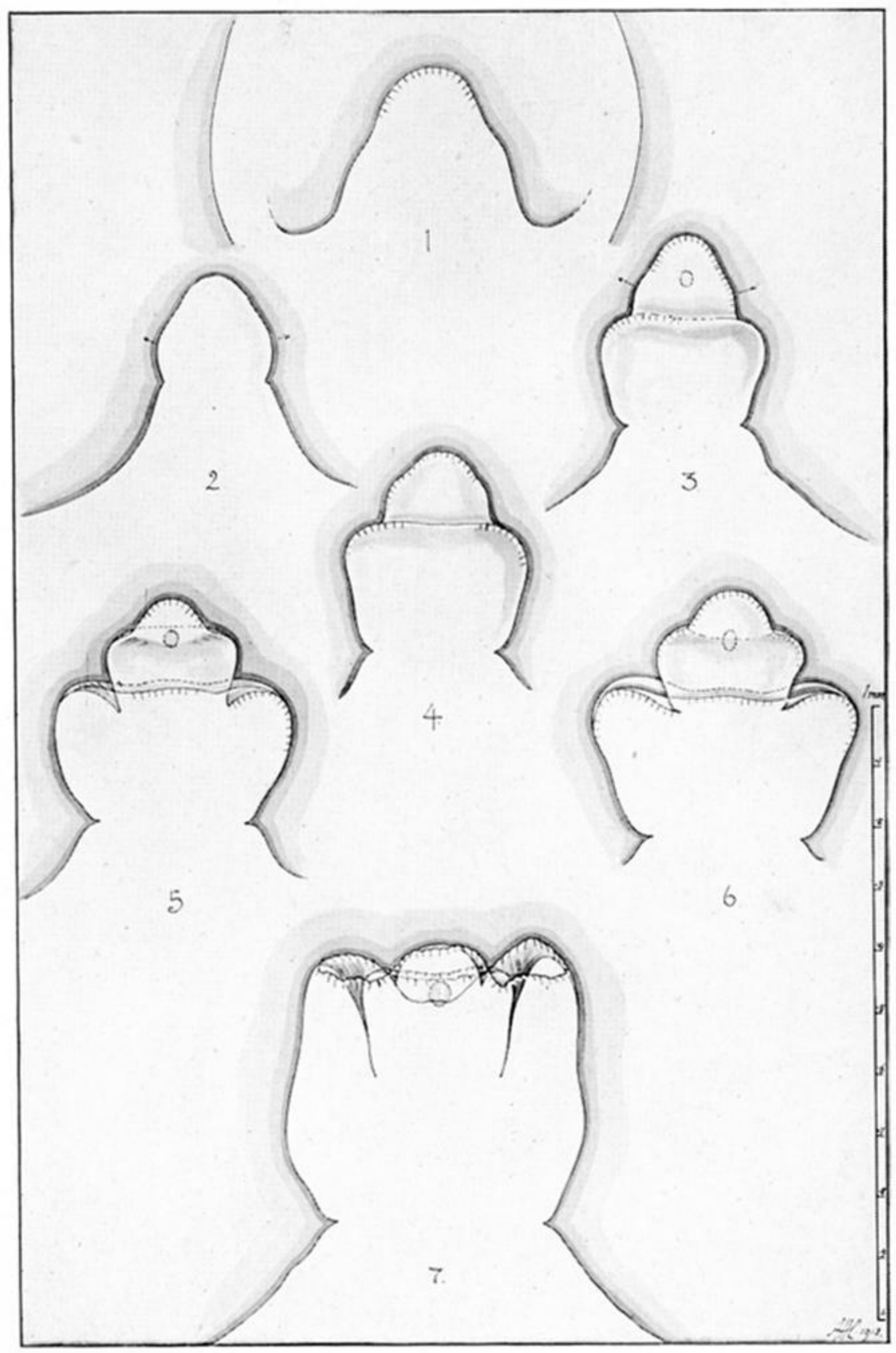


Fig. 6

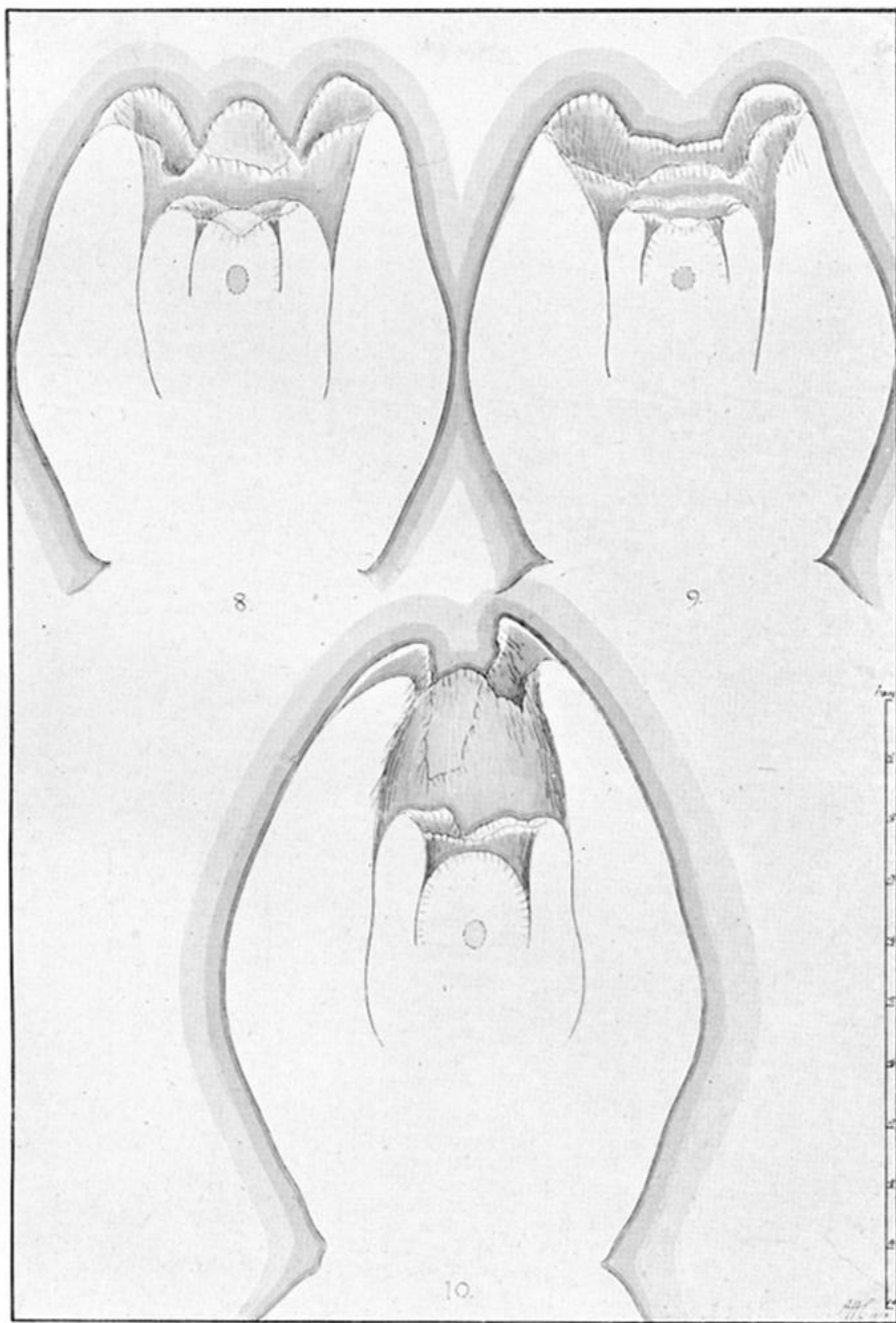


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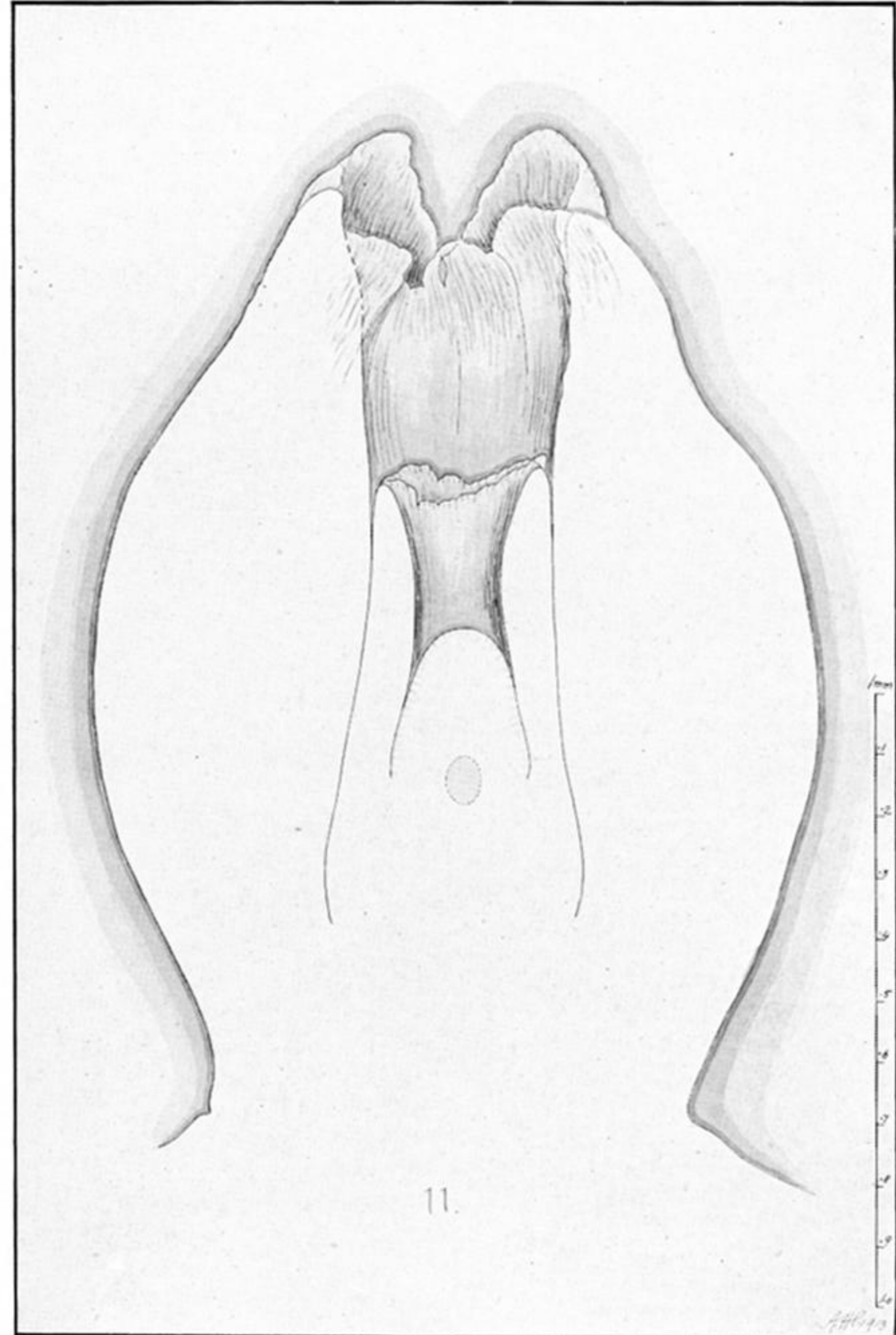


Fig. 8

PLATE 10.

Fig. 5.—Ovulate cone. Development of the ovulate flowers in serial succession behind the apex of the cone. Elevation to scale in the radial plane of the cone (median plane of the individual flowers); essential stages in the origin of the perianth and integument.

Fig. 6.—Corresponding stages of the young ovulate flowers, drawn to the same scale and numbered 1-7, for the transverse plane of the floral diagram in sectional elevation.

Fig. 7.—Similar stages, to the same scale, numbered in series 8, 9, 10.

Fig. 8.—Older stages to correspond 11; Nos. 3, 7, 10, 11 in this series represent the transverse elevations of the median elevations of fig. 5, numbered to correspond.

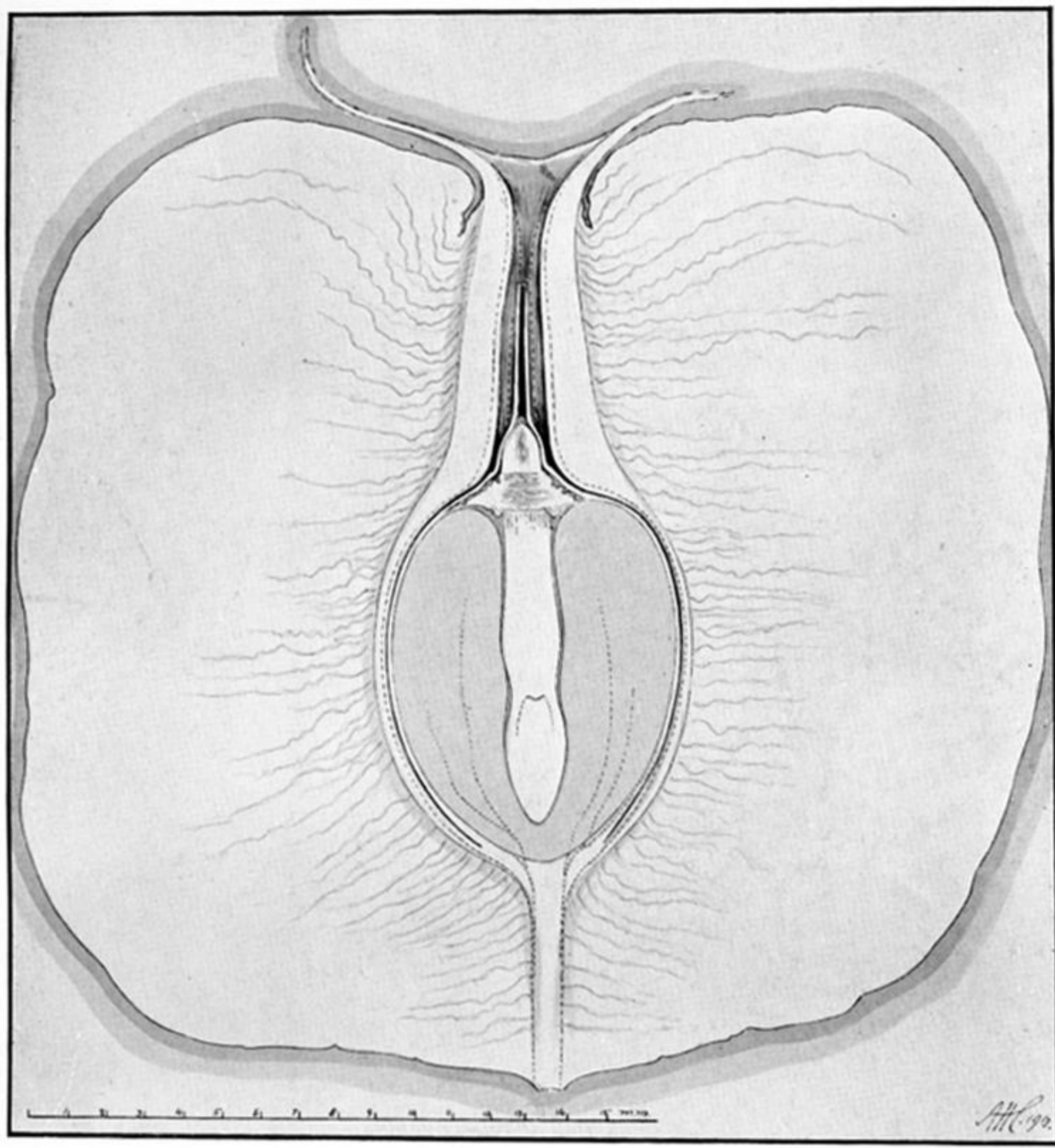


Fig. 9

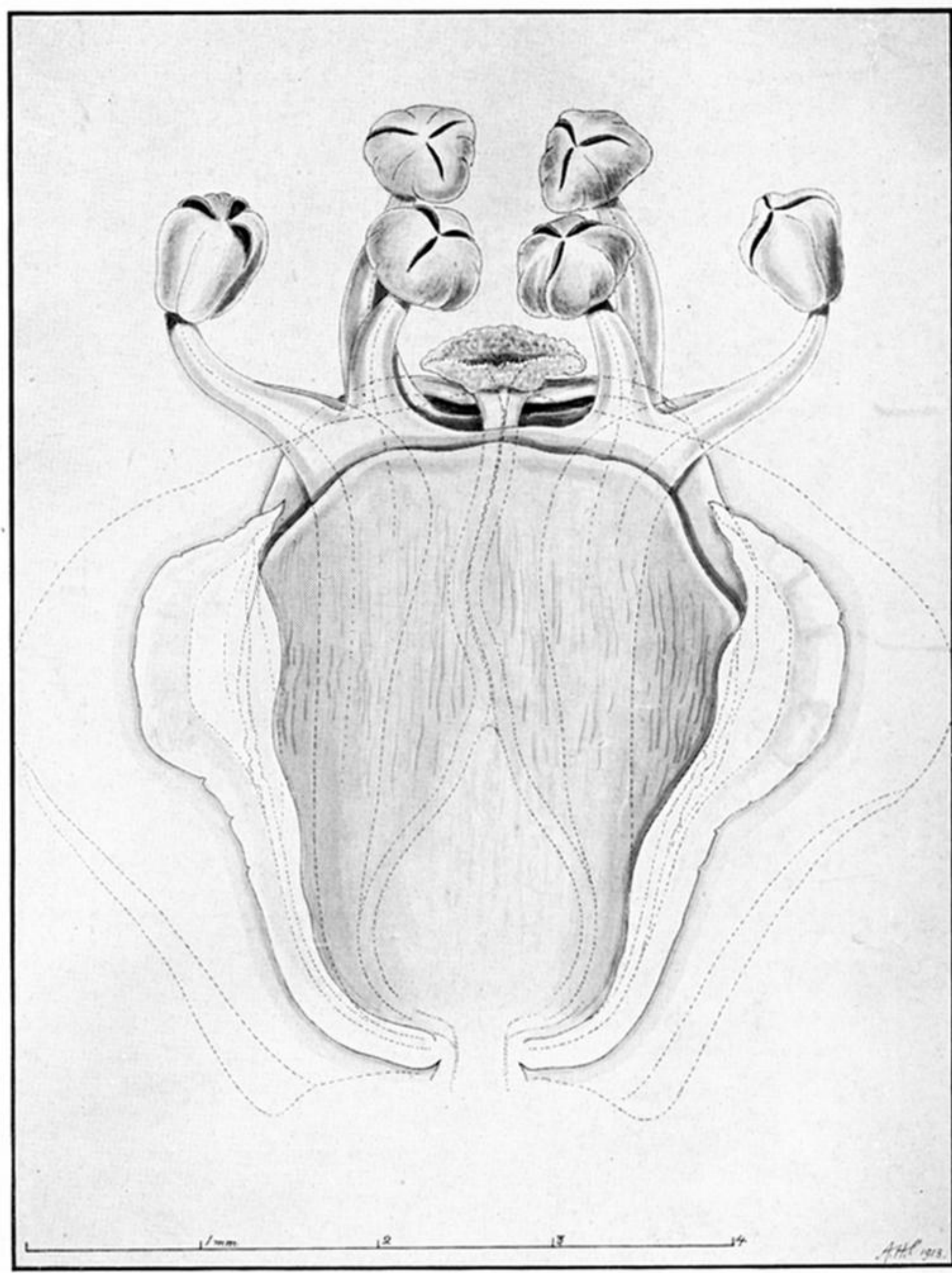


Fig. 11

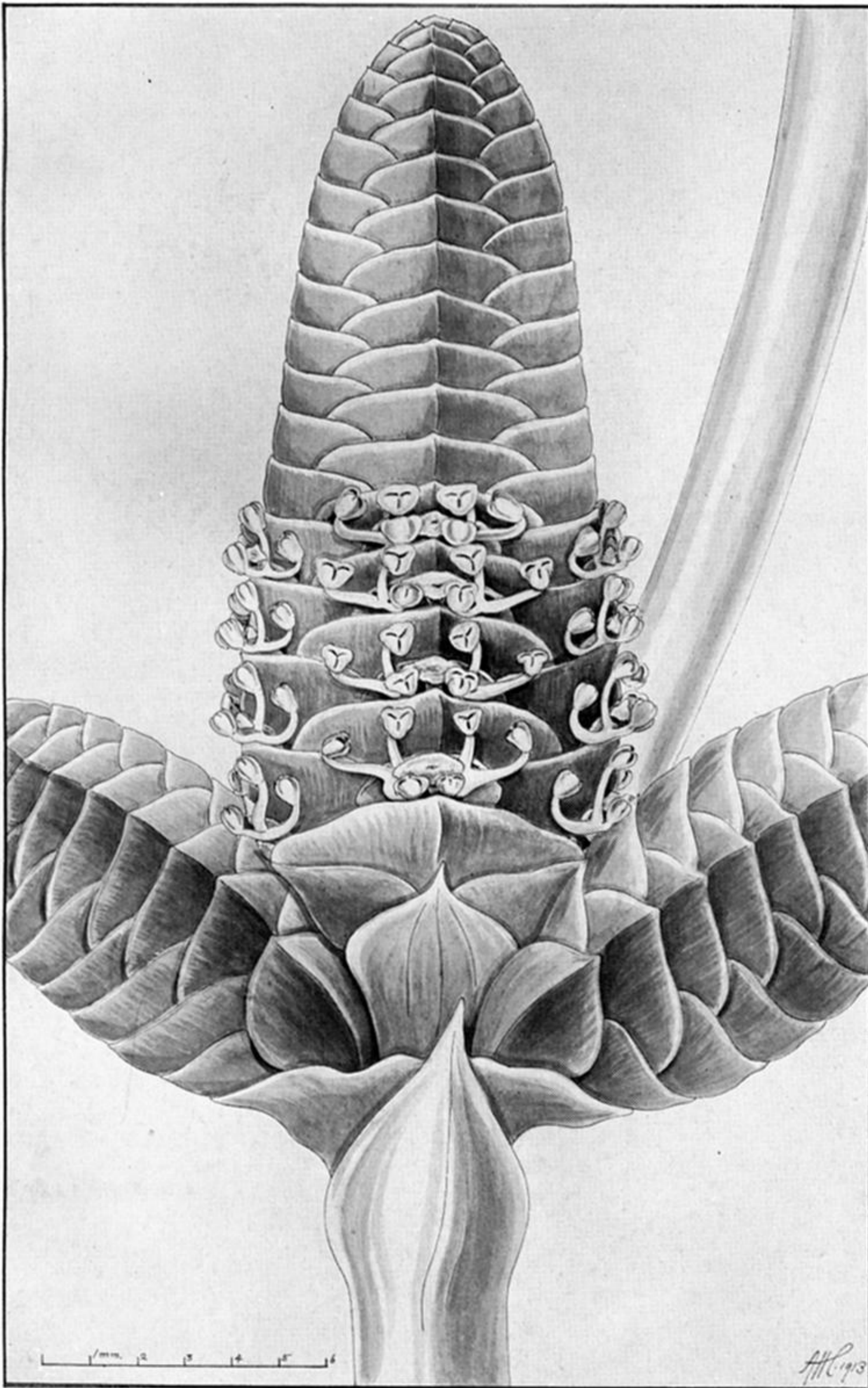


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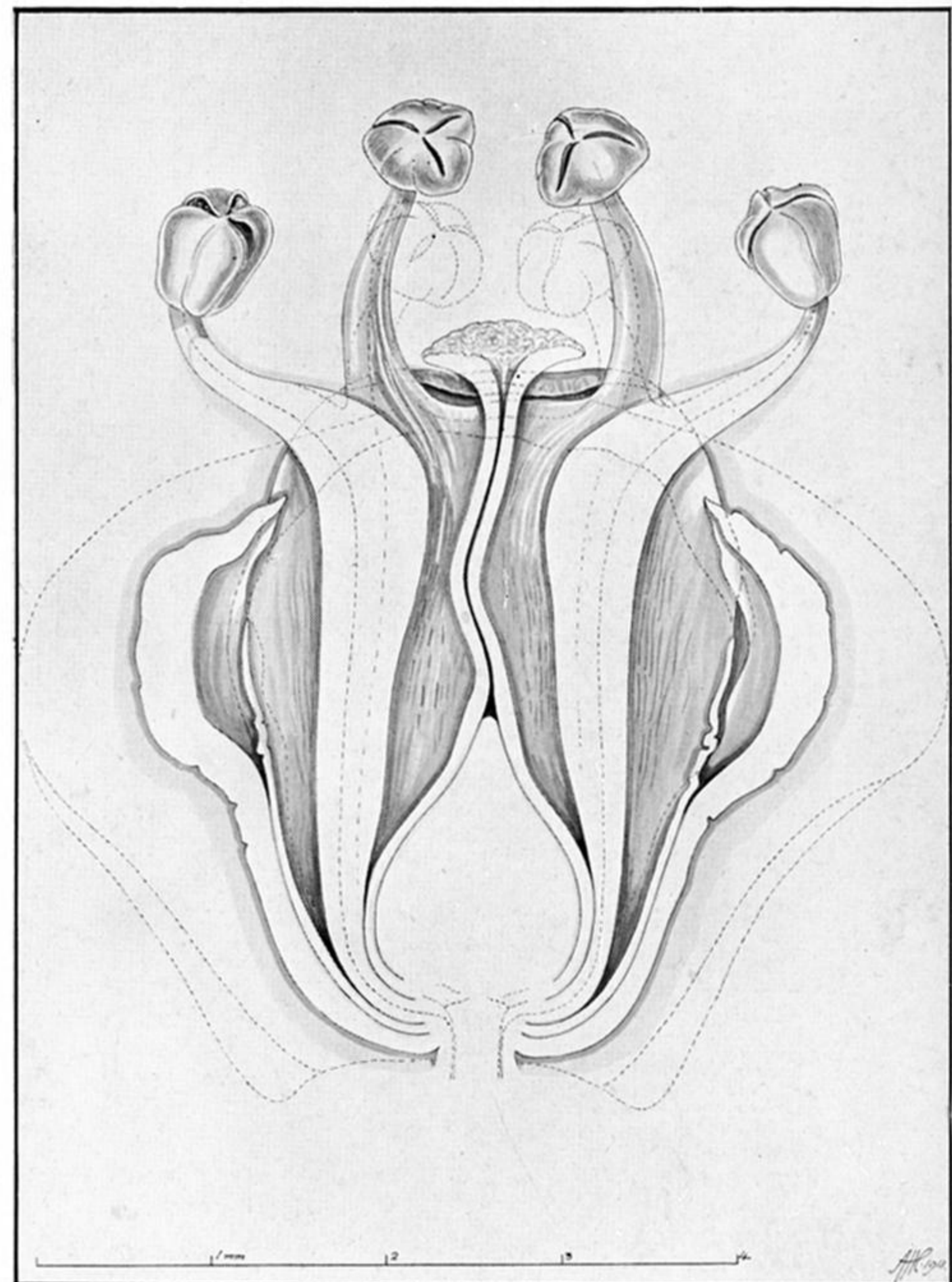


Fig. 12

PLATE 11.

Fig. 9.—Ripe seed (dry material), in median section, to correspond with the sectional elevation in transverse plane of ovulate flowers.

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Fig. 11.—Elevation of functional staminate flower in the axil of subtending bract (dotted); external view on removal of the bract; internal structures dotted.

Fig. 12.—The same flower in sectional elevation for the transverse plane of the floral diagram; missing parts dotted to correspond with preceding figure.



Fig. 13

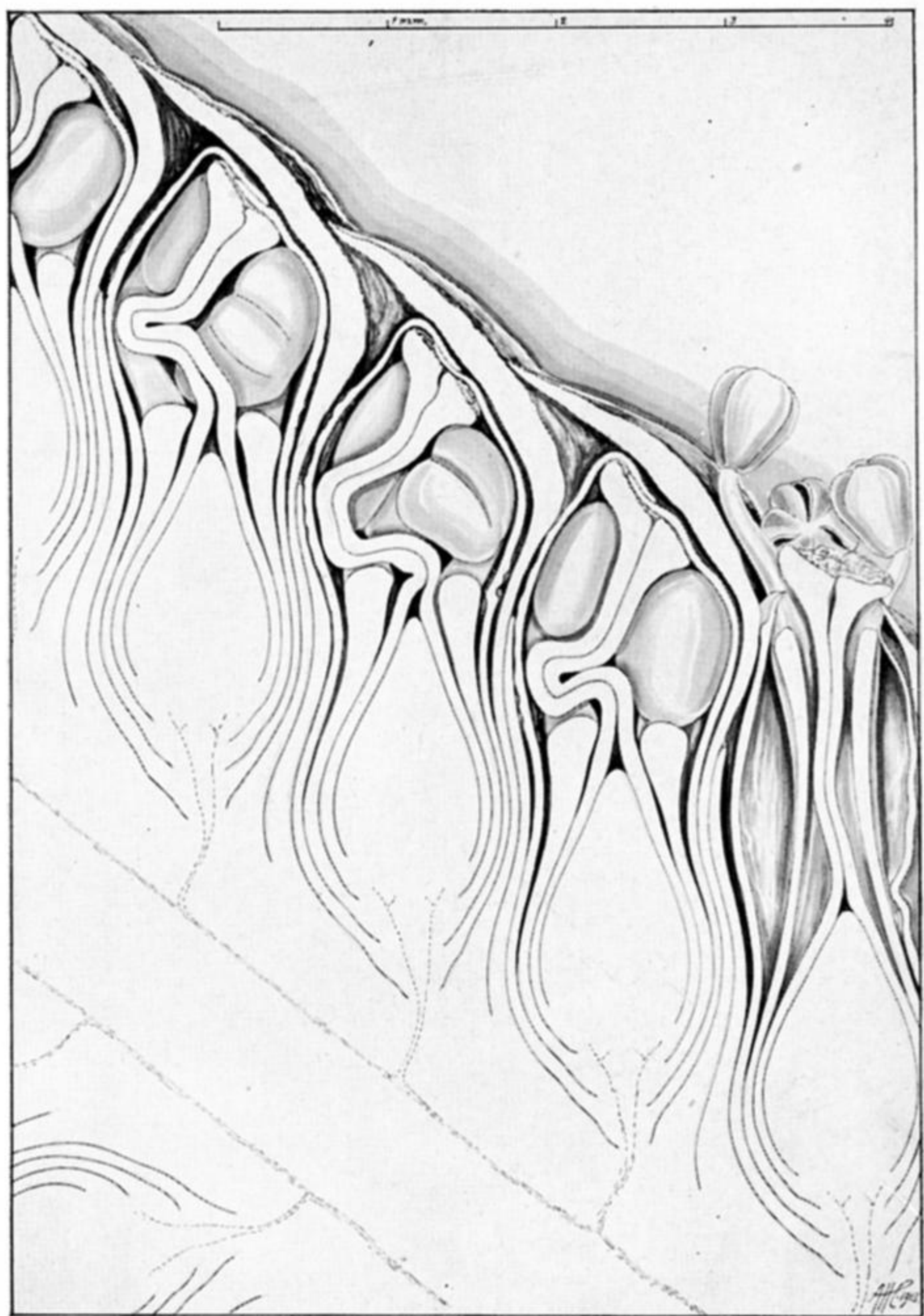


Fig. 14

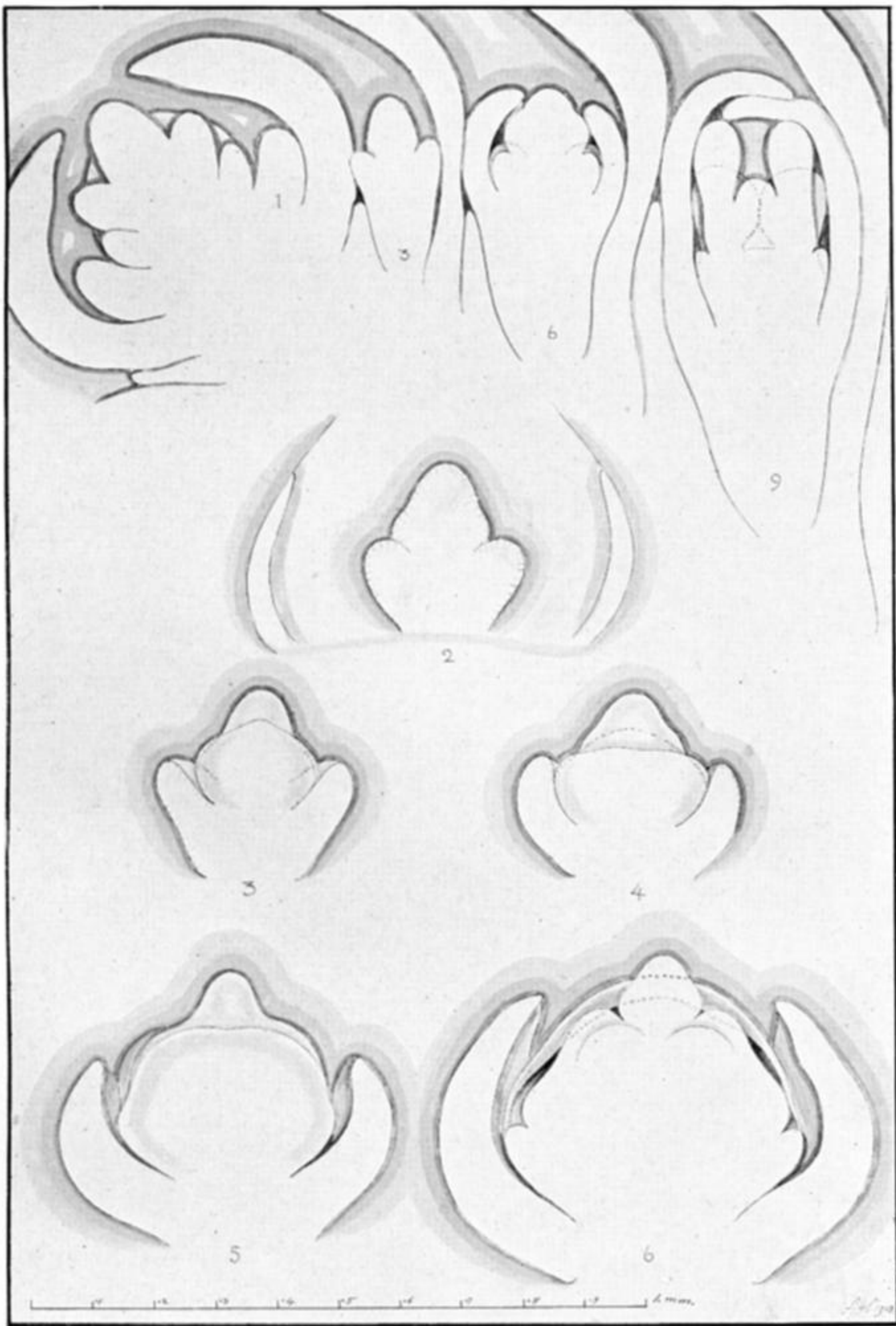


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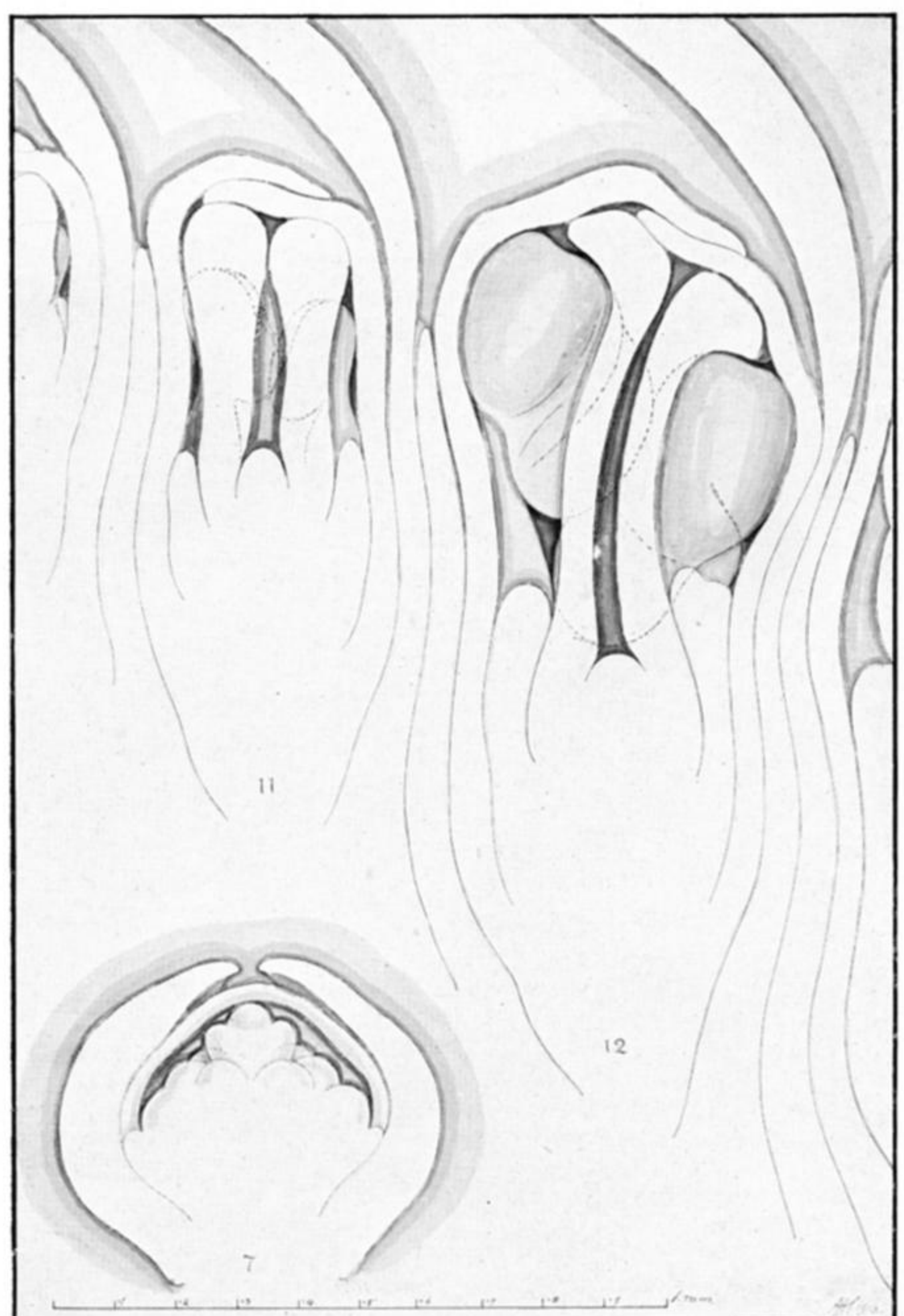


Fig. 16

PLATE 12.

Fig. 13.—Sectional elevation scheme for the median plane of the floral diagram for a series of four functional florets; constructed to the same scale as the preceding elevations.

Fig. 14.—Corresponding sectional elevations of the three next buds in the same vertical series. (Stage of the adult bud.)

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Fig. 16.—Developmental stages in continuation of the preceding; median elevations 11 and 12; transverse elevation of 7, showing six equal stamen primordia making contact on the crested compressed androecial region.

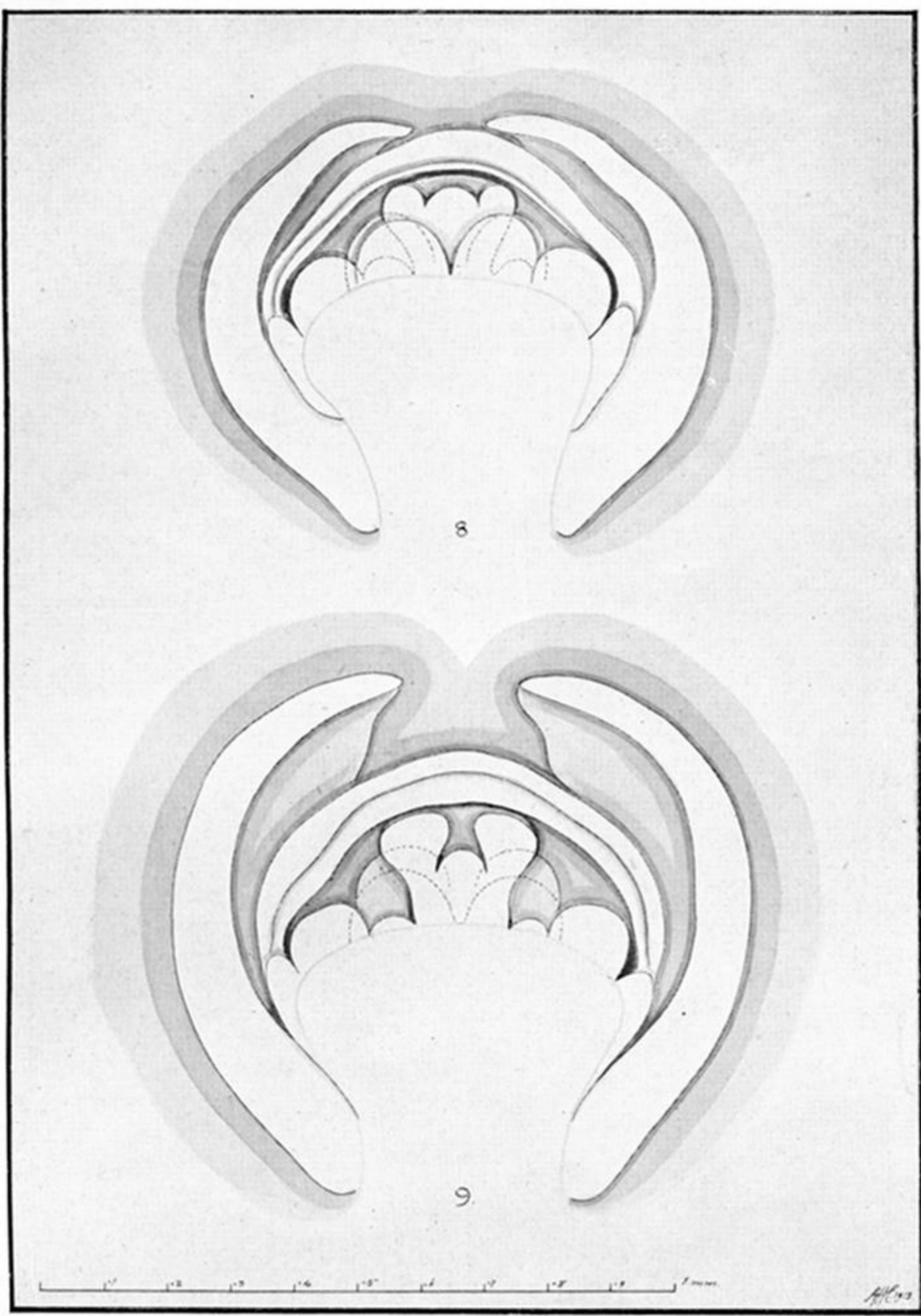


Fig. 17

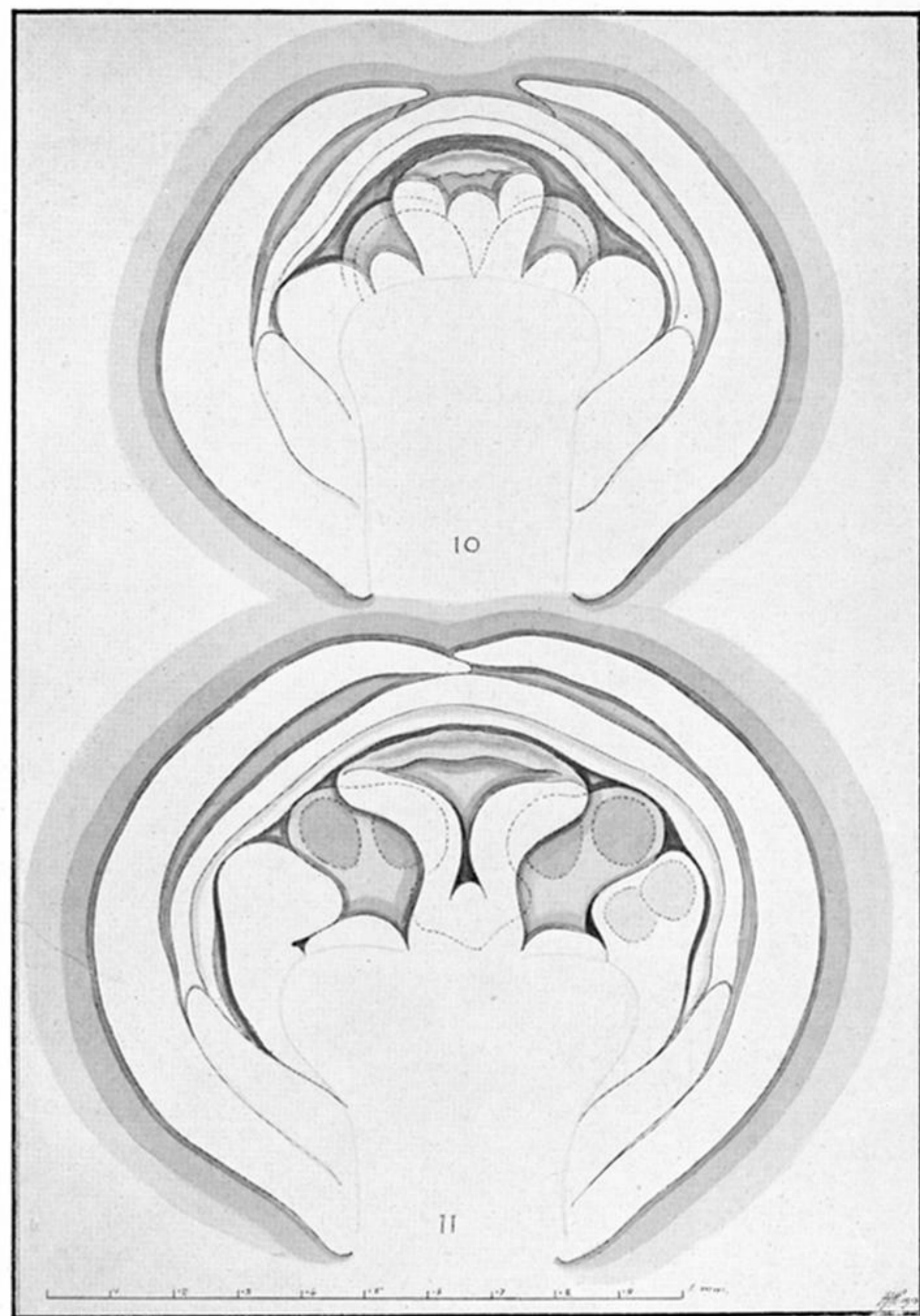


Fig. 18

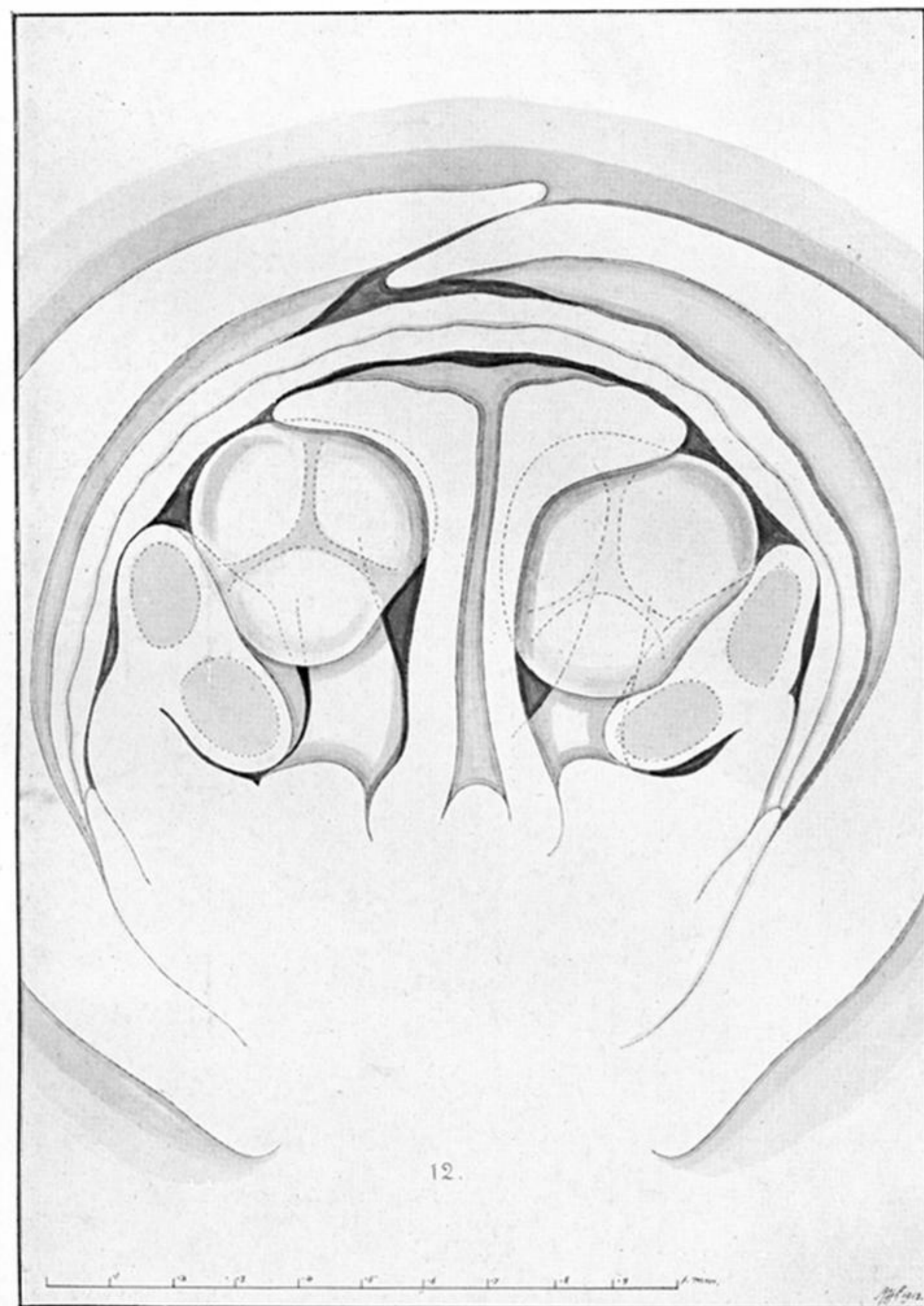


Fig. 19

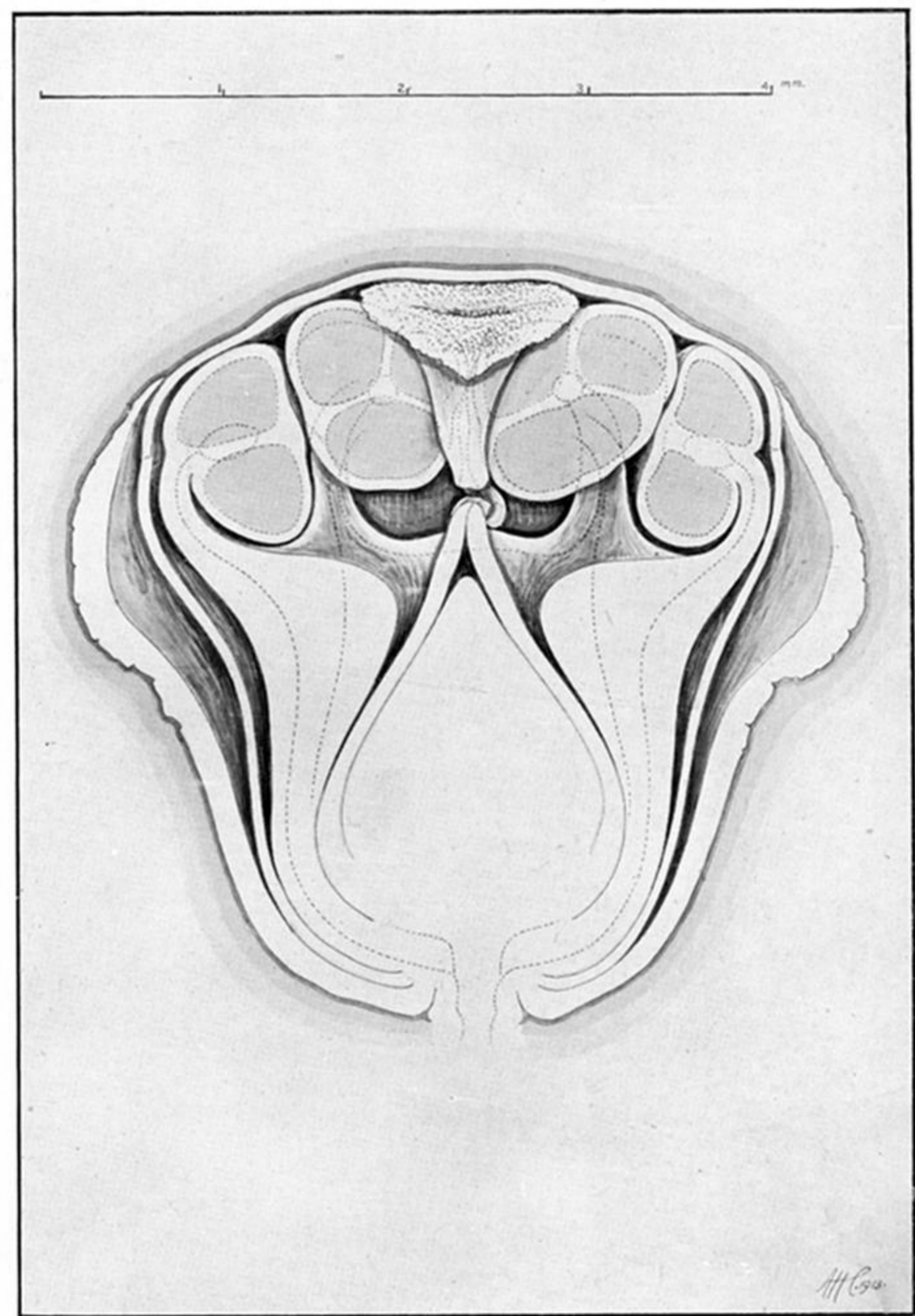


Fig. 20

PLATE 13.

Fig. 17.—Continuation stages in transverse-plane elevations 8 and 9. Progressive and equal differentiation of six stamen-primordia.

Fig. 18.—Continuation stages to correspond, for stages 10 and 11.

Fig. 19.—Sectional elevation of older bud to correspond, stage 12, showing differentiation of "stigma" and "stylar tube," also the first trace of the staminal tube (figs. 15–19, all constructed to the same scale).

Fig. 20.—Sectional elevation in transverse planes of adult bud, to correspond with elevations in fig. 14.