On the Development of the Leaf and Sporocarp in Marsilia quadrifolia[1], L.

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With Plates X, XI, and XII.

ALTHOUGH *Marsilia* and the related *Pilularia* have been frequently studied during the present century, the exact origin and morphological significance of the sporocarp has never been satisfactorily made out in either genus, the chief reasons for this being apparently the complexity of the apical bud and the dense covering of trichomes over all the younger parts. The present work was undertaken at the suggestion of Dr. J. P. Lotsy, then of the Johns Hopkins University, in the hope that a detailed study of the development of the leaf and the sporocarp of *Marsilia* would give some indication of the morphological nature of the latter. The work has been carried on during the winters '95–'96, '96–'97, in the biological laboratory of the Johns Hopkins

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University, under the stimulating direction of the late Prof. J. E. Humphrey, to which any value the work may have must be largely attributed.

The material was collected, partly at New Haven, Conn., through the kindness of Prof. W. A. Setchell, and partly at Cromwell, Conn. It was fixed in 95% alcohol, 1% chromic acid or a 5% sublimate-acetic mixture. For staining, gentian-violet or Mayer's haemalum, the latter either alone or in combination with Bismarck brown, were found most satisfactory.

The Development of the Leaf.

Our knowledge of the development of the leaf in *Marsilia* is due almost entirely to the work of J. Hanstein on the embryo, and frequent reference to this will be necessary in the following pages.

The leaves arise in two rows, one on each side of the median line on the dorsal surface of the stem. Each leaf is developed from a typical two-sided apical cell formed from part of one of the dorso-lateral segments of the tetrahedral apical cell of the stem. This apical cell of the leaf is recognizable when the stem-segment in which it is formed is only the third or fourth in its series from the apical cell of the stem. It is larger in size and projects more than the neighbouring cells (*L*, Fig. 1), and its position is such that its edges are directed toward the base and the apex of the stem.

Hanstein ('65) has already shown the shape and position of the apical cell to be as above described in all but the very earliest leaves of the embryo of *Marsilia*, which agrees thus with most other Leptosporangiates that have been studied. They have been thus described by Hofmeister ('62) in *Aspidium*, by Kny ('75) in *Ceratopteris*, by Klein ('87) in *Polypodium*, by Meunier ('87) and Bower ('89) in *Pilularia*, by Campbell ('87) in *Onoclea*, and by Bower ('89) in *Trichomanes*. *Pteris* is apparently the only known case where,

according to Hofmeister ('62) and Klein ('84), the position of the two-sided apical cell is transverse to the stem.

This apical cell of the leaf in *Marsilia* continues its growth and activity, cutting off segments alternately toward the right and left of the young leaf, which has its ventral side facing toward the stem-apex. When about fifteen or sixteen pairs of segments have been formed, the activity of the apical cell is ended, probably by a periclinal wall like that seen by Sadebeck ('73), Kny ('75), and Bower ('84) in other Lepto-sporangiates, and that to be described later in the sporocarp of *Marsilia*. The great regularity of the segments of the leaf in *Marsilia*, as well as the fact that certain of the cells remain of the full length of the segment (Fig. 3), make it possible to determine quite definitely the number of segments formed (Fig. 2). The only doubt is in regard to the first segments, some of which fuse with the tissue of the stem, and it is thus not certain that the segment numbered 1 in Fig. 2 is not really the second one. The young leaf is about 1 mm. long and ·15 mm. in diameter at the base when the activity of the apical cell ceases, and is a slightly tapering conical organ curved upward (Fig. 2) and ventrally over the stem-apex. It is almost exactly circular in cross-section until the formation of the pinnae begins, and is not at all spatulate as described by Hanstein ('65) in *M. Drummondii*, and by Campbell ('96).

The segments of the apical cell of the leaf, or 'primary marginal cells' of Hanstein ('65) and Sadebeck ('74), are nearly semicircular blocks with the upper and lower surfaces slightly concave toward the apex (Figs. 4–6). The first division-wall appearing in these segments is a longitudinal and radial anticline (*I*, Fig. 6), cutting off about one-third of the segment toward the dorsal side to form what we may call a *section*, and leaving on the ventral side a secondary marginal cell. Wall I is apparently the 'tangential wall' of Sadebeck ('74), and *section* I is the 'Schichtzelle' of Hanstein ('65), but this terminology does not seem appropriate when the real position of this and later section-walls is taken into

account, since it refers to the position of these walls at the intersection with the surface, when the thing of importance is, as we shall see, their position in the interior.

The second wall formed in the segment is also a longitudinal anticline in the secondary marginal cell, and nearly parallel to the inner or median border of the segment (*II*, Figs. 4, 6); and thus is formed a tertiary marginal cell (*mc.*^{3}, Fig. 6). This latter is then divided by a transverse anticline (*t. a.*^{1}, Figs. 4, 5), the radial wall of Sadebeck, into an upper and a lower tertiary marginal cell. Then in each of these further section-walls, to the number of three, are formed near and parallel to the dorsal and ventral sides alternately (*III*, *IV*, *V*, Figs. 4, 5, 7, 8), and there are thus formed two marginal cells of the sixth grade in each segment (*mc.*^{6}, Fig. 8). In a less frequent type of division only four section-walls are formed, and the ultimate marginal cells are thus of the fifth grade.

The Petiole.

The first nine or ten pairs of segments of the leaf go to form the petiole, and the six primary divisions of the segments (taking the type where the ultimate marginal cell is of the sixth grade) break up into cells, as will now be described. About the same time that wall II is formed, there appears in section I a pericline (*pl. w.*, Fig. 6), cutting off at the inner end a part of the plerome contributed by this section to the longitudinal bundle of the petiole. This is followed by a longitudinal and radial anticline, the *halving anticline*, cutting the outer cell into two (*h. a.*, Figs. 5, 7, 8). Each of the other sections and the marginal cell in turn cuts off plerome at the inner end (*pl. w.*, Figs. 7, 8), but no halving anticline is formed in any of them. Then there appears a pericline in the outer end of the halves of section I, in the outer ends of each of the other sections and of the marginal cell, separating a layer of outer cells which give rise to the epidermal structures of the petiole from an inner one of cells forming the mesophyll. We may for the sake of brevity,

though not with strict propriety, call these layers dermatogen and periblem, and the pericline itself a dermatogen-wall (*d. w.*, Fig. 7, *d.*, *pb.*, Fig. 22).

The dermatogen soon splits by another pericline into hypodermal and epidermal layers (Figs. 8–10, 22), each of which remains of one cell in thickness even at maturity, though numerous anticlines, both longitudinal and transverse, are formed in each. On the line of the median wall, of each section-wall and of the halving anticline of section I, there are formed intercellular spaces (*a.*, *c.*, Figs. 8, 22) between the periblem and hypodermis, which are the beginnings of the fourteen (primary) longitudinal air-canals of the petiole (*a. c.*, Fig. 9).

The single periblem-cell of each half of section I cuts off by a pericline at the inner end a second portion of plerome (*pl.*, Figs. 8, 22). Then each of the remaining periblem-cells of section I, the single periblem-cell of each of the other sections and that of the marginal cell, divides by a pericline into an inner and outer cell (Figs. 8, 22). Of these the inner cell divides by anticlines and periclines to form the loose mesophyll-tissue of the mature petiole (*mp.*, Figs. 8–10), while the outer cell gives rise to both the longitudinal and transverse partitions between the adjacent air-canals (*p. c.*, Fig. 8). These latter cells swell in the middle (as seen in cross-section of the petiole) and grow out at the ends into papilla-like tips (Figs. 8, 11, 12), touching their fellows of the adjacent sections, but leaving an intercellular space surrounding each tip. The tips thus formed are soon cut off by longitudinal anticlines (Figs. 8, 11), forming a pair of nearly isodimentional cells (*c. p. c.*, Figs. 8, 11) in each air-canal, opposite each primary partition-cell, of which there are usually eight in the length of each segment. From these eight pair of cells are developed the eight transverse partitions of the air-canal in each segment. These remain one cell thick even at maturity, but during their later development many intercellular openings or pores are formed, allowing the passage of air through them (*c. p. p.*, Figs. 9, 10, 13).

The portion remaining of each primary partition-cell (*l. p. c.*, Fig. 11) grows in a radial direction and splits by periclines, while it at the same time grows in the direction of the length of the petiole and divides by transverse anticlines. Thus are formed the longitudinal partitions between the adjacent air-canals, which are also one cell in thickness (Figs. 9, 10, 13). As each of these primary longitudinal partitions elongates with the lengthening of the petiole, it is seen (*l. p. c.*, Fig. 12) that the primary cross-partition cell at one end is nearer the upper wall and that at the other is nearer the lower wall. Then when the first transverse anticline is formed it is somewhat oblique and forms thus two wedge-shaped cells, each with a cross-partition cell at the broad end and none at the narrow one (*l. p. c.*, Fig. 12). The cross-partitions in adjacent canals are thus alternate. These wedge-shaped cells continue to elongate and divide by transverse anticlines (Fig. 13) till in the mature petiole the cross-partitions are far apart. Here again in the longitudinal partitions we find at maturity many small intercellular openings or pores, the 'méats' of Meunier (*l. p. p.*, Figs. 10, 14).

When the epidermal surface of a section is two cells broad and four cells long (Fig. 15), there is cut out of each cell, by a semicircular anticline at the upper end, a small cell which gives rise to one of the numerous trichomes that clothe the young leaf. The rest of the epidermal cell then divides further by anticlines (Fig. 15), and more trichomes arise in the cells thus formed, while the epidermal cells at maturity become much elongated (Fig. 16). Each trichome-cell grows out beyond the surface of the epidermis, and swells to a knob at the outer end (*tc.*, Figs. 2, 3, 9), which soon elongates in the direction of the length of the petiole. On the lower or basiscopic side it projects but little (Fig. 3), while it grows out toward the apex of the leaf to the long multicellular hair (*tc.*, Fig. 17) that is supported by the basal or stalk-cell which remains wedged in between the epidermal cells (*b. c. tc.*, Figs. 9, 16, 17); later in the development most or all of these trichomes are cast off, and the petiole thus becomes naked at maturity.

Stomata also occur on the petiole, but apparently not until quite a late stage, and their development was not studied.

When the longitudinal partitions are about three or four cells in width (radially), longitudinal rows of mesophyll-cells, usually one opposite each partition, have become specialized to form the so-called tannin-sacs (*t. s.*, Figs. 9, 10). The cells composing these are, like the surrounding mesophyll-cells, about twice as long as broad at maturity and rounded off laterally, forming many small intercellular spaces connecting with the large air-canals.

While the dermatogen and periblem have been developing as described above, the plerome of sections I–IV has given rise to the axial vascular bundle of the petiole. The plerome of section II divides by two longitudinal anticlines into quarters, of which the one in the angle between I and III never divides further in any direction, but forms the large trachea of its side of the bundle (*tr.*, Figs. 3, 8–10, 22). The nucleus of this cell may divide many times, so that in a trachea of half a millimeter in length (Fig. 3) we may find twenty-five or thirty nuclei, but these and all other protoplasmic contents disappear later and the end-walls assume the characteristic oblique position, always with the dorsal edge directed towards the base of the leaf.

The remaining three quarters of this section and all the plerome of sections I, III, and IV break up by numerous longitudinal walls (Figs. 8–10), and later by fewer transverse walls (Fig. 3), to form the remaining tissues of the bundle which later still develops a bundle-sheath (*b. s.*, Figs. 9, 10). The portion of the marginal cell within what we have called the plerome-wall never forms any part of the vascular bundle, and the same is usually true of the same portion of section V, though it does occasionally form a small portion of it (Fig. 9).

The Lamina.

Just before the activity of the apical cell ceases, the tenth and eleventh (or eleventh and twelfth) segments on each side begin to grow out laterally and ventrally to form the first

pair of pinnae (p^1., Fig. 18). Each pinna is formed from the whole length of one segment (usually the lower one) and most, but not all, of a second (Fig. 19). In this respect the pinnae resemble those of *Ceratopteris* (Kny '75) and differ from those of *Asplenium serpentini* (Sadebeck '73) and *Onoclea* (Campbell '87), in which the pinnae are equal in extent to the segments.

Soon after the apical growth ceases, the segments beyond the first pair of pinnae, except part or all of the one next the lower pinna on each side, begin to swell out in a similar manner to form the terminal pair of leaflets.

In a transverse section of the leaf through the pinnae, which is practically the same for both pairs, we see that the swelling mentioned is due to the continued activity of the marginal cells (Fig. 20). No pericline is formed in these, as in the marginal cells of the petiole, but anticlines parallel alternately to walls IV, V are formed continually until the pinna is two millimeters broad or more (Fig. 21). The additional sections thus formed divide like the earlier ones by periclines to form the three meristem-layers of the lamina. The marginal cells also divide frequently by anticlines perpendicular to the edge of the pinna, thus constantly increasing in number and giving the pinna a fan-like shape with rounded outer edge formed by the actively dividing marginal cells (Fig. 19), as was shown by Hanstein. The pinnae are directed more ventrally than laterally from the petiole, and the upper pair soon come to have their upper or ventral surfaces nearly in contact, while the lower and older pair fold together (Fig. 21) to enclose the younger ones between them in the bud (Fig. 25).

A branch of the axial bundle is given off to each pinna, which branches to form the anastomosing veins characteristic of *Marsilia*; but the exact development of these bundles of the pinna was not studied, and I cannot state whether they arise, as Sadebeck ('74) has shown them to, in *Asplenium*. The epidermal cells of the leaf give rise to stomata on the upper or both sides, and to deciduous trichomes like those of the petiole.

The Sporocarp.

The bean-shaped sporocarps of *Marsilia quadrifolia* are usually borne in pairs, the stalks of the two uniting below, as shown by A. Braun ('70), to form a common stalk joining the petiole of the fertile leaf on its inner side near the base. Occasionally but a single sporocarp is found, or two with stalks separately inserted on the petiole, or more rarely three or four, usually with a common stalk. In the half-grown sporocarp we find the smaller or younger one of the pair is borne on the side of the stalk toward the petiole. If sporocarps occur on any leaves of a given branch they are usually found on all.

Plants of *Marsilia* which were left out of water in September by the drying up of a pond, matured many more sporocarps than plants growing where the water-level was constant. Although the latter had an equal number of young sporocarps in July, nothing but small and often shrunken rudiments were found on most of the plants in September; these might, however, be borne on large and well-developed petioles, so that there is no regularity in the retardation in development of the fertile leaves.

Bischoff ('28) says the sporocarp of *Marsilia* arises as a slight prominence on the anterior side of the petiole, while Mettenius ('46) states that it originates endogenously, and later breaks through the epidermis of the petiole to form a solid mass of tissue, in the interior of which later the sori and canals are developed. The youngest sporocarp studied by Russow ('72) had a two-sided apical cell, but was already differentiated into stalk and capsule (probably about the stage of that shown in Fig. 42). He thought the soral canals arose by the splitting apart of certain cells in the interior of the capsule and the formation of pits on the ventral surface into which these slits opened, to close again later by the growth of the cells on the ventral surface. On the walls of these canals arose the 'soral cells,' in each of which later a tetra-

hedral apical cell was formed, which cut off a number of segments that, according to Russow, gave rise to the placenta with its vascular bundle and to the microsporangia, while the apical cell itself finally became the macrosporangium. Goebel ('82) states that the soral canals of *Marsilia* are external in origin, and that the sporangia arise from superficial cells; Büsgen ('92) describes the first rudiment of the sporocarp as 'eine scheinbare grosse Lücke' in the tissue of the young leaf, and he thinks it probable that all the soral cells of each sorus are derived from a single superficial cell of the ventral surface. The placenta, microsporangia and macrosporangia, he states, are formed as Russow has described from these soral cells.

According to my own observations on *M. quadrifolia*, the sporocarp makes its appearance when the young fertile leaf consists of about six or seven pairs of segments, and thus long before the appearance of the lamina. It is developed from an apical cell exactly like that of the leaf, formed in one of the ultimate marginal cells of the inner side of the petiole (*F. m. c.*, Fig. 22) and placed transversely to the latter. The marginal cell involved may be either the upper or lower of (apparently always) the second segment of the inner side of the petiole, though, because of the crowding together of the various rudiments of the bud, this could not be made out with certainty (*F.*, Fig. 23). The sporocarp is thus not, strictly speaking, epidermal in origin, but resembles closely in its origin the single sporangium of *Lygodium* from a marginal cell of the fertile pinnule, as described by Prantl ('81).

The apical cell of the sporocarp thus formed goes on cutting off segments, alternately toward the base and apex of the leaf, or to the right and left of the sporocarp itself, until about twenty-three pairs of segments are formed. It thus gives rise to a papilla, much like the very young leaf, which bends laterally to grow up beside the petiole with its ventral side facing in the same direction (Fig. 24), and then bends ventrally upon itself at the point where the stalk joins the capsule (Fig. 25). Finally, at about the time that the

activity of the apical cell is ended, by the appearance in it of a periclinal wall, the capsule or upper part of the sporocarp lies with its ventral side nearly in contact with that of the stalk (Fig. 31 *a*). The capsule is at this time about 1 mm. long, and the sori at the base about as far developed as that shown in Fig. 36. There is never any curling in of the extreme tip of the capsule, suggesting the circinate coiling of the leaf, and the sharp bending mentioned above is partially straightened out later, as Russow has shown, by the more rapid growth of the capsule at the base.

The shape and size of the segments of the apical cell are very nearly like those formed in the leaf, and their earlier divisions are exactly the same. Walls I and II (Fig. 27) are followed by the transverse anticline dividing the marginal cell (*t. a.*[1], Fig. 34), and wall III is formed in the same position as in the leaf. This is followed, however, by another anticline parallel to III (*IV*, Fig. 27), and then the regular alternation is resumed, wall V being on the ventral side, and VI, the last wall, on the dorsal side of the marginal cell (Fig. 28). We thus have one more section dorsal to the marginal cell than in the leaf, and the ultimate marginal cell is of the seventh grade instead of the sixth.

The position of the section-walls given above is in general that found in all of the segments of the sporocarp, but certain exceptions are worthy of note. Thus wall IV, instead of running through to wall II as usual, often bends down to meet wall III at some distance from II (dotted line, Fig. 27). This type of division, however, was never seen in the lower or basiscopic marginal cells of the soral segments of the capsule. Again, section V is usually narrower in the basiscopic marginal cells of the soral segments of the capsule (*V*, Fig. 34), and hence the basiscopic ultimate marginal cells, which are evidently 'the sorus mother-cells' of Büsgen, are the largest ones of the ventral side of the capsule. Finally, any marginal cell of the sporocarp, except the basiscopic one of the soral segments, may form a pericline instead of wall VI, and thus make the ultimate marginal cell of the sixth grade. This

behaviour is apparently analogous to that of certain marginal cells of the fifth grade in the leaf.

When the second sporocarp of a pair is formed, it arises usually from a marginal cell of the second or third segment of the first sporocarp on the side of the latter toward the petiole on which it is borne (F^2, Fig. 26), and a third probably arises in the same way from the second. The position of the apical cell of this second sporocarp, with reference to the first, is transverse, like that of the apical cell of the first with reference to the petiole. This mode of origin of the younger sporocarp from older ones shows that the common stalk of the pair is simply the portion of the stalk of the older one below the point of origin of the second, and the same is true of the stalk common to the second and third sporocarps of a trio. It is probable that where two or more sporocarps are inserted on the petiole by separate stalks, as happens occasionally in *M. quadrifolia*, and constantly in forms like *M. polycarpa*, we should find them to originate from marginal cells of successive segments of the petiole, but the early stages of this type were never seen.

The Stalk.

The further development of the seven divisions of each segment mentioned above differs in the different regions of the sporocarp. In the four or five oldest pairs of segments that form the stalk, their later history is very like that of the segments of the petiole, except that the axial bundle is here formed entirely from the plerome of sections I and II and a part only of that from section III. All the remaining portions of these segments, and all of the other segments, give rise to mesophyll and to hypodermal and epidermal structures, but no tannin-sacs are formed among the mesophyll-cells, and only very small air-canals between these and the hypodermis. A structure is thus formed of smaller diameter than the petiole, and of much firmer tissue, which swells out at the upper end (*l. t.*, Fig. 44) to form the lower tooth of the capsule.

The Capsule.

In the seventeen or eighteen segments forming this part of the sporocarp, we find that plerome- and dermatogen- walls are formed in each section, as in those of the petiole (Figs. 27, 28), and the halving anticline of section I is followed by periclines cutting off another portion of plerome from each half. The dorsal bundle, which is a continuation of the axial bundle of the stalk, is made up entirely from the plerome of section I (*d. b.*, Fig. 31), some of the cells of which differ from all others of the capsule by remaining of the full length of the segment. The bundle is thus much more restricted in origin than that of the petiole.

The dermatogen-layer in the capsule splits, as in the leaf, into epidermal and hypodermal layers, of which the former remains one cell in thickness and gives rise to stomata and deciduous trichomes, while the latter divides (*hy.*, Figs. 29, 31) to form the two layers of thickened cells of the wall of the mature capsule, differing thus from the hypodermis of the leaf (Fig. 10). The periblem of the capsule gives rise to the several layers of loosely packed cells between the vascular bundle and the hypodermis, and between these cells and the latter are developed the numerous but small air-canals confined mostly to the dorsal side (*a. c.*, Fig. 29) and separated by partitions arising like those in the petiole.

In the first three segments at the base of the capsule no sori are formed, but there is formed in the youngest pair from the plerome of sections III and IV, in a way to be described in treating the soral segments, a forked lateral branch of the dorsal bundle (Fig. 44). The plerome of sections II, V, and VI of this pair of segments, and all but section I of the next older pair, is apparently devoted to the formation of the basal portion of the gelatinous ring on which the sori are borne when the capsule bursts. In the oldest pairs of segments there is formed a two-layered wall of thickened cells, like those of the hypodermis, stretching completely across the

base of the capsule (*b. w.*, Figs. 31 *a*, 42, 44). In the periblem above the dorsal bundle in these segments and in several of the older soral ones is developed a wall of thickened cells, enclosing between it and the dorsal hypodermal wall a lens-shaped mass of looser cells, the 'linsenförmige Raum' of Russow (*l. c.*, Fig. 44). There is an opening into this space just above where the dorsal bundle pierces the basal wall, and another at the anterior end, out of which there projects a rod of brown-walled cells (*br.*, Fig. 44). The epidermal cells above this cavity swell out later to form the upper tooth of the capsule (*u. t.*, Fig. 44).

Each segment of the next eight or nine pairs give rise to a sorus. Section I in these segments develops much as in the segments of the stalk, as we have seen above. But the other sections have a peculiar history. Sections III, IV, and VI, dorsal to the marginal cell, widen rapidly at their outer ends, while sections II and V do not. The ultimate marginal cell is thus pushed around to a ventral position, the interpolated section IV contributing largely to this end (Figs. 27, 29 ; cf. Figs. 8, 9). Finally, all other cells in this region grow out beyond the cells formed from the basiscopic ultimate marginal cell, and grow together over the outer ends of them, completely enclosing them (Figs. 29–33).

The Vascular Bundle-System.

The dorsal bundle, arising from the plerome of section I in all the segments of the capsule, gives rise in each soral segment to a lateral branch that runs down back of each sorus, between this and the lateral wall of the capsule. At a point about opposite the middle of the sorus the lateral bundle splits to three branches, as Russow has shown. Two of these (*l. b. f.*, Fig. 33) continue on in the course of the single part of the bundle, while the third turns abruptly inward to connect with the placental bundle of the sorus (*p. br.*, Figs. 33, 44). The dorsal and single portion of the lateral bundle arises from the basiscopic half of the plerome

of section III, and from a part of the same region of section IV (*l. b.*, Figs. 29, 31, 32). Of the two outer forks of this bundle one arises in the basiscopic quarter of the acroscopic half of the plerome of the same segment (*l. b. f.*, Figs. 35, 39, 40), and the other from the acroscopic quarter of the acroscopic half of the next older segment. These forks are formed very early, but grow in length with the sorus, and finally on beyond it to the ventral edge of the capsule (Figs. 33–44), where their ends become connected in a more or less regular way with those of their fellows of the same side of the capsule (*l. b. f.*, Fig. 44). The third or placental branch of the lateral bundle arises from a part of the plerome of the basiscopic half of section VI (*pa.*, *br.*, Figs. 31, 32, 33, 42), and the placental bundle with which this connects is developed from the plerome of the same part of this section (*pa.*, *b.*, Figs. 30, 32, 36, 41, 42).

The Sori.

Of the sections on the ventral side of the marginal cell, the plerome of section II develops ultimately into the large-celled tissue of the dorsal portion of the gelatinous ring (*pl.*[2], Figs. 29, 31, *g. r.*, Figs. 32, 33), described by Hanstein ('62) and Russow. The plerome of section V grows around under the inner end of the marginal cell (Figs. 28–32), and probably takes part ultimately in the formation either of the gelatinous ring or perhaps of the stalks by which the indusia are attached to the latter, but this was not determined with certainty. The periblem of both these sections apparently develops very slightly, and seems to form a part of the stalk of the indusium (*pb.*, Figs. 28–31), but the boundary between this and the dermatogen soon becomes indistinguishable. The dermatogen of both sections grows rapidly in a radial direction (*d.*, Figs. 28–31, *o. ind.*, Figs. 32, 33), and gives rise to that portion of the indusium on the median side of the sorus. The outer or ventral cells of these sections soon grow over laterally to meet section VI, and thus enclose the cells of the sorus, while certain cells of these just below the ventral wall give

rise to part, if not all of the ventral portion of the gelatinous ring. The inner portion however, in the basiscopic half of the segments at least, remains of a single cell in thickness in each, even at maturity.

We come now to the most important division of the soral segment, the basiscopic ultimate marginal cell (Figs. 34–38), from which are derived all the sporangia of the sorus. This is the 'Sorusmutterzelle' of Büsgen, but this name seems inappropriate as there is no single mother-cell of the sporangia of the sorus alone, nor of the whole sorus including the indusium after the single marginal cell of the third grade. No dermatogen-wall is formed in these marginal cells, and the sori being derived thus, like the young sporocarp itself, from a cell capable of forming at least two of the meristem-layers, are not of strictly epidermal origin. As the young sporocarp increases in size, we find that soon after the formation of section VI the basiscopic marginal cell elongates in the direction of the length of the organ, and divides by a transverse anticline into halves, of which the acroscopic one soon comes to be the larger (Figs. 34–38). Then each of these divides by another anticline (Fig. 38), forming thus four cells, of which the basiscopic one of the acroscopic pair soon becomes the largest (*p. ma-sp. m. c.*, Fig. 38), while its sister-cell on the acroscopic side splits by still another anticline. We have formed thus a series of five cells, of which the middle and larger one (*p. ma-sp. m. c.*, Figs. 34, 38) is the primary macrosporangium mother-cell giving rise to all the macrosporangia of the sorus. The adjacent cells on either side of the latter (*p. mi-sp.*, *m. c.*, Figs. 34, 35, 38) are the primary microsporangium mother-cells, while the outer cells of the five (*i. ind.*, Figs. 34, 38) give rise to the inner layer of the indusium on each side. The outer layer of the indusium on each side is formed by the splitting in two of the acroscopic marginal cell by a transverse anticline (*o. ind.*, Figs. 35–38), one half helping to form the indusium of the sorus of its own segment, and the other of the sorus of the next younger segment.

In horizontal section it is seen that the three middle or sporangial cells become more densely filled with protoplasm than the indusial cells (Fig. 35), and also become separated at the ventral surface from the cells of section V (*s. c.*, Figs. 29, 35), thus forming the beginning of the soral canal. Otherwise the development of all of the five cells is much alike at first, and if we take transverse sections in the plane of the sporangial cells, we find that each elongates considerably in a radial direction (Fig. 29), and later divides into two by a pericline (Fig. 30). Then by the further growth and division of both of these cells (*ma.-sp. m. c.*, Fig. 31), there is formed a row of seven or eight cells reaching from about the centre of the capsule nearly to the ventral surface (Fig. 32), all of them separated by the soral cavity or canal from that part of the indusium formed from section V. In sagittal section (Fig. 43) it is seen that the microsporangial and indusial cells have divided in a similar manner.

From the occurrence in them of nuclear spindles and their relation to the surrounding cells, there can be no doubt that all the sporangial cells of the sorus are derived from the marginal cell, and none from cells dorsal to this in the interior of the capsule, as Büsgen thought possible. In the bending of the soral canal that takes place as it increases in length, the sporangial cells may come in contact with the inner layer of the indusium, but there is certainly no growing together, and the phenomenon has no significance. It is during the development of this row of soral cells that they are outgrown and finally enclosed by the surrounding cells, forming at first a 'funnel-like pit' at the ventral end of the soral canal (Figs. 30, 31), but finally closing entirely, though leaving traces of the fusion for a long time (*s. c.*, Figs. 32, 33).

While the sporangial and indusial cells have increased in numbers by the radial growth and division, there have been other important changes. The macrosporangium mother-cells (*ma-sp. m. c.*, Figs. 35, 36) are pushed by the growth of the plerome of section VI (*pa. b.*, Figs. 36, 37) out into the soral cavity, far beyond the microsporangium mother-cells, swell

laterally to several times their former size, and in so doing push the microsporangial cells around (Figs. 36, 37) to a position nearly at right angles to their former one. The macrosporangium mother-cell finally divides by three inclined walls to form the tetrahedral apical cell of the macrosporangium (*ma. sp.*, Figs. 32, 37). This apical cell cuts off two more segments on each of the three sides below (Fig. 41), which form the stalk and basal wall of the sporangium; then a pericline is formed near the outer end of the apical cell, cutting off the archesporium (*arc.*, Fig. 41) and completing the sporangium wall. The archesporium, as Russow has shown, then gives rise to the tapetum and spores.

While the microsporangial cells are being pushed aside as described above, each has divided by anticlines approximately parallel to the segment wall, first to two (Fig. 36) and then to four (Fig. 41). These come to lie parallel to the segments of the apical cell of the macrosporangium, and are evidently the cells which Russow supposed to be segments of this, but there can be no doubt that they are really derived as described above.

Of the four cells formed from each of the microsporangial cells as just described, the lower three go to form sterile tissue of the placenta (*pa.*, Fig. 41), while only the upper one, next to the macrosporangium, actually forms microsporangia. Each of these upper cells divides by walls transverse to the axis of the sorus to form four cells on each side of each macrosporangium (which are well seen in a sagittal section of a capsule somewhat older than that shown in Fig. 43). Then each of these four cells swells out from the placenta, and divides into a basal cell (*st. c.*, Fig. 41) and an outer cell, in which is formed later the tetrahedral apical cell giving rise to the stalk, walls, and archesporium. This basal cell of the microsporangium may be considered as homologous with the stalk-cell found in other Leptosporangiates, but nothing was seen in the development of the macrosporangium that could be regarded as such. In this latter respect *Marsilia* appears to differ from *Pilularia*, where Campbell ('93) states that such a cell is formed, at least occasionally.

In the development of the sporangial cells just described, the plerome of the acroscopic part of the basiscopic half of section VI has played an important part. The cells derived from this (*pa. b.*, Figs. 35, 36) push in back of the swelling macrosporangium mother-cell and between the placental cells (*pa.*, Figs. 37, 41) derived from the primary microsporangium mother-cells. Most of these cells derived from section VI form the middle portion or axis of the placenta, but a row of them next to the base of the macrosporangium (*pa. b.*, Fig. 36), and running the whole length of the sorus (*pa. b.*, Figs. 32, 33, 44), develop the vascular bundle of the placenta, while at a point about opposite the middle of the sorus these same cells become modified across the whole width of section VI (*pa. br.*, Figs. 31–33, 42, 44), to form the placental branch connecting the placental bundle with the lateral bundle.

During this activity of the other cells of the sorus the indusial cells have been developing also. The acroscopic part of section V and the acroscopic marginal cell have each split by a transverse anticline (Figs. 35, 36) to form, in connexion with the cells of section II, the complete outer layer of the indusium (*o. ind.*, Figs. 35–37, 41, 43). The inner indusial cells derived from the basiscopic marginal cell and the basiscopic portion of section V (*i. ind.*, Figs. 32–37, 41, 43) complete the inner layer also. Each of these layers remains one cell in thickness throughout; but by growth of the cells in a direction parallel to, and division by walls perpendicular to the surface of the indusium, the latter pushes out so as to accommodate the growing sporangia. During the growth of the indusium intercellular spaces appear at many points between the two layers (Fig. 41), and other larger ones between the outer layers of the indusia of adjacent sori, both laterally and along the median wall (*i-s.c*, Figs. 41, 42). By the increase in size of the latter spaces the indusia of adjacent segments become entirely separated, and the sori of each side of the capsule push into the furrows between the sori of the opposite side (Fig. 42). At a time a little

before this happens the sori may appear opposite each other, though they are really alternate in origin, as we have seen above (Fig. 34).

Finally we come to speak briefly of the last six or seven pairs of segments of the capsule, beyond the youngest soral segments. In these there is no single dorsal bundle, as this divides to two just beyond the origin of the lateral bundles of the last pair of sori. These two divisions run along nearly parallel to each other near the dorsal wall of the capsule (Fig. 44), and each gives off three or four branches which arise, like those in the soral segments, from the plerome of sections III and IV, and are joined like those also with their fellows of the same side near the ventral margin. The exact region of origin of the two divisions of the dorsal bundle was not made out satisfactorily. All the plerome of this region, except the little devoted to the dorsal and lateral bundles, is apparently devoted to the formation of the gelatinizing tissue of this part of the capsule.

Summary and Conclusions.

The leaves of *Marsilia* arise in two rows on the stem each from a cell quite near the growing-point. The two-sided apical cell formed in this leaf mother-cell cuts off fifteen pairs of segments, and these are divided by radial anticlines into six main divisions, five sections, and an ultimate marginal cell of the sixth grade. Four of these divisions on each side take part in the formation of the axial bundle of the petiole, while all of them help to form the mesophyll and epidermal tissues. One quarter of the vascular tissue contributed by section II develops without further division to the large trachea of its side of the bundle, which has its oblique end-walls always inclined in the same direction. Fourteen air-canals are formed between the mesophyll and hypodermis of the petiole, and a single longitudinal row of the mesophyll-cells gives rise to both the longitudinal and transverse partitions between

these. Another longitudinal row of the same cells gives rise to each of the tannin-sacs.

The pinnae or divisions of the lamina are formed by the continued activity of the marginal cells of certain segments, but their limits do not correspond exactly with those of the segments, the lower pair being nearly two segments in length and the upper pair about three.

In its mode of origin, then, the leaf of *Marsilia* agrees closely with that of other leptosporangiate Ferns, as it does also in its further growth by the segmentation of a two-sided apical cell. But the position of the first division-walls in these segments, while very like that described for *Asplenium serpentini* by Sadebeck ('74), is apparently quite unlike that described for *Ceratopteris* by Kny ('75), for *Onoclea* by Campbell ('87), and that given by Campbell ('95, p. 325) for the Leptosporangiates in general. In the development of the lamina also *Marsilia* is unlike other described forms except *Ceratopteris*, since the pinnae are not co-extensive with the segments as in *Onoclea* and *Asplenium*, though all agree in having the pinnae formed by the activity of a series of marginal cells. There is however great need of more detailed work on the origin of the leaf and the differentiation of this into petiole and lamina.

The sporocarp of *M. quadrifolia* is developed from a transversely placed apical cell, arising in a marginal cell on the inner side of the young leaf. The second sporocarp when present (usually) arises in the same way from a marginal cell of the first. The two are thus respectively primary and secondary branches of the leaf.

More rarely we may find two or more sporocarps inserted separately on the petiole, both on the same side. Then the suggestion is a tempting one, more especially in cases like *M. polycarpa*, where ten or more sporocarps may be borne in the same way, that the sporocarps represent pinnae homologous with those at the tip of the petiole, and the study of abnormal pinnae by Büsgen may perhaps seem to favour this. But before accepting this we have to account for the

occurrence of the sporocarps on one side of the petiole only, and also for their origin by a single apical cell instead of a series of marginal cells like the pinnae.

Growth by the apical cell continues till more than twenty pairs of segments are formed. In the primary division of the segments one more section is formed dorsal to the marginal cell than in the leaf. The epidermis is formed much as in the leaf, but the mesophyll and its air-canals are less developed, while the hypodermis is of two much-thickened layers. The longitudinal bundle (axial in the stalk and dorsal in the capsule) is derived from section I only; the lateral branches of this in the capsule are formed in sections III and IV; and the placental bundle and branch from section VI. The sporangia of each sorus are all derived from one macrosporangial cell, and two microsporangial cells are formed in the basiscopic marginal cell of each soral segment.

The microsporangia and the macrosporangia are thus derived from sister-cells, and the former do not come from segments of the apical cell of the latter as described by Russow and Büsgen; neither is the view of these authors as to the origin of the placental bundle from these same segments the correct one, as was stated a few lines above. A stalk-cell, homologous perhaps with that of the other Leptosporangiates, is formed in the development of the microsporangium, but nothing that could be so interpreted was seen in the macrosporangium.

The soral canals arise by the separation of the primary sporangial cells from the outer cells of section V, and are entirely external in origin. The indusium surrounding each sorus arises by the more rapid growth of the superficial cells of the ventral side of the capsule which grow out and close together over the ends of the sporangial cells. Its development thus seems to warrant the statement that it is a true indusium morphologically as well as physiologically. The gelatinizing tissue of the dorsal part of the capsule is apparently the equivalent of a part of the vascular tissue of the petiole, while that at the ventral edge probably comes

from the outer, and that at either end of the capsule from all three meristem-layers.

The walls of the capsule, including the vascular bundle-system, are developed entirely, or practically so, from the four sections in each segment dorsal to the marginal cell. Hence the two valves into which the capsule splits at bursting cannot be homologized with the divisions of the lamina, since these are developed from the numerous sections formed on both sides by the continued activity of the marginal cells. For this reason also any seeming similarity in the branching of the vascular bundle-systems of the two organs can have no meaning in the direction of homology.

We have here then another reason, in addition to the one mentioned above in speaking of the mode of origin of the sporocarp from the petiole, for not believing with Goebel that it represents a single leaflet or pinna with its edges folded in to meet at the ventral margin of the capsule. And the same objections hold against other views involving a belief in the laminar nature of the valves, such as that of Russow and Büsgen, who regard the capsule as made up of two leaflets with ventral surfaces facing each other, or that of Campbell and Meunier, who compare it to a folded pinnate leaf with a sorus for each pinna.

As far as developmental history gives any clue, the sporocarp of *Marsilia* is homologous with the petiole only of the sterile branch of the leaf. But before adopting this unreservedly we have to explain why there should be the marked difference in the development of the longitudinal vascular bundle in the two, especially in such very similar structures as the petiole and stalk.

So far as we have light at present, then, we may consider the capsule as the swollen end of a petiole in which the marginal cells are devoted to the formation of the sporangia instead of a lamina.

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[1] I regret that Poirault's work did not come to my notice before the present paper went to press, so that I might have mentioned certain points in his work concerning the origin of tissues in the leaf of *Marsilia* which my own work confirms.

EXPLANATION OF FIGURES IN PLATES X, XI, AND XII.

Illustrating Dr. Johnson's paper on the Development of *Marsilia quadrifolia*.

Abbreviations used :—*A.*, direction of the apex ; *a. b.*, axial bundle of the petiole ; *a. c.*, air-canal ; *arc.*, archesporium ; *a. s. w.*, acroscopic segment wall ; *B.*, direction of base ; *b. c. tc.*, basal cell of the trichome ; *b. m. c.*, basiscopic marginal cell ; *br.*, branch (axial bud) ; *b. r.*, rod of brown-walled cells ; *b. s.*, bundle-sheath ; *b. s. w.*, basiscopic segment-wall ; *b. w.*, basal wall of the capsule ; *c.*, capsule ; *c. p.*, transverse partition ; *c. p. c.*, transverse partition-cell ; *c. p. p.*, spores in transverse partition ; *D.*, dorsal side ; *d.*, dermatogen ; d^1., d^2., &c. dermatogen of sections I, II, &c. ; *d. b.*, dorsal bundle of sporocarp ; *d. w.*, dermatogen-wall ; *ep.*, epidermis ; *F.*, sporocarp ; F^1., first sporocarp ; F^2., second sporocarp ; *F. m. c.*, mother-cell of sporocarp ; *g. r.*, gelatinous ring ; *h. a.*, halving anticline of section I ; *hy.*, hypodermis ; *ind.*, indusium ; *i. ind.*, inner layer of indusium ; *i. s.*, intercellular space ; *i. s. c.*, inter-soral cavity ; *L.*, leaf ; *l. a.*, first longitudinal anticline in plerome of section V ; *l. b.*, lateral branch of dorsal bundle ; *l. b. f.*, fork of the lateral branch ; *l. p.*, longitudinal partition ; *l. p. c.*, longitudinal partition cell ; *l. p. p.*, pores in longitudinal partition ; *l. t.*, lower tooth ; *ma-sp.*, macrosporangium ; *ma-sp. m. c.*, macrosporangium mother-cell ; *m. c.*, marginal cell ; $m. c^1$., $m. c.^2$, &c., marginal cell of the first, second, &c. grade ; *mi-sp.*, microsporangium ; *mi-sp. m. c.*, microsporangium mother-cell ; *mp.*, mesophyll ; *m. w.*, median wall ; *o, hy.*, outer layer of hypodermis of capsule ; *o. ind.*, outer layer of indusium ; p^1., lower pinna ; p^2., upper pinna ; *pa.*, placenta ; *pa. b.*, placental bundle ; *pa. br.*, placental branch ; pb^1., periblem of section I ; pb^2., periblem of section II ; *pb.*, periblem ; *p. c.*, partition-cell ; *pl.*, plerome ; pl^1., plerome of section I ; pl^2., plerome of section II ; *pl. w.*, plerome-wall ; *p. ma-sp. mc.*, primary macrosporangium mother-cell ; *S.*, stem ; *sc.*, soral cavity ; *st.*, stalk ; *st. b.*, stalk-bundle ; *st. c.*, stalk-cell of microsporangium ; *s. w.*, segment-wall ; ta^1., ta^2., &c. first, second, &c. transverse anticlines of marginal cell ; *tc.*, trichome ; *tp.*, tapetum ; *tr.*, trachea ; *t. s.*, tannin-reservoir ; *u. t.*, upper tooth ; *V.*, ventral side ; *X.*, apical cell ; *I. II. III.*, &c. first, second, &c. section-walls ; 1. 2. 3., &c. first, second, &c. segments of the apical cell on one side.

All figures are camera drawings, and all are from microtome-sections, except Figs. 25, 31^a, and 44.

PLATE X.

Fig. 1. Transverse section of stem through apical cell of young leaf. × 300.
Fig. 2. Sagittal section of a leaf nearly at the end of apical growth. × 200.
Fig. 3. Part of a sagittal section of the petiole of an older leaf. × 300.
Fig. 4. Ventral surface of tip of a young leaf. × 400.

Fig. 5. Dorsal surface of the tip of a similar leaf. × 400.

Fig. 6. Half of a nearly transverse section of a young leaf showing the shape of a segment and the position of the first two section-walls. × 700.

Fig. 7. The same still older. × 750.

Fig. 8. Transverse section of petiole in which epidermal and hypodermal layers are completed and the partition-cells are nearly ready to cut off the cross-partition-cells. × 750.

Fig. 9. The same section of a still older petiole. × 400.

Fig. 10. Transverse section of a nearly mature petiole. × 60.

Fig. 11. Tangential section of petiole showing the air-canals and partitions. × 400.

Fig. 12. The same in a slightly older petiole. × 400.

Fig. 13. The same still later showing the lengthening of the longitudinal partition. × 400.

Fig. 14. Surface view of a longitudinal partition showing the pores in a nearly mature petiole. × 125.

Fig. 15. Surface view of petiole showing the arrangement of the trichomes. × 750.

Fig. 16. Nearly mature stage of same. × 300.

Fig. 17. Nearly mature trichome. × 60.

Fig. 18. Horizontal section of the tip of a leaf, showing the beginning of the first pinnae. × 400.

Fig. 19. Sagittal section of a leaf through one of the well-developed lower pinnae. × 400.

Fig. 20. Transverse section of a leaf through pinnae, a little later than Fig. 18. × 300.

Fig. 21. A similar section still later. × 125.

Fig. 22. A transverse section of petiole showing origin of sporocarp. × 750.

Fig 23. Part of an approximately horizontal section of base of a leaf showing the apical cell of sporocarp. × 750.

Fig. 24. Transverse section of stem, and a young leaf with two sporocarps, all three nearly parallel to the stem. × 150.

Fig. 25. Inner side of a young leaf with a sporocarp in which the segmentation of the apical cell is nearly finished. × 25.

PLATE XI.

Fig. 26. Nearly horizontal section of a stem through two leaves, an axillary branch and two sporocarp-rudiments, showing the under surface of part of older leaf, and cross-section of the first sporocarp arising on this; also the origin of a second sporocarp from the first. × 400.

Fig. 27. Transverse section of a young sporocarp. × 750.

Fig. 28. Transverse section through the basiscopic ultimate marginal cell of a sporocarp after all six sections are formed. × 750.

Fig. 29. The same section of a capsule at the time of beginning of soral canal, showing relative thickness of older and younger walls. × 750.

Fig. 30. Part of transverse section of older capsule. × 750.

Fig. 31. The same still older. × 400.

Fig. 31[a]. A slightly older sporocarp than Fig. 25, on a petiole, showing capsule bent against the stalk.

Fig. 32. The same as Fig. 31 at the time of closing of soral canal. × 500.

Fig. 33. The same still later. × 45.

Fig. 34. Ventral surface of capsule a little older than Fig. 25. × 750.

Fig. 35. Part of horizontal section of about the age of Fig. 30 near the ventral surface. × 750.

Fig. 36. Horizontal section of capsule about the age of Fig. 31 near the ventral surface. × 750.

Fig. 37. The same of about the age of Fig. 32. × 750.

Fig. 38. Sagittal section through the marginal cells of capsule about the same age as Fig. 29. × 750.

Fig. 39. Sagittal section through sections III and IV of capsule, the same age as the last. × 750.

PLATE XII.

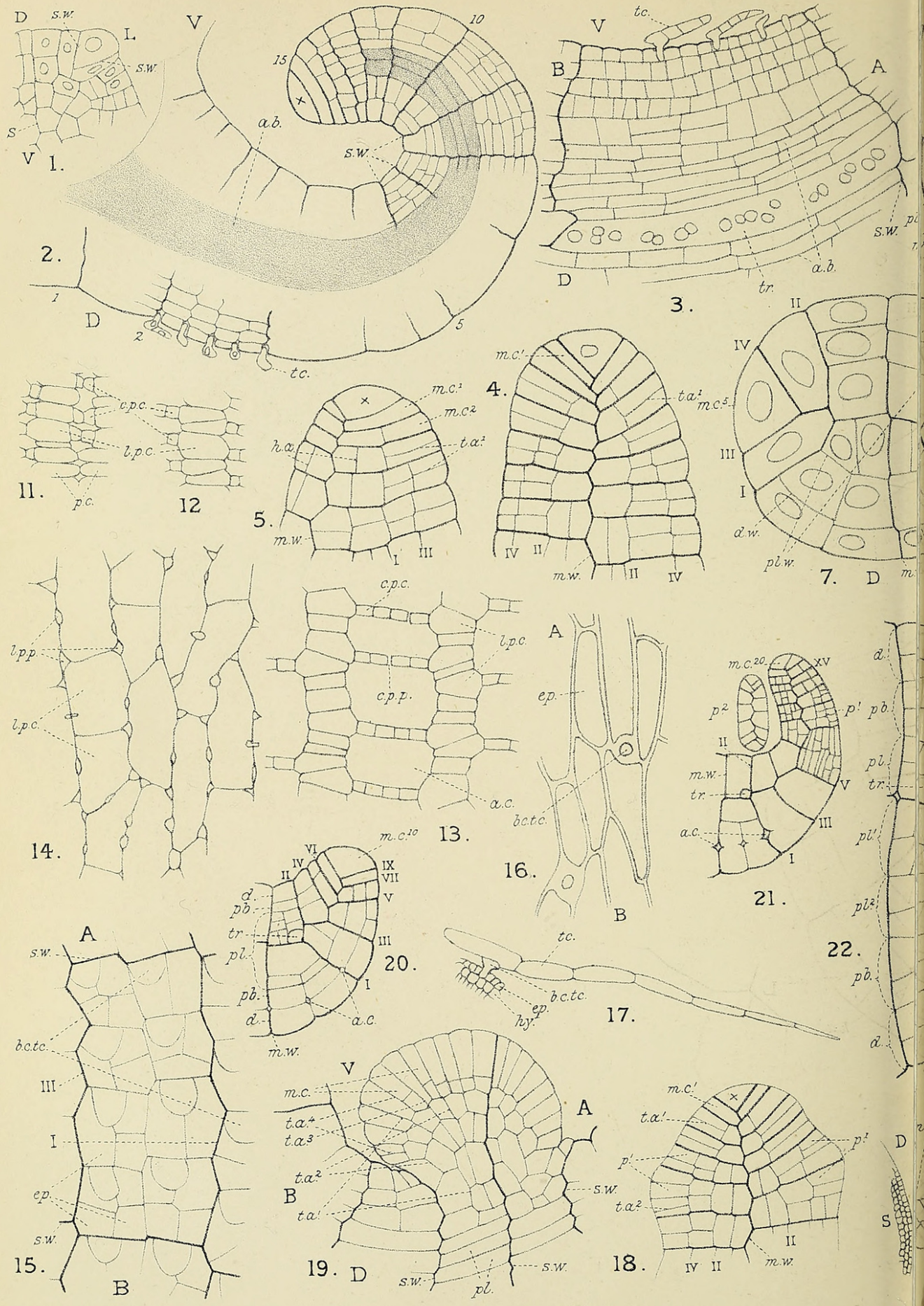
Fig. 40. Sagittal section through sections III and IV of a capsule of about the age of Fig. 31. × 750.

Fig. 41. Part of horizontal section of capsule of the age of Fig. 33. × 750.

Fig. 42. The same of whole capsule of same age as Fig. 41. × 50.

Fig. 43. Sagittal section through sori of same capsule as Fig. 40. × 750.

Fig. 44. View of inner side of one of the valves of a nearly mature capsule. × 8.



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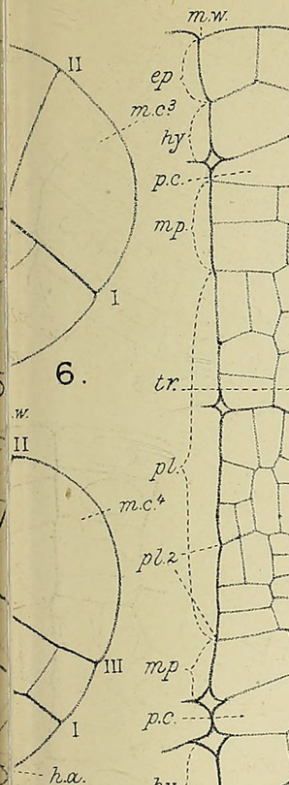

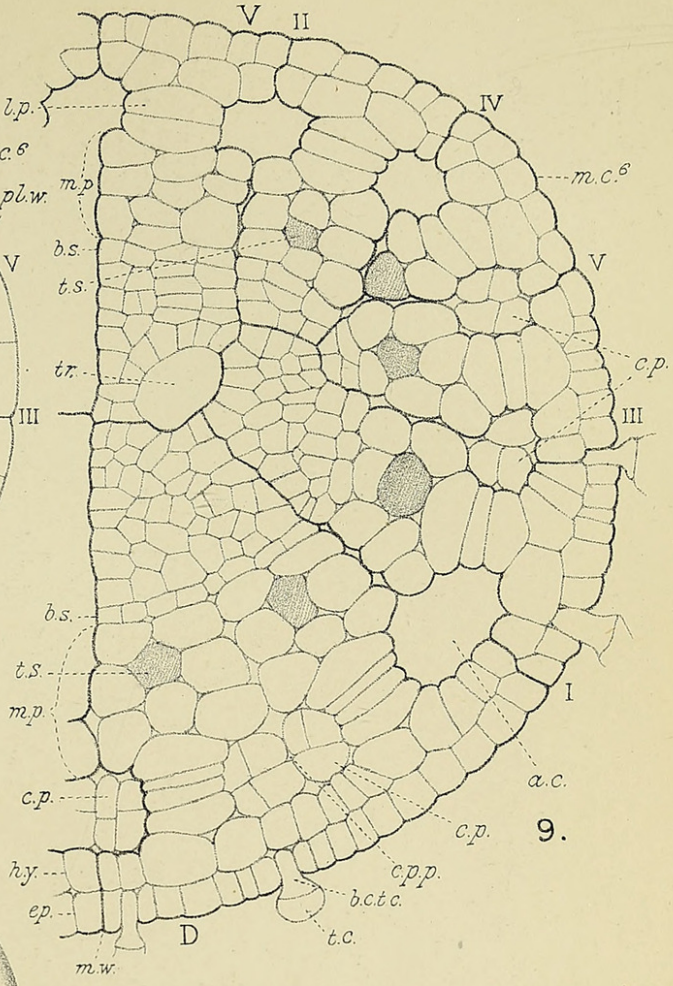

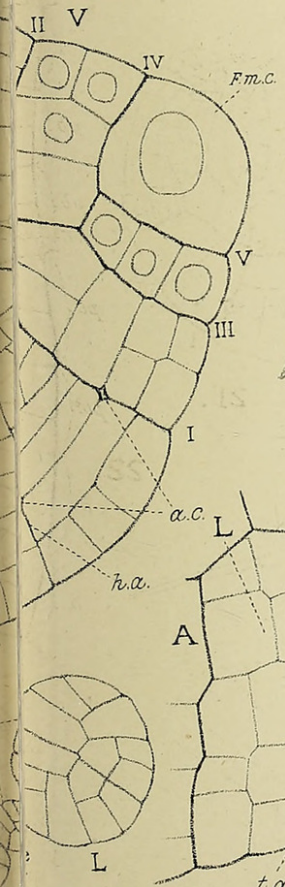

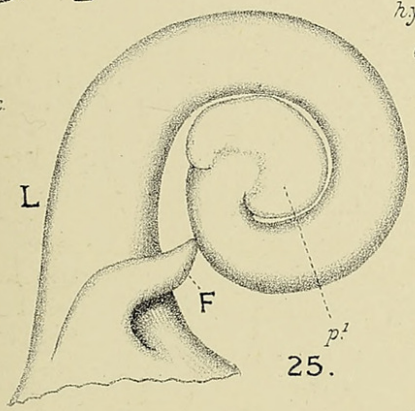

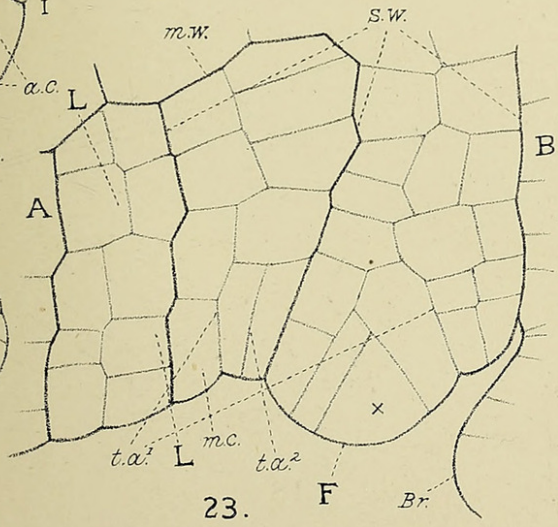

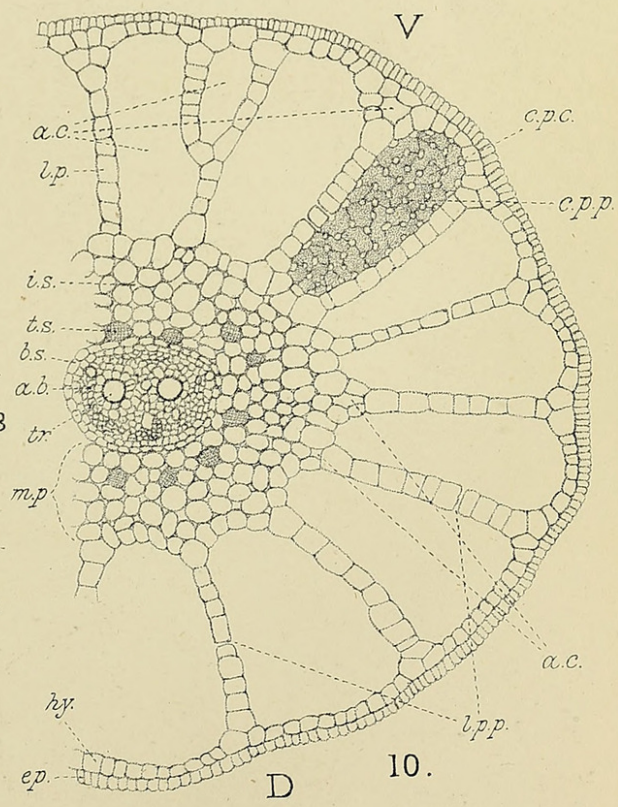

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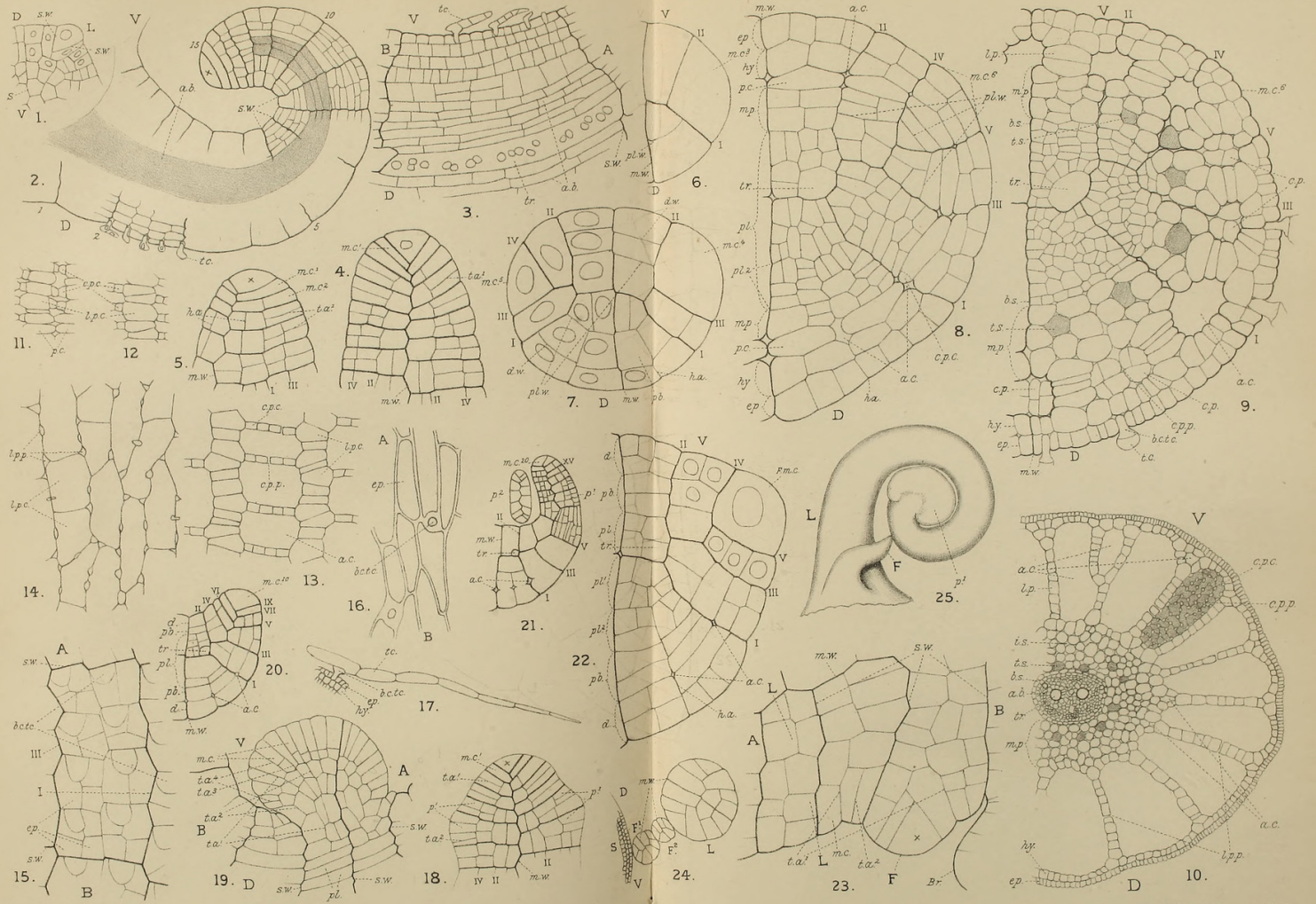

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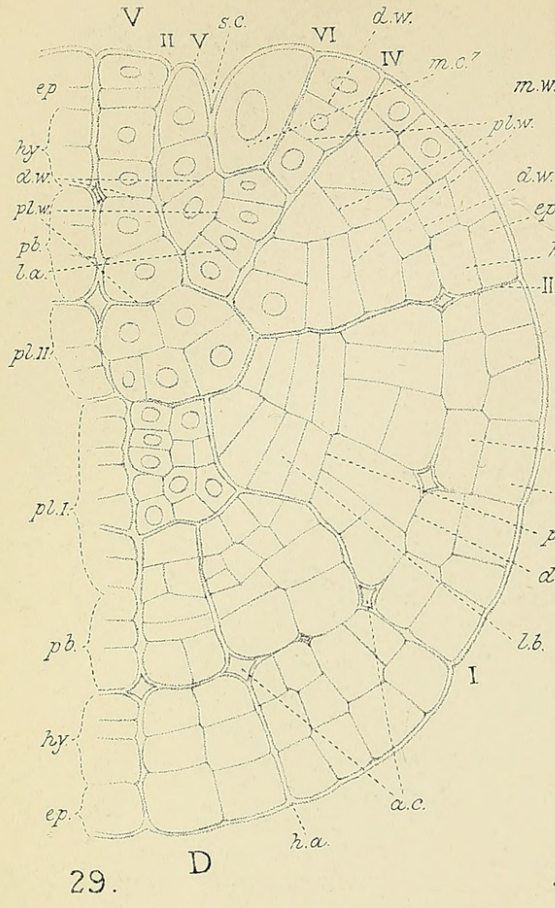
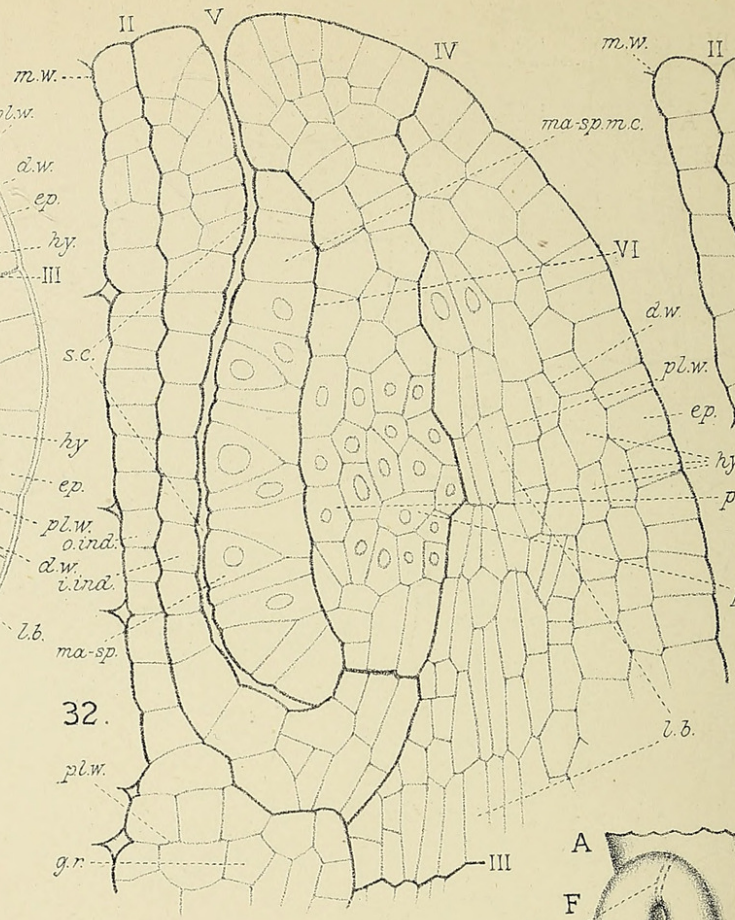


29.



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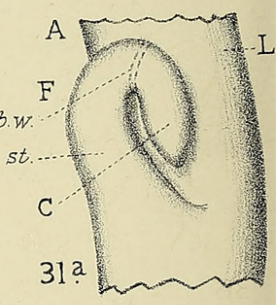

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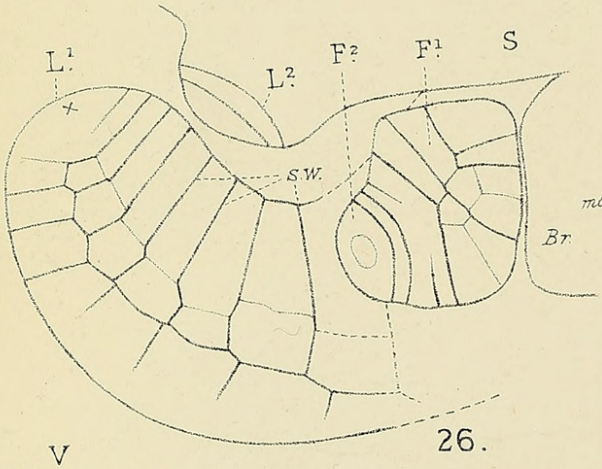

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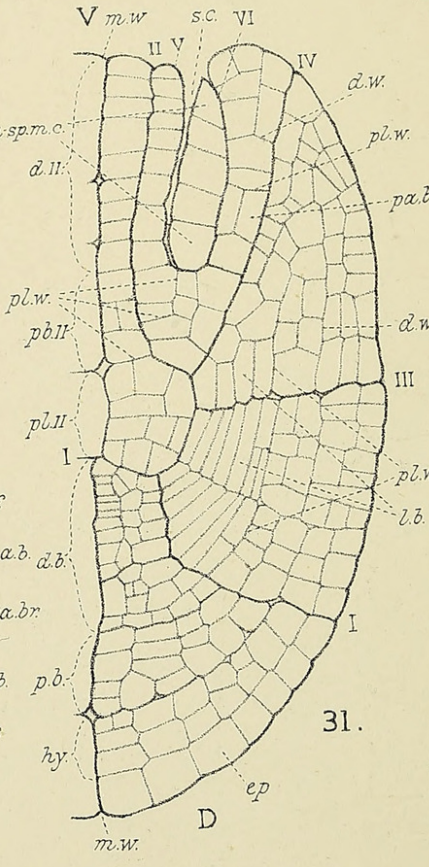

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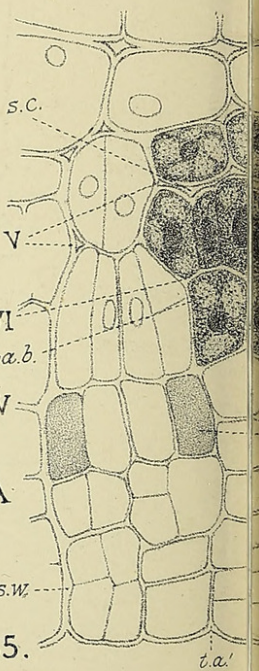

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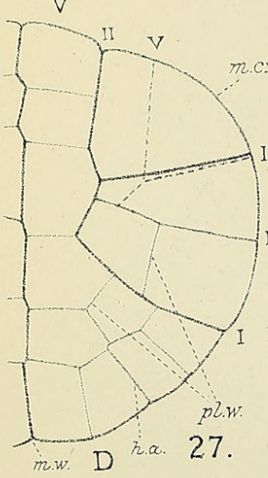

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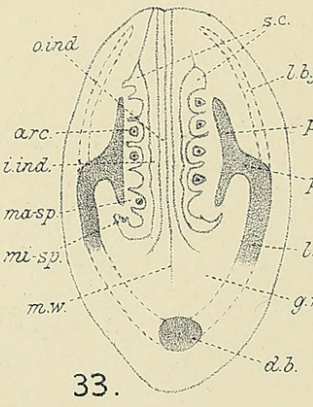

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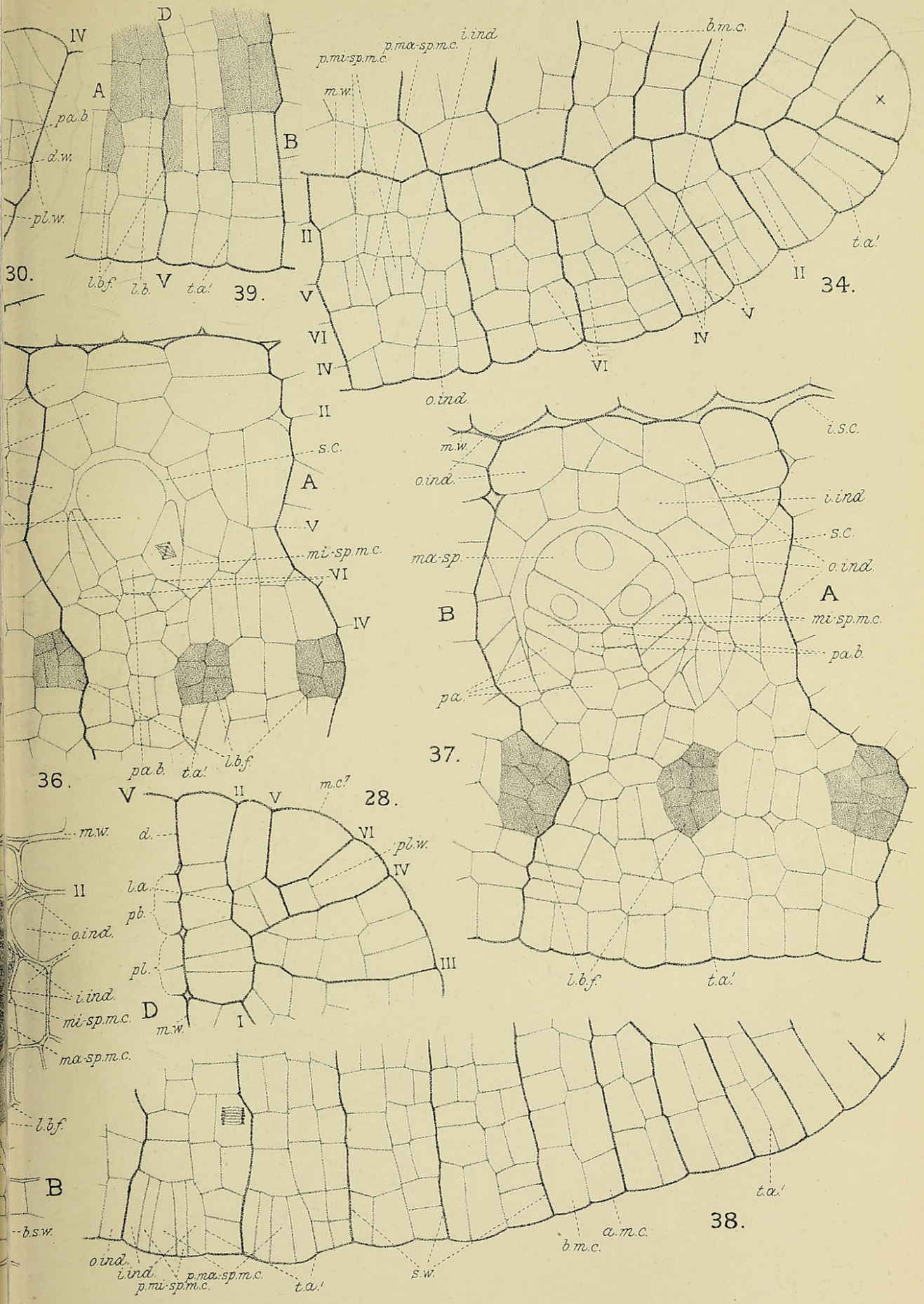

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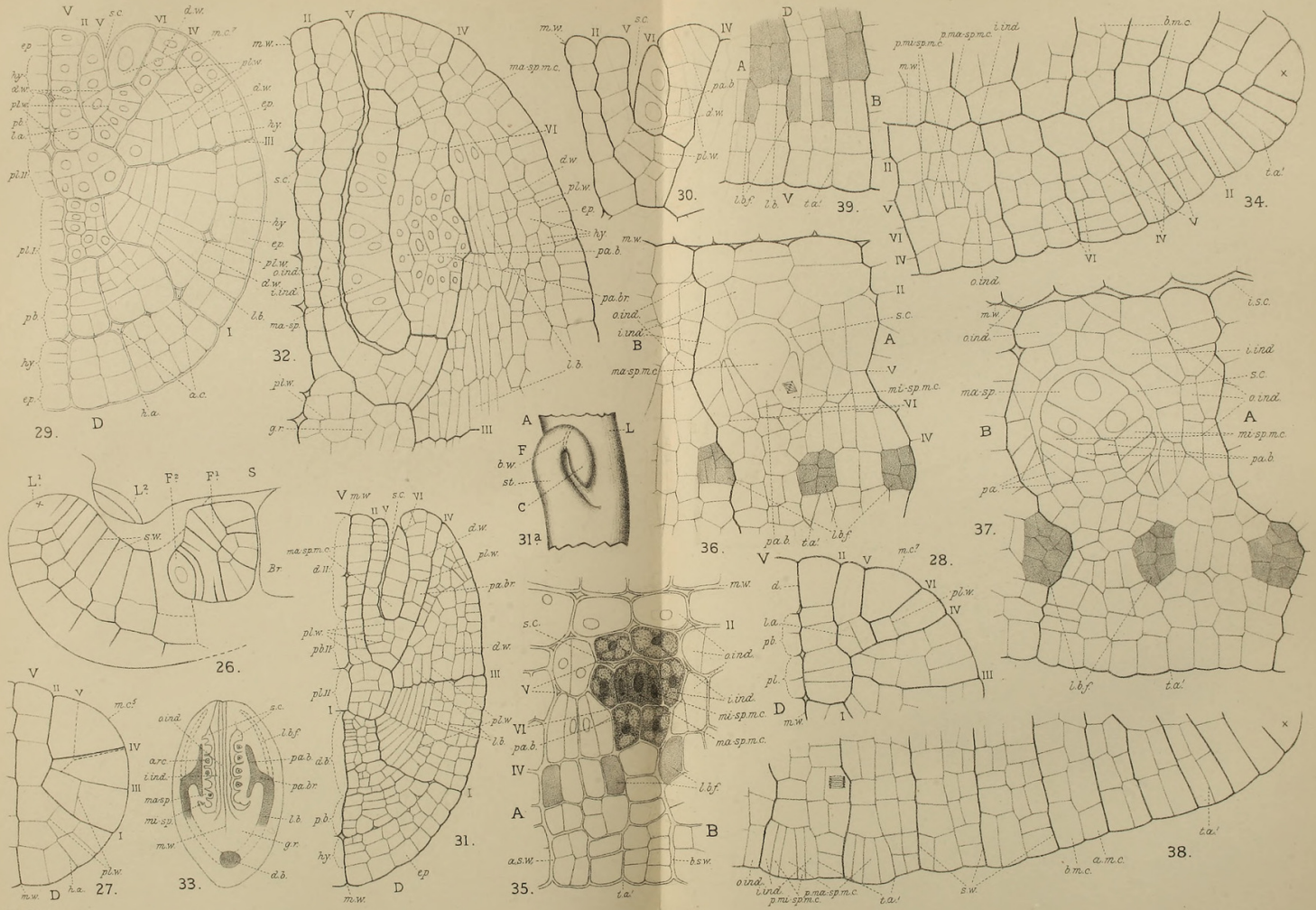

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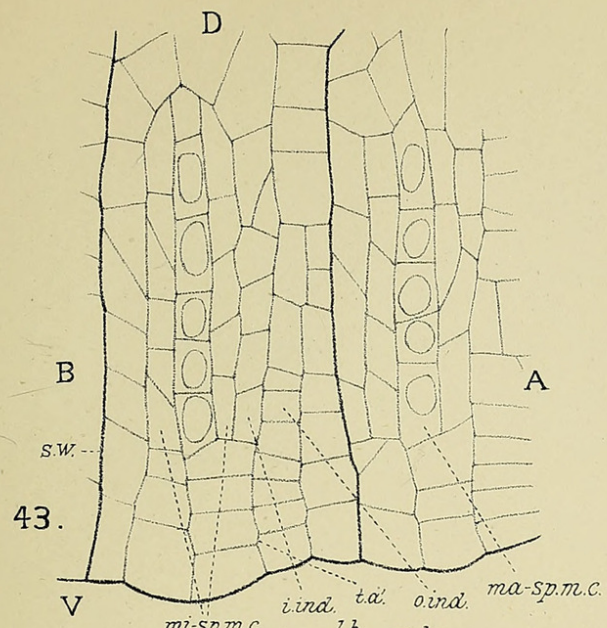

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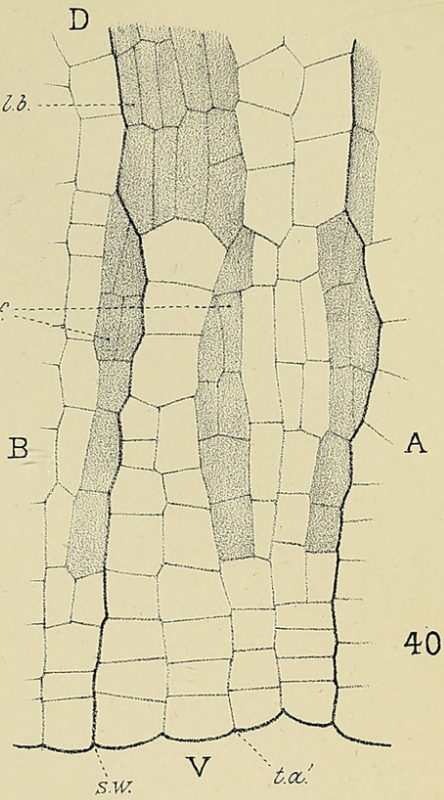

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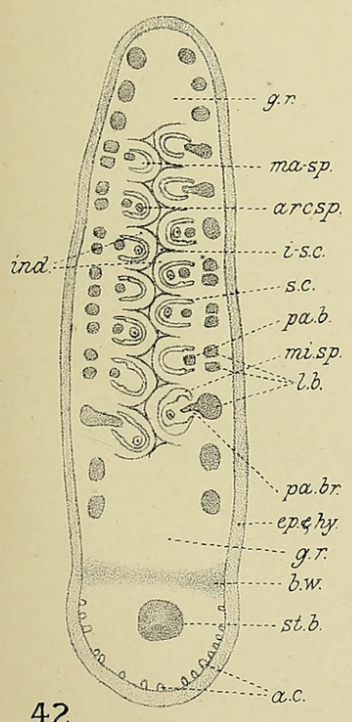

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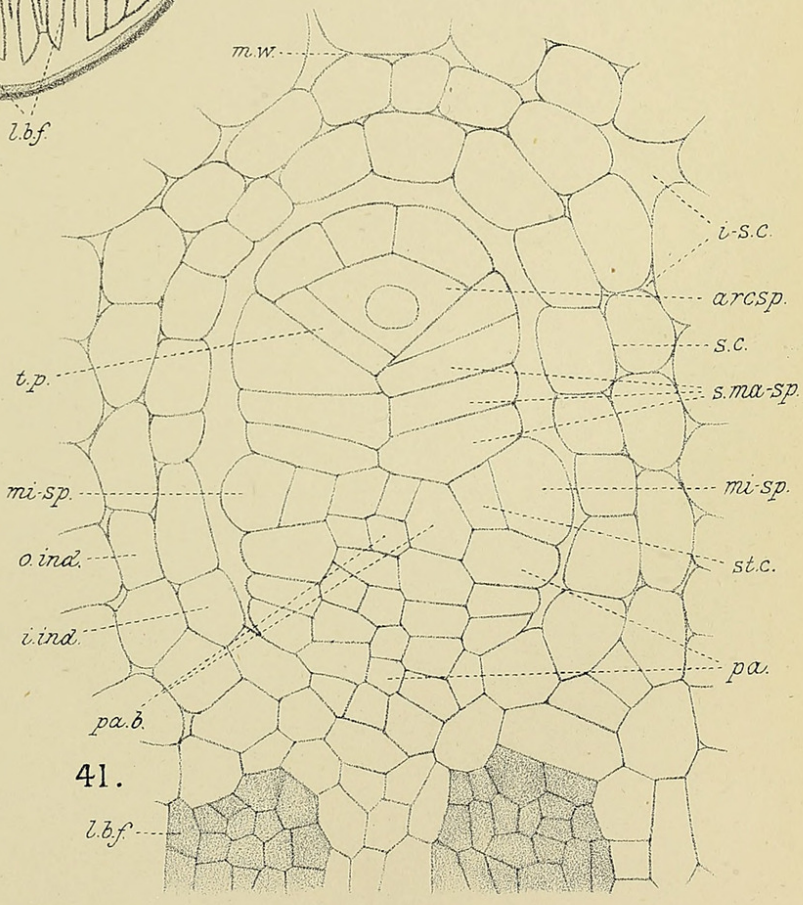

41.

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