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ON THE DEVELOPMENT OF THE
LEAF AND SPOROCAEP
IN MARSILIA QUADRIFOLIA, L.

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Dissertation presented to the Board of
University Studies of the Johns Hopkins Uni-
versity for the Degree of Doctor of Philosophy,

by

Duncan S. Johnson.

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The Leaf and Sporocarp of Marsilia.

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Bot' genera of the Marsiliaceae have been the subject of frequent study by botanists since the early part of this century. But in spite of this the exact origin, sequence and development of the various organs of the mature sporophyte, and especially the morphological significance of the sporocarp, have never been made out satisfactorily in either genus. This is undoubtedly due ~~in the main~~ to the dense covering of trichomes, over all the young organs, which practically prevents the successful study of these parts in toto as transparent objects. But it is due partly also to the complexity of the apical bud with its confusion of numerous and crowded, root, branch, leaf and sporocarp rudiments, developing, except the last, in rapid succession from the segments of the apical cell of the stem. Still much has been accomplished even with this method and with hand sections, by Biscoff, Mettenius, Hanstein and Russov. The introduction of the paraffine method of sectioning has largely overcome the first difficulty, while making the second perhaps more puzzling still. This method in the hands of Menuier, Russon, Campbell and others, has added considerably to our knowledge of the minuter details of development in these forms.

The present work was undertaken at the suggestion of

Dr. J. P. Lotey, of the Johns Hopkins University, for the purpose of determining the origin and early development of the sporangium in *Marsilia*, in the hope that thus some light might be thrown on the question of its morphological nature. It was very soon decided, that the best way to reach this end would be to study in detail the origin and development of the leaf also, for comparison, and thus if possible to complete the detailed developmental history between the leaf mother cell and the sporangium.

The work has been carried on during the last two winters in the biological laboratory of the Johns Hopkins University, under the direction of Dr. J. E. Humphrey, to whom for his constant assistance and encouraging interest, I wish here to express my sincere thanks. I am indebted also to Dr. W. A. Setchell, then of Yale University, for aid in obtaining material.

The material used was obtained from New Haven, Conn. and Cromwell, Conn. It was fixed in either 95% alcohol, 1% chromic acid, or a sublimate-acetic mixture (5% of glacial acetic acid in a saturated solution of corrosive sublimate). All of these gave good results, but the sublimate mixture was the best on the whole, since the chromic acid specimens did not always stain well and at certain stages of development the alcohol caused shrinkage. The material was stained either in toto in Mayer's haemalum, or on the slide with this alone or in combination with Eosin or Iron, with fasten-

violet or alcoholic cochineal. Of these the cochineal and haemalum with Bismark brown gave the best results.

The Development of the Leaf.

Practically all that we know of the development of the leaf in *Marsilia*, is due to the work of J. Harstein, on the leaves of the young embryo, and it will be necessary to refer to this often as we proceed.

The leaves of *Marsilia* arise in two rows, one on each of the dorso-lateral surfaces of the stem. Each leaf arises from one of the cells derived from a dorso-lateral segment of the tetrahedral apical cell of the stem. The leaf mother cell is first recognizable when the segment in which it arises, is about the third or fourth in it's series from the apical cell. It is soon distinguished by its larger size, usually by a larger nucleus and by it's bulging beyond the general surface of the stem apex, (L. Figs. 1. 2.).

The first division of the leaf mother cell, is usually by a curved longitudinal anticline, appearing toward the dorsal edge of the cell and with it's concavity facing laterally, (S. W. Fig. 2). The second wall is also a longitudinal anticline near the lateral edge of the mother cell and with it's concavity facing dorsally, (S. W. Fig. 1). These walls are also inclined to each other, (Fig. 2.) and there is thus left between them the typical two sided apical cell

of the leaf, curved like the half of a double convex lens, and with its edges directed respectively toward the base and apex of the stem.

Hanstein ('65) has already shown that the leaf of *Marsilia* has a two sided apical cell, and he figures it (pl.XIII 15. 17) as having approximately the position given above, but he did not describe the origin of the apical cell except in the leaves of the very young embryo. This agrees in origin, shape and position with the apical cell of the leaf as found in most of the other Leptosporangiate Ferns that have been studied. They have been thus described by Hofmeister ('62) in *Aspidium*, by Strasburger ('73) and Campbell ('92) in *Azolla*, by Kny ('75) in *Ceratopteris*, by Klein ('87) in *Polypodium*, by Bower ('89) in *Trichomanes*, and by Campbell ('87) in *Onoclea*. In *Pteris* however, while the origin and shape of the apical cell are the same, its position, as shown by Hofmeister ('62) and Klein ('84) is exactly at right angles to that found in the other genera mentioned. That is the edges are directed transversely to the stem and segments are cut off toward and away from the stem apex alternately.

In *Pilularia*, the only other genus of the *Marsiliaceae*, Bower ('89) and Mennier ('37) describe the apical cell of the leaf as two sided, while Campbell ('93¹ pl. 42. '95 pl. 13) states that it is tetrahedral, and differs thus from that of

Marsilia. The study of the growth of *Ptiloris* also uniformly shows that in both cases the position of the segments entirely with *Marsilia* and thus with the other *Adiantum* mentioned above except *Pteris*.

The two sided apical cell thus formed in *Marsilia*, continues its growth and activity, cutting off segments alternately towards the dorsal and lateral sides of the stem (Fig. 38), or, since the ventral side of the young leaf looks towards the apex of the stem (Fig. 3), the segments are cut off alternately toward the right and left of the leaf itself. This goes on until about fifteen or sixteen segments have been formed on each side, when the apical cell ceases to function as such and apical growth ends. The exact fate of the apical cell was not made out in the leaf, but it is probable that a periclinal wall is finally formed instead of the usual segment wall, as such a wall was seen several times in the apical cell of the sporocarp. Sadebeck ('73), Kny ('77) and Bower ('84) have actually observed such a wall in the apical cell of the leaf, but they were not able to make out just how many segments were cut off before it appeared.

In *Marsilia* the great regularity of the divisions in the segments of the leaf, as well as the fact that certain cells remain of the full length of the segment (Fig. 5), make it possible to determine quite exactly the number of segments cut off (Fig. 4). The only doubt is in regard to

the first segments, which fuse with the tissue of the stem, so that it is not certain that the segment numbered 1 in Fig. 4, may not really be the second one. Aside from this the several leaves examined in which apical growth had not proceeded very closely as to the number of segments formed.

The young leaf at the end of segmentation of its apical cell, is about 1mm. long and .15mm. in diameter at the base, and nearly up to this time it has the form of a slightly tapering cone, capped by the bulging apical cell, which curves upward and ventrally (Fig. 4) over the stem axis, by more rapid growth on the lower and dorsal sides. The cross section of the leaf at this stage is almost exactly circular. The leaf not being, until the formation of the pinnae, at all flattened ^{or} ~~or~~ undulate, as described by Campbell ('95) and figured by Hanstein ('65) in *M. Drummondii*.

Just before the last few segments are formed, the tenth and eleventh, or eleventh and twelfth, segments from the base on each side, begin to swell out laterally and ventrally to form the first pair of pinnae of the lamina (p¹, Fig. 31). Soon after the last segment is cut off from the apical cell, the segments beyond the first pair of pinnae develop the second and terminal pair of leaflets (p², Fig. 32). If the leaf bears one or more sporocarps, the first of these arises on the lower and anterior side of the petiole from the second segment on its side from the base (Fig. 33). The second

sporocarp is present, or also arise from a segment of the petiole above the second, but usually arise on the first sporocarp near its base, and on the side turned toward the petiole.

The segments of the apical cell of the leaf, or primary marginal cells of Hanstein ('65) and Sadebeck ('74), are quite regular in shape, being curved slices, slightly thicker at the middle of the outer border (Fig. 6) and with a slightly curved inner border where the segments overlap (Fig. 8). The first division wall to appear in these marginal cells is a longitudinal and radial anticline (Fig. 9), running from about the middle of the inner border to the dorsal part of the outer border, so as to cut off about a third of the whole semicircular segment toward the dorsal side (I, Figs. 7 - 10). We may call the third thus cut off a section, and the part still left of the primary marginal cell is the secondary marginal cell (m.c.², Fig. 9). 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 here, when the real position of this and the later section walls is taken into account, since it refers to the position of the walls at the surface of the leaf only, when the thing of real importance is their position in the interior, as we shall see.

The second wall formed in the segment is also a longi-

tudinal anticline (II Figs. 6, 10), but instead of being radial it is nearly parallel to the inner or median border of the segment, running from wall I to the ventral outer border of the secondary marginal cell, thus cutting off section II and leaving a tertiary marginal cell (p.c.³, Figs. 10, 11). In each of these sections and in the tertiary marginal cell walls are formed in various planes nearly simultaneously as the leaf grows. In section I there is formed first a pericline (pl. w., Fig. 11), at about one third of the distance outward from the center of the leaf, cutting off thus at the inner end a part of the plerome contributed by this section to the axial bundle of the leaf. Then a longitudinal and radial anticline, which we may call the halving anticline, cuts the outer cell into two (h.a., Figs. 7, 11). Meantime the plerome of section II is cut off by a pericline (Fig. 11), while the tertiary marginal cell divides by a transverse anticline (t.a.¹, Figs. 6, 7) into an acroscopic and a basisopic marginal cell. This anticline is the "radial wall" of Sadebeck.

The further divisions can best be described by taking up first the fate of the two tertiary marginal cells. In each of these there is formed first an anticline (III, Fig. 11) nearly parallel to wall I and toward the dorsal side of the marginal cell; then a similar wall is formed toward the ventral side parallel to wall II (IV Figs. 6, 11). There

are thus left two marginal cells of the fifth grade in each segment. The next wall formed in each of these may have either one of two positions. In the more frequent type of division, another longitudinal anticline appears in each (V, Fig. 13) parallel to wall III, forming thus the fifth and last section and leaving an ultimate marginal cell of the sixth grade. Then a pericline appears, running from wall IV to wall V , and the function of the marginal cell as such is thus ended. In the other and less frequent type of division, the marginal cells of the fifth grade are divided immediately by periclinal lines running from wall III to wall IV , the marginal cell of the fifth grade playing the same role here as that of the sixth grade in the first type; and their further development is also practically the same in both cases. The fate of all the segments of the leaf is in other respects the same, with the exception of those giving rise to the lamina and to the sporocarp, in which the pericline is never formed in the marginal cell.

THE PETIOLE.

Taking the first type of leaf for the study of the further development of the segments of the petiole, we find that during the divisions of the tertiary marginal cells, sections I and II, and the other sections as fast as formed,

to on dividing actively. Section I cuts off a dermatogen layer by a pericline near the outer end of each half, then a second plerome portion is cut off from the inner end of each (d. and pl., Fig. 13) and section II, followed by each of the others in turn, cuts off plerome and dermatogen (Figs. 13 - 15), while the ultimate marginal cell is lost of all to form, first the dermatogen wall as described above, and then still later the plerome wall (pl. w., Fig. 16). The dermatogen soon splits by a pericline into two layers around the whole circumference of the petiole, and these break up by anticlines, both longitudinal and transverse, to form the epidermis and hypodermis, each of which remains of one cell in thickness even in the mature leaf (ep. hy. Figs. 14 - 19). On the line of the median wall, of each of the section walls, and of the halving anticline of section I, small intercellular spaces soon appear between the cells of the periblen and those of the hypodermis (a.c., Figs. 13 - 19). These are the beginnings of the longitudinal air canals of the petiole, of which, as can be seen from their origin, fourteen are formed altogether in leaves where the segments divide according to this type.

The single periblen cell formed in each half of section I, in each of the other sections and in the ultimate marginal cell (pl., Figs. 13 - 15), soon divides by a pericline into two cells (Fig. 15). Of these the inner cell di-

sides of anticlines and pariclines to form the mesophyll cells of the mature leaf (m., Figs. 15 - 19), while the outer cell gives rise to both the longitudinal and the transverse partitions between the air canals (n.c., Figs. 15, 16). These latter cells swell out in the middle (Figs. 16 - 18) and grow out at the ends into papilla like tips, which are in contact with those of their fellows of the adjacent sections (Figs. 17, 21), leaving an intercellular space between these and the mesophyll cells and also one above and below each papilla, connecting this with the primary air canal formed between the partition cells and the hypodermis (Figs. 16, 17, 21). These papillae are soon cut off by longitudinal anticlines (Figs. 17, 21 - 23), and thus is formed a pair of small nearly isodiametric cells, in each canal opposite each of the primary partition cells, of which there are usually eight in the length of a segment. From these eight pairs of cells, one cell in each pair being from each of the opposite primary partition cells bordering on an air canal, are developed the eight transverse partitions of the air canal in each segment. These remain one cell thick even till maturity, but later in their development many intercellular openings or pores are formed, allowing the passage of air through them (c. . ., Figs. 19, 20, 21). Except for these pores, the partitions of the mature leaf stretch completely across from end to

parallel to the end walls and the cross partition is parallel to the next.

That part of each primary partition cell left after the separation of the single cross partition cell at each end, does not divide further by longitudinal anticlines, till very much later, but immediately gives rise to the longitudinal partition between the adjacent air canals. As these cells grow in a radial direction they are divided by periclinal walls until, in the mature leaf, the partitions may be fifteen cells or more in radial breadth and form one third the diameter of the petiole, but they are only one cell thick (L.p., Fig. 19, 20). These cells grow with the longitudinal growth of the leaf (Figs. 21 - 24). As each cell elongates it is seen that the primary cross partition cell at one end (c.p.c., Fig. 21) is nearer the acroscopic wall of the longitudinal partition cell, and at the other end is nearer the basiscopic wall. Then when the transverse anticline appears it is somewhat oblique, and thus forms two wedge shaped cells, each with a cross partition cell at the broad end and none at the narrow one (Fig. 22). The cross partitions in adjacent air canals are thus not opposite but alternate. These wedge shaped cells continue to grow and divide frequently by transverse anticlines, till in the mature petiole the cross partitions are far apart. Here in the longitudinal partitions also we

find a maturity; many small intercellular openings or "pores" of Mowbray, which allow communication between adjacent canals (L.p.p., Figs. 19, 20, 21).

In the type of petiole with five sections in each segment, there are, as we have seen, fourteen primary air canals. When the segments of both sides of the petiole form only four section walls, there are but twelve canals, while when, as occasionally happens, one side forms four and the other five sections, we find thirteen canals. All three types are found in the older petioles, but it is interesting to note that the only figure of a cross section of a petiole that I have seen, that of Bischoff ('23), is a petiole of the ⁴⁺⁵frequent type with thirteen canals.

At a comparatively late stage of the development of the leaf, when the longitudinal partition is already many cells broad radially, the outer cells, next to the epidermis, or the inner ones next to the mesophyll cells, may split by a longitudinal anticline. The daughter cells then separate laterally (a.c., Fig. I), and divide by periclinals, forming thus a new canal bordered by these cells and the hypodermis or meso and the mesophyll cells. This splitting of the primary partition may apparently proceed through its whole radial width, and thus form a secondary canal between two layers, easily to be distinguished from the primary canals in the mature leaf. The number of the sec-

smaller canals thus formed is always small, fewer than of the primary ones, but there is apparently no regularity either in number or position.

When the epidermal layer of a section has divided by one longitudinal anticline and three transverse ones (Fig. 27), forming thus eight cells altogether, four in the length of a segment and two in the width of a section, there is cut from each of these cells, by a circular anticline at the acroscopic end, a small cell which gives rise to one of the numerous trichomes that clothe the young leaf. The rest of the original epidermal cell then divides to four cells with the trichome at the acroscopic end of one of the upper pair (Fig. 28), then further divisions follow and at maturity the epidermal cells become much elongated (Fig. 29), as has been shown by Russow ('72) and also by Meunier for *Pilularia*, while some of them may later form more secondary trichomes. Each trichome cell grows out beyond the surface of the epidermis (Fig. 28) and swells at its outer end to a knob, which soon elongates, in the direction of the length of the petiole. On the basiscopic side it projects but slightly, while it grows out toward the tip of the leaf into the long multicellular hair, which is supported by the basal or stall cell that remains wedged in between the other epidermal cells (Fig. 30). Before the leaf reaches maturity these hairs separate

from their basal cells and thus leave the leaf gap. The later development and mature structure of these trichomes have been studied by Russow, and have been worked out in great detail by Heunier for the similar ones of *Pilularia*.

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

By the time that the longitudinal partitions are two or four cells in radial width, a longitudinal row of the large mesophyll cells opposite each partition, usually in the next to the inner layer of these, becomes specialized to form one of the so-called tannin sacs (i.e., Figs. 18, 19). The contents of these are distinguished by a brownish color in the unstained alcoholic material, but usually stain very darkly with haemalum. In the mature leaf these cells are about the same size as the surrounding mesophyll cells. The latter are about twice as long as broad and fit together quite squarely at the ends, while laterally they are rounded off from each other, leaving between them many small intercellular spaces (Fig. 20) which connect with the large air canals.

While these structures have been developing from the dermatogen and periblem layers of the petiole, the plerome portions of the first four sections have given rise to the axial vascular bundle. The first plerome cell cut off from

section I together with the two cells adjacent to it from the apical portion of this section, divide again by many periclinal and longitudinal anticlines (Figs. 1, 12 - 17). Later transverse anticlines appear, the first one being in about the tenth segment from the apical cell of a leaf of the size shown in Fig. 1. In section II a longitudinal anticline is formed in the pleurone cell parallel to the median wall; then a similar wall perpendicular to this divides the pleurone into quarters (Figs. 18 - 19). Of these, the cell in the angle between sections I and III (br., Figs. 3, 14 - 19) never divides further, but becomes directly the large trachea of its side of the axial bundle. Though no division walls are formed in this its nucleus divides actively, so that in a trachea of half a millimeter in length (Fig. 5), there may be twenty-five or thirty nucleipresent. Later these and the other protoplasmic contents of the trachea disappear, while the end walls, which are portions of the original segment walls, assume gradually the oblique position characteristic of these in the mature trachea (Fig. 5). Their inclination is always downwards and dorsal as shown in the figure. This is the only cell of the segment that remains of the full length of a segment for any considerable time during the development.

The other three quarters of this section, and all the

plerome of sections III and IV divide up like the plerome of section I, by frequent periclinal and longitudinal anticlines, and by fewer transverse anticlines, to form with this the remaining tissues of the axial bundle. The small cells of the outer layer of the bundle gradually become more regular in shape and uniform in size, forming thus the characteristic bundle sheath (b.s., Figs. 18, 19).

The plerome of the ultimate marginal cell never takes any part in the formation of the axial bundle, but in some cases that of section V apparently contributes to the formation of the sheath and of a few cells within this (Fig. 18).

The Lamina.

By the time that the apical cell of the leaf has ceased to cut off segments, the tenth and eleventh (or eleventh and twelfth) segments from the base on each side, have begun to grow out laterally and ventrally to form the first pair of pinnae (pl, Fig. 31). These pinnae do not correspond in extent exactly with the segment, as has been shown to do in *Asplenium serpentini* by Sadebeck ('70) and in *Onoclea struthiopteris* by Campbell ('87). In this respect they agree rather with the pinnae of *Ceropteris thalictroides*, as described by Kny ('73). The lower border

of a pinna (Fig. 33) may correspond exactly with a segment wall while the upper border falls short of the second segment wall above, or perhaps the reverse may be true though it was never seen satisfactorily. It is certain, however, that the lower pinna on each side is formed from the whole length of one leaf segment and the larger part of another, and never of a single segment or of more than two. After cutting off its last segment the apical cell of the leaf, as stated above, probably breaks up to form marginal cells like those formed in the segments. By the time that this has happened, the segments beyond the first pair of pinnae, except all or part of the one next to the pinna on each side, have begun to swell out (Fig. 32) to form the terminal pair of pinnae. Later on the marginal cells arising from the apical cell probably take part also in the development of these pinnae.

The beginning of the development of a pinna is best seen in a transverse section of the leaf through the pinna, and is practically the same for both pairs. While in the segments of the petiole there are only five section walls formed, and the marginal cell of the sixth grade is the ultimate one, in the segments giving rise to the lamina no periclinal (dermatogen and plerome) walls are ever formed in the marginal cells. These on the contrary continue to form walls parallel to the lateral section walls

ill late in the development of the lamina (Figs. 34, 35). The next wall formed after wall V is toward the ventral side of the marginal cell (VI, Figs. 34, 35), continuing thus the regular alternation of the section walls. Then wall VII is formed toward the dorsal side of the cell, wall VIII toward the ventral side, and so on till a large number of sections, if we may still call them such, have been formed (Fig. 35), the marginal cell being still distinguishable, and probably active, when the pinnae are more than two millimeters broad. These additional sections divide like the earlier ones by periclinal walls to form the epidermis, pericycle and dermatogen layers and later by anticlinal walls (Fig. 35), forming thus the various tissues of the lamina. Meanwhile the marginal cells divide also by anticlinal walls perpendicular to the edge of the pinna (Fig. 33). They thus constantly increase in number and form a rounded growing edge, as Hanstein ('65) has shown, the pinnae finally becoming wedge shaped with a broad rounded outer end, in the mature leaf. The pinnae are directed more ventrally than laterally from the petiole even at the beginning, and those of the upper or younger pair soon come to have their ventral surfaces nearly in contact, while the lower and older pair are folded together in the leaf bud so as to enclose the younger ones between them (Fig. 36).

A branch of the axial bundle of the petiole is given off to each pinna, and each of these branches in the pinna to form the anastomosing veins characteristic of the leaves of *Marsilia*. The detailed development of the bundles of the pinna was not studied, and it is not certain whether they originate as Sadebeck ('74) has shown them to in *Asplenium*. The epidermal cells of the leaf give rise to stomata on the upper side, or on both upper and under sides, and to deciduous trichomes like those of the petiole.

In the leaf of *Pilularia*, which was examined for comparison with *Marsilia*, the segments of the two sided apical cell form but three sections, and leave thus an ultimate marginal cell of the fourth grad. The sections correspond in relative position to the first three in *Marsilia*, but they and the ultimate marginal cell are broader than in the latter, since the whole semicircular segment is here made up of the four divisions, instead of containing six divisions as in *Marsilia*. Here as in *Marsilia* the outer part of section I is split by a pericline in two cells, each of which plays the same role as one of the other whole sections, in the development of the periderm and dermatogen structures. The marginal cell, as well as all of the sections, here takes part in forming the axial bundle, and as will be seen from the number of sections, there

There are only two primary tracheae formed in it, as is figured by Bischoff ('92, VIII, 13) and Campbell ('02, XV, 10). The partitions like the sections from which they arise are thicker, and seem to be much more irregular in both size and position, than in Marsilia. The trachea formed in section II of each segment is therefore less prominent from its size than in the petiole of Marsilia.

The Sporocarp.

The bean-shaped sporocarps of Marsilia quadrifolia are most often borne in pairs, the stalks of the two apparently uniting below to form a common stalk, which joins the petiole of the fertile leaf on its inner side near the base. Occasionally only one sporocarp is found on a leaf, or there may be two with their stalks inserted separately on the petiole, and these may be several millimeters apart at maturity. Again, more rarely still, there may be three or four sporocarps, all with a common stalk, or one may arise separately from the petiole while the others are joined to it by a common stalk. In the former cases, when the sporocarps are not yet fully grown, it is usually found that the smaller or younger one of a pair or of three, is borne on the side of the stalk toward the

reduced to a single rudiment.

It is usually found that where any sporocarp occurs on a branch of the stem, they are present on practically all the leaves of this branch. This fact was of very great assistance in the study of sections of the buds, or slightly developed branches, since the absence of sporocarp rudiments on the older leaves of a bud enabled one to avoid a fruitless search for the less easily recognizable earliest rudiments, on the younger leaves of the same bud.

It is an interesting fact that of the several localities from which material was obtained, the plants from those habitats where the water level lowered considerably toward the end of the growing season, leaving the plants to grow on the wet mud and in the air, matured many more sporocarps than those which were submerged throughout the entire growing season. This appears not to be due to the fact that fewer sporocarps arise on the leaves of the submerged plants, but rather to the fact that the rudiments which are formed do not complete their development. At the end of July many young sporocarps are found on plants from either habitat, while at the end of September plants that have been left out of the water, by the fall of the water level, have many matured sporocarps on them and those that are still submerged have very few. Closer examination of the leaves of the sub-

pinnae, however, both the half-grown sporocarps of normal appearance, and many more of the same or smaller size which have evidently been arrested in their development, and appear shrunken or withered. The leaves of which these are borne have gone on in their development, and we may thus find on full grown leaves sporocarps of the same size as those found on other leaves of which the pinnae have not yet unfolded. There is thus, on the whole, no great regularity in the retardation in development of the fertile or sporocarp bearing leaves.

Of the origin of the sporocarp of *Marsilia*, Bischoff ('28) says, that it arises as a slight prominence or papilla on the anterior side of the base of the petiole. Mettenius ('44) on the other hand, states that it arises endogenously and later breaks through the epidermis of the petiole, to form a projecting solid mass of tissue in the interior of which the various internal structures of the capsule are formed. The youngest sporocarps found by Russo ('72), had a two sided apical cell, but were already differentiated into sterile stalk and a fertile tip or capsule, being probably in about the same stage as that shown in Fig. 42. He traced the development of the soral canals, stating that they arise by the splitting apart of certain cells in the interior of the capsule, and the development of pits on the ventral surface of the

into which the spines finally open, leaving the soral canals thus open to the exterior for a time, to be closed again later by the growing together of the cells of the ventral surface. On the outer walls of these cavities arise the "soral cells", in each of which walls appear later so as to cut out a tetrahedral apical cell. This cuts off a number of segments, which according to Russow give rise to the placenta with its vascular bundle, and to the microsporangia, then a pericline appears at the inner end of the apical cell forming thus the archesporium of the single macrosporangium arising from it. Goebel ('82) states that the soral canals of *Marsilia* are external in origin and that the sporangia arise from superficial cells. Büsgen ('90) described the earliest stage of the sporocarp as in one case a "gap" (Lücke) in the epidermal tissue of the young leaf near its base, and in another place as a swelling or prominence in the same region. The sporocarp grows for a time by a two sided apical cell, and he thinks it probable that all of the soral cells are derived from an epidermal cell of the ventral side of the capsule. The placenta macrosporangia and microsporangia he states are all formed as Russow has shown from these soral cells.

In the similar sporocarp of *Pilularia*, Holmeister ('62) and Juranyi ('79) describe the soral cavities as arising internally, while Goebel ('82), Holmeister ('87) and

Campanella (1914) seems to have been of the opinion that the origin of Goebel and Bispson had found to be the case in Marsilia.

According to my own observations on Marsilia quadrifolia, the sporocarp first makes its appearance when the young leaf on which it is borne, consists of about six or seven segments on each side; thus long before the lamina, or even the segments that are to develop it, have been formed. It arises by the increase in size and bulging out, of apparently either, the acroscopic or the basiscopic ultimate marginal cell, of what is probably the second segment on its side from the base of the leaf (Fig. 37). Because of the beginning of curvature of the leaf, the proximity of the sporocarp rudiment to the axillary bud of the same leaf and the resulting difficulty in orientation so as to get exactly longitudinal sections of the leaf through the sporocarp rudiment, it was impossible to decide certainly in which segment the latter arises. It is probably the second rather than either the first or third segment, and cannot be a younger one than the latter in any of the cases seen, and though no indication of this was seen, it is possible that the exact point of origin may be shown, on further observation to vary. The sporocarp always arises from a marginal cell of the inner and ventral side of the young petiole (Fig. 3), the tip of which at this time is beginning to take a position normal

parallel to the stem (Fig. 41). Soon after its formation the sporocarpial cell, a curved anticline nearly parallel to the axis of its acropscopic or its basiscopisic wall, than a similar transverse anticline on the opposite side of the mother cell (Figs. 37, 38), and there is thus formed a two sided apical cell like that of the leaf, with its edges directed across the leaf. The sporocarp, as it arises thus from the whole of a marginal cell, which has not yet given rise to the three meristem layers that it is capable of forming, is not, strictly speaking, epidermal in origin. In its origin, by a two sided apical cell formed in a marginal cell of the leaf, the sporocarp resembles closely the solitary sporangium of *Lygodium*, which as was shown by Prantl (Sadebeck '82, Fig. 64) arises from a marginal cell of the fertile pinnule.

The apical cell of the sporocarp thus formed goes on cutting off segments alternately toward and away from the leaf apex, which are to form the right and left sides of the sporocarp, till more than twenty have been formed on each side. It thus gives rise to a slightly tapering conical structure, much like the young leaf, which bends laterally to grow up beside the leaf (Fig. 41) with its ventral side facing in the same direction, but soon begins to bend ventrally upon itself (Fig. 42). Finally about the time that apical growth ceases, the upper part or cap-

sule lies with its ventral side nearly in contact with that of the lower or stalk portion of the sporocarp (Fig. 43). There is never any curling in ^{of} the extreme tip of the sporocarp suggesting the circinate coiling of the leaf, and the bending mentioned is later partially straightened out, as Russow ('72) has shown by the more rapid growth of the ventral side of the capsule. The activity of the apical cell as such, is ended by the appearance in it of a wall, which in a horizontal section is apparently a periclinal, but its exact direction was not made out satisfactorily in sagittal sections. At the time when this wall appears the bending mentioned above has taken place, the capsule is a millimeter long,, and the sori at the base of this are developed as far as that shown in Fig. 40.

The first few pairs of segments of the sporocarp, probably four or five, form the sterile stalk, and the rest develop the fertile tip or capsule. Of the segments of the capsule the first three pairs do not develop sori and only the youngest one forms a lateral bundle. Each segment of the next eight or nine pairs gives rise to a single sorus and to a lateral branch of the dorsal bundle of the capsule. Beyond the last of the soral segments are six or seven pairs, of which only the three or four oldest form lateral bundles and none form sori. The capsule

soon becomes flattened into a plate (Fig. 7), and in its early development is closely appressed to the petiole (Fig. 12) and thickly covered by the trichomes arising from the capsule itself and from the wall of the sporocarp. These trichomes have been omitted in all drawings because if they had been drawn they would have hidden the more important details in many of the figures.

The shape and size of the segments cut off from the apical cell here, are very nearly like those of the leaf, and their early divisions are exactly the same. Section walls I and II (Fig. 14) are formed in the same position as in the segments of the leaf, then the transverse anticline appears in the marginal cell (t.a.¹, Fig. 15) forming two of these of the third grade, and section wall III is formed in each of these in the usual position (III, Fig. 14). Thus up to this stage the series of figures given for the leaf (Figs. 7 - 11), is equally suitable for the sporocarp. After the formation of wall III, however, the regular alternation, that continues in the leaf till the last section wall is formed, is here broken by the appearance of wall IV on the dorsal side of the marginal cell and parallel to III, instead of on the ventral side as in the leaf (IV, Fig. 15). Wall V in the sporocarp is then formed toward the ventral side of the marginal cell, in the position of wall

IV of the leaf segments (V, Fig. 40), and consequently this the last section - II (VI, Fig. 43) is formed near the dorsal side of the marginal cell. The ultimate marginal cell is thus of the seventh grade here, and not of the sixth grade as in the leaf.

When a second sporocarp is formed on a leaf, it usually arises from a marginal cell of the second, or third segment of the first sporocarp on the side of the latter that is turned toward the petiole which bears it (F.², Fig. 40), and a third sporocarp may probably arise from the second in the same way. The exact origin of the apical cell here in the marginal cell was not seen but it is reasonable to expect it to be like that of the first sporocarp in the marginal cell of the leaf, and the earliest ^{stages} [^]seen also indicate that this is true. This origin of the younger sporocarps from the older ones, explains the occurrence of the mature sporocarps in pairs or trios on a common stalk, that was mentioned above. But the portion of the stalk of a pair that is common to both is not, as suggested by A. Braun ('70), formed by the fusion of two originally separate stalks, but it is the lower portion of the single stalk of the older sporocarp, and so of the common stalk of the second and third sporocarps of a trio. Where two sporocarps are inserted on the petiole of a leaf-

adult stage, it is probable that these cells arise from marginal cells of the petiole, and this is a comparatively rare occurrence and was not actually seen in the early stage of development.

We may return now to the further development of the segments of the sporocarp. The positions of section walls as given above is in general that found in all the segments, but there are frequent exceptions to this in various segments that are worthy of note. Thus section V is usually broader in the acroscopic marginal cell of the soral segments than in the basiscopic cell (V, Figs. 49, 50). Sometimes section IV is also slightly broader and thus since section VI does not vary greatly in size, the basiscopic ultimate marginal cells, which are evidently the "sorus mother cells" of Büsgen, are the largest ones of the whole sporocarp. It quite frequently happens also that wall IV when formed, in the acroscopic marginal cells of the soral segments and in either marginal cell of the other segments, may bend down at the inner end and intersect wall III instead of running through to meet wall II as usual (IV, Fig. 44). This was frequently seen in the younger stages as figured and in later stages in the segments of the stalk but was never seen in the basiscopic marginal cell of the soral segments. Again, the marginal cell of the sporocarp except on the inside is one of

total width of the petiole of the leaf is equal to the width of the stalk of the leaf. This is approximately analogous to the behavior of some marginal cells of the fifth grade in the leaf.

The Stalk.

If we follow out the development of each of the sections of the different regions of the sporocarp, we may best begin with the four or five pairs of segments of the stalk. We shall find that these together produce at maturity a structure much like the petiole of a leaf, or about half a millimeter in diameter and from ten to twenty millimeters in length. Each of the sections of these segments cuts off phloem and dermatogen cells, and section I cuts off a second portion of phloem as in the leaf, but only the phloem of sections I and III, and usually only part of section III (Fig. 0), take part in forming the axial bundle of the stalk. The phloem of the other sections, together with the pericycle of all the sections, develops into the thick walled sclerenchyma cells, if we may call them such, which give the mature stalk its rigidity and strength, and some of which grow

one of the most important of the tissues of the lower part of the capsule, the base of the capsule (l.i., Fig. 49). The dermatogen gives rise to the pericycle to the hypodermis, and to the epidermis with its trichomes and stomata, while between the hypodermis and the pericycle are formed the small and irregular air canals. There are often more than twenty of these, and six on each side of the pericycle between the pericycle and hypodermis of sections I and III. It is worthy of note that the dermatogen of sections II and V soon splits by longitudinal anticlines (Fig. 50) as was seen in the leaf (Figs. 15, 16), and differs from the dermatogen of the same sections in the same segments of the capsule, as we shall see later. None of the mesophyll cells either here or elsewhere in the gynoecium become specialized as tannin reservoirs as we have seen them do in the leaf.

The Capsule.

Turning now to the development of the seven-seeded or septid seed pods of the capsule, we find that each section forms a portion of the dermatogen as in the stem, and the pericycle between (pl., pb., d., Figs. 49 - 51), and that only the two pericycle portions of section I take part in forming the dorsal wall of the capsule (Fig. 52).

sheath (a.c., Pl. . .). Seen in the cells of the . . .
 . . . portion of section I . . . of the full length
of the segment no other cells of the capsule were
found to do this. The longitudinal vascular bundle of the
sporocarp is thus very much more localized than that of
the leaf, which has been seen to arise from the . . .
 . . . of four of the sections. The dermatogen of all the sec-
tions in all the segments of the capsule splits as in the
leaf into epidermal and hypodermal layers. Of these the
former remains, as in the leaf, of one cell in thickness
and gives rise to trichomes and stomata. The latter
has been shown by Russo . . . and in *Pilularia* by Meunier,
divides (hy., Figs. 53, 54) to form the two layers of
thickened cells of the wall of the mature capsule, and
differs thus from the one layered hypodermis of the peti-
ole (Fig. 13). In general the periblex of all the sections,
in all the segments, gives rise to the few layers of loose-
ly packed cells between the vascular bundle and the hypo-
dermis. Between these cells and the hypodermis are formed
the small and irregular air canals, which in the capsule
are confined largely to the dorsal side and thus to sec-
tions I and III (a.c., Fig. 51).

It will be best now to examine in detail first the
further development of the eight or nine dorsal segments
then of the three basal segments and finally of the . . .

...and

We have seen above that section I in the, as well as in the other segments of this part of the carp, develops much as in the segments of the stalk or of the petiole except for the peculiar specialization of the hypodermis. All the other sections on the contrary have a peculiar history differing from those of either the stalk or the leaf. Sections III, IV and V, dorsal to the marginal cell, widen rapidly at their outer ends, and, as sections II and V do not widen in this way, the ultimate marginal cell is pushed into a ventral position (Figs. 15, 40, 51). Of course the interpolation of the extra section IV, dorsal to the marginal cell, would give the latter a more ventral position than it has in the petiole (Figs. 15, 17), and this is evident from the use of its formation out of the normal sequence, but this result is greatly enhanced by its very vigorous expansion at the outer end. Finally, section VI grows out at the ventral end, beyond the cells arising from the basisopic marginal cell and spreads over into contact with the cells of section V at the ventral surface (Figs. 52, 53). The plerome of the basisopic or soral half of section III breaks up by one anticline and then by periclinal (Figs. 51, 55) to form the dorsal part of the lateral bundle. The more dorsal part of section IV does likewise, while

in the more ventral part, as well as later, the forms of the lateral bundle arise in ^{the} basicopic or indusial halves of the segments (l.b.f. Fig. 40). In section VI the plerome of the basicopic half gives rise to the pleu-
cental bundle of the sorus and to the branch connecting this with the lateral bundle (pa.b., pa.br., Figs. 48 - 50, 52).

Of the sections on the ventral side of the marginal cell, the plerome of section II divides to form rather large isodiametric cells (pl.^{II} Figs. 51, 54) which ultimately form the gelatinizing tissue of the dorsal part of the capsule described by Hanstein ('62) and Russow ('71). The plerome of section V divides by a longitudinal and radial anticline (l.a., Figs. 47, 51) and grows around under the inner end of the cells of the sorus, and the inner end of section VI (Figs. 51 - 54). The ultimate fate of the plerome of this section is probably to help form the dorsal part of the gelatinous ring along with that of section II. It may also help to form the stalk by which the indusium is connected to this ring, but the development of this was not followed out in detail in the later stages and therefore no definite statement can be made. The periblem of both these sections develops very slightly as far as followed, and as that of section V is pushed around under the base of the sorus (Fig. 42) it

apparently, was taken part in the formation of the shell of the indusium. The development of both these sections grows very rapidly in a radial direction, keeping pace with the lengthening of the sorus, and giving rise thus to a part of the indusium surrounding the latter (Figs. 51 - 54), becoming finally more than half the width of the capsule (i.ind., o.ind., Fig. 55). The outer end of these layers later spread out peripherally to meet the ventral end of section VI and thus enclose the cells of the sorus. This portion of each of these two sections becomes several cells in thickness (Figs. 54, 55), and gives rise to a part at least of the ventral portion of the gelatinous ring, while the inner portions (o.ind., i.ind., Fig. 54) remain one cell thick even till maturity. This latter statement, however, is strictly true only of the basicopic portions of these segments, as we shall see later.

The Sporangia.

It remains to describe the development of the most important division of the soral segments, the basicopic ultimate marginal cell. This has a very interesting and significant history, since each is the mother cell of all the sporangia of the sorus formed in its segment. It is the "sorus mother cell" of B¹ogen, located at the base

not only to the sporangia but to a part of the indusium as well, this name is not strictly appropriate. There is, as we shall see, no single cell after the two tertiary marginal cells are formed which gives rise to the placenta and sporangia only, nor to these and the whole of the indusium. No true dermatogen wall is ever formed in this marginal cell, hence the placenta and sporangia are not of strictly epidermal origin. They are formed rather, as was found in the origin of the sporocarp from the leaf, from a cell that is capable of forming at least two meristem layers, as it actually does in the segments of the stalk (Fig. 50).

In the growth of this part of the capsule that takes place soon after section VI is formed, the marginal cell elongates in a radial direction. At the same time its wall begins to separate at the outer or ventral end from the outer cells of section V (s.e., Fig. 51). Meanwhile the marginal cell has grown in the direction of the length of the sporocarp also (Figs. 52, 64). It soon splits by a transverse anticline into halves, of which the acroscopic one soon comes to be the larger. Then each of these divides by another transverse anticline (Fig. 61) forming thus four cells, of which the basicopic cell of the first pair soon becomes the largest (p.m. - sp.m.c., Fig. 64), the size of

cell also divides to form the mother cell of all the microsporangia of the sorus, we may call it the primary macrosporangium mother cell. The sister cell of this latter divides once more by a transverse anticline (Figs. 50, 51) and thus five cells are formed from the basicopic marginal cell, two on each side of the primary macrosporangium mother cell. Of these the one next to the latter on each side (p.mi - sp.m.c., Figs. 50, 54) is a primary microsporangium mother cell, each giving rise to all the microsporangia of the sorus on its side of the placenta. The outer cell on each side (i.ind., Figs. 50, 54) forms the inner layer of the lateral part of the indusium. These five cells are at first much alike as they appear in a transverse section of the capsule (Fig. 51), but the contents of the three middle ones soon become much denser (Fig. 57).

In horizontal section it is soon seen that while the outer or indusial cells, of the five, remain in contact with the cells of section V, the three middle macrosporangium mother cells are separated from these by a narrow slit (s.c., Fig. 57). This is the beginning of the soral canal that we have already noticed in the cross section (s.c., Fig. 51). This cavity constantly increases in size by the pushing out of the indusial cells on each side of the sorus and the forcing away from the cells of section V from the sporangium mother cells.

During this development of the basiscopic marginal cell the periscopic one splits, usually by the transverse anticline (Figs. 52-53, 54), into two cells, one of which helps to form the outer layer of the indusium in its own segment, while the other does likewise for the sorus of the next younger segment (o.ind., Figs. 55, 56).

Returning now to the development of the five cells formed in the basiscopic marginal cell as seen in a cross section of the capsule, we find that at first it is very similar for all, and we may take for further study, sections in the plane of the macrosporangium mother cell. This is seen to elongate radially and then to divide by a pericline (Fig. 52), then by further growth and division of both of the cells thus formed (ma-sp.m.c., Fig. 53) there arises a row of seven or eight cells reaching from about the center of the capsule nearly to the ventral surface (Fig. 54), all of which are separated by the soral cavity from the cells of the inner layer of the indusium arising in section V. From the increase in size of both of the cells formed from the marginal cell by the first pericline, from the occurrence of nuclear spinules in both, and from their relation to the surrounding cells, it can be no doubt that both divide further and give rise to

all of the microsporangia which are in the serus. None of the latter then can be developed from cells in the capsula dorsal to the marginal cells Bäsgen ('00) thought possible. In sagittal section (Fig. 4) it can be seen that, as suggested above, periclinal cells are formed in the microsporangium mother cells and the inner indusial cells about opposite those in the macrosporangium mother cells, as they keep pace with these in radial growth.

By the time that the whole number of macrosporangium mother cells has been formed in the serus, the soral canal has been away from the median wall below an oblique toward the median wall at the ventral end (Fig. 5). It is sometimes the case as Bäsgen has pointed out that the sporangial cells may grow over into contact with the inner layer of the indusium, but there is certainly no growing together after the first separation and the phenomenon has no significance. Soon after the soral canal has taken this curved form the cells of sections V and VI come into contact and thus close the outer end of the canal. These soon fuse together finally but the line of junction remains visible for a long time, (Fig. 7).

While the five divisions of the basiscopic seral cell have increased in numbers by radial growth they have also been developing in other directions. The soral canal is at first confined to the ventral

surface (s.c., Figs. 17, 18), forming a narrow band along the inner margin of the soral cavity (Fig. 19). The microsporangium mother cells push out into the soral cavity (mi - sp.m.c., Figs. 17, 18), far beyond the microsporangium mother cells and swell so that they fill the soral cavity. For this reason sagittal sections all the way across the median wall than that shown in Fig. 27 could not show anything of the microsporangium mother cells, but simply the soral cavity and the two layers of the inner wall on each side of the macrosporangium mother cells, and the microsporangium mother cells might thus easily be overlooked.

As the macrosporangium cell grows and swells laterally to a wedge like form, with a rounded outer end, it is also pushed out into the soral cavity, by the growth of the phloric cells of the acroscopic part of the basicopic half of section VI (p.a.b., Figs. 28, 29). Meanwhile the microsporangium mother cell on each side also increases in thickness and is divided by an annulus parallel to the segment wall (mi - sp.m.c., Fig. 30). When each of these resultant cells is divided by a similar wall (Fig. 31) and thus four cells are formed on each side of the macrosporangium mother cell. These are pushed down by the growth of the macrosporangium mother cells to a position nearly at right angles to their original one (Fig. 32). The growth

... (') ...
formed ...
microsporangium.

The microsporangium mother cell divides by mitosis in three planes: first, then, forms a tetrahedral micell cell relation when (m.sp., Figs. 51, 61). The first cell row-
ed is seen in a cross section of the embryo is usually
toward the ventral side of the mother cell (Fig. 52).
There is no remaining of the mother cells from the
other in the series as described by Basgen ('10) and as
figured in *Pilularia* by Munier ('37), but those are
squarely against each other (Figs. 53, 54). The apical
cell of the microsporangium cuts off two separate micelle
side which form the lateral and basal cells of the spo-
rangium and that part of the placenta or stalk which lies
between the sporangium and the region of the placental
bundle (Fig. 55). Then a pericline is formed near the
outer end of the apical cell and the archesporium is thus
cut off (arch., Fig. 56) and the sporangium wall is laid.
the former giving rise as Rostov has shown to the integument
and spores.

While the microsporangium has been developing, there
has been some important changes in the cells derived
from the microsporangium mother cell and in the cell
section VI that are pericline in between them. But in
the four cells on either side of the pericline in the

divides by walls perpendicular to the axis of the sporangium into four cells (Figs. 31, 32). These are produced in four rows, of approximately thirty-two cells each, on either side in the length of a sorus of eight macrosporangia. There would thus be four cells opposite each macrosporangium in a longitudinal section of a capsule 11-12 older than that shown in Fig. 30. Each of the cells arising from that one of the original four nearest the macrosporangium (mi - sp., Figs. 31, 32) swells and from the placenta and divides into a basal cell, and an outer cell which gives rise by inclined walls to the tetrahedral apical cell of a microsporangium; while the cells derived from the original four furthest from the macrosporangium, form the outer cells of the placenta in that region (pa., Figs. 31, 32). The basal cell of the microsporangium can perhaps be considered as homologous with the stalk cell

found in the sporangia of many of the homosporous *Lepidosporangiates*, but there was nothing seen in the development of the macrosporangium that could be regarded as such, and *Marsilia* thus differs from *Pilularia*, in which Campbell ('88) has described such a cell as being sometimes formed.

The cells derived from the plerome of section VI as described above, continue to divide, giving rise to two rows of cells, as seen in horizontal section (Figs.

0 - 10), and the outer part of the placental branch, cells on one side derived from the microsporangial cells. From certain of these initial cells, in the embryo described in detail later, are formed the placental handle and the placental branch.

Meanwhile the inner and outer indusial cells, on each side of the sori, have kept pace with the growth of the sporangial cells. The acroscopic part of section V and the acroscopic marginal cell have each split by a transverse anticline (Fig. 75) to form the lateral part of the outer layer of the indusium of the adjacent sorus, and these, in connection with the cells of section II, complete the outer indusial layer, surrounding the sori through its whole length (o.ind., Figs. 54, 70 - 72).

The lateral inner indusial cells, arising from the basiscopic marginal cell, together with the cells of the basiscopic half of section V complete the inner layer of the indusium also. Each of these layers remains only a single layer in thickness even at maturity, and no division walls are formed in their cells except those very infrequently at the surface, and by growth in this manner the indusium constantly increases the size of the sorus enclosing it. Spores are pushing out in o.n.s. (Figs. 70 - 72). During the growth of the indusium some intercellular spaces appear, between the two layers, the space between the

The Vascular Bundle System.

We have now turn to the vascular system of the lateral bundle and its termination in the capsule, as described in connection with the development of the leaf, in order to avoid unnecessary complication. The proximal portion of each lateral bundle arises from the vascular half of the next older stem (III and IV (l.b., Figs. 41 - 51, 55, 56). At a point above the capsule the inner end of the lateral bundle splits into two branches as has been shown by Russon. Two of these continue on in the course the single bundle round the half of the capsule (l.b.f., Fig. 55, 56), while the other two branch out, inward toward the vascular joins on peripheral bundle (p.b.f., Figs. 55, 56, 57). Of the two outer branches of the lateral bundle, one arises in the mesoscopic quarter of the mesoscopic half of the same stem (l.b.f., Figs. 55, 56), while the other arises from the mesoscopic quarter of the mesoscopic half of the next older stem (l.b.f., Figs. 55, 56, 57). These four are formed while the marginal cell is still undivided, by the periclinial wall that form from it the cells of the soma (Fig. 55), and grow in length with the soma (l.b.f., Figs. 55, 56, 57). They increase also in diameter as the capsule grows and

and of the (1000, Fig. 30 - 31), and near the base of the capsule. These cells are connected with those of lower level of the series in a more or less regular way by the formation of vascular tissue from the cells lying between them (Fig. 32).

It has been shown above that the placenta of the basiscopic half of section VII divides into two portions (Fig. 37) and that the acroscopic one of these portions is the median cells of the placenta (1a., Fig. 32). Most of these cells form a part of the general parenchyma of this region of the placenta, but several rows of these cells at the point between the opposite microsporangia are in contact with the first segments of the apical cell of the macrosporangium, give rise to the placental bundle which runs through the whole length of the placenta. In a region about opposite the inner ends of the series (1a.br., Fig. 37, 38) these same cells also become specialized to form the placental branch which runs across the whole breadth of section VI from the single portion of the lateral bundle to the placental bundle (1a.br., Figs. 37, 38, 39).

The sterile Segments of the Capsule.

We continue on the capsule, and the capsule is now

to the capsule wall. The capsule wall is at the base of the capsule, giving rise, in the basal segments, to its portion of the basal wall. From the base of section I. The capsule wall of the basal segment also forms a lateral bundle, formed in the pleura of sections III and IV as in the basal segments (Figs. 10, 11). No trace of the pleural branch of the pleural bundle is seen here, and in the other basal segments no lateral bundle is developed. The pleura of sections II, V and VI, in the young's segment of the tube, and probably that of all the sections except section I of the middle segment, is apparently devoted to the formation of the basal portion of the gelatinous wall (i.e., Figs. 12, 13). In the basal or basal segment of the tube the pleura and peribion of all the sections are combined to form the basal wall of two layers of thickened cells (b.w., Figs. 14, 15), like the hypodermal cells of the capsule wall, and stretching across from the dorsal to the ventral wall. In the peripheral of section I in the basal segment, and probably in the first two basal segments also, there is developed a wall of thickened cells, like those of the hypodermis, enclosing a lens-shaped space of two thickened cells, the "lens-shaped space" of Figs. 16 (i.e., Fig. 16). Into a small opening to the outside of this space project a few of the basal cells

(... , Fig. ...). Just above the dorsal bundle there is a small ... (Fig. ...). By the ... of the ... calls ^{above this place} the ... of the ... (... , Fig. ...).

Lat 17, in ... six or seven pairs of ... of the capsule there is no single dorsal bundle, but this divides into two just before the lateral bundles of the youngest sordal segments arise. These two divisions then run nearly parallel near the dorsal ... of the capsule and each gives off three or four branches, which arise like those of the sordal segments, from the ... of sections III and IV (Figs. ...), and are joined, like these also, with their fellows of the same side near the ventral margin. The exact origin of the two parallel divisions of the dorsal bundle can be made out ... The place of the first three or four segments aside from ... the ... of that of the remaining segments probably ... in ... this position of the ...

Summary.

The seniclerous sponges of the genus *Senecella* are characterized by longitudinal canalicles into six or seven segments, the marginal cell of the seventh segment. The dorsal portion of the capsule is formed entirely from the plates of section I, the lateral bundles in each of sections III and IV and the pleural bundle and branch in section VI. The epidermis is of one layer of cells and the hypodermis of two, both layers of the latter consisting of very thick-walled cells. The canalicles of the epidermis and the canals under the hypodermis are like those of the setiole, except that the latter are smaller and more irregular. The sporangia of each seta are all derived from a basiscopic ultimate marginal cell, which gives rise also to the cells forming an inner layer of the lateral portion of the indusium. The single primary macrosporangium mother cell and the two primary microsporangium mother cells of each seta are side cells, formed by the first divisions of the marginal cell. They are thus superficial, but not strictly epidermal, in origin. The so-called canal arises by a split between the cells of the primary sporangium mother cells and those of the cells of section V, beginning at the ventral end of the capsule and extending later to the inner end of the seta. From the space so formed is developed the

The leaf canal, as we have seen, is formed by the growth and division of the primary sporophyllous cell, which forms also the ultimate sporangium of the leaf. A stalk cell is formed in the development of the microsporangium, but nothing homologous with this was seen in the case of the macrosporangium. The indusium of each sorus arises partly within its own segment, but partly also from the next older segment. It is derived from the dermatogen cells of sections II and V and from the marginal cells. The gelatinizing tissue of the dorsal part of the capsule arises largely, if not entirely, from the plerome of section II; that of the ventralside from the dermatogen of sections II and V, and that at either end of the capsule probably comes from all three meristematic layers.

Conclusions.

The leaf of *Marsilia* agrees closely with those of most of the leptosporangiate Ferns which have been studied, in its origin, in its growth by a broad sided apical cell, and in the development of the lamina by the continued activity of the marginal cells of certain of its segments. The position of the primary or section cells in the segments of the leaf, while somewhat varied, is

both found in *Asplenium* & *Adiantum*. Sauer (1911), is very different from the description of Greville (1811, p. 32) for the *Leptosporangiales* in general, so far as one can judge from the description alone. It is very evident that, as Bower has suggested, there is great need of a detailed work on the origin of the sporangia layers in the various organs of the Ferns. Many of the accounts at present available, of the development of the prothallium and gametophyte are very unsatisfactory because of the lack of details in both descriptions and figures.

The sporocarp is certainly to be considered as a branch of the leaf, since it is derived from the apical cell of the leaf. The second sporocarp is usually a branch of the first and hence a secondary branch of the leaf, while the third may in like manner be a tertiary branch. In the shape of its apical cell and of the segments cut off from this, the sporocarp agrees exactly with the leaf, while in the primary divisions of the segments, it differs from the leaf only in the introduction of an extra section dorsal to the marginal cell. The capsule, so far as its development gives any clue, is homologous with the apical cell of the leaf. There is no indication from this source that the sporocarp contains anything homologous with the lamina of the leaf. The out-growths of the sporophylls, the so-called paraphyses, are certainly

... (G...) ...
... We may ...
... as well as in ...
... .

It is difficult however to see ...
... the capsule of ...
... together with the ...
... margin of the capsule, is ...
... of development as given above. The same difficulty is
of course found in the interpretation of ...
... the capsule as a pair of leaflets, and in ...
... and Campbell who consider it a pinnate leaf with
... at the dorsal margin and ...
sorus.

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Fig. 1. A nearly vertical section of the stem apex showing the surface of the stem and the leaf mother cell with one segment wall. x300.

Fig. 2. Transverse section of stem (from apical cell of young leaf). x300.

Fig. 3. Section of stem between vertical and horizontal planes, showing surface of stem apex and transverse section of leaf. x300.

Fig. 4. Sagittal section of a leaf nearly at the end of apical growth. x200.

Fig. 5. Part of a sagittal section of the petiole of an older leaf. x200.

Fig. 6. Ventral surface of tip of a young leaf. x400.

Fig. 7. Dorsal surface of the tip of a similar leaf x400.

Fig. 8. Surface of the tip of a very young leaf showing the shape of the two young segments on one side and the apical cell seen so as to show the shape of the lateral wall and hence the shape of the segments etc. x500.

Fig. 9. Half of a nearly transverse section of a young leaf, showing the shape of a segment and the position of the lateral cell wall. x500.

Fig. 10. A similar section of a leaf showing the shape of the segments etc. x500.

Fig. 11. A transverse section of a petiole showing still older segments. x100.

Fig. 12. The same still older. x500.

Fig. 13. Transverse section of a petiole showing still older segments. x100.

Fig. 14. Transverse section of a petiole showing an ultimate marginal cell of the fifth grade. x500.

Fig. 15. Similar section showing the ultimate marginal cell of the sixth grade. x500.

Fig. 16. Transverse section of petiole in which epidermal and hypodermal layers are completed and the parenchyma cells are now ready to cut off the cross partition cells. x500.

Fig. 17. Part of similar section of a still older petiole. x100.

Fig. 18. The same section of a still older petiole. x100.

Fig. 19. Transverse section of a nearly mature petiole. x100.

Plate II .

Fig. 20. Part of transverse section of a petiole. x100.

Fig. 21. Tangential section of petiole showing the same cells in longitudinal section. x100.

- Fig. 22. The same section as Fig. 21. x 60.
- Fig. 23. The same section as Fig. 21. x 100.
- Fig. 24. The same section as Fig. 21 showing the beginning of the longitudinal partition. x 100.
- Fig. 25. Surface view of a longitudinal section showing the bases of a novel set of petioles. x 100.
- Fig. 26. Sagittal section of petiole, same section of segment five or six of Fig. 1. x 500.
- Fig. 27. Surface view of petiole in the same section showing the arrangement of the trichomes. x 100.
- Fig. 28. Lower edge of the same. x 100.
- Fig. 29. Novel nature stage of the same. x 100.
- Fig. 30. Novel nature trichomes. x 100.
- Fig. 31. Horizontal section of the same leaf, showing the beginning of the three pinnae. x 100.
- Fig. 32. The same leaf showing origin of terminal pinnae. x 100.
- Fig. 33. Longitudinal section of leaf showing the origin of the well developed pinnae. x 100.
- Fig. 34. Transverse section of long, straight pinna, a little larger than Fig. 31. x 100.
- Fig. 35. A similar section still larger. x 100.
- Fig. 36. A similar section showing a little more of the same. x 100.
- Fig. 37. A similar section showing a little more of the same. x 100.

Fig. 9. Longitudinal section of stem . x70.

Fig. 10. Approximate longitudinal section of stem showing the first leaf and sporocarp . x70.

Fig. 11. The same as Fig. 10 . x70.

Fig. 12. Near longitudinal section of stem showing the leaves, an undulating rhomboid sporocarpial segments, showing the under surface of part of side leaf, and cross section of the first sporocarpial leaf on the 1st whorl of stem side leaf from the first . x100.

Plate III .

Fig. 13. Transverse section of stem, and a young leaf with two sporocarps all nearly parallel to the stem . x10.

Fig. 14. Inner side of young leaf with a sporocarp in which the segmentation of the apical cell is nearly finished . x25.

Fig. 15. An older sporocarp on a pedicel showing capsule bent against the wall . x25.

Fig. 16. Transverse section of a young sporocarp . x70.

Fig. 17. The same in an older stage . x70.

Fig. 18. Transverse section of capsule at the base of the seedling . x70.

Fig. 19. The young plant on a pedicel . x100.

Fig. 19. Transverse section of shell of *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell, and the position of the siphon (Fig. V) in the ventral margin of the shell. $\times 700$.

Fig. 20. The same *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell and the position of the siphon (Fig. V) in the ventral margin of the shell. $\times 700$.

Fig. 21. Transverse section of shell of *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell. $\times 700$.

Fig. 22. The same section of *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell, and the position of the siphon (Fig. V) in the ventral margin of the shell. $\times 700$.

Fig. 23. Part of transverse section of *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell. $\times 700$.

Fig. 24. The same still older. $\times 400$.

Fig. 25. The same at the time of closing of the siphon. $\times 400$.

Fig. 26. The same still older. $\times 400$.

Fig. 27. Ventral surface of *Mytilus* showing the position of the siphon (Fig. V) in the ventral margin of the shell. $\times 700$.

Plate IV.

Fig. 28. Part of transverse section of *Mytilus* showing the position of the siphon (Fig. IV) in the dorsal margin of the shell. $\times 700$.

Fig. 29. The same still older. $\times 400$.

Fig. 10. Vertical section of capsule, showing the internal structure of the capsule. x100.

Fig. 11. Horizontal section of capsule, showing the internal structure of the capsule. x100.

Fig. 12. The same, of capsule, showing the internal structure. x100.

Fig. 13. The same, still lower, showing the internal structure. x100.

Fig. 14. The same, of whole capsule, showing the internal structure. x100.

Fig. 15. Sagittal section through the capsule, showing the internal structure. x100.

Fig. 16. Sagittal section through the capsule, showing the internal structure. x100.

Fig. 17. The same, of capsule, showing the internal structure. x100.

Fig. 18. Sagittal section through the capsule, showing the internal structure. x100.

Fig. 19. View of inner side of one of the valves of a non-ferrous capsule. x10.

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V i t a .

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The writer of this is born in Cromwell, Conn., on the twenty-first day of July 1891. He received his early education in the public schools of Cromwell and Middletown Conn., and took his college course at Wesleyan University, in the latter town, receiving the degree of B. S. in 1898. During the college year of 1897-8, he was a graduate student at Wesleyan. Since the fall of 1898 he has been a graduate student at Johns Hopkins University, with Botany as a major subject and Zoology and Physiology as minors.

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