TRENDS OF SPECIALIZATION IN THE SPOROCARP AND SPORES IN THE LIVING AND FOSSIL MARSILEACEAE

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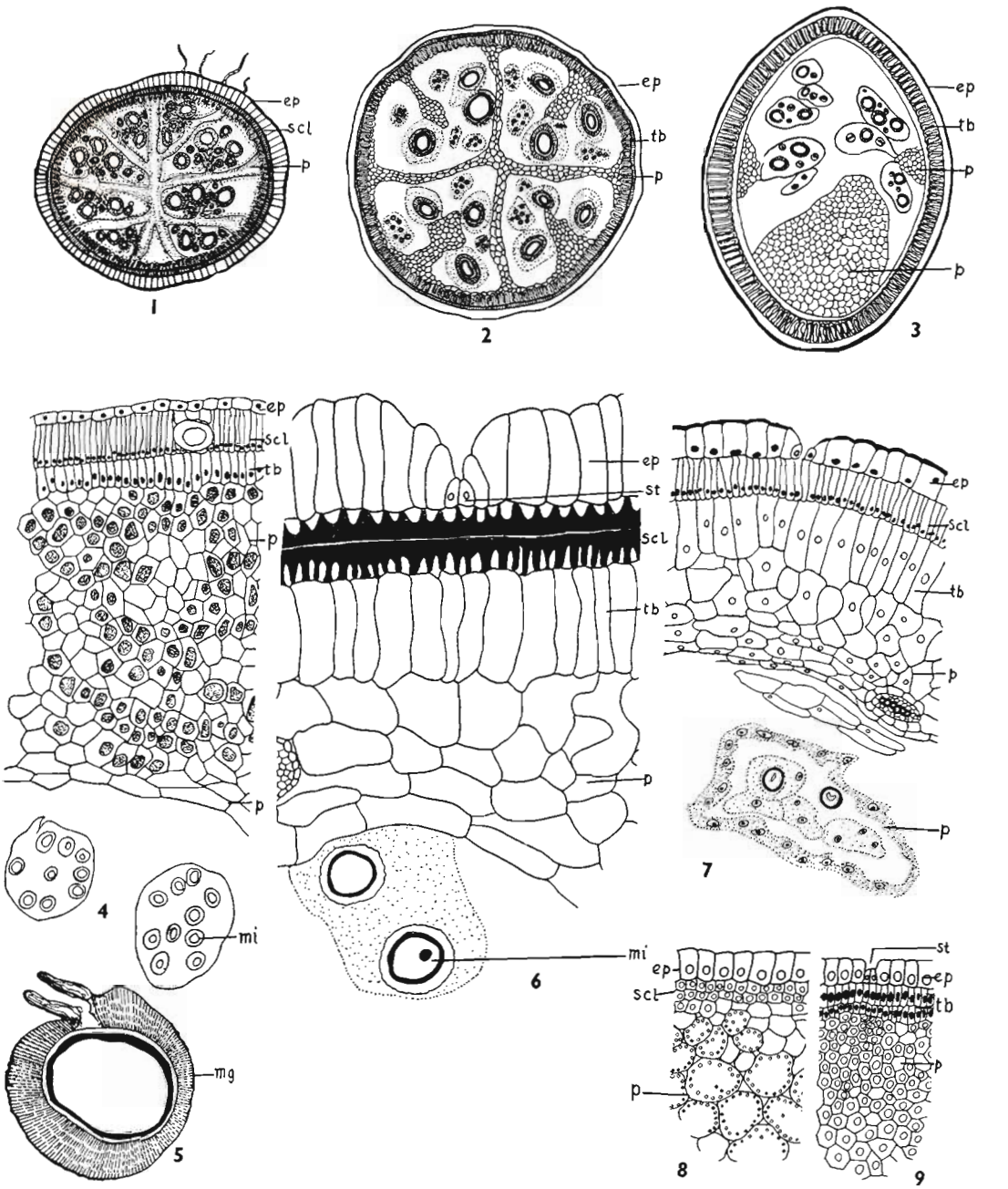
ABSTRACT

The paper gives an account of the trends of specialization in the structure of the sporocarp and spores in three living members of the Marsileaceae, *Marsilea*, *Pilularia* and *Regnellidium*, and in the only definitely known fossil member of this family, belonging to the genus *Regnellidium* named as *Rodeites dakshini* by Sahni (1943), from one of the Tertiary horizons of India, the Deccan Intertrappean Series of Mohgaon Kalan (Dist. Chhindwara). Apart from morphological differences in shape, size, position of spines and their position on a sporocarp, it is the sporocarp wall which shows a good deal of variation and specialization in the three genera. The tabular layers of elongated cells forming a column below epidermis, sporoderm, and the mode of germination of mega- and microspores differ in different species. The spore wall is 4-layered in all genera, but the spore size and episporial ornamentation are different in them. In the spores of all these plants prismatic layer is conspicuous in both kinds of spores, but more so in megaspores. The sori are bilaterally arranged in the living members and also in the fossil member, *Rodeites*. The sporocarp wall, however, seems to have been less differentiated in the fossil member, *Rodeites dakshini* Sahni than in the living species *Regnellidium diphyllum* Lind., as the tabular cells are not apparent in the former. The raphe, on the other hand, in this member is more prominent than that in the living species.

HYDROPTERIDINEAE comprise two families, the Salviniaceae and Marsileaceae, both of which possess a structure, sporocarp, in which sori bearing mega and microsporangia are lodged. On the basis of the morphology of sporocarp, the two families are considered to be related to Hymenophyllaceae and to two other families, the Schizaeaceae or Cyatheaceae. The Marsileaceae is considered to be related to the Schizaeaceae on the basis of its soral structure, particularly the indusium. This family consists of three genera, *Marsilea* with about 65 species, *Pilularia* having 6 species, and the monotypic Brazilian genus *Regnellidium*, with its single species, *R. diphyllum* Lind. The sporocarps in these genera show a good deal of variation in their morphology, structure of the wall, scales or hairs on them, sori, and the method of spore dispersal. In *Pilularia* the round sporocarp arising from the petiole a little above the ground is slightly conical at the top. It is profusely covered with ramental scales or hairs. It gives an impression to be radially symmetrical, but a careful examination of its serial sections shows bilateral symmetry (TEXT-FIG. 2 and PLS. 1, 2, FIGS. 7, 20). There are four or in some species three or two chambers in it, in which the sori are lodged. In *Marsilea* the kidney-shaped sporocarp is definitely bilateral (TEXT-FIG. 3) and the coenosorus is partitioned into a number of chambers 8-12 on each side (TEXT-FIG. 3 and PL. 2, FIG. 19). This number, however, varies in different species. In *Regnellidium* the round and large sporocarp is without a hump, like that in the sporocarp of *Pilularia* (TEXT-FIGS. 11, 14) or spines as those in *Marsilea* (TEXT-FIG. 10). It possesses only a red-coloured raphe. It is also few-chambered, 6-7, and bilaterally symmetrical (TEXT-FIG. 1), though externally round (PL. 2, FIGS. 18, 23, 24).

The structure of the sporocarp wall in these three genera is quite different (TEXT-FIGS. 4, 6, 7-9 and PL. 1, FIGS. 1-3). In *Marsilea* the wall having peltate scales or hairs is heavily thickened and mucilaginous (TEXT-FIG. 7 and PLS. 1, 2, FIGS. 2, 19). Two distinct layers of elongated, tabular cells lie below epidermis, in close association with the parenchymatous layers secreting mucilage and filling the cavities of the chambers (TEXT-FIG. 7 and PL. 1, FIG. 2). In *Pilularia* the outer epidermis is not thick, but there are two contiguous layers of cells below it having heavy sclerenchymatous thickening on opposite sides (TEXT-FIG. 6 and PL. 1, FIGS. 3, 7). These two layers constitute a strong, subdermal, thick wall in the sporocarp of *Pilularia* (TEXT-FIG. 6 and PL. 1, FIG. 3-*scl.*). The cells below these thick subdermal layers are mucilaginous and they fill the cavities of sporocarp chambers (PLS. 1, 2, FIGS. 7, 20). In *Regnellidium* the wall of the sporocarp is quite massive (TEXT-FIG. 1 and PL. 2, FIG. 18-*scl.*). It



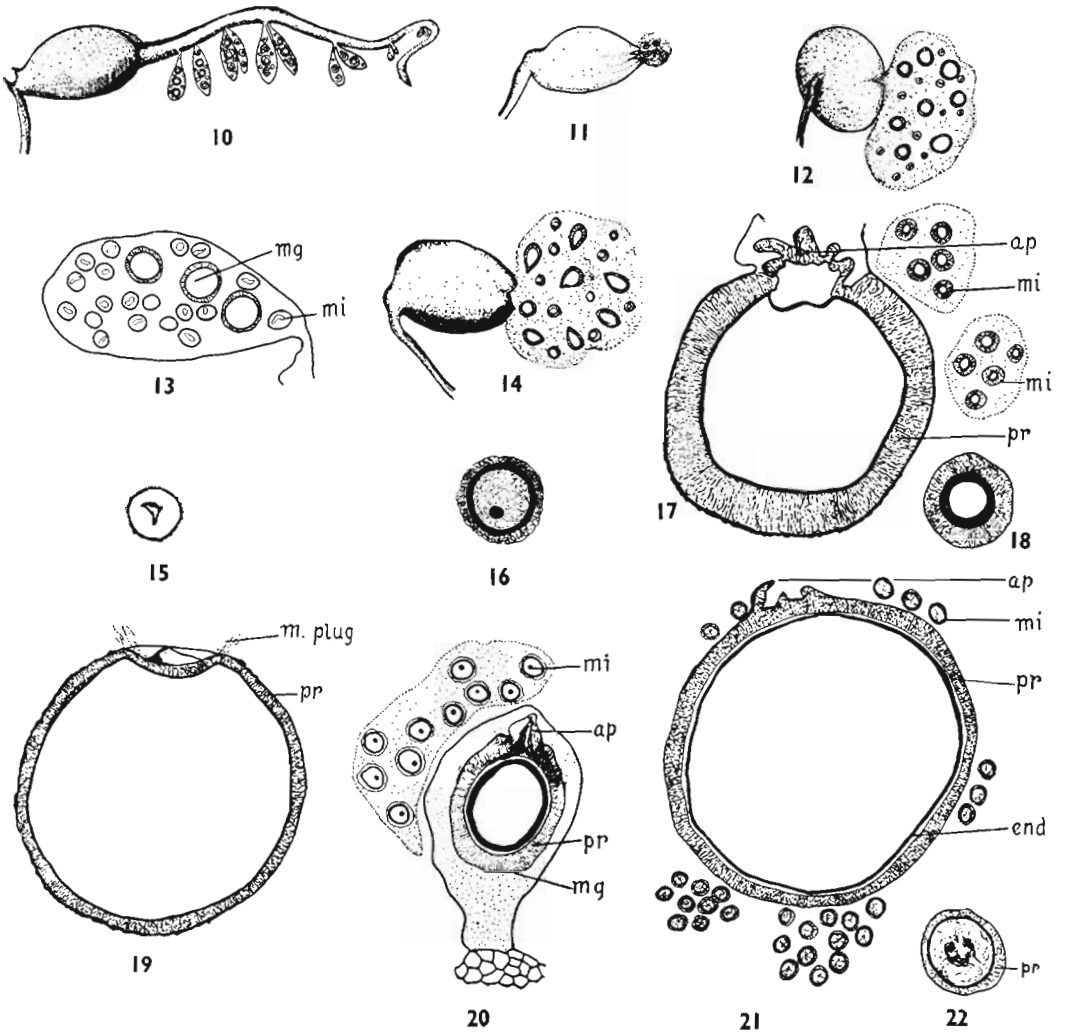
TEXT-FIGS. 1-9 — Sporocarp and its wall in the Marsileaceae. (Abbrev.: *ep*, epidermis; *scl*, sclerenchymatous cells; *st*, stomium; *tb*, tabular, columnar palisade-like cells; *p*, parenchyma secreting mucilage; *mi*, microspores; *mg*, megaspores; *p*, prismatic layer; *ep*, warty episporium; *end*, double-layered endosporium; *ap*, appendages.) 1-3 — T.S. of sporocarps showing bilateral symmetry in *Regnellidium*, *Pilularia* and *Marsilea*. 1, *Regnellidium diphyllum* Lind. T.S. of sporocarp. × 6. 2, *Pilularia americana* A. Br. T.S. of sporocarp. × 13. 3, *Marsilea poonensis* Kolhat. T.S. of sporocarp. × 13. 4, *Regnellidium diphyllum* Lind. T.S. of sporocarp wall. × 44. 5, Ibid. A megaspore of the same lying below microsporangia. × 44. 6, *Pilularia americana* A. Br. T.S. of sporocarp showing structure of the sporocarp wall and two microspores below it engulfed in mucilage. × 166. 7, *Marsilea poonensis* Kolhat. T.S. of sporocarp showing epidermis with a stomium (*st*), small tabular cells, elongated palisade-like cells below them, parenchyma secreting mucilage, a vascular bundle (*vb*) and a sporangium with two developing megaspores. × 166. 8, 9, wall of the sporocarp in young sporocarps of *Regnellidium diphyllum* Lind. showing differentiation of the tabular cells in young condition. × 166.

contains elongated tabular cells below epidermis and several layers of parenchymatous cells, about 15, traversed by mucilage ducts and vascular bundles. The elongated cells become differentiated at a very early stage in the development of the young sporocarp (TEXT-FIGS. 8, 9). The mucilage-secreting cells are very conspicuous in the subdermal tabular cells of this genus. The sori and spores lie fully enveloped in the mucilage secreted by these cells in all species of the three genera (TEXT-FIGS. 1-7 and PL. 2, FIGS. 17-20), but the development and extent of the tabular, parenchymatous and mucilage-secreting cells in the sporocarp of different species of *Marsilea* and *Pilularia* greatly vary (TEXT-FIGS. 2-7 and PL. 1, FIGS. 1-3).

Dehiscence of the sporocarp in *Marsilea*, as is well known, is by means of a long mucilage cord, the sorophore, to which the sori are attached ventrally (TEXT-FIG. 10). It emerges generally from the distal end of the sporocarp and is quite long, several times longer than the sporocarp. In *Pilularia* the sporocarp lies just in flush with the soil and dehisces by means of more than one valve or pores at the top, generally 3 or 4, producing a drop of mucilage which, absorbing water, enlarges considerably (TEXT-FIGS. 11, 14). The spores are spread in it. They germinate on moist soil of the pond in which the plants grow and produce sporophytes which root in the soil. In *Regnellidium* the sporocarp dehisces irregularly and gives out a large irregular mass of mucilage, in which numerous sori containing both mega- and microspores lie together in the mass of mucilage secreted (TEXT-FIG. 12 and PL. 2, FIG. 17).

The development of microspores and megaspores in the three genera proceeds more or less along a similar pattern of the Polypodiaceae up to 16 spore mother cells stage. But after that, the development of the mega- and microsporangia becomes different in different species. However, in all species, 16 microspore mother cells divide to form 64 microspores, or sometimes less due to sterilization and apogamy. In megasporangium, on the other hand, megaspore tetrad or tetrads in different sori lie mixed with young microspore mother cells and young spores (TEXT-FIG. 18 and PL. 1, FIGS. 5-7). They show a characteristic development further. Of the 16 spore mother cells only a few, generally one or two, develop at the cost of the developing microspores in various stages, which eventually degenerate, resulting in a varying number of megaspores in each sporangium (cf. TEXT-FIGS. 13, 17, 29 and PL. 1, FIGS. 4-7). Consequently in different species of *Marsilea* and *Pilularia*, and in *Regnellidium diphyllum* the number of megaspores in a ripe sporocarp varies (PLS. 1, 2, FIGS. 4-7 and 20, 23). The largest number of megaspores is in *Regnellidium* (PL. 2, FIGS. 17, 23), next to that in *Pilularia* (PLS. 1, 2, FIGS. 7, 20) and the smallest in *Marsilea* (PL. 1, FIG. 5). In different species of *Marsilea* this number varies from 1 to 9 per sporocarp. In *Regnellidium diphyllum* there are 40-80 megaspores engulfed by numerous microspores lying in a mass of mucilage. In *Pilularia* the number of megaspores is also generally large, but in some species it is comparatively small, varying from 8 to 25 (cf. PLS. 1, 2, FIGS. 7, 20). Both mega- and microspores lie together in the mucilage collected in sori lying in chambers. The mucilaginous mass is mostly dorsal (PL. 2, FIG. 19) and in the form of a cord in *Marsilea* (TEXT-FIG. 10), globular and lying in the distal terminal half in *Pilularia*, and spread all around the sporocarp in *Regnellidium* (TEXT-FIG. 17 and PL. 2, FIG. 17). The peculiarities of the wall structure and the mucilage-secreting cells, thus, largely account for the difference in the mode of dehiscence of the sporocarp in the three genera and in their different species. It looks as if the whole sporocarp of Marsileaceae, after early stages, is a large mucilage or gelatine-secreting body, in the midst of which the sori and spores get dispersed.

Spores in the Marsileaceae, like the sporocarp wall, greatly differ in the three genera, but all of them have some common features, namely the presence of mucilage and other substances in the spore wall which enable them to absorb lot of water and to swell. The sporoderm is four-layered, the most conspicuous layer amongst them being second which is prismatic, and lies below warty perine. The exospore in mega- and microspores in *Marsilea* has the least thickening (TEXT-FIGS. 15, 19 and PL. 1, FIGS. 10, 15). The triradiate mark is clear in microspores (TEXT-FIG. 15), but not in megaspores (PL. 1, FIG. 15). The latter is thrown off during germination and a mucilage funnel develops around this projection after its lid or the upper portion is thrown off. The spermatozoids are caught in this funnel of mucilage. In *Pilularia* and in *Regnellidium* the mega- and microspores have



TEXT-FIGS. 10-22 — Mode of dehiscence of sporocarp in the Marsileaceae and the mega- and microspores. 10, *Marsilea poonensis* Kolhat. Dehisced sporocarp showing sorophore and sori. × 3 approx. 11, *Pilularia minuta* Dur. A sporocarp dehiscing by apical pores and throwing out a mucilage drop. × 5. 12, *Regnellidium diphyllum* Lind. A sporocarp broken open, from which a large mass of mucilage with sori and spores has come out. × 3 approx. 13, *Marsilea poonensis* Kolhat. A sorus showing a single sporangium with three developing megaspores. × 63. 14, a dehiscing sporocarp of *Pilularia americana* A.Br. throwing out a mass of mucilage containing mega- and microsporangia and spores. × 5. 15, *Marsilea poonensis* Kolhat. A microspore. × 240. 16, a microspore of *Pilularia americana* A.Br. × 240. Note the different layers in the spore wall. 17, *Regnellidium diphyllum* Lind. L.S. of megaspore showing prismatic layer in the sporoderm and terminal appendages (*ap*) and two microsporangia cut transversely. × 44. 18, *Regnellidium diphyllum* Lind. A microspore. × 166. Note the prismatic and other layers of sporoderm. 19, *Marsilea poonensis* Kolhat. L.S. of megaspore. × 441. 20, L.S. of sorus of *Pilularia americana* A.Br. showing sporangia with a megaspore showing prismatic layer (*pr*), terminal cluster of appendages (*ap*) and the rim formed by the prismatic layer around the apical appendages. × 44. 21 *Rodeites dakshini* Sahni. L.S. of megaspore having outer prismatic layer and thick inner layer surrounded by microspores. × 44. 22, *Rodeites dakshini* Sahni. L.S. of microspore of the same showing prismatic layer. × 166.

curious appendages at their top (TEXT-FIGS. 5, 16, 20, 21 and PL. 1, FIGS. 8, 9, 11-14). The spore wall is uniformly thickened in *Regnellidium* and has four layers (PL. 1, FIGS. 9, 13, 14). The outermost of these is warty and the second below it is prismatic (TEXT-FIGS. 17, 18 and PL. 1, FIGS. 9, 13, 14-*pr*.). The other two inside belong to endosporium, one thick and dark and the other shining and transparent. In *Pilularia* also the spore wall has four layers (TEXT-FIGS. 16, 20 and PL. 1, FIGS. 7, 11, 12, 16), but the prismatic layer forms a kind of inflated rim or a constriction at the top of megaspore in some species (TEXT-FIG. 20 and PL. 1, FIGS. 12, 16). The inflated wing-like layer helps the spores in floating erect. The two layers of endospore form a cone or a papilla at the top of the mega- and microspores (TEXT-FIG. 20 and PL. 1, FIG. 16). As the megaspores swell, this cone of appendages opens out and allows the papillate prothallus to come out, especially after the embryo has been formed. In *Regnellidium* the terminal appendages of mega- and microspore form a twisted, quincuncial funnel-shaped apparatus, highly characteristic of this genus (TEXT-FIGS. 5, 17, 18 and PL. 1, FIGS. 8, 9, 13, 14). The microspores adhere to these appendages of megaspores as in *Pilularia*, and facilitate thereby fertilization like the glochidia of *Azolla*. The whole mechanism of the sporocarp and spore dispersal thus seems to depend largely on the peculiar structure of the sporocarp wall, the sporoderm, and the capacity of spores to absorb water from surrounding mucilage. The latter also helps spores in germination or to remain dormant during the period of desiccation, which is spread over several years sometimes. Very often when the mucilage gets hardened, germinating spores are not much affected thereby. This method of bringing spores closer for fertilization with the help of mucilage secreted strongly reminds one of the mucilage drop mechanism in pollination and fertilization met with in some gymnosperms.

Fossil history of the Hydropteridineae clearly shows that the Marsileaceae is essentially a Tertiary family. The only definite member of this family so far known is the genus *Rodeites* discovered by Sahni and Rao (1940) in the Tertiary Flora of the Deccan Intertrappean Series of India. The sporocarp of this member and its other parts are fairly well preserved in cherts at Mohgaon Kalan (Dist. Chhindwara), and at a few other places such as Vikarabad (SHARMA, 1947). The species was named *Rodeites dakshini* Sahni by Sahni (1943) after the discoverer of this locality, Dr. K. P. Rode of the University of Rajputana. This fossil species has a sporocarp which is bilaterally symmetrical and has 6-7 chambers on either side (PL. 2, FIGS. 22, 21). It contains numerous megaspores fully packed in the midst of microspores in several sori (PL. 2, FIGS. 21, 22, 25, 26), like those in the present-day *Regnellidium diphyllum* (cf. PL. 2, FIGS. 21, 24 and FIGS. 22, 23, 25). The sporocarp here, however, is more elliptical and elongated, about 10 mm., than that in the living species, *R. diphyllum*, where it is round, about 6-7 mm. in diameter. The raphe appears to have been more prominent in the fossil member (PL. 2, FIG. 21-*r*). The sporocarp wall also is not much differentiated into tabular and parenchymatous cells (PL. 2, FIG. 26-*p*) as in the living species (cf. PLS. 1, 2, FIGS. 1, 26). For example, in the fully matured fossil sporocarp shown in Pl. 2, Fig. 26, there are only 10-12 rows of parenchymatous cells but no elongated palisade-like cells. The number of megaspores per sporocarp appears to be larger in the fossil species, 80-120, than in the living having 60-90. The spore size and their ornamentation are more or less similar (*see* table *below*), but the sporocarp

SPECIES	SIZE OF THE SPOROCARP, mm.	THICKNESS OF THE SPOROCARP WALL μ	MEGASPORE DIAMETER μ	MICROSPORE DIAMETER μ
Marsilea poonensis Kolhat	2·0 × 3·0	310-375	660 × 840	45-60
Pilularia globulifera L.	3·0 × 3·2	156	365 × 425	45
Pilularia americana A.Br.	3·5 × 4·0	225	312 × 425	45
Regnellidium diphyllum Lind.	7·0 × 6·0	416-525	600 × 580	40-50
Rodeites dakshini Sahni	*ca.* 7·0 × 13·0	*ca.* 420	*ca.* 600 × 550	*ca.* 47

All measurements are based on an average of ten counts.

wall and sporoderm are less thick in the fossil species than in the living.

The ornamentation of the sporoderm and size of the spores in fossil and living species being similar, there is no doubt that the spores in the fossil species were fully matured; and hence the sporocarps that produced them must also have been fully ripened (cf. PL. 2, FIGS. 23, 26). The mode of dehiscence in the fossil species, however, seems to have been somewhat similar to, but intermediate between, that in the sporocarps of *Pilularia* and the present-day species of *Regnellidium*, since the sporocarp wall of the fossil species *Rodeites dakshini* has no conspicuous layers of elongated tabular cells, found in the living species of both *Regnellidium* and *Pilularia*. It is these cells which greatly help in the expulsion of mucilage engulfing sori and spores. There is a definite mechanism of maintaining connection between epidermis of sporocarp and mucilage secreting cells below, which will be described later.

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EXPLANATION OF PLATES

PLATE 1

Figs. 1-16 — *Structure of the sporocarp wall, sori and spores in the Marsileaceae.*

1. *Regnellidium diphyllum* Lind. Sporocarp wall showing epidermis (*epl*) layers of tabular cells (*tb*), elongated mucilaginous cells (*mc*), and parenchyma below them (*p*). × 45.

2. *Marsilea poonensis* Kolhat. showing different layers of sporocarp wall. × 45.

3. *Pilularia americana* A.Br. Sporocarp wall showing different layers. × 45. Note the two sclerenchymatous layers (*scl*) below epidermis (*ep*).

4. *Regnellidium diphyllum* Lind A microsporangium with microspores. × 15.

5. *Marsilea poonensis* Kolhat. A sporangium showing mega- and microspores. × 22.

6. *Pilularia globulifera* Linn. Sporangium showing microspores. × 22.

7. *Pilularia globulifera* Linn. One-fourth sectant of a sporocarp showing mega- and microsporangia. × 12.

8. *Regnellidium diphyllum* Lind. A developing megaspore and a group of microspores above it. × 40.

9. *Regnellidium diphyllum* Lind. A microspore magnified to show the prismatic and other layers of sporoderm. × 150.

10. *Marsilea poonensis* Kolhat. Two microspores, × 80.

11. *Pilularia americana* A.Br. Microspores. × 80.

12. *Pilularia globulifera* Linn. A megaspore magnified to show the wing formed by the prismatic layer of the sporoderm. × 75.

13. *Regnellidium diphyllum* Lind. A fully developed megaspore showing five appendages at the top. × 40.

14. The same in V.S. × 60. Note the prismatic layer (*pr*), warts on epispore (*w*).

15. *Marsilea poonensis* Kolhat. A megaspore showing the central cavity and plug. × 22.

16. *Pilularia americana* A.Br. A megaspore. × 22.

Plate 2

Figs. 17-27 — *Sporocarp in the living and fossil Marsileaceae.*

17. *Regnellidium diphyllum* Lind. A dehisced sporocarp showing mass of mucilage in which spores are germinating. Note the large megaspores (*mg*), and numerous microspores (*mi*) lying in the mucilage thrown out by the sporocarp (*sp*). × 1·5.

18, 19. Sporocarp of *Regnellidium diphyllum* Lind. and *Marsilea poonensis* Kolhat. showing bilaterally arranged sori. × 10.

20. *Pilularia americana* A.Br. T.S. of sporocarp showing four chambers, each containing several megaspores and some microspores. × 10.

21. *Rodeites dakshini* Sahni, a fossil species of *Regnellidium* from the Deccan Intertrappean Series of Mohgaon Kalan (Dist. Chhindwara; Age, Eocene). V.S. of sporocarp showing bilaterally arranged sori, thin wall (*w*) and prominent raphe (*r*). × 5.

22. Ibid. The same magnified to show the megaspores (*mg*). lying in the midst of numerous microspores (*mi*). × 10.

23, 24. *Regnellidium diphyllum* Lind. T.S. of sporocarp showing bilateral distribution of sori containing mega- and microsporangia. Compare Figs. 21 and 22 with Figs. 21 and 24, Fig. 22 with Fig. 23. × 10.

25, 26. *Rodeites dakshini* Sahni. Median L.S. of sporocarp showing mega and microsporangia and spores. × 5. Note the elliptical elongated shape of the sporocarp in Fig. 26 as contrasted with the round shape of sporocarp in *Regnellidium diphyllum* Lind. shown in Pl. 2, Figs. 18 and 24.

27. *Rodeites dakshini* Sahni. Sporocarp wall magnified to show epidermis (*ep*), parenchymatous cells (*p*) below it, dark cells (*dp*), probably mucilaginous, megaspores (*mg*), and microspores (*mi*) × 20. Note that elongated tabular cells are not obvious.

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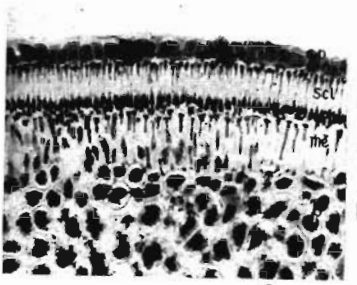

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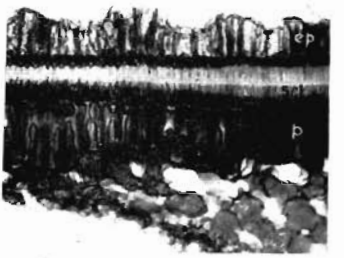

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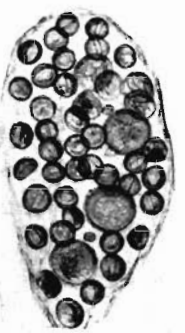

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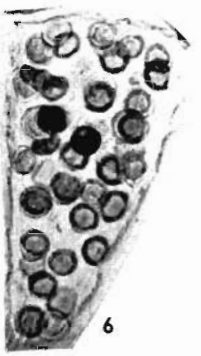

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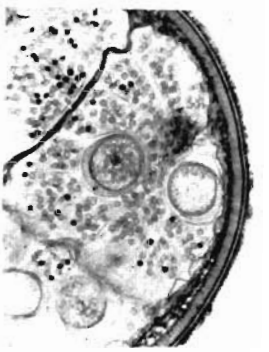

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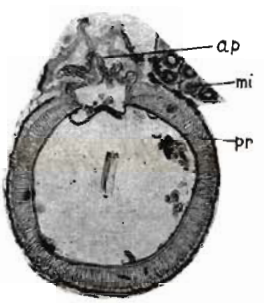

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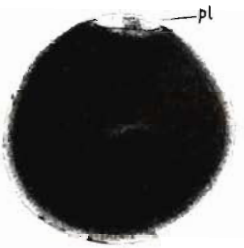

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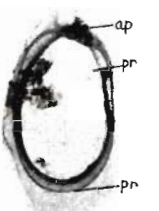

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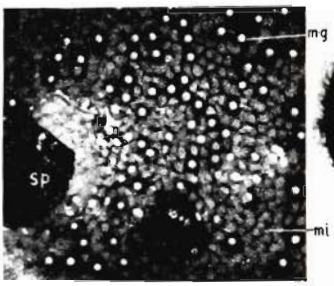

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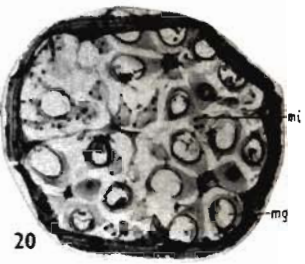

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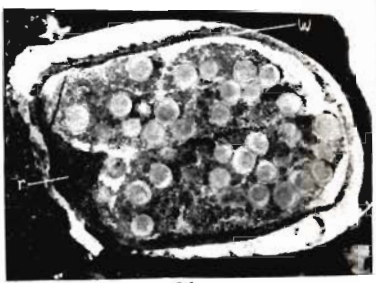

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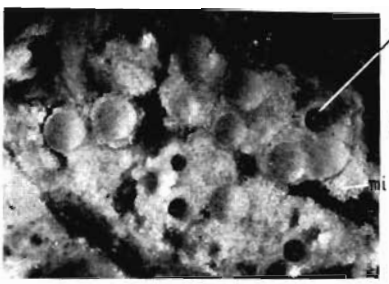

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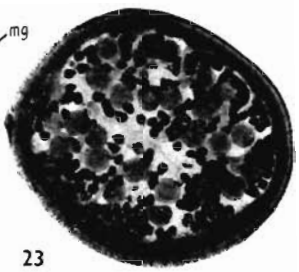

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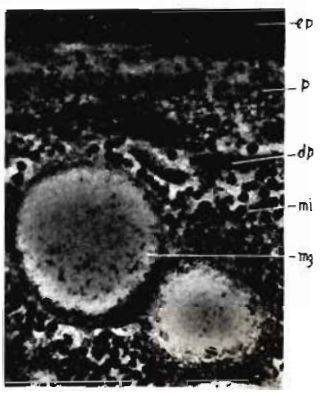

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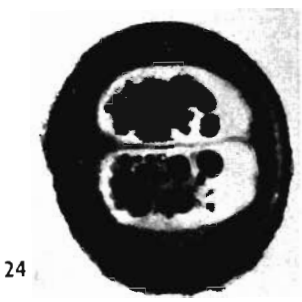

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