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MARSILEALES AND SALVINIALES — "LIVING FOSSILS"?

A. D. J. MEEUSE

(*Hugo de Vries Laboratory, University of Amsterdam*)

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According to current opinion (see, e.g., CHRISTENSEN 1938, REED 1954, ZIMMERMANN 1959, PICHI-SERMOLLI 1959) there is no close relationship between the Marsileales and the Salvineales, so that they should not be united into one class as "Hydropteridales". Their taxonomic position with regard to the *Filices Leptosporangiatae*, to which class they have up to now usually been referred, has always been unsatisfactory. Not only has a close relationship with any group of real ferns never been demonstrated, but their heterospory—to my mind an extremely fundamental character—and the absence of a true annulus distinguish them sharply from the Leptosporangiate ferns.

The resemblance between certain fossil "seeds", later identified as fructifications of the *Caytoniales* (THOMAS 1925, 1927), and the sporocarps of *Marsilea* has in the past lead to the interpretation of these Caytonialian fructifications and the associated *Sagenopteris* leaves as remains of *Marsileaceae*. When Thomas recognised these remains as those of advanced Pteridosperms, this interpretation was abandoned. However, ZIMMERMANN (1930) again suggested that *Marsileales* might be descendants of Caytonialian stock in the same way as *Isoëtes* is a dwarfed "survivor" of the *Lepidodendrales*. Thomas and HARRIS (1951) critisized this idea and mentioned several differences between the two groups under discussion. Indeed it is not very likely that *Marsilea*, which is undoubtedly more primitive than the *Caytoniales* in several respects, could have descended from the latter. Among other things, the *Caytoniales* produced unisexual strobili and seed-like fructifications, whereas *Marsilea* has bisexual sporocarps which are shed before fertilisation takes place and do not produce "seeds", the embryo developing at once into a young plant.

On the other hand I agree with Zimmermann that the differences mentioned by Thomas and by Harris are not so important as to preclude any relationship. However, the interpretation of a possible relationship must be based on an entirely different assumption, *viz.*, that instead of *Marsilea* being a form descended from the Caytonialian ancestors, the *Caytoniales* descended from a group of more primitive plants of which the *Marsileaceae* are the survivors. I am personally convinced of the fact that the basic ancestral stock of the *Caytoniales*, the *Cycadophyta* and ultimately of the Angiosperms is to be sought among the *Glossopteridales*. Consequently, the above-mentioned suggested derivation of the *Caytoniales* from Marsileaceous ancestors

would imply that the *Marsileales* represent surviving members of the large Pteridospermous class of the *Glossopteridales*. Indeed, the *Marsileaceae* show several agreements with seed ferns of this type. Bisexual reproductive organs were described from *Glossopteris* (s.l.) by PLUMSTEAD (1956) and, barring the *Bennettitales* and the Angiosperms, no other group of the *Pteropsida* shows this singular character, except the *Marsileales*. The general habit of the *Marsileales*, *i.e.*, a rhizomatous stem producing fronds of which the fertile ones bear in the basal region one to several *stalked* sporangium-bearing organs, is known from several *Glossopteridales* (Plumstead, see also HARRIS 1958). The frond segments of *Marsilea* resemble those of the common form-genus *Sagenopteris* and possess a type of venation which is "glossopteroid". Recently, cells resembling sieve-tube members have been found in *Marsilea* (WHITE 1961), an advanced condition unknown in ferns. The structure of the megasporangium resembles that of gymnospermous types, especially those of the *Cycadales* and the female gametophyte is as much reduced as one would expect in a seed fern. The multiciliate spermatozoids are of a type suggesting a relation with those of the *Cycadales* but they are obviously more primitive than the latter, because they uncoil before fertilisation whereas the spermatozoids of the Cycads have a spiral band of cilia which is fused with the protoplasmic "body". Neither of these characters alone is sufficiently convincing, but the complex of similarities is thought to be fairly significant. I am, therefore, of the opinion that at least one may accept the above-mentioned suggestion as an alternative hypothesis concerning the relationships of the *Marsileales*—the *Marsileaceae* do not show any clear affinities to the true ferns whereas there are some, though admittedly slender indications of a relationship with Glossopterid seed ferns and higher Gymnosperms. As far as I can ascertain there are no arguments strongly pleading against this assumption and, therefore, I am inclined to regard the *Marsileaceae* as surviving members of the *Glossopteridales*.

Similarly, the *Salviniales* can be interpreted as descendants of the *Lyginopteridales* (*Lagenostomales*). *Salvinia* produces rhachis-borne "sporocarps" and is markedly heterosporous. Its vegetative parts are built like those of certain pinnate types of Pteridospermous fronds; the similarity between the "leaflets" (i.e., the pinnae!) of *Salvinia* and the pinnae of *Neuropteris* is rather striking. The structure of the megaspore of the Salviniaceae is so strongly reminiscent of that of the *Lagenostomales* (see Fig. 1), that this is, to my mind, not likely to be a mere coincidence. The "perisporium", then, would be the homologue of a pteridospermous cupule, which has become reduced to a unicellular layer as a result of the adaptation to an aquatic habitat. Significantly, the perisporium develops as an outgrowth of the megasporangiophore and gradually envelops the megaspore. It is still provided with an apical pore in *Azolla*. Current opinion among pteridologists is that the *Salviniales* must be divided into two families, the *Salviniaceae* and the *Azollaceae*. Indeed, the sporangia are borne on the frond in the *Azollaceae*, but this is a condition known to have

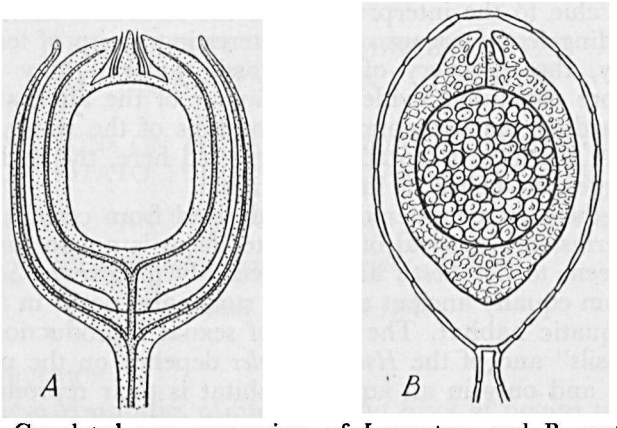

Fig. 1. A, Cupulated megasporangium of *Lagenostoma* and B. mature megasporangium of *Salvinia*, both in optical longitudinal section.

occurred in several types of seed ferns such as *Pecopteris*. Rather recently, REMY (1953) described a fossil type of reproductive organ (*Saarotheca sphenopteroides*, see Fig. 2) which had not previously been encountered. This organ was attached to a sphenopteroid frond and Remy suggested as one of several tentative interpretations that this fossil might be related to the water ferns. I think that this discovery provides some additional evidence of the relationship between the *Salviniales* and the *Lyginopteridales*, for *Saarotheca* might be interpreted as an ancestral form of the male "sporocarp" of the *Salviniales*.

The eventual transfer of the *Marsileaceae* to the *Glossopteridales* and of the *Salviniaceae* and *Azollaceae* to the *Lyginopteridales* would allow us to consider the features of the living plants to be (necessarily rough) approximations of the respective conditions in the related classes of seed ferns thought to be long extinct. It is, for instance, not at all improbable that at some later date, when fossilized Glossopterid fertile organs with retained anatomical structure become available for study, the morphology of the sporocarps of the Marsileaceae might

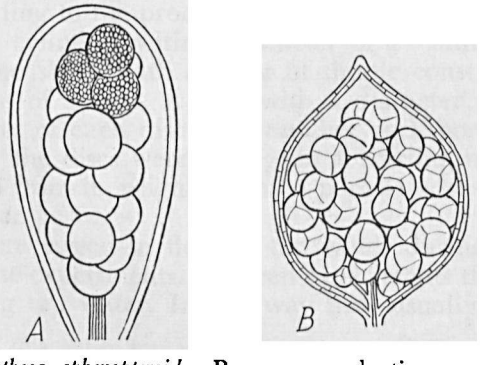

Fig. 2. A, *Saarotheca sphenopteroides* Remy, reproductive organ, and B. male sporocarp of *Azolla filiculoides*.

provide a clue to the interpretation of the structural features of the corresponding fertile organs of this interesting group of fossil plants. Conversely, the discovery of more fossil material may eventually supply more conclusive evidence in favour of the alternative hypothesis regarding the taxonomic relationships of the water ferns and that is why the idea is tentatively suggested here, the main purpose of the suggestion being to invite criticism.

Even if they are considered to be derived from certain groups of Pteridosperms, the survival of the water ferns is not so surprising as it might seem to be. *Isoëtes* and the recently discovered *Stylites*, descended from equally ancient ancestral stock, also occur in an aquatic or semi-aquatic habitat. The mode of sexual reproduction of these "living fossils" and of the *Hydropteridales* depends on the presence of free water and only in an aquatic habitat is their reproduction not at a great disadvantage in respect of the very efficient method of sexual reproduction of the Angiosperms, so that they can still successfully compete, undoubtedly assisted by their vegetative reproduction, whereas the terrestrial seed ferns already long ago were ousted out by the competitive pressure of the more efficiently reproducing seed-forming plants (*Cycadophyta* and *Angiospermae*).

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