

FOSSIL EVIDENCE ON THE CONDENSATION THEORY OF THE ORIGIN OF MARCHANTIACEOUS THALLUS

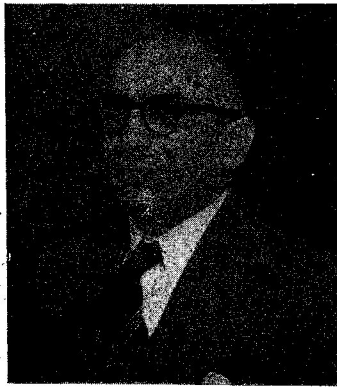
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ABSTRACT.—Pertinent fossil data of the Marchantiales is reviewed and its bearing on the Condensation Theory of the Origin of Marchantiaceous Thallus postulated earlier by the writer is discussed. It is pointed out that the pattern of thallus structure in the earliest known of the Marchantiales *Marchantiolites porosus* Lundblad and *Ricciopsis scanica* Lundblad conforms to the primitive type envisaged on the basis of this theory.

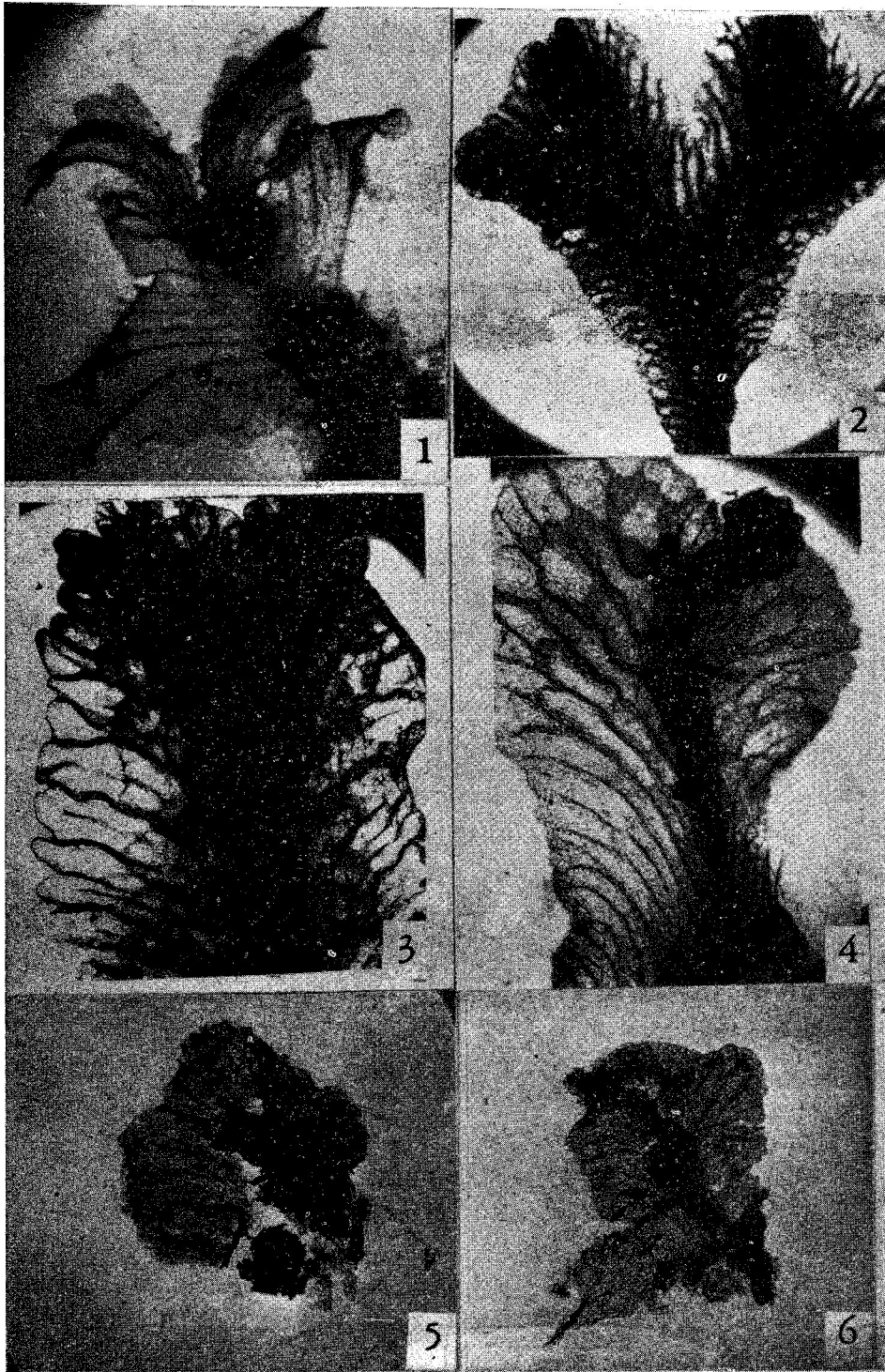
INTRODUCTION

IN an earlier communication the writer (Mehra 1957a, b) postulated the Condensation Theory of the Origin of Marchantiaceous Thallus based upon a comparative study of the thalli in this group of plants, which was supplemented by evidences from other sources. The chambered thalli were broadly classified into three groups, (1) the *Stephensiella* type, (2) the *Plagiochasma* type, and (3) the *Marchantia* type. Characteristics of each type of thalli were described. The *Stephensiella* type was shown to be the most primitive type from which thalli of other types with complex construction were derived secondarily and the probable methods of their evolution were discussed. The *Stephensiella* type is the simplest in configuration and consists of a rather narrow midrib in the centre, with flattened wings on either side bearing a single layer of chambers without any assimilating filaments. The architectural construction of these thalli was brought out in the transparencies prepared by a special technique and it was shown that the wings possessed a single layered parenchymatous basal layer which bore systemati-



cally one cell thick parenchymatous lamellae which projected forward and outward from the mid-rib extending upto the margin (Pl. 5, figs. 2-4). The roofing of the chambers was considered to be by the inward growth of the margins of the lamellae—a process adequately illustrated during the ontogenetic development of the thalli from sporelings. It was stated that the ancestral type of thallus in the Marchantiales was rather narrow with a single row of linear chambers on either side of the mid-rib but during the course of flattening of the thalli secondary lamellae transverse to the original ones transformed the thalli into areolate structures, and this was evidenced in forms like *Asterella blumeana* Nees and *A. reticulata* Kash. Summing up, the primitive thallus structure according to this theory was merely two layered in the region of wings, an upper and a lower layer supported by primary lamellae radiating outward from the mid-rib which in many cases show on the under surface of the thallus as feeble 'ribs'. The chambers thus organised are empty without assimilating filaments.

As to how such a primitive marchantiaceous thallus originated was conceived on a comparison of this with *Petalophyllum indicum* Kash.—a member of the Anacrogynous Jungermanniales. In this plant conclusive evidence was brought out indicating its origin from foliose ancestors by a process of condensation. The lamellae which characterise the genus were shown to be the posterior upturned portions of the succubously arranged leaves which had undergone congenital concrescence at the points of contact (Pl. 5, fig. 1). The lamellae



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of *Petalophyllum* are so similar to the primary lamellae organising chambers in *Stephensiella brevipedunculata* Kash. (Pl. 5, fig. 3) or *Asterella blumeana* Nees (Pl. 5, fig. 4) or *Riccia crystallina* L. (Pl. 5, fig. 2) that it gives the impression that in its origin the marchantia-ceous thallus had passed through a 'Petalophyllum like' stage. The original progenitors of the Marchantiales were thus conceived to be leafy forms belonging to the Jungermanniales.

On the basis of comparative data from the life-history of plants representing this group, it was surmised that amongst the living forms the genus *Asterella*, particularly members like *A. blumeana* and *A. reticulata* approach the ancestral type most closely not only in possessing simple construction of the thallus but also in relatively simple type of pores, filamentous type of embryo, and the presence of a perianth which reminds one of the almost persistent condition met with in the Jungermanniales.

While evidences from other sources like chromosome numbers, embryogeny and general morphology, etc., were brought forward to bear upon this theory, fossil data was not adequately touched. It is the purpose of this paper to elaborate on this aspect in some measure of detail.

FOSSIL DATA

Liverworts are a poor material for fossilisation on account of the delicate nature of their tissues and hence they are not abundantly represented, particularly in the early geological horizons.

The earliest positive record of the occurrence of the Marchantiales goes back to the Rhaetic-Liassic period of Scania in Sweden

from where in the upper coal beds at Skromberga a Swedish palaeobotanist Lundblad (1954) recently described two genera of undoubted marchantialean affinity. One of these was designated *Marchantiolites* with a single species *M. porosus* Lundblad and the other *Ricciopsis* with two species *R. florinii* Lundblad and *R. scanica* Lundblad. Earlier to this period there is no positive proof of the occurrence of forms which could with confidence be assigned to the Marchantiales.

Both *Marchantiolites porosus* and *Ricciopsis scanica* have been discovered in a fairly good state of preservation and using maceration and transfer techniques it has been possible to get an insight into their internal structure which seems to be full of interest.

In the case of *Marchantiolites* only fragments of thallus were preserved and consequently details of its habit and general form are unknown. Photographs of the type specimens representing the distalmost portion of two segments, are shown in Pl. 5, figs. 5, 6 through the kind permission of its author. Lundblad states that the lamina was formed of two layers of cells of which the upper layer possessed definite air pores which were circular in outline and were surrounded by a concentric ring of 5-7 cells whose inner and radial walls were strongly cutinised. The most interesting feature is the presence of what Lundblad called 'ribs' which seem to extend from the mid-rib to the margin of the thallus and are 0.1-0.2 mm. *apart. There is no indication of any assimilating filaments although Lundblad believes that they are not expected to be preserved in fossil materials of the compression type. Drawing a comparison of the pore structure of *Marchantiolites* with the living representa-

EXPLANATION OF PLATE 5

FIGS. 1-4—Transparencies of the thalli.

1—*Petalophyllum indicum* Kash.

2—*Riccia crystallina* L.

3—*Stephensiella brevipedunculata* Kash.

4—*Asterella blumeana* Nees.

5, 6—*Marchantiolites porosus* Lundblad.

*Lundblad states on p. 395 of her paper that the ribs are 1-2 mm. apart. This appears to be a misprint as the actual measurements in her photograph show them to be in the neighbourhood of 0.2 mm. Moreover, the entire length of the preserved fragment as stated by her is only 2.6 mm.

tives of Marchantiales she remarks, "The nearest equivalents to the Marchantiolites type are found in the Grimaldiaceae (=Rebouliaeeae)—where both *Plagiochasma* and *Grimaldia* have similar pores. In *Plagiochasma* these are surrounded by only one ring consisting of 4-6 cells, in *Grimaldia* there are 2-3 rings of 6-7 cells. In the other genera of Grimaldiaceae—*Reboulia* and *Fimbriaria* the pore is surrounded by a large number of cells (6-8), and they have respectively 4-5 and 2-5 rings". It may, however, be stated that in some species of *Fimbriaria* (= *Asterella*) like *A. reticulata* and *A. blumeana* there are only 1 or 2 rings of cells with 6-7 cells in each ring.

The structural organisation of the thallus of *Marchantiolites* seems to be remarkably similar to that represented by members of the *Stephensoniella* type. As stated previously, in this group of forms the thallus is only two layers of cells thick and pores are present on the upper layer. A comparison of figs. 5, 6 of *Marchantiolites* with figs. 3, 4 of *Stephensoniella brevipedunculata* and *Asterella blumeana* (posterior region) respectively shows a striking similarity of the so-called 'ribs' of the former with the lamellae of the living forms in the matter of their disposition and arrangement so that one is tempted to believe that they are morphologically similar entities and represent really the partitions in *Marchantiolites* that separate the chambers. On the basis of this interpretation the chambers in the latter are long linear, without cross partitions, and just what are expected to be on the basis of the Condensation Theory and comparable with those present in the posterior region of *Asterella blumeana* or *Stephensoniella brevipedunculata*. Also the absence of assimilating filaments in *Marchantiolites* may be a reality as is true of the living representatives of *Stephensoniella* type rather than due to non-preservation. Lundblad's comparison of the pores of *Marchantiolites* with those of Grimaldiaceae (Rebouliaeeae) is particularly interesting in view of the conclusion of the present author (Mehra 1957b) drawn independently on the basis of several criteria that this family, particularly the genus *Asterella*, approaches the ancestral type more closely than any other in the Marchantiales.

A slight reference to the two species of *Ricciopsis*, also from the Rhaetic-Liassic beds of Scania, will not be out of place. The genus has been so designated because of its apparent resemblance with *Riccia*. In *Ricciopsis florinii* the thallus is of a rosette type with crowded dichotomously branched lobes such as characterise some species of *Riccia*. A median prominent groove is present on these. The rhizoids on the lower surface are differentiated into smooth-walled and what appears to be tuberculate ones. Scales are not seen, probably they were not preserved. The specimens do not permit of any elucidation of the internal organisation. But in the other species *Ricciopsis scanica* it has been possible to obtain a knowledge of the internal structure from some translucent areas of the fragments referred to this species. The thallus here is also of rosette type with four principal dichotomies which further dichotomise twice. No well defined rhizoids or scales are observed. According to Lundblad, the thallus in this species, like that of *Marchantiolites porosus*, is only two layers of cells thick and possesses 'arcuate ribs running obliquely to the margin' which are clearly seen in the photographs presented by her. It is not without interest to remark that in some living members of *Riccia* like *R. crystallina* a very similar internal organisation is observed (Pl. 5, fig. 2). The thallus is two layers of cells thick and is partitioned internally into air-chambers by outwardly directed primary lamellae comparable to the 'ribs' although one or two slanting cross partitions are also present between them.

It thus appears that the most ancient members of the Marchantiales so far known conform to the pattern of thallus structure present in the *Stephensoniella* type which is visualised to be the most primitive on the basis of the Condensation Theory.

Coming to the late Mesozoic and Tertiary periods quite a number of forms have been referred to the Marchantiales under the form genus *Marchantites* mostly on the basis of forms and size of the thalli. A review of those reported from North America has been undertaken by Steere (1946) in his interesting paper dealing with the Cenozoic and Mesozoic Bryophytes of North America. Of all these only two, namely,

Marchantites hallei Lundblad and *Marchantites sezannensis* Brongniart are known in some measure of detail to justify fully their inclusion in this group. *M. hallei* was originally discovered by Halle and studied intensively by Lundblad (1955) who proposed this name. The plant occurs in the lower Cretaceous of Patagonia in Southern Hemisphere and is known in a sterile state from a few fragments. A central mid-rib about 1 mm. wide is present and the lamina shows on the under surface arcuate 'lateral ribs'. There are two close rows of scales along the mid-rib reminding one of a similar condition in some living members of this group. The rhizoids occur in clusters associated with the 'lateral ribs' at their bases and are presumably of two types although tubercles on the inner walls of any of these have not been clearly observed. Pores are present on the upper surface but their structure cannot be deciphered.

The other species *Marchantites sezannensis* Brongniart discovered from the Eocene of France was described by De Saporta (1868). The thallus is dichotomously branched and of somewhat greater dimension than the former. Here also the under-surfaces of the mid-rib shows two rows of closely situated scales. Air pores are present. The thallus bears pedunculate receptacle like structure showing apparent resemblance to the male receptacle of *Marchantia*. Certain structures are observed on the surface of the thallus showing some semblance of the gemma cups.

Unfortunately, the internal structure of none of these two species is known, so that comparison with earlier Mesozoic forms or with the living genera of Marchantiales is not possible. But the presence of 'arcuate ribs' on *Marchantites hallei* is significant.

The Condensation Theory envisages that the foliose members of the Jungermanniales were the progenitors of the Marchantiales. Fossil evidence at present available seems to support this view. While there is no positive proof of the occurrence of the Marchantiales in the geologic horizons lower than the Rhaetic-Liassic, the Jungermanniales are known with certainty to have existed in the Palaeozoic.

Of course the negative evidence in fossil botany has to be considered with caution.

Walton (1925, 1928, 1940) discovered undoubted members of the Jungermanniales from the British Upper Carboniferous period in an excellent state of preservation which he described under the form genus *Hepaticites*. Four species were described of which *H. kidstoni* is leafy, *H. lobatus* occupies a status intermediate between the thalloid and leafy forms, while *H. langi* and *H. metzgerites* are both thallose which have been compared by Walton with the living genera *Aneura* and *Metzgeria* respectively. *Hepaticites kidstoni* is worthy of some attention. It is known from the Middle Coal Measures of England preserved in shale. The plant was in an excellent state of preservation and apparently looked very much like a small sized modern representative of foliose hepatics. There is a rather flattened mid-rib which bears on either side a row of large one cell thick leaves in which practically every cell is clearly defined. The leaves overlap slightly at the base. In addition to these there are present two alternating rows of much smaller leaves, also one layer of cell thick, but in the absence of rhizoids it is difficult to interpret whether they were borne on the upper or lower surface of the mid-rib. In the larger leaves several scattered cells with dark contents are observed which may be compared to the oil cells met with in the living forms. No reproductive bodies are known. Walton considers the plant to belong probably to the Anacrogynous Jungermanniales and compares it with the living genera *Fossombronia* and *Treubia*. The main interest of the fossil lies in respect of the two rows of smaller leaves which are very systematically arranged. Walton suggests a comparison with the small scales that are borne on the upper surface of the mid-rib in relation to the sex organs in *Fossombronia*. In the first place it may be mentioned that these scales or bracts in *Fossombronia* are not borne with such precise regularity as are the small leaves in *H. kidstoni*—more often they are irregularly spaced and not in very regular rows. Secondly, if these were comparable structures, it is indeed sur-

prising to find complete absence of any trace of reproductive organs in specimens which are otherwise so excellently preserved. In *Treubia insignis* each leaf has a relatively larger lobe and a smaller dorsal one which is borne on the upper surface of the mid-rib orientated transversely. In *H. kidstoni* the larger and smaller leaves are separate entities, each having a definite positional arrangement. The comparison of the fossil with either of these forms therefore does not hold. It seems not unlikely that the smaller leaves may as well have been ventral in position although this could have been finally settled only if the position of the rhizoids on the plant were located. Unfortunately they are lacking on the specimens.

Also in the absence of reproductive organs it is not possible to assign *H. kidstoni* with confidence to Anacrogynous Jungermanniales. It could as well have belonged to the Acrogynous forms. In any case in the Carboniferous period both the foliose and thallose Jungermanniales were represented and one would agree with Walton in stating that a comparatively high degree of differentiation had already been achieved in the Palaeozoic members of this group which thus indicates a much longer fossil history. The pertinent fact remains that as far as the present evidence goes the Jungermanniales—both the thallose as well as foliose ones—seem to have preceded the complex thalloid Marchantiales.

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* Not studied in original.