Advances in
BOTANICAL RESEARCH

Edited by

R. D. PRESTON

VOLUME 1

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The Astbury Department of Biophysics
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PREFACE

As in most other scientific disciplines, research in the various aspects of botany has grown vigorously since the war and on the way has achieved spectacular results which have received much publicity. These developments have led, and will progressively lead still further, to a corresponding growth, steadily accelerating, in the number of papers published over a wide spectrum of learned journals until it is even now virtually impossible for any worker to stay abreast of his own field and remain active in research. The classical type of review article is still a valuable help; but the reviewing journals are too few in number to give a satisfactory cover. Consisting as they normally—and properly—do, moreover, of little more than ordered sequences of abstracts of papers published over the past year or so, they can neither examine the subject concerned against the background of less recent knowledge or of matter from cognate fields nor allow authors freedom to express opinions and to speculate on the future. This undoubtedly goes far to explain the appearance over the past few years of volumes, either singly or in series, sometimes but not always confined to one field of botanical science, such as Physiology or Cytology, which deal with the retrieval of information in a different way. In these the authors are allowed freedom not only to collate facts but also to express opinions—to deal not only with the letter but also with the spirit. The present series is designed to be of this kind.

It is the intention, however, that this series should have special features at present unique to it, in our view features which will make all the articles of special merit and some of them of lasting value. The authors of this first volume have been asked to do three things. They have been asked to write about some special topic within their chosen field, of especial current interest to them and upon which they have been actively engaged; they have been asked to set their own work against the background of cognate researches in other laboratories both past and present; and they have been asked to express opinions freely and to speculate as widely as they dare upon future trends and future developments. This will remain the policy of these volumes. The articles will, moreover, range over the whole field of botanical enquiry dealing both with the more spectacular modern chemical and physical approaches and the less well publicized developments in more classical fields upon which all else depends. In this again the first volume sets the standard.

In these publicity-minded days it is by no means an easy matter for an editor to persuade scientists, already deeply immersed in paper, to write yet another article. We are all the more grateful to the authors of this volume that they accepted their tasks cheerfully and presented manuscripts punctually. They are all recognized authorities in their fields and we need say no more about them. Their articles range from the classical fields of anatomy and palaeobotany to the most modern treatments of irreversible thermodynamics and electron spin magnetic resonance. There should therefore be something here for all; though it is my sincere hope that both the clasically- and the modern-minded readers will at least dip into each other's pages so that each may appreciate the other and learn "what it is all about".

The editing of volumes such as these could not possibly be attempted without the assurance of co-operation with many whose names will not appear in these pages. To all of these I offer my sincere thanks, particularly to my colleagues for their support and encouragement and especially to my secretary, Miss Eunice D. Lister, for her untiring attention to detail and for her skill in ensuring that I have not lost a manuscript. I am especially indebted to the publishers who have throughout smoothed my path in every possible way and who have carried out their own part of the task without fuss and with quiet efficiency.

R. D. PRESTON

Leeds, 1962

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The Status of Some Fossil Plants

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I. Introduction

The aim of this article is to present to the general reader a survey of some of the more interesting contributions that have been made in the field of palaeobotany during the past decade or two. It will be seen that relatively few topics have been selected for treatment, but in this way it has been possible to present detailed, though not necessarily exhaustive, discussions in each case. It is felt that this may be a more useful method of approach since to have attempted a complete coverage of all the numerous and specialist minutiae of palaeobotanical research published over a short period of time would have meant devoting a disproportionate amount of space to listing discoveries and statements, with little, or no, opportunity for extended discussion of any particular example. Consequently some groups of fossil plants and certain aspects of their study receive scant, or no, attention, but this in no way signifies

belittlement of the many authors whose names and valuable contributions have inevitably and regrettably to be excluded.

Though the treatment of the several topics varies somewhat according to the subject matter, an endeavour has been made to indicate current attitudes and the extent to which they may be accepted. Historical considerations cannot pass unnoticed in most cases, and reference has been made to previous knowledge where it is of relevance to new discoveries or modified interpretations. In addition, some emphasis has been placed on the difficulties which palaeobotanists continually encounter in their studies of fossil plants and which the non-specialist does not always readily appreciate.

II. Fossil Liverworts

Apart from spores, liverwort remains are poorly represented in the fossil record on account of the small size and delicate nature of their bodies. Unless fossilization has occurred under optimum conditions, preservation is usually so poor that, at best, no more than a non-committal name may be assigned to them. The chances of a fossilized thallus being the remains of a marine alga or a terrestrial hepatic are equal, especially when it is wholly sterile. In the absence of knowledge about the structure of the cells of the plant body, and rhizoids should they be present, the affinities of any thalloid fossil must always remain doubtful.

Unfortunately much of the fossil material of this type has acquired names recalling those of living genera, which has resulted in implied relationships even though such may not have been intended by the original investigators. To avoid further confusion and misconjecture, it has now become customary to follow the proposal made some years ago by Walton (1925, 1928) to name all those showing characters exclusive to the liverworts as *Hepaticites* and those which agree equally with algae as *Thallites*, unless there be some special character indicating relationship with some more narrowly limited taxon of the group (Harris, 1942a, 1961a; Lundblad, 1954). Examples of this latter type that may be noted are *Marchantites* Brongn. *emend.* Walton (Walton, 1925; Lundblad, 1955), *Metzgeriites* Steere and possibly *Jungermannites* Goepp. *emend.* Steere (Steere, 1946), and the lately described *Ricciopsis* and *Marchantiolites* (Lundblad, 1954). There is also, of course, the very fully known *Naiadita lanceolata* Buckman *emend.* Harris (Harris, 1938).

Yet the number of Pre-Tertiary forms that may be regarded as having belonged to the Hepaticae is not particularly large and amounts to probably no more than twenty, of which about fifteen are species of *Hepaticites*. There are, in addition, probably a dozen good species of

Thallites, but their affinities are unknown at present and they could equally represent algal remains.

Nothing new has been added to our knowledge of the small assemblage of Upper Carboniferous liverworts (Walton, 1925, 1928), except that Walton now finds that his original *Hepaticites willsii* should be more correctly called *Thallites* since it lacked rhizoids (1949a). These Carboniferous hepatics were thalloid plants with a habit recalling that of certain modern members of the anacrogynous Jungermanniales, though one of them, *Hepaticites kidstoni* Walton, was definitely leafy. This latter type has been compared with the acrogynous Jungermanniales by some authors, but there seems little reason for doubting Walton's opinion that it too was another anacrogynous form very much like *Treubia*.

There is a greater number of satisfactory records of liverworts from the Mesozoic but, with the exception of *Naiadita* which has been tentatively referred to the Sphaerocarpales (Harris, 1938), sterile remains alone are known. These nearly all take the form of dichotomizing thalli and are mostly referable to the anacrogynous Jungermanniales, but recent investigations by Harris (1961a) and Lundblad (1954, 1955) indicate that plants with undoubted marchantialean characters existed during the Period.

Two species of *Hepaticites* from the Jurassic rocks of Yorkshire have been assigned to the Marchantiales, though the attribution of one of them, *H. wonnacotti* (Harris, 1942a, 1961a), is rather uncertain since neither tuberculate rhizoids nor ventral scales have been found. The other species, *H. haiburnensis* (Harris, 1961a), is only known from one specimen, but it is clear that the dichotomously branched thallus possessed numerous rhizoids arising from the underside of the midrib, as well as two rows of conspicuous ventral scales (Fig. 1, B). Harris has not been able to see details of the walls of the rhizoids, or to recognize pores in the centres of the oblique polygons which he considers to represent the outlines of air chambers within the lamina. For such reasons he justifiably refrains from attempting a more precise classification of the specimen.

On the other hand, some material from the Swedish Liassic, comprising rather complete sterile thalli (*Ricciopsis florinii* and *R. scanica*), fragmentary segments with cellular structure and air-pores (*Marchantiolites porosus*), and associated *Riccia*-like spores (*Ricciisporites tuberculatus*), quite clearly represents the remains of plants that belonged to the Marchantiales (Lundblad, 1954). *Ricciopsis florinii* consisted of small, dichotomously branched thalli, which occurred "singly or in groups, of more or less circular shape, forming rosettes of crowded segments" about 2·5 cm in diameter. The segments were channelled and

bore ventral rhizoids which were "tuberculate or smooth-walled, unicellular or multicellular, with oblique transverse walls". Ventral scales have not been observed, but the resemblance between this species and modern members of the Ricciaceae (Marchantiales) is remarkable (Fig. 1, A). The same is also true for *R. scanica* which, though no ventral scales or rhizoids have been seen, was composed of dichotomous thalli

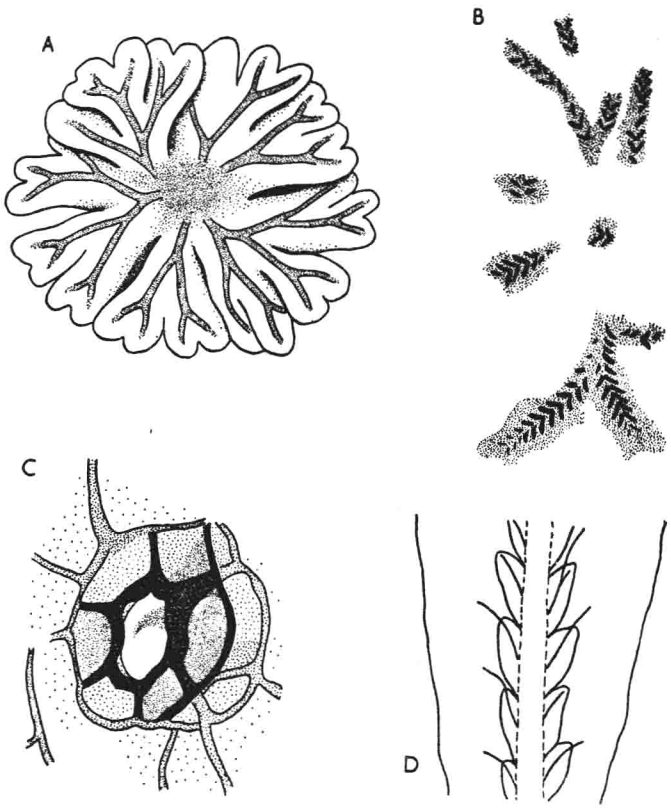

FIG. 1. Mesozoic Liverworts. A. *Ricciopsis florinii* Lundblad; reconstruction of a thallus (redrawn from Lundblad, 1954). B. *Hepaticites haiburnensis* Harris; fragments of a thallus with ventral scales (redrawn from Harris, 1961a). C. *Marchantiolites porosus* Lundblad; air-pore (redrawn from Lundblad, 1954). D. *Marchantites hallei* Lundblad; reconstruction of a segment of thallus, showing ventral scales (redrawn from Lundblad, 1955).

with rather more slender segments. Though the two forms appear to be quite distinct, Lundblad points out the possibility of their representing two different growth forms of a single species resulting from different environmental conditions or even a difference in sexuality. Amongst modern liverworts the aquatic form of *Riccia fluitans* has narrower segments than, and lacks the rhizoids and ventral scales of, the terrestrial form, and there may be considerable differences in size and shape

between the male and female thalli of the dioecious *Riccia cupulifera* Duthie and Garside.

Only fragments of the thallus of *Marchantiolites* are known, and since the fossil material is of the compression type no more than the limiting layer of cells is preserved. Thus the upper and lower epidermis alone have been seen and nothing is known of the internal structure. One of these layers is pierced by a number of elevated air-pores, each of which is surrounded by a concentric ring of cells (Fig. 1, C). Ventral scales are not known, nor is it clear whether some of the rhizoids were tuberculate or not. Nevertheless the remains are undoubtedly marchantialean. The comparatively simple air-pores of the fossil do not resemble the compound barrel-shaped openings of the air chambers of the living Marchantiaceae, nor are they so simplified as in the Ricciaceae. The nearest equivalent is to be found in such living genera as *Plagiochasma*, *Grimaldia* and *Oxymitra*, but to attempt any very close comparison between *Marchantiolites* and living forms is impossible until more complete specimens become available.

Another species with air-pores is now known to have existed during the Mesozoic, but it differs considerably from the Liassic *Marchantiolites* just described. This is *Marchantites hallei* (Lundblad, 1955), based on three specimens from the Lower Cretaceous of Patagonia which were collected and figured some years previously as "*Marchantites* ? sp." by Halle (1913). The specimens represent segments of dichotomous, sterile thalli, but only one of them is actually branched. There is a median thickened zone from which arcuate lateral ribs diverge towards the margins. There are two distinct rows of ventral scales along the sides of the midrib (Fig. 1, D), and dense clusters of unicellular rhizoids attached to the proximal part of the lateral ribs. The rhizoids were apparently of two kinds, but owing to their unsatisfactory state of preservation Lundblad has not been able to make out details. The structure of the air-pores is not preserved, yet it seems that they were barrel- or cone-shaped.

The arcuate lateral ribs, the two rows of ventral scales and the large size of the air-pores are features in favour of the classification of *Marchantites hallei* within the sub-order Marchantiineae, if not in the Marchantiaceae *sens. strict.*, rather than near the ricciaceous types which have small pores and a single row of ventral scales.

While these discoveries are extremely interesting as recording the undoubted existence of the Marchantiales as far back as the older Mesozoic, they afford no data towards a better understanding of the evolution of the liverworts which must still be based purely upon comparative morphology of the living forms. They do, however, indicate that the group was already reaching a world-wide distribution towards the end

of the Mesozoic Period, and possibly even earlier if the less convincing record from the Lower Jurassic of Australia (Medwell, 1954) is also taken into consideration.

III. Early Vascular Plants

Vascular plant remains have long been known in rocks of Devonian age, but whence the varied and highly organized vegetation which they represent came and what its antecedents were have been unanswered questions around which much interest, and often highly speculative discussion, has centred. In some cases, preservation of specimens is so good that it has been possible to obtain reasonably accurate reconstructions of the original plants and some indications of their relationships, but in others the specimens are so fragmentary or obscure as to offer no more evidence than that there had existed other types of plant.

The dramatic discoveries by Kidston and Lang (1917–21) of petrified remains in the Middle Old Red Sandstone of Scotland almost 50 years ago, and their recognition of the Psilophytales, still ranks as the most outstanding contribution to our knowledge of early vascular plants. The deposit at Rhynie has given a remarkable glimpse of one type of vegetation of the early Devonian period. The four higher plants have the double interest of being not only the most ancient fully-known vascular cryptogams, but also the most simply organized members of the group. These discoveries had a profound influence on morphological thought and theories of evolution of the higher plants, and the Psilophytales rapidly achieved importance as the basis of ideas which became crystallized in the Telome Theory of Zimmerman. This theory, which has received wide acceptance, derives all vascular plant groups, by a few elementary processes, from ancestors of *Rhynia*-type with simple, dichotomous, vascularized, but rootless, axes with terminal sporangia.

There is much supporting evidence for many aspects of the telomic concept, but it inevitably favours a monophyletic origin of the vascular plants. It apparently makes no provision for the unquestionable fact that the lycopsid line, represented by the Silurian *Baragwanathia longifolia* (Lang and Cookson, 1935), was already well defined and strongly established prior to the appearance of the rhyniaceous types which are conceived as ancestral to all other forms. There seems little doubt, too, that the sphenopsid and pteropsid lines were already marked out by mid-Devonian time and that the average level of differentiation of the plant association was too advanced to have originated from the contemporaneous representatives of the Psilophytales. However, as will be shown in a later paragraph, the evidence may not be quite so con-

flicting. Yet Leclercq (1954) inclines to the view "that the Psilophytales represent a division possibly equal in importance to that of the Lycopsides, Sphenopsides, Pteropsides, running parallel with them, instead of being their converging point", and goes on to add that "if this conception were confirmed, the Psilophytales might be considered as a resulting point instead of a starting point". The idea of polyphylesis may by no means be ruled out, and Andrews (1959, 1961; Andrews and Alt, 1956), amongst others, has recently pleaded very strongly in favour of its acceptance.

The appearance of such a relatively complex form as *Baragwanathia* during the late Silurian indicates that a fairly long period of evolution of the vascular plants had occurred prior to that moment, and that a search must be made for their real origin at least in the early part of the Period, if not before. Indeed, evidence from plant microfossils from rocks of an even earlier age suggests that vascular plants may have already been in existence in pre-Silurian time. As will be learnt from the next two sections, however, much of this evidence still awaits confirmation and is insufficiently convincing as the basis for extended evolutionary arguments.

It has sometimes been suggested that the simplicity of the Rhynie plants had resulted from reduction in response to some environmental stimulus, rather than being a manifestation of genuine primitiveness. Yet, if this be the case, what more simple form of construction for a primitive vascular plant may be expected? This writer, for one, believes that the plants are primitive both in their vegetative and sporangial construction. Anything more primitive than a simple sac-like terminal sporangium, with a wall several layers thick and no provision for dehiscence, cannot be conceived. And though they are antedated by other more complex vascular plants, is it not satisfactory to consider these plants as being the last surviving members of a family of *Psilopsida* which had existed under favourable conditions and remained unaltered since the moment of its inception until the mid-Devonian?

From this point of view, it is particularly significant that every Devonian flora contains records of genuine psilopsid remains. These are even to be found side by side with *Baragwanathia* in the Australian Silurian. This co-existence of both the psilopsid and lycopsid lines at an early period in time offers, of course, no evidence as to whether one antedated the other or whether they represent quite distinct and separate lines of evolution as polyphyletism demands. Therefore, until such evidence as may settle this point is forthcoming, it would seem that the more conventional outlook, which favours psilopsids of *Rhynia*-type as having provided the ancestral stock for all other groups of vascular plants, will remain without serious challenge.