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FOSSIL BRYOPHYTES

By WILLIAM S. LACEY

School of Plant Biology, University College of North Wales, Bangor

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I. INTRODUCTION

At the turn of the century virtually nothing was known of the early geological history of bryophytes. No less an authority than Robert Kidston, writing on the flora of the Carboniferous period in 1900, stated that only one authentic Palaeozoic bryophyte had been described. This was a moss, *Muscites polytrichaceus* of Renault & Zeiller (1888), preserved as a compression in shales from the Stephanian (Upper Carboniferous) of Commentry in France. No Palaeozoic liverworts were known. Kidston himself, in the paper cited, claimed the honour of finding the first Carboniferous liverwort in rocks of Calciferous Sandstone age in Scotland, but later changed his mind and decided that his fossil was probably an alga.

Just before the First World War Lignier (1914) described a second moss from beds of Stephanian age in France, this time in a petrified condition from near St Etienne; and in the same year Wills (1914) discovered in the Coal Measures of Staffordshire, England a thalloid plant that is probably the first record of a Carboniferous liverwort. Both of these interesting papers seem to have passed almost unnoticed, perhaps because they were over-shadowed by events at the time of their publication; it remained for Walton (1925, 1928*a*) to accord them due notice in his work on Carboniferous Bryophyta. Walton's two papers marked a turning-point in the study of early fossil bryophytes, for they not only described in detail five liverworts and two mosses of Carboniferous age but they also indicated techniques likely to be successful in retrieving the fossilized remains of these delicate plants.

Since Walton's important work there has been a steady and increasing flow of contributions from many countries describing real or supposed bryophytes from many geological formations. A considerable variety of Palaeozoic and early Mesozoic mosses and liverworts is now known from work done in Britain, France, Sweden, South Africa, U.S.A. and U.S.S.R., to mention only countries which have made major contributions and the record for the earliest known bryophyte has been extended back to the lowermost Upper Devonian. There have also been impressive additions to the knowledge of Tertiary and Quaternary bryophytes.

Three particularly valuable papers on fossil bryophytes have appeared in recent years. Lundblad (1954) reviewed the progress in work on fossil liverworts up to that time; shortly afterwards Savicz-Lubitzkaja & Abramov (1959) provided a summary of the whole field of bryophyte palaeobotany; and Jovet-Ast (1967) has written an extensive, detailed and up-to-date account of all known fossil bryophytes. A comparison of the two last-mentioned works is particularly instructive in indicating the very rapid progress that is being made. For example, Savicz-Lubitzkaja and Abramov list a total of 33 pre-Tertiary bryophytes (9 mosses and 7 liverworts in the Palaeozoic; 3 mosses and 14 liverworts in the Mesozoic), while less than 10 years later Jovet-Ast records twice the total number of taxa (17 mosses and 9 liverworts in the Palaeozoic; 8 mosses and 34 liverworts in the Mesozoic).

The main purpose of this article is to review the present state of knowledge of the geological history of bryophytes in the light of recent research. This will be done systematically, primarily from a botanical standpoint, presenting the stratigraphical data within a botanical classification. After this, some phylogenetic speculations based on the available fossil record will be offered. Before proceeding to these tasks however, it is desirable to consider briefly the conditions necessary for the fossilization of bryophytes.

II. THE PRESERVATION OF BRYOPHYTES AS FOSSILS

Liverworts and mosses are, for the most part, small and delicate plants, devoid of true vascular tissues, lacking extensive resistant mechanical tissue and with little or no cuticle covering their exposed surfaces. It is therefore hardly to be expected that such plants would lend themselves to fossilization. Their delicate nature has often been quoted as the explanation for the apparent scarcity of fossil remains. Parihar (1959), for example, states that 'our knowledge of the fossil history of the Bryophyta is very defective, on account of the relatively fragile nature of the plant body'.

Yet, contrary to the popular belief exemplified by this quotation, patient palaeobotanical studies during the last 40 years have shown that fossil bryophytes are, in fact, widespread both geographically and stratigraphically and that their remains are often very well preserved, even in the oldest deposits.

It is clear that the chances of preservation do not always depend necessarily on the presence of resistant structures, but on the occurrence of the appropriate kind of sedimentation in the right situation at the right time. Neuberg (1958) also makes this point when she states that 'the absence or extreme rarity of mosses among the remains of a subtropical Upper Palaeozoic flora of the Euramerican region is apparently connected with conditions unfavorable not so much for the development of mosses as for their burial'. Except for the special case of preservation in Baltic Amber, all the examples of well-preserved fossil bryophytes have one feature in common; effective preservation has depended on the inclusion of the plants in fine sediments, probably accumulated in fresh water under anaerobic conditions. The impervious matrix thus produced ensured that little of the original carbon content of the plant is lost. Since also the organic remains so preserved have been found to withstand quite drastic maceration in the laboratory it is very tempting to believe that the chemical changes which take place during the fossilization process may result in the formation of resistant membranes or, indeed, that in some cases at least a cuticle-like layer was present in the first place. This second suggestion is not without support, for Dr J. M. Pettitt of the British Museum (Natural History), London, has recently shown (personal communication) that acetolysis of certain *Riccia* L. (*Ricciella* (Braun) Boulay) gametophytes releases a very thin and delicate membrane from the surface of the thallus which may represent a cuticle.

It is rather curious that bryophytes have not been recognized in the extensive studies on coal-balls that have been carried out in Britain, Holland, Belgium, the U.S.A. and U.S.S.R., for the solitary record due to Lignier (1914) shows that petrified bryophytes can occur. A possible explanation may be found in the fact that coal-ball floras consist for the most part of the accumulated and sometimes drifted debris of large and small vascular plants, while the bryophytes which have been found in Carboniferous shales may represent mud or soil-dwelling species preserved in the original place of growth.

The absence of bryophytes in coal-balls seems to indicate that the forest trees of the Carboniferous coal-swamps were not clothed with the thick festoons of epiphytic species that characterize both temperate and tropical rain-forests at the present day. Although the trunks of arborescent lycopsids and ferns, such as *Lepidodendron* Stbg. and *Psaronius* Cotta, would seem to have provided suitable lodgement for epiphytes, and, indeed, a small number of epiphytic ferns is known (Mamay, 1952), no epiphytic bryophytes have been described.

The best hope for finding further examples of early fossil bryophytes probably lies in the systematic searching of very fine-grained deposits—clays, soapstones and shales—of known freshwater origin, by the bulk maceration methods first described by Harris (1926).

III. SYSTEMATIC REVIEW OF THE FOSSIL RECORD

Three difficulties confront the writer of a review of this kind. These are (*a*) the lack of agreement among bryologists as to the most suitable scheme of classification for living bryophytes, (*b*) the impossibility of assigning most of the Palaeozoic and Mesozoic forms to a satisfactory place in whatever scheme of classification is adopted, owing to the absence of reproductive structures, and (*c*) limitations of space which permit reference to only a small fraction of the very large number of fossil bryophytes which have been recorded.

In this article these difficulties have been met somewhat arbitrarily by (*a*) using a scheme of classification essentially the same as that used by Jovet-Ast (1967), but recognizing only three Classes—Hepaticopsida, Anthocerotopsida and Bryopsida; (*b*) by referring Palaeozoic, Mesozoic and some Tertiary genera or species to a taxonomic level not lower than Order or, in some cases, Sub-Class; and (*c*) by dealing only with the earliest geological records of the various taxa and with certain subsequent records selected for their particular interest.

(1) Class HEPATICOPSIDA Rothmaler

(*a*) Order *Jungermanniales* Rupp

The earliest stratigraphic record is *Hepaticites devonicus* described by Hueber (1961) from the lowermost Upper Devonian (Frasnian) of New York State, U.S.A. This plant consisted of a thallose part and a 'rhizomatous' part. The former is a ribbon-like structure with an axial region of elongate cells and lateral wings with finely serrate margins, while the latter resembles the axial region of the thallose part but bears rhizoids. No reproductive organs are known. Like the records of hepatics from Carboniferous rocks, this species is referred to Jungermanniales Anacrogynae on the basis of vegetative morphology. Hueber compares his material with the extant genera *Pallavicinia* Gray and *Metzgeria* Raddi.

Walton (1925, 1928*a*) had previously described *Hepaticites willsi* from the Upper Coal Measures of Staffordshire and *H. kidstoni*, *H. lobatus*, *H. langi* and *H. metzgerioides* from the Middle Coal Measures of Shropshire and Nottinghamshire in England. *H. kidstoni*, *H. lobatus* and *H. metzgerioides* were compared respectively with the extant genera *Treubia*, Goeb., *Fossombronia* Raddi, and *Metzgeri* Raddi. *H. langi* and *H. willsi* were compared with *Riccardia* Gray (*Aneura* Dumort.). Subsequently Walton (1949) removed *H. willsi* to his genus *Thallites* on the grounds that the absence of rhizoids in that species was a serious difficulty in definitely assigning it to the Hepaticopsida.

The recent recognition by Oschurkova (1967) of *H. metzgerioides* Walton in various localities in the Upper Carboniferous of the Karanganda Basin, U.S.S.R., indicates quite clearly that thalloid hepatics were widespread in Carboniferous times.

Jovet-Ast (1967) lists many other species of *Hepaticites* Walton, *Thallites* Walton and *Metzgeriites* Steere from Jurassic and Cretaceous deposits. Most of these are too incompletely known for anything but the most tentative classification, but some seem to be clearly referable to Jungermanniales Anacrogynae, others to Marchantiales.

The 'Leafy Liverworts' (Jungermanniales Acrogynae) do not appear with certainty before the Tertiary. Jovet-Ast (1967) lists some fifty species distributed in twenty genera from Tertiary and Quaternary deposits. Most of the Tertiary species are placed in the two pre-Quaternary genera *Jungermannites* Goeppert, as emended by Steere (1946), and *Plagiochilites* Straus (1952), but a few of the Tertiary species and all the Quaternary ones are referred to extant genera in the families Trichocoleaceae, Lophoziaceae, Jungermanniaceae, Lophocoleaceae, Plagiochilaceae, Lejeuneaceae and Frullaniaceae. Some of the most beautifully preserved examples occur in the Oliocene Baltic Amber deposits, the flora of which has been reviewed by Savicz-Lubitzkaja and Abramov (1959) and by Czeczott (1959). Steere (1946) has reviewed the occurrence of leafy liverworts in the Tertiary of North America.

(*b*) Order *Marchantiales* Schiffner

The Marchantiales are not known with certainty from the Palaeozoic. *Thallites willsi* Walton (1949) from the Coal Measues of Staffordshire, England, and *T. lichenoides* (Matthew) Lundblad (1954) from the Coal Measures of New Brunswick, Canada, have some similarity to the extant genus *Riccia* L., while *Marchantites lorea* Zalessky (1937) from the Middle Permian of Bardinsky, Urals, U.S.S.R., is said to resemble the living species *Marchantia polymorpha* L. in some respects. But these three taxa do not seem to be sufficiently well characterized to constitute reliable evidence of the Marchantiales.

The thalloid plant from the Upper Carboniferous shales at Dollar, Clackmannanshire, Scotland, which Walton (1949) cautiously described as cf. *Hepaticites* sp., presents a problem. If the plant is a bryophyte at all, which has yet to be proved, it has close similarity to the extant genus *Riccia* L. (Ricciaceae, Marchantiales) as well as to *Riccardia* Gray (Jungermanniales).

The earliest acceptable record is *Hepaticites cyathodoides* described by Townrow (1959) from the Middle Triassic shales in the Upper Umkomaas Valley, Natal, South Africa. Townrow compares *H. cyathodoides* with the extant genus *Cyathodium* Kze., formerly placed in the Targioniaceae, but now in a family of its own. There are similarities in habit, rhizoids, ventral scales and midrib structure but the pores on the upper surface of the thallus in *H. cyathodoides* differ from those in the genus *Cyathodium*.

Later Mesozoic records of plants of undoubted marchantialean affinity include species in the genera *Ricciopsis* (resembling *Riccia* L.) and *Marchantiolites* (close to Marchantiaceae), both established by Lundblad (1954) for material from the Rhaeto-Liassic (Triassic–Jurassic) of Skromberg, Scania, Sweden; also several species of *Hepaticites* resembling Marchantiaceae described by Harris (1961) from the Bajocian (Jurassic) of Yorkshire, England; and a *Marchantites* (probably belonging to Marchantiaceae) from the Lower Cretaceous of Patagonia (Lundblad, 1955).

From Tertiary and Quaternary deposits about sixteen species have been described (Jovet-Ast, 1967); these consist of five species each in the genera *Marchantites* (Brongniart) Walton and *Marchantia* L. and two species of *Riccia* L. in the Tertiary; and from the Quaternary the extant species *Riccia fluitans* L., *Marchantia polymorpha* L., *Clevea hyalina* (Somm.) Lindb. and *Conocephalum conicum* (L.) Dumort.

Apart from the Quaternary species, the most completely known fossil representative of the Marchantiaceae is *Marchantites sézannensis* Brongniart from the Eocene Travertine of Sézanne, Marne, France. The large dichotomous thallus shows not only the air-pores characteristic of the family but also gemma-cups on the thallus surface, ventral scales and stalked structures similar to the antheridiophores of *Preissia* Corda and *Marchantia* L. *M. sézannensis* is one of the very few pre-Quaternary bryophytes in which the reproductive organs are known.

(*c*) Order *Sphaerocarpales* Cavers

A narrow subdivision of the English Rhaetic, known as the Cotham Beds, extends from Somerset east of the Mendip Hills north-eastwards to Worcestershire and Warwickshire. In these beds there occurs locally an abundance of fragments of the minute leafy plant *Naiadita lanceolata* Buckman, emend. Harris. The plant has been known for more than 100 years and has had a very chequered history, having been regarded in turn as a Monocotyledon resembling *Naias* L., a moss close to *Fontinalis* Dill., a lycopod and finally a liverwort. Indeed, as late as 1928 Walton wrote 'the genus *Naiadita* of Buckman, once regarded as being Bryophytic, is now known to belong to the Lycopodiales'. However, Harris (1938, 1939) has proved conclusively that this plant is a bryophyte. Stems, leaves, rhizoids, gemma-cups and gemmae, archegonia, sporophytes and spores are all described. Only the antheridia are lacking. Thanks to Harris's detailed work, *Naiadita lanceolata* remains to this day the most fully known fossil bryophyte. Harris considers it to be a submerged aquatic liverwort and assigns it tentatively to the Riellaceae (Sphaerocarpales).

(2) Class ANTHOCEROTOPSIDA Proskauer

(*a*) Order *Anthocerotales* Schiffner

Very little is known of the early history of the Anthocerotales. Neither gametophyte thalli nor sporophytes have been found as fossils and the earliest occurrences of Anthocerotales are based on certain kinds of Tertiary spores. Thiergart (1942) and later Krutzsch (1963) record *Anthoceros* L. spores from the Upper Oligocene, Miocene and Pliocene at various localities in Eastern Germany. Stuchlik (1964) has described from the Miocene of Poland a spore known as *Rudolphisporis rudolphi* Krutzsch which he refers to the extant genus *Anthoceros*.

(3) Class BRYOPSIDA *sensu lato*

The earliest geological records of what would seem to be undoubted mosses are *Muscites polytrichaceus* Renault & Zeiller (1888) and *M. bertrandi* Lignier (1914) from the Stephanian (Upper Carboniferous) of France, but their affinities are obscure. Palaeozoic mosses which can be classified more satisfactorily are the undoubted representatives of the Sphagnidae and Bryidae described by Neuberg from the Permian of the U.S.S.R.

1. Sub-Class SPHAGNIDAE Reimers

(*a*) Order *Protosphagnales* Neuberg

One of the most outstanding advances in the knowledge of early fossil bryophytes during the last ten years results from the extensive researches of the late Professor Maria F. Neuberg (1956, 1958, 1960). Before her untimely death in 1962, this author established 14 species of mosses distributed in 10 genera (of which 12 species and 9 genera were new to science) from the Lower and Upper Permian deposits of the Petchora, Kuznetsk and Tunguska Basins, Angarida, U.S.S.R. The plants were embedded in fine shales and were so beautifully preserved as to permit the preparation of cellulose peel and balsam transfers.

Three of the species (*Junjagia glottophylla*, *Vorcutannularia plicata* and *Protosphagnum nervatum*) have leaves resembling those of the extant genus *Sphagnum* L. in possessing two kinds of cells. They differed from modern *Sphagnum* in not showing a marked differentiation into narrow photosynthetic cells and large hyaline water-holding cells. In addition they had a midrib and sometimes a suggestion of lateral nerves as well. Realizing that these mosses had a close similarity to the modern genus *Sphagnum* but differed too much to be placed in the Order Sphagnales, Neuberg created the Order Protosphagnales for them.

Her work is being continued by S. V. Meyen (1963, 1966), who has extended the geographical range of the Protosphagnales with the discovery of a probable second species of *Protosphagnum* in the Upper Permian of Southern Priuralia.

(*b*) Order *Sphagnales* Engler

Undoubted *Sphagna* have been recorded from Mesozoic, Tertiary and Quaternary deposits. Reissinger (1950), for example, has described authentic leaves and spores of a *Sphagnum* from the Liassic (Lower Jurassic) of Nuremberg in Bavaria, while Arnold (1932, 1947) claimed to have *Sphagnum* leaves from the Upper Cretaceous of Disko Island, Western Greenland. A little caution is necessary in accepting this latter record for Steere (1946) suggested that it could have been due to the contamination of the Cretaceous material by recent *Sphagnum* fragments. Jovet-Ast (1967) lists some twelve Mesozoic species of *Sphagnum* based on spores. The same author records about twelve Tertiary species of *Sphagnum* and about thirty, many of which are modern, from Quaternary deposits.

2. Sub-Class ANDREAEIDAE Reimers

The fossil record for Andreaeales, like that for the Anthocerotales, is almost blank. Fleischer (1919) mentioned an *Andreaea*-like capsule and spores from the Devonian of Roros, Norway, but this has never been proved to be a true *Andreaea* Ehrh. Apart from this record of very doubtful value, nothing is known until the Quaternary, when the three extant species *Andreaea huntii* Limpr., *A. petrophila* Ehrh. and *A. rothii* Web. et Mohr have been found in glacial, interglacial or post-glacial deposits in Bavaria, Poland and Scotland (Szafran, 1952; Jovet-Ast, 1967).

3. Sub-Class BRYIDAE Reimers

The earliest true moss floras known so far are those described by Neuberg (1956, 1958, 1960) from the Permian of various localities in Angarida, U.S.S.R. No less than eleven species, referred to seven genera, occur variously distributed throughout both Lower and Upper Permian strata as shown in the Table 1.

Some of the mosses described by Neuberg, especially the four species included in the genus *Intia*, have striking similarities to the extant genera *Mnium* L. (B. and S.) and *Bryum*. Dill.; others are quite unlike any living mosses. Although all the species are undoubted members of the Bryidae, the absence of sporophytes and capsules makes further classification difficult. Jovet-Ast (1967) places all except *Muscites uniforme* in a 'Famille incertaine' within the Order *Eubryales* Fleischer. *M. uniforme* is placed in Bryophyta Incertae Sedis.

Mesozoic records of mosses are scarce. However, *Muscites guescelini* described by Townrow (1959) from the Middle Triassic of Natal, South Africa, is of some interest as it is sufficiently well preserved to permit comparison with extant members of the family Leucodontaceae.

By Tertiary times mosses are abundant and widespread and many of them can be referred to living genera (Savicz-Ljubitskaja & Abramov, 1959; Jovet-Ast, 1967).

Table 1. *Permian mosses in the U.S.S.R.*

Species	Locality	Geological age
Muscites uniforme	Kuznetsk	Upper Permian
Bachtia ovata	Tunguska	
Bajdaievia linearis	Kuznetsk	
Polyssaievia deflexa	Petchora	
P. spinulifolia	Kuznetsk and Tunguska	
Uskatia conferta	Kuznetsk	
Salairia longifolia	Kuznetsk	Lower Permian
Intia vermicularis	Petchora	
I. variabilis	Petchora	
I. falciformis	Petchora	
I. angustifolia	Petchora	

The numbers increased steadily throughout the Tertiary and Quaternary and many hundreds are known, mostly referable to extant species. Jovet-Ast (1967), for example, described examples in at least forty families referable to Fleischer's Orders Polytrichales, Fissidentales, Dicranales, Pottiales, Grimmiales, Funariales, Tetraphidales, Eubryales, Isobryales, Hookeriales, and Hypnobryales. Dickson (1967) states that macroscopic remains of more than 100 species of mosses are known from British deposits of the last glaciation alone but it is beyond the scope of the present article to include any extended treatment of Tertiary and Quaternary records.

Many of these more recent records of mosses relate to beautifully preserved material, as, for example, the Upper Miocene Moss Flora of Arjuzanx in Landes, France, recently described by Jovet-Ast & Huard (1966). Despite good preservation, the majority of Tertiary and Quaternary mosses are known only from vegetative remains. Fertile mosses worthy of note are *Muscites florissanti* (Knowlton) Steere (1946) from the Upper Miocene of Florissant, Colorado, U.S.A.; *M. yallournensis* Clifford & Cookson (1953) from the Oligocene of Yallourn, Victoria, Australia; and *Plagiopodopsis cockerelliae* (Britton & Hollick) Steere (1946) from the Oligocene of Florissant, Colorado, U.S.A.

IV. PROBLEMATIC BRYOPHYTE-LIKE FOSSILS

A number of Palaeozoic plants of uncertain affinity have been described which show varying degrees of similarity to liverworts or mosses. They merit some consideration in a review of the geological history of the Bryophyta. Six categories of plants or groups of plants, ranging in age from allegedly Ordovician to Upper Carboniferous, are selected for discussion. Two of these categories relate to material long known, four relate to discoveries within the last ten years. They are the genus *Protosalvinia* Dawson (1884); the genus *Sporogonites* Halle (1916*a*); the genera *Musciphyton* and *Hepaticaephyton* of Greguss (1959, 1961); the genus *Tetrapterites* Sullivan & Hibbert (1964); a 'bryalean sporogonium' from the Rhynie Chert (Lemoigne, 1966); and 'an early moss' from South Africa (Plumstead, 1966).

Protosalvinia Dawson

Small detached spore-bearing organs or 'sporocarps' of unknown plants found in the Upper Devonian Black Shales of East-Central U.S.A. have been placed in the genera *Sporocarpon* Williamson, 1878, *Protosalvinia* Dawson 1884 and *Foerstia* White & Stadnichenko (1923). The name *Sporocarpon* is unsuitable as it is now known to refer to fungal perithecia, and Arnold (1954) has shown that *Foerstia* is indistinguishable from *Protosalvinia*. *Protosalvinia* therefore takes precedence as the valid name, even though it has unfortunate suggestions of fern affinity.

The sporocarps of *Protosalvinia* usually occur as once-forked objects, 2–5 mm. wide, that were probably borne in large numbers on a dorsoventrally-flattened thalloid plant body. Occasionally two closely placed dichotomies give a four-lobed sporocarp. The outer surface is covered by an epidermis-like layer which seems to have been formed from the compact packing of the ends of filaments. Tetrads of large spores, each about 200 μ, occur in cavities in the internal tissues. According to Arnold (1954) the cavities are bounded by a distinct limiting layer and are arranged in a row beneath an apical groove that extends between the lobes of the sporcarp (Fig. 1*a*).

The position of *Protosalvinia* in the plant kingdom remains uncertain. White & Stadnichenko (1923) believed that it was an alga of some kind and that the internal cavities were oogonia containing eggs; Kidston & Lang (1924) claimed that it was intermediate between the algae and the lowest vascular plants; Kräusel (1941) believed it to be intermediate between algae and fungi and suggested for it a new Class of the Thallophyta, the Algomycetes. Arnold (1954), however, remains uncommitted, except to say that 'it had evolved to a level comparable to that of the lower bryophytes'. In the same paper Arnold also states that 'there is no apparent reason for classifying *Protosalvinia* with the bryophytes'. While this remains substantially true, it would appear that the recent discoveries of thalloid liverworts in older Devonian rocks of the U.S.A. (Hueber, 1961), of rosette-forming *Riccia*-like plants in the Carboniferous of Scotland (Walton, 1949) and Pettitt's demonstration of the presence of an acetolysis-resistant cuticle-like outer layer in living *Ricciella* all add weight to the idea that *Protosalvinia* may be the terminal branches of a rosette-forming liverwort in which large tetrads of spores were produced in simple sporophytes sunk in the

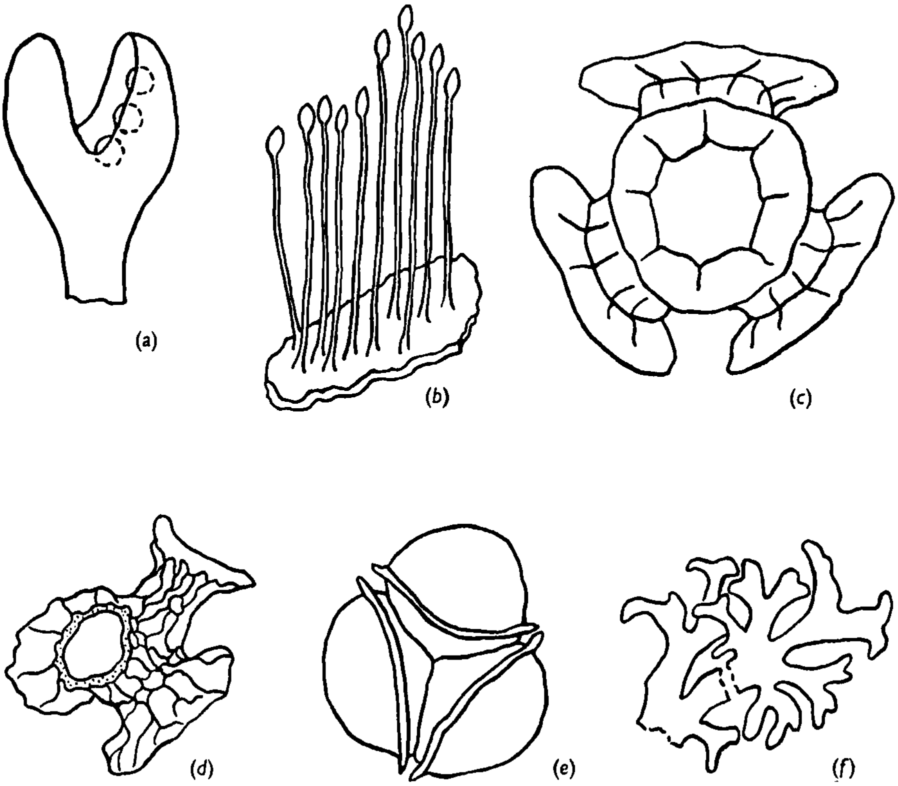

Fig. 1. (*a*) Sporocarp of *Protosalvinia furcata* (Dawson) Arnold, greatly enlarged (redrawn from Arnold, 1954); (*b*) portion of a plant of *Sporogonites exuberans* Halle, about ½ nat. size (redrawn from Andrews, 1960); (*c*) diagram of *Tetrapterites visensis* Sullivan & Hibbert, to show the tetrahedral form and wing-like expansions, greatly enlarged (redrawn from Sullivan & Hibbert, 1964); (*d*) *Tetrapterites visensis*, showing details of the surface ornament × 190 (drawn from Hibbert, 1967); (*e*) spore tetrad of *Naiadita lanceolata* Buckman, emend. Harris (three spores drawn), to show the extended margin, greatly enlarged (redrawn from Harris, 1938); (*f*) outline drawing of fragments of a thalloid plant, referred by Walton to *Rhodea* Presl, × 5 (redrawn from Walton, 1928*b*).

gametophyte thallus, much as in the living genus *Riccia*. Pettit himself (personal communication) inclines to the view that *Protosalvinia* is bryophytic.

Sporogonites Halle

This genus was first established by Halle (1916*a*, *b*) for slender unbranched stalks bearing spore-containing capsules found in the Lower Devonian of Norway. At first Halle believed that *Sporogonites* was possibly closely related to the bryophytes, but in a later, more detailed, account (Halle, 1936), possibly as a result of the description of the Rhynie plants during the intervening period, he changed his mind and stated that it was 'probable that *Sporogonites* represents part of a Pteridophyte belonging to or related to the Psilophytales'.

Additional material referred to the genus has also been described from the Lower Devonian of Australia (Lang & Cookson, 1930; Cookson, 1949), South Wales (Croft & Lang, 1942) and Belgium (Lang, 1937; Stockmans, 1940). More recently Andrews (1960) has re-examined certain of the Belgian specimens and has drawn attention to two features of particular interest; first, many of the specimens exhibit large numbers of sporangiophores showing a parallel alignment; and secondly, several specimens show attachment of the sporangiophores to a thin basal carbonaceous film, tentatively called a thallus. These features, coupled with the absence of any vascular strand (a feature already known) lead Andrews to suggest that *Sporogonites* was a non-vascular plant with an irregularly shaped flat thallus, bearing numerous slender erect sporangiophores, each unbranched and terminating in a single sporangium (Text-fig. 1*b*). Andrews decides in favour of a bryophytic affinity and suggests that *Sporogonites* is possibly related to the liverworts or represents an independent group of bryophytes. This seems to be an entirely reasonable suggestion. Nevertheless, as in the case of Arnold's (1954) account of *Protosalvinia*, Andrews' description implies that the spore-bearing organs are attached directly to the thallus. This would mean that the thalloid body is sporophytic and not gametophytic, an arrangement not yet known in any living groups of bryophytes, but familiar in many algae.

Musciphyton Greguss and *Hepaticaephyton* Greguss

In 1959 Kozlowski and Greguss announced in a preliminary communication the discovery of Ordovician land plants in Poland. The plants were obtained from a glacial erratic block, said to be derived from Scandinavia. They consisted of small cylindrical or flattened multicellular fragments, with rhizoids and an internal conducting strand but devoid of leaves or clearly recognizable reproductive organs. Greguss (1959) established two new genera, *Musciphyton* and *Hepaticaephyton*, for these plants which he believed to have bryophyte affinities. The photographs in the original paper were almost impossible to interpret, but later papers (Greguss, 1961, 1962) were better illustrated. Jovet-Ast (1967) has reviewed these genera at some length. Indeed, it is somewhat surprising to find that so much space is devoted to them, for they are not only problematical as bryophytes, to say the least, but also their provenance as fossils of Ordovician age is questionable. Many palaeobotanists are firmly of the opinion that the supposed Ordovician fossil plants of Kozlowski and Greguss are no more than contaminating fragments of recent plants. The late Professor R. Kräusel, in particular, expressed the view (personal communication) that some of the fragments were roots of modern *Carex* L. Certainly the alleged sporogonia of *Musciphyton* closely resemble the root-tubercles borne by some species of *Carex*.

It does not seem that *Musciphyton* and *Hepaticaephyton* are sufficiently authenticated to play any part in a consideration of the early fossil history of bryophytes.

Tetrapterites Sullivan & Hibbert

Tetrapterites is the name given to an unusual type of spore tetrad occurring in Lower Carboniferous shales in the Menai Straits, Caernarvonshire and in the Forest of Dean, Gloucestershire.

The tetrad is enclosed by a non-cellular membrane which has a tetrahedral shape and possesses a large wing-like expansion near each of its four apices (Text-fig. 1 *c*). The whole spore-containing unit is about 200 μ in diameter. Recent studies with the scanning electron microscope (Hibbert, 1967) show that the enclosing membrane is strongly ornamented with anastomosing ridges (Text-fig. 1 *d*).

In discussing the comparative morphology of this interesting fossil, Sullivan & Hibbert (1964) put forward the suggestion, among others, that the whole *Tetrapterites* unit bears some similarity to the structures found during spore formation in certain Hepaticae, notably to the early stages in *Pellia* Raddi and even more strikingly to the mature condition in *Sphaerocarpos* Ludwig, where spores are liberated in the form of large tetrads.

The possibility that *Tetrapterites* may indeed be bryophytic seems very real. The idea is not without support of an indirect kind from several sources. First, liverworts are now known as far back as the Upper Devonian, so they should not be unexpected in Lower Carboniferous deposits; secondly, the Sphaerocarpales are represented by *Naiadita* in the Rhaetic of Britain, and this fossil bryophyte (which may be expected to have originated from some pre-Rhaetic ancestor) also has large spores in persistent tetrads, with a prominent flange-like ornament on each member of the tetrad (Text-fig. 1 *e*); and thirdly, the Menai Straits beds which yield *Tetrapterites* also contain fragmentary remains of a thalloid plant which Walton (1928 *b*) thought might be minute pinnules of a species of the pteridosperm genus *Rhodea* Presl. (Text-fig. 1 *f*). It seems equally possible to the writer that these fragments could be part of a *Riccia*-like plant (similar ones are already known in Upper Carboniferous rocks in Scotland) and the parent plant of *Tetrapterites*. Before such an explanation could be accepted it would be necessary to discover the *Tetrapterites* tetrads in place in the thalloid plant body. Bulk maceration of the shales and careful examination of a sufficient number of thallus fragments might provide just such evidence.

An alleged bryalean sporogonium of Devonian age

Lemoigne (1966) has described a spore-bearing organ from the Rhynie Chert Beds, Aberdeenshire, Scotland, which is claimed not merely as indicating for the first time the occurrence of bryophytes in the Chert, but more than that, the sporogonium of a moss. On the basis of this somewhat far-reaching claim, it is stated that 'in the Lower Devonian the Bryales had already reached a degree of differentiation comparable with that found in extant species'. As far as can be judged, these claims are based on the examination of one slightly oblique longitudinal section. Cellular structure is admitted to be poorly preserved but it is nevertheless stated that the apex of the organ shows an 'operculum'. Such a feature is difficult to detect in the single published photograph; certainly it is not as clear as the two line-drawings accompanying the photograph would suggest. It is further stated that progressive polishing of the single section revealed a central columella, which could not be illustrated photographically. Even if a columella and operculum are present, it is difficult to see why the author goes so far as to claim this fossil as a moss. No diaphragm or peristome is detectable in the material below the operculum. Apart from the presence of larger spores (stated to be about 150 μ, but this figure may refer to the whole tetrad) the new material does not differ essentially from the psilophyte *Horneophyton* Barghoorn & Darrah. At the present time Lemoigne's claims seem to be far from substantiated. It is greatly to be hoped that additional better-preserved specimens will clarify the position.

An early moss from South Africa

Plumstead (1966) has described from four localities in the Transvaal, South Africa, a small herbaceous leafy plant. The shoots are up to 3 cm. long and grew crowded together, almost forming mats or cushions. They have no vascular tissues. These features strongly suggest that the plant is a moss. This is further supported by the form of the leaves. They are fine, linear and tapering, about 5 mm. long, composed of elongated cells; indeed, the whole aspect of the plant is strikingly similar to modern species of *Dicranum* Hedw. Plumstead claims that this is probably 'the oldest known well-preserved moss'. A moss it almost certainly is, but 'oldest known' is another matter not yet substantiated, since the age of the deposits in relation to the European Carboniferous is not yet known with precision but given only as 'Upper Carboniferous Stage, Proto-Glossopteris Zone'.

V. BRYOPHYTE EVOLUTION

Many well-known bryologists (for example, D. H. Campbell, G. M. Smith, J. Proskauer, to mention but three) have suggested at various times that the Anthocerotales occupy an important ancestral position in the evolution of the Hepaticae. More recently, Jeffrey (1962) goes farther and considers that the Anthocerotales possess not only characters ancestral for the Hepaticae but also characters in common with the Psilotales, Bryales, Sphagnales and Andreaeales. It would be fine if the fossil evidence furnished additional support for these views based on comparative morphology, anatomy and cytology of recent species. Unfortunately it does not, for so far no Anthocerotales are known before Tertiary times.

Other bryologists have suggested a 'down-grade' line of bryophyte evolution; that is, the gametophyte was at first a 'leafy' structure which became flattened and thalloid, either by the loss of the leaves and enlargement of the axis (A. W. Evans) or by the fusion of the leaves (P. N. Mehra, B. R. Vashist). If the Palaeozoic bryophytes do not yet establish the Anthocerotales as an early ancestral group, do they throw any light in general terms on the question of 'up-grade' as against 'down-grade' theories of bryophyte evolution? The earliest known example, *Hepaticites devonicus* from the Upper Devonian of the U.S.A., is thalloid and tips the scales slightly in favour of the 'up-grade' view, but the occurrence of a wide range of foliose or near-foliose forms relatively soon afterwards in the Upper Carboniferous and Permian must cast doubt on the wisdom of basing arguments on a single record (or even several records, if *Protosalvinia* and *Sporogonites* are accepted as bryophytes) from the Devonian. Putting this another way, although thalloid liverworts appear from the fossil record to have arisen before foliose ones, and liverworts in general to have arisen before mosses, the complexity and diversity of the moss floras from the Permian of Russia, for example, must surely imply an evolutionary origin considerably earlier in the Late Palaeozoic and probably contemporary with that of the liverworts.

Within the liverworts, on present fossil evidence, the Jungermanniales Anacrogynae seem to have pre-dated the Marchantiales and these in turn predated the Sphaerocarpales, but if the Lower Carboniferous *Tetrapterites* is ever shown to have Sphaerocarpalean affinities this order would be largely reversed. Jungermanniales Acrogynae, Anthocerotales and, within the Musci, the Andreaeales all appear, so far as fossil evidence goes, to be of relatively recent origin.

On a lower taxonomic level a similar situation exists within Orders. In the Marchantiales, for example, the Ricciaceae are sometimes placed in an ancestral position, but sometimes the reverse view is held. The Late Palaeozoic and Early Mesozoic marchantialean fossils give no unequivocal answer. The Mid-Triassic *Hepaticites cyathodoides* from South Africa, pre-dating by a few million years the Rhaetic-Liassic *Ricciopsis scanica* from Sweden, might be taken to support a Marchantiaceae Ricciaceae 'down-grade' line of evolution, but should the *Riccia*-like cf. *Hepaticites* sp. from the Upper Carboniferous of Scotland prove to be a *Riccia* the position would be reversed.

Early fossil bryophytes, then, give no clear answers so far to most phylogenetic questions. They permit perhaps one firm conclusion and one reasonable conjecture, namely (*a*) that, as Watson (1964) has already pointed out, the principal groups of both liverworts and mosses (Jungermanniales, Marchantiales, Sphagnales s.l. and Bryales) have all been differentiated before the end of the Palaeozoic, and (*b*) a polyphyletic origin of the Bryophyta seems highly probable. To speculate beyond this without much more fossil evidence than is presently available is an exercise which is hardly worth while.

VI. SUMMARY

1. The rapid increase in the knowledge of the early geological history of bryophytes which has taken place in recent years is emphasized.

2. An explanation for this unexpected development is sought in a consideration of the conditions necessary for the preservation of bryophytes as fossils.

3. It is concluded that the chances of preservation depend not so much on the conditions suitable for the growth of bryophytes or the possession of resistant structures (although both can be important contributory factors) but on the occurrence of the right kind of sedimentation in the right place at the right time.

4. The fossil history of the main Orders of the Bryophyta is then systematically reviewed, with special reference to first records in the Palaeozoic and Mesozoic.

5. A number of problematic bryophyte-like fossils of Palaeozoic age are also reviewed. Four (*Protosalvinia* Dawson, *Sporogonites* Halle, *Tetrapterites* Sullivan and Hibbert, and a *Dicranum*-like plant from South Africa) are accepted as probably bryophytic; three (*Musciphyton* Greguss, *Hepaticaephyton* Greguss, and an alleged bryalean sporogonium from the Rhynie Chert) are rejected on the grounds of insufficient evidence.

6. The bearing of the fossil evidence on bryophyte evolution is briefly considered.

7. It is shown that the principal groups of both liverworts and mosses had already been differentiated before the end of the Palaeozoic.

8. A polyphyletic origin of the Bryophyta is therefore highly probable.

9. Beyond this, the early fossil evidence as yet gives no unequivocal answers and more detailed phylogenetic speculation based on the present state of knowledge of fossil bryophytes has little value.

10. Further knowledge of the early fossil history of bryophytes is needed and it is suggested that this is most likely to be obtained by patient systematic search in fine-grained freshwater sediments by bulk maceration techniques.

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VIII. ADDENDUM

Nagy (1968), in a recent well-illustrated paper on bryophyte spores from the Neogene of Hungary, makes an important addition to the knowledge of Tertiary Anthocerotopsida, Hepaticopsida and Bryopsida.

In the Anthocerotopsida the Anthocerotaceae are represented by one new species of *Rudolphisporites* (*Rudolphisporis*) Krutzsch and two new species of *Phaeocerosporites*, a new genus established by Nagy, all from the Upper Helvetian (Miocene) at Zengovarkony, and one new species of *Saxosporites* Krutzsch from the Upper Pannonian (Pliocene) at Hidas.

The Hepaticopsida are represented by the Ricciaceae with two new species in another new genus, *Ricciaesporites*, established by Nagy, also from the Upper Helvetian locality at Zengovarkony.

Mosses are represented by one new species in each of the two new genera *Encalyptaesporites* Nagy and *Ephemerisporites* Nagy, referred respectively to the Encalyptaceae, Pottiales, and Ephemeraceae, Funariales. The *Encalyptaesporites* is from the same Pliocene locality at Hidas which yielded the *Saxosporites*, while the *Ephemerisporites* is from somewhat older Lower Pannonian deposits at Bogacs. Spores of four recent species of *Riccia*, of *Ephemerum serratum* (Schreb.) Hampe and of *Encalypta vulgaris* (Hedw.) Hoffman are figured at high magnification for comparison with the fossil spores and strongly support the reference of the latter to the families suggested by Nagy.

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