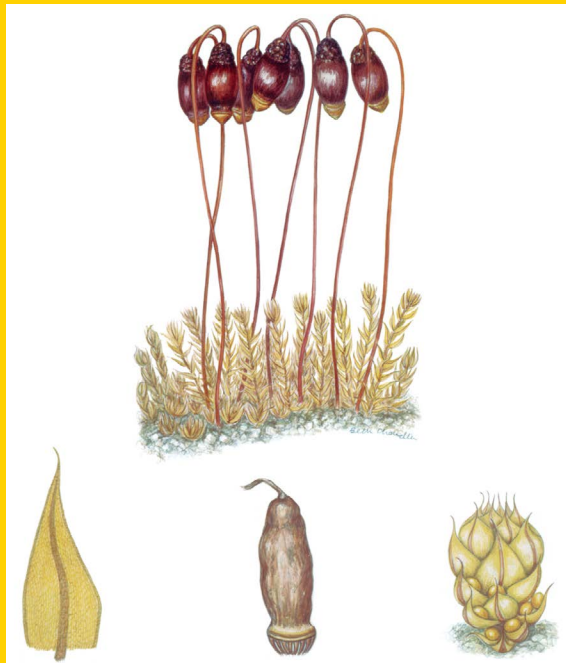




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Fossil Record of Bryophytes

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FOSSIL RECORD OF BRYOPHYTES

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The fossil record of bryophytes is poor compared to that of vascular plants, and the Australian record is particularly sparse. Bryophytes are probably rarely fossilised because they lack the resistant structures typically found in vascular plants, e.g. thick cuticles and lignified vascular tissues. Fossil bryophytes may also have been ignored because of their small size, or they may have been destroyed by many of the commonly used methods of extracting vascular plant fossils from sediments.

There are certain clear biases in the fossil record of bryophytes. Some higher order taxa are undoubtedly preserved more readily than others (e.g. more robust mosses rather than hepatics; see Schuster, 1981). Other taxa (e.g. certain thallose hepatics) might have been overlooked due to their non-descript gross morphology. Moreover, fossil spores of some hepatics, anthocerotites and *Sphagnum* are more readily recognised because these taxa have large, distinctive and resistant propagules. Preserved spores of other bryophytes may well occur in sediment, but they are often overlooked, either through loss in processing or due to an absence of distinctive features.

Records of fossil bryophytes are more common from higher latitudes (Ovenden, 1993) than from the subtropics and tropics (Frahm, 1993). This is due in part to the greater relative abundance of mosses in cool-climate floras, and probably also because of more rapid weathering of sediments at low latitudes. Similarly, records from glacial periods are more informative than those from interglacials during the Pleistocene (Miller, 1984). Records are also more numerous in younger than in older sediments, presumably because of the comparative paucity of resistant structures, and perhaps also because global cooling during the Cainozoic favoured bryophytes.

Nevertheless, there is a long and rich fossil record of bryophytes. Figure 1 provides a time scale annotated with some of the major events in the bryophyte fossil record. Beautifully preserved macrofossils are sometimes isolated from various types of rock, including fine-grained permineralised sediments, unsubstituted fine-grained sediments with organic preserved fossils, from Quaternary peats and in amber.

The types of structures preserved and the state of systematics influence our understanding of the fossil record of bryophytes. The record is dominated by spores and the leafy or thallose parts of gametophytes. The gametophytes of most bryophytes tend to be larger and longer-lived than the sporophytes, and the spores are highly resistant, widely dispersed and produced in great numbers. Gross morphology and the anatomy of bryophyte leaves and thalli are often highly distinctive, and some species can be readily distinguished using these features. These attributes can also be preserved in the fossil record, and they are well documented in the taxonomic literature (including keys and floras descriptions). Unfortunately, identification can be complicated by convergence among families and genera. Consequently, there is a high probability of readily and reliably identifying well-preserved fossils of species closely related to extant taxa; when the relationship is more remote any inferred affinity to living taxa rapidly becomes less reliable. Thus, extant species and, often, extinct species of extant genera can be accurately identified, and well-preserved Cenozoic fossil bryophytes can often be named. On the other hand, the affinities of older fossils are often very obscure, even to the point of being uncertain whether they represent mosses, liverworts, hornworts or, indeed, bryophytes. Apart from the exceptions noted above,

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spores are rarely identified more precisely than to family level, presumably due to the absence of taxonomically meaningful characters and a general lack of knowledge of bryophyte spore morphology, particularly among palaeo-palynologists.

Recent reviews of aspects of the fossil record of the bryophytes include those of Lacey (1969), Dickson (1973), Krassilov & Schuster (1984), Miller (1984), Taylor & Taylor (1993), Balme (1995) and Kenrick & Crane (1997).

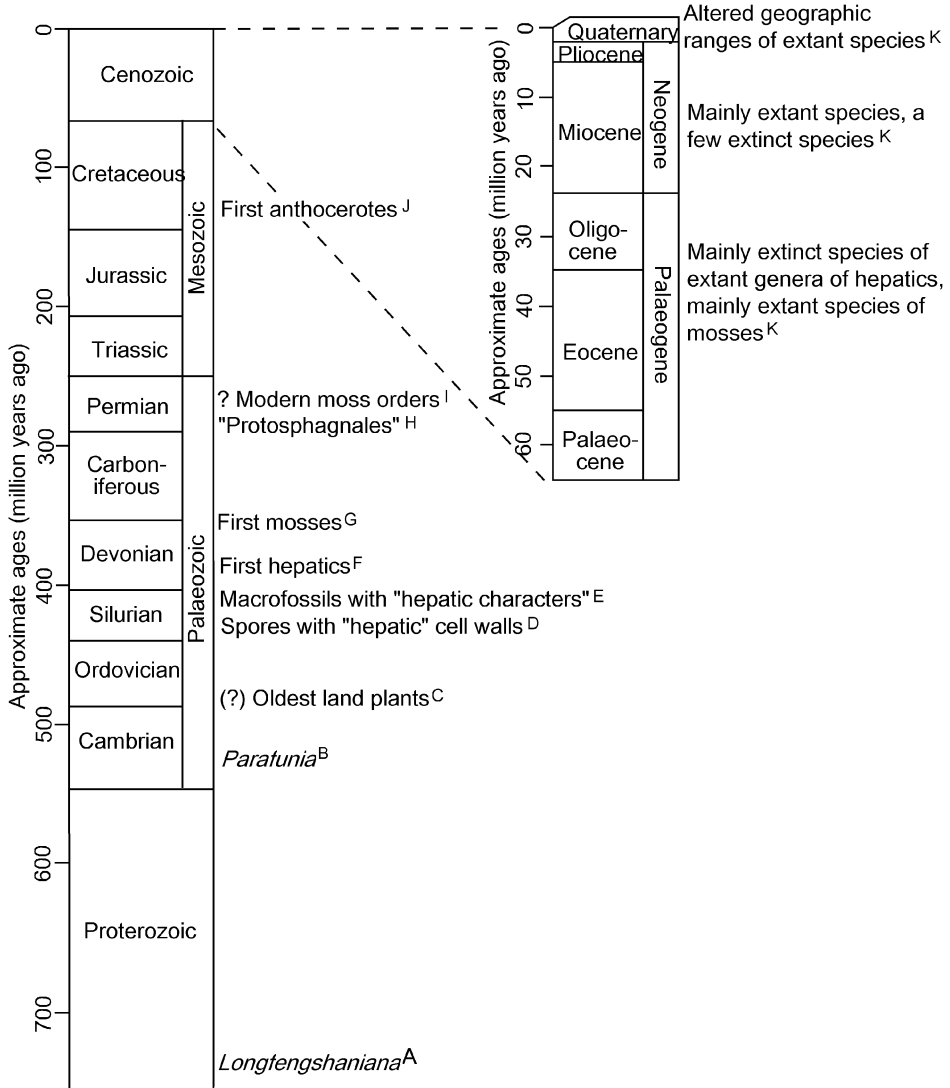


Figure 1. The geological time scale with some of the major events in the fossil record of bryophytes (ages are approximate). Sources of information: A, Zhang (1988); B, Yang *et al.* (2004); C, Gray (1985); D, Taylor (1995); E, Edwards *et al.* (1995); F, Thomas (1972); G, Schuster (1981); H, Neuburg (1960); I, Ignatov (1990) and Smoot & Taylor (1986); J, Dettman (1963), Jarzen (1979) and Drinnan & Chambers (1986); K, Krassilov & Schuster (1984) and Miller (1984).

Origin of the Bryophytes

A combination of the fossil record and phylogenetic analysis of modern taxa indicates that the major groups of bryophytes are very ancient and arose near the time of the earliest land plants (Shaw & Renzaglia, 2004). The land plants, including bryophytes, are probably monophyletic and, within this larger group, the tracheophytes are also very likely to be monophyletic. However, the relationships among the tracheophytes and the three major lineages of bryophytes (mosses, hepatics and anthocerotales) remain unclear, with different phylogenetic analyses showing almost all possible arrangements of these groups. While it is often very difficult to recognise features of modern plants in many early land plants, the fossil record does provide some hints about the origin of the bryophytes.

Some of the oldest of all terrestrial plant fossils resemble hepatics. An extreme example is the claim that the Precambrian *Longfengshania* is probably a liverwort (Zhang, 1988; Fig. 1), although it could also be interpreted as an alga. Moreover, Yang *et al.* (2004) described a bryophyte-like fossil, *Parafunia sinensis*, from Early-Middle Cambrian sediments, with structures they interpreted as whorled leaves, a capsule, seta and complex rhizoidal structures. This fossil occurred in the same sediments as cryptospores (spores having some of the features of terrestrial plant propagules), and the sediments also contained a diverse fossil assemblage of shallow marine organisms.

The earliest convincing evidence of terrestrial plants is found in Ordovician spores with resistant walls suggesting a terrestrial existence (Gray, 1985). Silurian spores, similar to one type of the Ordovician 'land plant' spores, have a wall ultrastructure similar to that seen in extant hepatics especially the Sphaerocarpaceae (Taylor, 1995). Earliest Devonian macrofossils with anatomical similarities to hepatics contained spores similar to another type of Ordovician 'land plant' spore (Edwards *et al.*, 1995). However, as discussed by Edwards (2000), differences between the morphology of ancient fossils and that of any living plant, the relatively poor preservation of some fossils and the primitive character of many of the structures (and hence similarity to only distantly related primitive taxa) together mean that the earliest fossil land plants are open to various interpretations. Consequently, such fossils are often described as evidence of terrestrial plants of a bryophyte grade, representing either ancient bryophytes, or land plants with primitive features that make them resemble bryophytes.

Fossil Record of Hepatics

Apart from the possible records listed above, hepatics were clearly present by the Devonian (*Pallavicinites devonicus* (Hueb.) R.M.Schust.; Heuber, 1961; Schuster, 1981). *Pallavicinites* has attributes of the comparatively advanced "simple thalloid I" group of hepatics (Schuster, 1981; Shaw & Renzaglia, 2004). It is, therefore, likely that hepatics were well differentiated by this time. Furthermore, most of the Mesozoic fossils are of the Metzgeriales (Krassilov & Schuster, 1984; Miller, 1984) which is an advanced group. Schuster (1981) argued that the early occurrence of apparently advanced forms is due to biases against fossilisation of primitive hepatic forms. Fossil evidence regarding the Sphaerocarpaceae may help to resolve this dilemma. The Triassic fossil *Naiadita lanceolata* Brodie has sporophyte characters and spore wall ultrastructure indicating a position in the Sphaerocarpaceae but, like Calobryales, the gametophytes are erect and radially symmetrical (Hemsley, 1989), i.e. key attributes of Schuster's (1981) putative ancestral hepatic. Together with the evidence from Taylor (1995) and Edwards *et al.* (1995) that very early land plants had sphaerocarpacean characters (see discussion above), this leaves open the possibility that the earliest hepatics were proto-sphaerocarpaceans with radially symmetrical gametophytes.

A number of Mesozoic fossil taxa can be assigned with some confidence to major groups of modern hepatics. Thus, the Cretaceous *Dietertia* is clearly a member of the order Jungermanniales and, apparently, a highly derived form within that order; this suggests an early origin for the order (Schuster & Janssens, 1989). Convincing fossils of the Marchantiales are known from the Jurassic including ones associated with spores consistent with the extant genus *Riccia* and other taxa (Lundblad, 1954; Balme, 1995). Few Mesozoic

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hepatics can be assigned to extant families, and although occasional fossils have been assigned to extant genera, there is considerable uncertainty about their identity. An Australian example, *Riccardia koonwarriensis*, was described from the Aptian Koonwarra Fish Beds in Victoria (Drinnan & Chambers, 1986).

In marked contrast to Mesozoic fossils, almost all well-preserved Cenozoic hepatic fossils are clearly attributable to modern genera, which suggests that many, including highly advanced taxa, were extant by the end of the Cretaceous (Schuster & Krassilov, 1984). The extant leafy liverwort genera *Porella* and *Frullania* are represented by beautifully preserved specimens in the Eocene Baltic amber (Grolle & So, 2004). Schuster (1981) argued that the high specific and generic diversity of hepatics in the Cenozoic reflects an sudden, dramatic increase in the diversity of epiphytic taxa, particularly of five families of the Marchantiales (Lejeuneaceae, Jubulaceae, Radulaceae, Porellaceae and Plagiochilaceae), in response to the Late Cretaceous and Paleogene expansion of angiosperm abundance and diversity. Palaeogene hepatics tend to be of extinct species, although a few are virtually identical to extant taxa (Miller, 1984). For example, of the 20 species of hepatic found in the Middle Eocene-Early Miocene Dominican amber, 12 represent extinct species, three are of extant species, and there is insufficient information to determine whether the remaining five are extinct or not (Gradstein, 1993). By contrast, most Neogene fossils are morphologically consistent with extant species (Miller, 1984). There is an implication that the typical turnover time of hepatic species is probably 10–30 million years, which is long, especially when compared with angiosperms. If hepatic diversity was greater in the past, these figures may be incorrect, either because there were many extinct species with similar gametophyte morphology (and hence the turnover time could be shorter), or because there were so many Palaeogene species that the extant species were masked in the fossil record by extinct species (and hence the turnover time could be longer).

Fossil Record of Anthocerotites

The only unambiguous, macrofossil anthocerotite is a member of the Dendrocerotaceae found in the Eocene-Early Oligocene Dominican amber (Frahm, 2005). Drinnan & Chambers (1986) described *Dendroceros victoriensis* from the Aptian (Early Cretaceous) Koonwarra Fish Beds in Victoria, Australia. Provided the detached structures considered by the authors to be sporophytes were actually part of the living plant, these fossils are undoubtedly anthocerotites, and they probably represent *Dendroceros*. If not, it is plausible that they were hepatics. Anthocerotite spores certainly occur in nearby correlatives of these sediments (Dettmann, 1986). There are Cretaceous spores in North America (Jarzen, 1979) and in Australia (Dettmann, 1994) that are almost certainly anthocerotites and resemble propagules of the extant genus *Phaeoceros*. Dettmann (1994) also recorded spores that probably represent other anthocerotite genera, and many anthocerotite spores are known from the Cenozoic (Jarzen, 1979).

Fossil Record of Mosses

Fossil mosses are less common than hepatics during the Mesozoic and especially the Palaeozoic, even though Cenozoic fossils of mosses are much more common than hepatics from that period. The oldest known fossil moss is the Early Carboniferous *Muscites plumatus* from Gloucestershire, England (Thomas, 1972). Neuberg (1960) observed a rich moss flora from the Early Permian which Krassilov & Schuster (1984) suggested were from a single group of mosses (Protosphagnales) of unknown modern affinities. A Late Permian flora from the Russian Platform is of particular interest since it contains beautifully preserved leaves and leafy gametophytes which appear to represent five extant orders, viz. Dicranales, Pottiales, Funariales, Leucodontales and Hypnales (Ignatov, 1990). The oldest Southern Hemisphere moss, and the oldest bryophyte with anatomical preservation of the gametophyte, is the permineralised *Merceria augustica* from the Transantarctic Mountains, which appears to confirm the differentiation of the Bryales, probably the Bryidae (Smoot & Taylor, 1986).

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The Mesozoic record of mosses is similar to that of the hepatics in that a number of extant major groups became known, but extant genera have rarely been identified (Krassilov & Schuster, 1984). Late Cretaceous (Campanian) sporophytes and gametophytes of an extinct member of the Polytrichaceae, *Eopolytrichum antiquum*, are known from North America (Konopka *et al.*, 1997). The presence of both sporophytes and gametophytes means that this is a highly reliable identification.

The Cenozoic fossil record of mosses is comparatively rich, with many more mosses than hepatics known from this time. The overwhelming feature of this record is the similarity to modern floras, and almost all of the fossils are indistinguishable from modern species, even in the Paleogene (Miller, 1984). For example, among 55 very well-preserved moss specimens from the Eocene Baltic amber, most have been identified as belonging to 11 extant species, the remainder are assigned to living genera, but without preservation of the organs necessary to identify them to species level (Frahm, 2004).

Occasionally, Cainozoic fossils clearly represent extinct species. For example, in the Neogene Ellesmere Island flora from the high Arctic, two of 57 moss taxa were different to all known extant species (Ovenden, 1993). A possible explanation is that the turnover time of moss species is very long, often tens of millions of years, and even slower than for hepatics among which Palaeogene fossils tend to be of extinct species. However, it is also possible that this difference might be partly due to a lesser amount of differentiation between species within moss genera in comparison with hepatics, and perhaps different attitudes to identification on the part of the palaeobotanists involved, i.e. whether they tended to assign fossils to living species, as opposed to describing new species on limited information, or to leave specimens without formal description.

The long species turnover time in mosses and hepatics may be due to a combination of factors, including rarity of sexual reproduction and resilience to macroclimatic change. This resilience may also be related to very high dispersal ability and a tendency for distributions to be determined by microclimate rather than macroclimate.

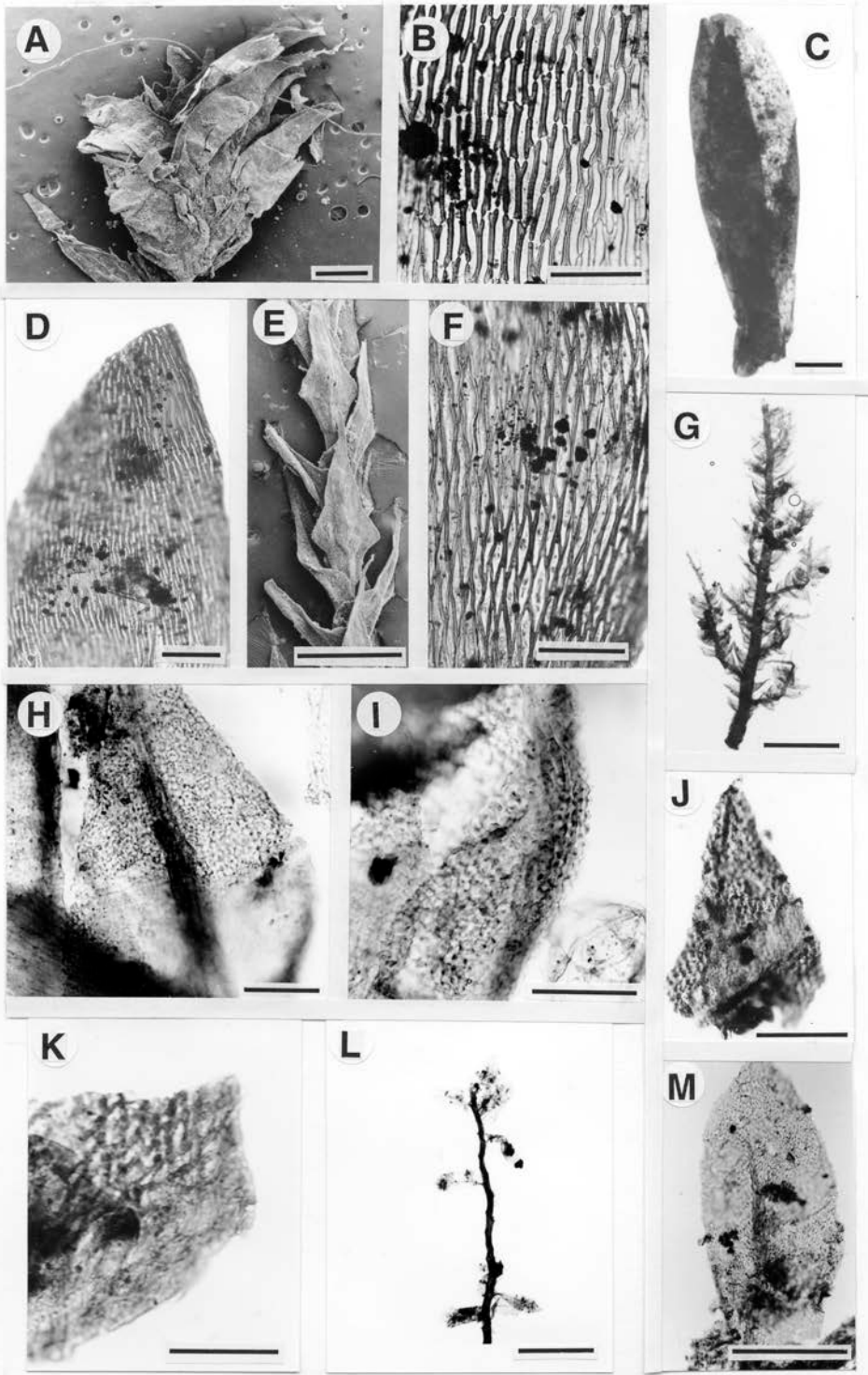
There have been marked changes in the distribution of taxa even in comparatively recent times. Some are of taxa tracking well-defined macroclimatic changes (e.g. bryophytes having more poleward distributions during warm interglacial periods than during glacials), but a few taxa appear to contradict the trends (Miller, 1984). These trends are consistent with the commonly held view, based on the ranges of modern taxa, that the distribution of most bryophytes is determined primarily by suitable microclimatic conditions rather than by macroclimate.

The Australian Fossil Record

Apart from spores, there are few fossil bryophytes of any age in Australia, and these show similar trends to the global fossil record. The Aptian (Early Cretaceous) Koonwarra Fish Beds contain the richest Mesozoic fossil bryophyte flora in Australia (Drinnan & Chambers, 1986). The preservation of these fossils is moderate at best, and all the identifications are

Figure 2 (opposite). Some fossil mosses from south-eastern Australia. **A–F**, Fossils from Early Pleistocene Regatta Point sediments in western Tasmania. **A**, Leafy stem fragment of *Ptychomnion aciculare* (Ptychomniaceae); **B**, Cells from mid-leaf of *Ptychomnion aciculare*; **C**, Leaf of *Weymouthia mollis* (Lembophyllaceae); **D**, Cells from apex and mid-leaf of *Weymouthia mollis*; **E**, Leafy stem fragment of *Papillaria* sp. (Meteoriaceae); **F**, Cells from mid-leaf of *Papillaria* sp. **G–M**, Fossil mosses from Mid-Miocene sediments at Elands, central-eastern New South Wales. **G**, Leafy stem fragment of unidentified Species A; **H**, Leaf of Species A; **I**, Folded portion of a leaf of Species A; note the papillae; **J**, Leaf of unidentified Species B; **K**, Mid-leaf cells of Species B; note the thick-walled, smooth, rhomboidal cells; **L**, Leafy stem fragment of unidentified Species C; note the sparse, possibly flattened phyllotaxy; **M**, Leaf of Species C; note the thin-walled, smooth, rhomboidal cells. Scale bars: A and E, 0.5 mm; B, D, F, H, I and K, 50 µm; C and M, 0.2 mm; J, 100 µm; G and L, 1 mm.

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open to alternative interpretations. The fossils included gametophytes of leafy hepatics (?*Jungermannia*, ?*Plagiochila* and Jungermanniales indet.), one probable thallose hepatic (*Riccardia koonwarriensis*), several possible thallose hepatics (*Hepaticites* spp. and *Thallites* sp.), and probable moss gametophytes (two types) and sporophytes (two types). The fossils described as the anthocerote *Dendroceros victoriensis* are discussed above.

Douglas (1973) described a Cretaceous thallose hepatic (*Hepaticites discoides*), but the state of preservation precludes recognition of its relationship to extant taxa. Selkirk (1974) identified persistent protonemata and haptera resembling the extant epiphyllous moss *Ephemeropsis* on Early Miocene cuticle from Kiandra. Clifford & Cookson (1953) described a moss capsule of unknown affinity from the Oligo-Miocene sediments at Yallourn, although re-examination of this specimen has led to some doubt about its identification (P.J.Dalton, pers. comm.). Although hepatic spores are common, particularly those similar to Ricciaceae, the only Cenozoic macro-fossil record is a member of Jungermanniales in the Early-Middle Miocene Yallourn Formation in the Latrobe Valley coal. Spores of *Phaeoceros* and Sphagnaceae occur in Australia from the earliest Cretaceous (Dettmann, 1994). Several types of hepatic spore (*Riella* or *Riccia* and others) also occur in the Early Cretaceous (Dettmann, 1994). Spores of most of these types and some other likely bryophytes occur in the Cenozoic (Macphail *et al.*, 1993, 1994). A fossil flora from Early Pleistocene at Regatta Point sediments in western Tasmania contains a suite of fossil mosses (Jordan & Dalton, 1995). Two of these, *Ptychomnion aciculare* and *Weymouthia mollis*, can be confidently assigned to extant wet-forest species and another, *Papillaria* sp., appears to be of a species which is at least regionally extinct (Fig. 2A–F). Several as yet unidentified moss taxa (Fig. 2G–M) occur in an Early-Middle Miocene fossil flora from Elands in eastern New South Wales (Barnes & Hill, 1999).

Conclusions

The fossil record shows that at least two of the major bryophyte lineages are very ancient. The hepatics were already differentiated into subgroups at least back to the Devonian, and the mosses to the Early Carboniferous. By inference, the anthocerotes are also likely to be Palaeozoic in age. Prior to this there are spores and traces of conducting tissue which have certain hepatic characteristics, and it is plausible that these fossils represent early hepatics or extinct lineages close to the common ancestors of bryophytes and vascular plants. Several of the major modern orders within the mosses first appear in the Late Permian, as well as at least one group (Protosphagnales) which is difficult to convincingly link with any modern taxon. The modern orders of hepatics mostly appear later, in the Cretaceous or Cenozoic, possible exceptions being the Metzgeriales and the Sphaerocarpaceae. Most Palaeozoic hepatics are assigned to the Metzgeriales, and many of the most ancient land plants share characters with the Sphaerocarpaceae. In both cases, it is possible that the fossils are identified on the basis of shared primitive characters, although this still suggests that the lineages leading to these orders are very ancient. Anthocerotes do not appear until the Cretaceous. Mesozoic and Palaeozoic mosses and hepatics are usually of extinct genera and probably families, but Cenozoic fossils are usually referable to modern genera. All first appearances based on fossil evidence are minimum ages for these taxa, and actual first occurrences may be much older, especially considering the sparseness of the bryophytes record. There are many moss fossils and some hepatics from Cenozoic sediments, indicating that moss species often exist for a very long time, perhaps tens of millions of years, i.e. much longer than angiosperm species. Hepatic species also appear to exist for millions of years, but perhaps not as long as mosses.

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