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the **TIMETREE** *of* **LIFE**

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Mosses (Bryophyta)

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Abstract

Living mosses (ca. 13,000 sp.) constitute the Phylum Bryophyta, with eight classes divided into acrocarpous mosses (23 orders), not an evolutionary group, and pleurocarpous mosses (4–7 orders, 42% of extant species). Two subclasses, Dicranidae (acrocarpous haplolepidae) and Bryidae (diplolepoidous-alternate mosses, with both acrocarpous and pleurocarpous members), account for 90% of extant species. The moss timetree shows lineage origin at ~380 million years (Ma) ago, the split between Haplolepidae and Diplolepidae at 220–195 Ma, and appearance of the first pleurocarp lineages at ~173 Ma. Major diversification occurred in the Cretaceous, 140–90 Ma.

Mosses are photosynthetic plants that exhibit a wide range of morphologies, based on the life cycle of alternation of haploid and diploid generations. The gametophyte generation starts with haploid spores that develop into threadlike protonema, from which grow erect or creeping axes usually up to a few centimeters tall. The plants are often branched, with leaves that are mostly one cell thick and usually radially arranged (Fig. 1). They form small cushions, velvety swards, open turfs, tufts, or deep mats. Long-lived clonal growth and specialized vegetative reproduction are common and widespread, with sexual reproduction rare or unknown in some taxa. Plants are male or female, or bisexual, with various different arrangements of gametangia. Male and female gametangia are distinct, with a basic morphology common to all mosses (and to most of the early-diverging land-plant lineages) but with variation in some groups. Motile spermatozoa travel through surface water to fertilize sedentary eggs. The resulting diploid embryo grows into a sporophyte that is largely dependent on the gametophyte, with

a single spore capsule and often with a complicated dehiscence (dispersal) mechanism (peristome). Spores are formed by meiosis and usually dispersed as monads.

The taxonomic diversity of living mosses reflects the morphological diversity, and is arranged in a pectinate grade of several small or very small but highly distinct clades, a few rather larger but also distinct clades (e.g., Sphagnales, Polytrichales) and two very large and poorly resolved clades, the Dicranidae and Bryidae, that together account for 90% of extant moss species diversity. The basal grade, the Dicranidae and part of the Bryidae are acrocarpous, with the principal vegetative axis terminated by gametangia, and consequently with terminal formation of sporophytes. A monophyletic group within the Bryidae is pleurocarpous, with gametangia

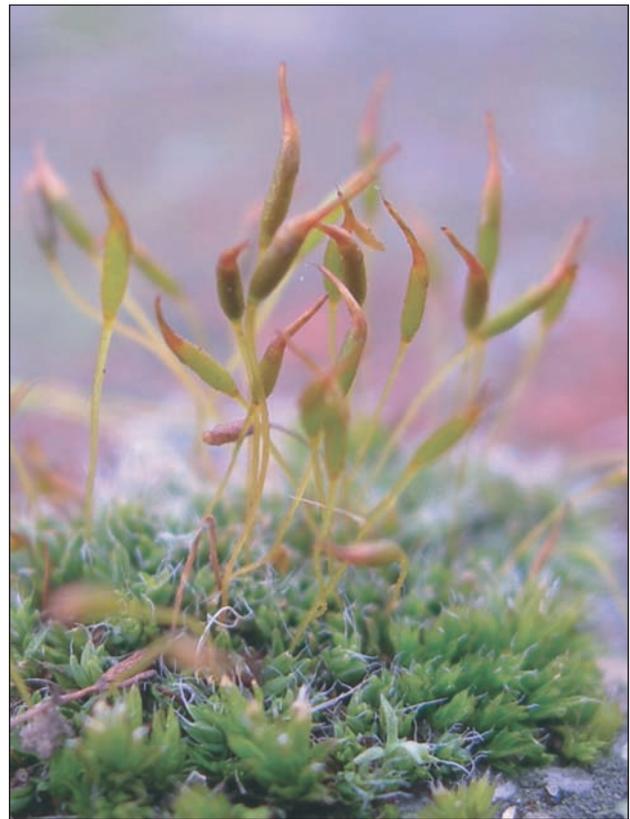


Fig. 1 Wall screw-moss (*Tortula muralis*) from a brick wall in Richmond, England. Credit: A. E. Newton.

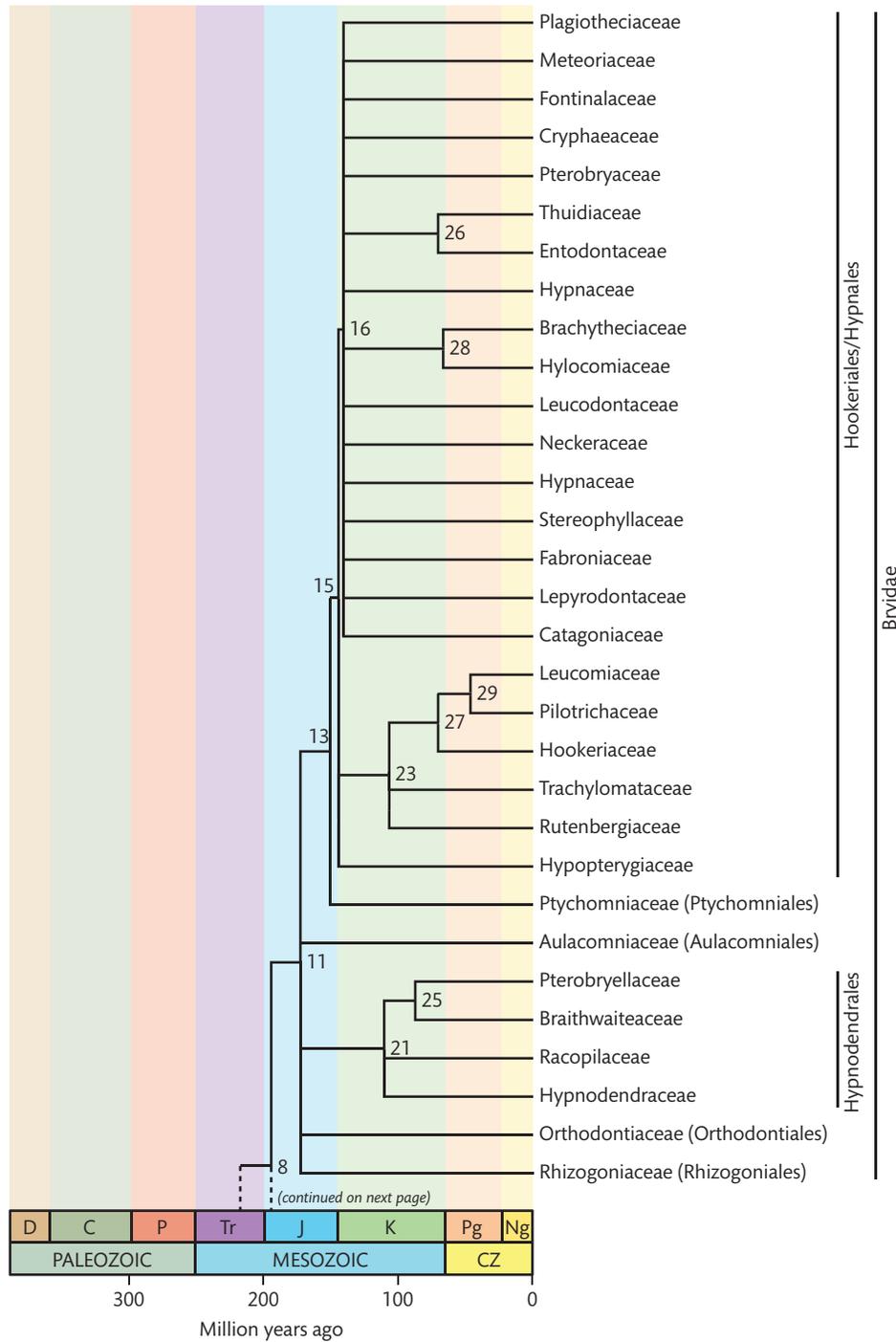


Fig. 2 Continues

terminating specialized lateral branches, so that sporophytes develop on branches. This innovation has been suggested to be a key in the evolution of the branching structure, contributing to the enormous species diversity in this group (1).

A similar morphological transition is seen in the structure of the dehiscence mechanism of the sporophyte. The earliest diverging lineages mostly have simple linear dehiscence while later diverging lineages have circumscissile dehiscence and (usually) a peristome. The peristome

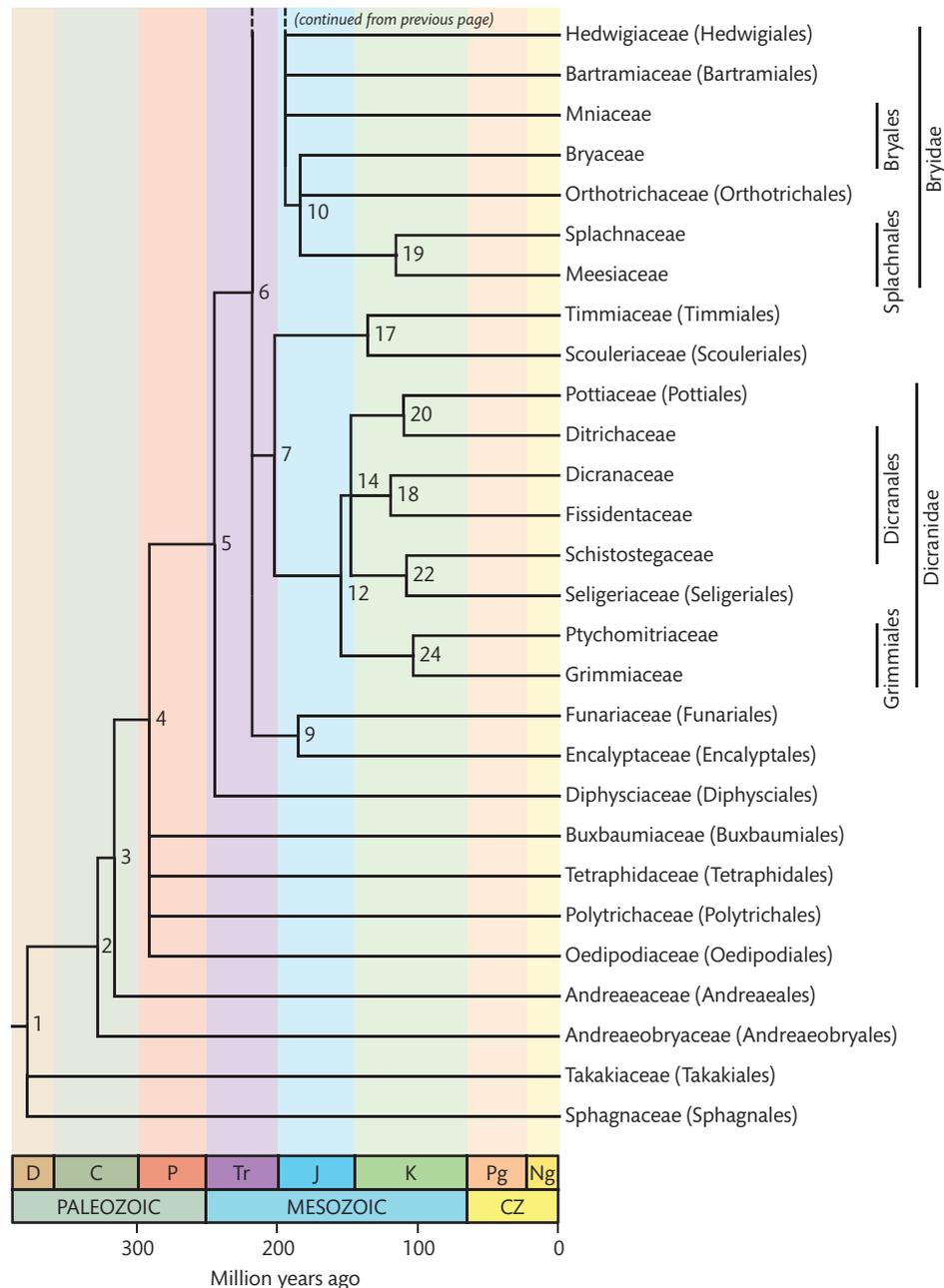


Fig. 2 A timetree of Bryophyta. Classification follows Bell *et al.* (35) for the pleurocarpids and Goffinet and Buck (4) for the remaining taxa. *Abbreviations:* C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), Ng (Neogene), P (Permian), Pg (Paleogene), and Tr (Triassic).

itself shows a transition from massive teeth composed of multiple cells (nematodontous) to more delicate and flexible teeth composed of cell walls (arthrodontous). In the arthrodontous mosses the peristome is composed of one or two rings of structures, the outer exostome teeth and the inner endostome segments, derived from the cell

walls between three concentric rings of cells. The patterns of the cell wall remnants on the peristome surfaces have allowed the correspondence of the structures to be identified (2). Mosses with both peristome rings are termed diplolepidous, and have an exostome that is robust and flexes with changes in humidity, while the endostome is

Table 1. Divergence times and their confidence/credibility intervals (CI) among Bryophyta, based on ref. (1).

Timetree		
Node	Time	CI
1	379.0	400–362
2	329.0	342–304
3	317.0	334–295
4	292.0	316–280
5	246.0	272–230
6	219.0	243–205
7	203.0	220–176
8	195.0	216–181
9	187.0	209–162
10	184.0	204–165
11	173.0	194–161
12	156.0	188–144
13	151.0	173–141
14	149.0	175–130
15	143.0	165–131
16	141.0	157–123
17	136.0	159–111
18	121.0	145–101
19	116.0	138–95
20	111.0	141–96
21	111.0	124–88
22	109.0	134–88
23	107.0	136–93
24	105.0	131–82
25	88.0	102–67
26	71.0	96–56
27	71.0	92–61
28	67.0	118–54
29	47.0	61–39

more delicate but less flexible. Changes in positions and symmetry of division patterns of the cell lineages during development (3) have allowed the recognition of opposite or alternate forms of the basic diplolepidous pattern. In the haplolepidous mosses only the endostome is well developed, consisting usually of 16 or more simple or bifid teeth, usually flexible and often highly ornamented with papillae. The exostome may be present as a very reduced ring referred to as a prostome. Other variations are also known, and in particular reduction or loss of parts of

the peristome is known in many different taxa. Both the haplolepidous- and diplolepidous-alternate forms appear to be derived from the diplolepidous-opposite group, but this area of the topology is not yet strongly resolved or supported. However, these forms comprise very large monophyletic groups, the haplolepidous Dicranidae and the diplolepidous-alternate Bryidae (*sensu* 4), with 30% and 60%, respectively, of extant species diversity (1).

Classification of the mosses has fluctuated wildly over the centuries since the starting-point publication by Hedwig in 1801 (5), depending on whether the sporophyte or gametophyte generation was given precedence (6). Certain groups in which the peristome is highly reduced or absent have been particularly problematic. However, some degree of stability was introduced with the work of Brotherus (7) and Fleischer (8) in the early twentieth century, although numerous small and not-so-small changes have continued to be made in taxon circumscription and relationships at all levels, and opinion has differed on particular taxa. For example, the Polytrichales, which have relatively well-developed vascular tissue, have been placed near the beginning (9) or end (8) of classifications, with implications of a primitive or derived status, respectively. The relatively small size and simple structures of mosses appears to have led to extensive parallelism and convergence, making the use of morphological characters for classification particularly difficult.

Cladistic methodology was adopted early by bryologists, one of the earliest applications of Hennigian principles was a generic revision (10) of the moss Family Mniaceae in 1968, and in 1984 a morphological cladistic analysis (11) of the bryophytes established the very basic elements of the pectinate grade (Sphagnales (Andreaeales (Tetraphidales (Polytrichales (Buxbaumiales (Bryales)))))) most of which is still accepted. A pioneering series of cladistic analyses (using morphological data) explored the relationships of the pleurocarpous mosses (12). However, it was not until the advent of DNA sequencing that sufficient data were available to explore relationships in detail. Since the late 1990s studies using single plastid or multigene phylogenies (often including morphological data) have established the topology now widely recognized. These have included both larger studies that established the “backbone” topology (13–17) and others that provided resolution of smaller taxonomic groups (18–20). However, although the general pattern emerged quite quickly, certain problem areas have resisted resolution.

A long-standing problem has been resolution of the relationships of the green algae and basal land plants, which also impacts the question of whether the mosses

are monophyletic. Many combinations of the four terrestrial groups (liverworts, mosses, hornworts, and vascular plants), with subdivisions, have been retrieved with strong support, using different data and taxon sampling (21–23). The genus *Takakia*, historically placed in the liverworts, was recognized as a moss when sporophytes were finally discovered (24), supported by molecular data that often showed a weak close relationship (15, 25) with *Sphagnum* as close to all other mosses. Different arrangements have been found, including *Andreaea* and the nematodontous mosses (Polytrichales, *Tetraphis*, etc.) close to *Sphagnum*, *Takakia* and all other mosses (25) but these do not contradict the evidence for monophyly.

The sparse and relict monotypic genus *Oedipodium*, found in cool temperate or montane habitats, lacks a peristome and had been placed with the diplolepidous-opposite Funariales until molecular evidence proposed a relationship either close to all peristomate mosses (15, 26), or basal in the Polytrichales clade close to all remaining peristomate mosses (26). These positions are both plausible morphologically.

Within the basal arthrodontous mosses relationships are still not conclusively resolved. The diplolepidous-alternate (Bryidae) and haplolepidous mosses (Dicranidae) both clearly form monophyletic clades, although the circumscription of the latter is not yet strongly supported (27). However, the mosses with arthrodontous peristomes that are neither clearly haplolepidous nor diplolepidous-alternate (Funariaceae, Disceliaceae, Encalyptaceae, Gigaspermaceae, Catascopiaceae, and Timmiaceae, see 28) have been variously placed. Some have traditionally been regarded as diplolepidous-opposite while others are anomalous or lack peristomes. Two hypotheses were suggested by Goffinet and Buck (4, p. 210): (1) Funariales and Encalyptaceae form a clade close to the haplolepidous mosses (1, 16, 27) and these share an “opposite” peristome arrangement and (2) the haplolepidous and diplolepidous-alternate mosses (Dicranidae plus Bryidae) form a clade (28–30). The diplolepidous-opposite and anomalous mosses have also been shown to be paraphyletic relative to the combined clade of Dicranidae and Bryidae (15–17). However, recent studies are beginning to converge on support for a topology with the clade of diplolepidous-alternate mosses close to a clade composed of paraphyletic diplolepidous-opposite and anomalous mosses with a monophyletic clade of haplolepidous mosses (1, 27).

Within the Dicranidae a number of clades have been established (27) although support for several of these is weak, and the backbone topology is mostly unsupported.

The Bryidae is strongly supported as monophyletic (14–16, 31) and includes several groups that are

morphologically distinct and in which some relationships have been established. However, with the exception of certain critical distal nodes, the relationships between most of the groups are obscure, either unresolved or unsupported, and with little congruence between analyses. In particular, the positions of the Orthotrichales and Hedwigiaceae, and the identity of the closest relative of the pleurocarpous mosses, are not clear. Several taxa have been proposed as candidates for closest relative of the pleurocarp clade, including Orthotrichaceae (28), Mniaceae (1, 32), Bartramiaceae (31), Bartramiaceae with Hedwigiaceae (17), or Bartramiaceae, Hedwigiaceae, and Mniaceae (33), *Orthodontium* (4), or *Aulacomnium* (14, 34). Recent work (35) has shown the Orthodontiaceae and Aulacomniaceae to be included within the monophyletic clade of pleurocarpous mosses, with the Orthotrichales closest to the pleurocarps and the Bartramiaceae placed in a more distant position. This relationship for the Orthotrichales has previously been proposed by other authors (32), but there is also evidence for a position of the Orthotrichales in a more basal position in the Bryinae (32). The monophyly of the clade including the lineages of pleurocarpous mosses (pleurocarpids = Aulacomniales, Orthodontiales, Rhizogoniales, Hypnodendrales, and Hypnidae) and the relationships of the basal clades of core pleurocarps (Hypnodendrales and Hypnidae) has recently been established (32, 33, 35, 36). However, problems remain unresolved in the homocostate pleurocarps, the vast majority of taxa traditionally classified in the Hypnales, Hookeriales, and Leucodontales, and characterized by an undifferentiated costa. The revelation that the Leucodontales and Hypnales s.s. are both polyphyletic (37) was tempered by the continued recognition of the Hookeriales and establishment of a new order, the Ptychomniales (38), but there is now increasing evidence (1, 39, 40) that the Hypnales s. l. are also paraphyletic relative to the Hookeriales. In addition to the Ptychomniales, two controversial lineages may be recognized—the Hypopterygiaceae as an entity separate from the Hookeriales (1, 34, 40), and a clade containing the Hookeriales and various taxa of Hypnales s. l. but of uncertain affinity, such as *Catagonium*, *Pseudocryphaea*, *Rutenbergia*, and *Trachyloma*. The circumscription of this clade has yet to be finalized, but where sampling was adequate and the topology not constrained, several published and unpublished studies have supported its existence (1, 28, 34). Finally, within the Hypnales s. l., there is very little resolution of relationships. Where published molecular studies exist, individual families may be shown to be monophyletic (e.g., Brachytheciaceae and Meteoriaceae, 41, 42) or polyphyletic (Amblystegiaceae,

43–45), frequently with changes in circumscription (46). A very few well-supported clades are consistently found by different studies, for example that consisting of exemplars of the Rigodiaceae, Lembophyllaceae, Echinodiaceae, Thamnobryaceae, Leptodontaceae, and Neckeraceae (28, 34, 37, 45, 47) although again the circumscription of this clade has yet to be finalized since the circumscription of the individual families is also being reassessed.

As yet there is only one published study proposing molecular divergence times for mosses (1), although a study on liverworts (48) includes a single relevant estimate, for the divergence of mosses from liverworts. A study of the pattern of diversification in the pleurocarpous mosses (18) did not include divergence time estimates. Until recently the lack of a resolved topology for the mosses hindered such work, but the shortage of moss fossils suitable for use for calibration or as constraints (1, 49) is also a problem, necessitating the use of fossils outside the group. Both studies providing divergence time estimates used a penalized likelihood approach using r8s and cross validation, for topologies derived by Bayesian inference with only nodes $\geq 95\%$ PP recognized. However, the topologies for the relationships of the basal land plants and the calibration ages differed. The first study used a fixed calibration age of 450 Ma for the origin of the land plants, based on a conservative date for the appearance of spore tetrads (50), and mosses were estimated to have diverged from other land plants at 403 Ma. The second study used a calibration point based on the earliest split in the vascular plants at 430 Ma (51), with a fixed maximum age constraint of 475 Ma for the oldest fossils (controversially) accepted as land plants (52). Here mosses were estimated to have diverged from other land plants (liverworts) at 454 Ma. However, the methodological differences between the studies prevent meaningful comparison.

The moss timetree (Fig. 2, Table 1) shows the first split in the lineage (Node 1—between *Sphagnum/Takakia* and the other mosses) at around 380 Ma, and the shift from predominantly linear to circumscissile sporophyte dehiscence (Node 4) at 292 Ma, with the appearance of the peristome presumably shortly thereafter. In the nematodontous mosses the Family Polytrichales shows diversification from at least the Triassic (226 Ma), with the earliest diverging extant taxon (1) a relict species (*Alophosia azorica*, not shown) found only on Macaronesia. This species lacks the photosynthetic lamellae and peristome structures characteristic of the order, while its closest relatives have the lamellae poorly developed and are also relictual in their distribution (26). One of the few

moss fossils sufficiently well characterized to be placed in phylogenetic topologies is *Eopolytrichum* (53), from the Cretaceous (Campanian) at 80 Ma. This species shows derived features that allow it to be placed in a quite distal position in the family (26, 54), but there is not yet sufficient resolution to allow its generic relationships to be finalized, and it therefore cannot yet be used as a constraint in molecular divergence analyses.

The first taxa with early forms of the arthrodontous peristome had appeared (Node 5) by 246 Ma, but this area of the topology is very sparse despite almost complete generic sampling. This relates to the period of the Permian through to the late Triassic, and it is assumed that very few lineages survived the Permian–Triassic extinction, although there is fossil evidence (55, 56) for a diverse Permian bryoflora markedly different from extant taxa. Only 10 lineages passed through this bottleneck to the present day (1), and of these the majority are either extremely depauperate or show evidence of recent divergence (e.g., Sphagnales, 57), while just one lineage, the arthrodontous mosses, contains 95% of extant species diversity. The arthrodontous mosses diverged (Node 6) around 219 Ma into various forms, including haplolepidous, diplolepidous-opposite, and diplolepidous-alternate. The haplolepidous mosses were found (1) to be derived from within a group of mosses with diplolepidous-opposite or anomalous peristomes, but the relationship was not supported. Considerable variation in peristome morphology is apparent in taxa in all the earlier diverging lineages, but during the Jurassic two major forms appear to have stabilized, the diplolepidous-alternate (Bryidae) from 195 Ma (Node 8) and the haplolepidae (Dicranidae) from 156 Ma (Node 12). Apart from the Orthotrichales, which have a distinctive morphology and probably diverged from the Bryidae from around 184 Ma (Node 10), further variation seems to have mostly been limited to differences in sculpturing and relative development of parts, with derived reduction and loss of features occurring in parallel in many lineages.

The circumscription of the Dicranidae and relationships within the clade have recently been established (27). The clades resolved by this analysis are mostly congruent with those recognized in the timetree, differing mainly in the placement of *Timmia*. The haplolepidae diverged (Node 7) around 203 Ma from the proto-haplolepidae (27), represented in the timetree by *Scouleria* and Timmiaceae, and further divergence of the major clades (Nodes 12, 14, 18, 20, 22, 24) occurred between 156 and 105 Ma. The split between the Grimmiaceae plus Ptychomitriaceae (27, Clade B) and the remaining Dicranidae (Node 12) occurred in the

Jurassic at 156 Ma, while further splits between genera representing major groups occurred in the late Jurassic through to early Cretaceous, at 105 Ma (Node 24).

The Bryidae diverged from the other arthrodontous mosses in the late Triassic, at 219 Ma, followed by the split (Node 8) at 195 Ma between a clade composed of the Splachnales, Orthotrichales, and the Bryaceae, and the remaining diplolepidous-alternate mosses, including the other members of the (paraphyletic) Bryales. Due to the lack of resolution of the backbone topology and low sampling, it was not possible to draw many conclusions about divergence times between most of these groups, but the few exemplars included show a pattern of divergence between families from the late Jurassic to the late Cretaceous. Although dates for the early-diverging Bryalean lineages could not be proposed, the pleurocarpid node (Node 11) is well supported by both molecular and morphological data. This node, at 173 Ma, represents the divergence of the lineages containing pleurocarpous taxa (with gametangia on lateral specialized branches). Not every lineage is exclusively pleurocarpous, and there are several variations in morphology, indicating that this feature was unstable between about 173 and 151 Ma. Again, most of the early-diverging nodes within the pleurocarpids were not sufficiently well supported for divergence times to be proposed, but the appearance of the homocostate pleurocarps (Node 13) at 151 Ma was followed by two divergences in a very short period. Within the homocostate pleurocarps there is a grade of four lineages diverging between 151 and 141 Ma, starting with the Ptychomniales and followed by the Hypopterygiaceae, which diverged from the remaining pleurocarps (Node 15) at 143 Ma. The most substantial split (Node 16) occurred at 141 Ma, between the clade containing the Hookeriales with some associated Hypnalean taxa, and the remaining members of the Hypnales. Within the expanded hookerialian clade (Nodes 23, 27, and 29) divergence occurred at about the family level from 107 to 47 Ma, that is through the Cretaceous and into the Cenozoic. Major diversification in the Hypnales clade also seems to have occurred in the Cretaceous but sampling within this very large clade was not sufficiently dense to allow more than two divergence estimates (Nodes 26 and 28, late Cretaceous). While it is not yet possible to date the divergence of most clades at the family level, several nodes in the original analysis (1) provide support for the divergence of genera within clades, indicating that divergences at this level have occurred, in different groups, over a wide range of time, so that some “species” may be older than “genera” in other groups.

After the split between the Ptychomniales and the remaining homocostate pleurocarps there were few changes in gametangial position, but greatly increased variation in branching architecture, leaf morphology, and peristome reduction and ornamentation. Much of this variation seem to have been associated with changes in habitat utilization, such as colonization of semiaquatic habitats, and the appearance of epiphytism as the increasing diversity of the angiosperm forest provided novel habitats (41). Studies of diversification patterns (18) in the pleurocarpous mosses indicate the possibility that rates of diversification were elevated early in the history of this group, but decreased in later periods. However, evaluation of these alternative hypotheses will depend on adequate resolution of the topology and estimates of divergence times for critical nodes of this very large clade.

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