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Ordinal relationships of pleurocarpous mosses, with special emphasis on the Hookeriales

Abstract Sequence data from four DNA regions, namely, chloroplast *trnL-trnF* and *rps4*, mitochondrial *nad5*, and nuclear 26S rDNA, were surveyed from 89 taxa traditionally associated with the Hookeriales, five Hypnales and five outgroups. Phylogenetic reconstruction was performed using the maximum parsimony and maximum likelihood optimality criteria and by Bayesian phylogenetic inference. Thirteen morphological characters were optimized on the resulting phylogeny using maximum likelihood. Inferences of character evolution based on the molecular phylogeny suggest that (1) the core of pleurocarpous mosses (i.e. the Hypnanae) is best defined and thus distinguished from the Ptychomnianaes by smooth rather than furrowed capsules, (2) a synapomorphy for the Ptychomnianaes is the short and double (or absent) costa and (3) the Hookeriales are defined by undifferentiated alar cells. The Ptychomniaceae plus Garovagliaceae are recognized as a single family in its own order, the Ptychomniales ord. nov. and superorder, the Ptychomnianaes, superord. nov. This superorder is sister to the combined Hypnales and Hookeriales, i.e. the Hypnanae. The Hookeriales are interpreted as consisting of seven families, the Hypopterygiaceae, Saulomataceae fam. nov., Daltoniaceae, Schimperobryaceae fam. nov., Hookeriaceae, Leucomiaceae and Pilotrichaceae. The Adelothechiaceae are embedded within the Daltoniaceae and considered synonymous with that family. Within the Ptychomniaceae, *Ptychomniella* is raised from a subgenus of *Ptychomnion* to generic status. *Euptychium setigerum* and its monospecific section, *Crassisubulata*, are transferred to *Garovaglia*. *Callicostella diatomophila* is transferred to *Diploneuron*. Additional alterations at the generic level await more data.

Introduction

The Hookeriales have long generated interest among bryologists. Compared with plants of the Hypnales, the order that encompasses almost all north temperate pleurocarpous mosses, those of the Hookeriales are exotic looking, often with large, lax cells, strong double costae and mitrate calyptrae. It is therefore not surprising that the order has garnered considerable interest in recent years, resulting in multiple hypotheses about relationships within the order and to other orders.

Brotherus (1925), following Fleischer (1923), recognized six families in the Hookeriales, the Nemataceae (Ephemeropsidaceae), Pilotrichaceae (including only *Pilotrichum* and *Pilotrichidium*), Hookeriaceae (with four subfamilies and 34 genera), Symphyodontaceae (monogeneric), Leucomiaceae (for *Leucomium* and *Vesiculariopsis*) and Hypopterygiaceae (with two subfamilies). This was the system most widely followed by bryologists for over 50 years (e.g. Welch, 1976). Miller

(1971) proposed a new classification for the order, recognizing eight families, Pilotrichaceae (with 15 genera) Hookeriaceae (with two subfamilies and 13 genera), Distichophyllaceae (with six genera), Daltoniaceae (for *Daltonia* and *Bellia* [= *Crosbya*]), Symphyodontaceae (monogeneric), Leucomiaceae (with seven genera), Ephemeropsidaceae (monogeneric), Hypopterygiaceae (with three genera) and Cyathophoraceae (for *Cyathophorum* and *Cyathophorella*). This system gained little support. Shortly afterward, Crosby (1974) proposed a new classification that was based solely on peristomial features. Those genera with striate exostome teeth were placed in the Hookeriaceae and those with papillose exostome teeth were relegated to the Daltoniaceae. Pairs of genera that are almost identical gametophytically, but differ by peristome features, were placed in different families. The next complete classification of the order was by Buck (1987, 1988). In this system, which stressed gametophytic rather than sporophytic characters, five families were recognized: the Hookeriaceae (with six genera), Daltoniaceae (with eight genera, including *Ephemeropsis*), Adelothechiaceae (for *Adelothecium*

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and *Bryobrothera*), Leucomiaceae (for *Leucomium* and *Rhynchostegiopsis*) and Callicostaceae (=Pilotrichaceae, with 23 genera). The Symphyodontaceae were transferred to the Hypnales and the Hypopterygiaceae to the Bryales. Subsequently, Whittmore & Allen (1989) adopted a conservative family classification for the Hookeriales, recognizing the Daltoniaceae (including the Adellotheciaceae), the Ephemeropsidaceae and the Hookeriaceae (including the Pilotrichaceae and Leucomiaceae) and tentatively suggested that the Hypopterygiaceae may belong in the order. Although *Symphodon* and putative relatives (*Chaetomitrium* and *Dimorphocladon*) are included in a morphological table, they are not otherwise mentioned in the text and presumably excluded from the order.

The advent of DNA sequencing has offered the possibility of independent phylogenies, unbiased by human interpretation of morphology. Two recent studies inferring phylogenetic relationships based on cpDNA (Buck *et al.*, 2000; De Luna *et al.*, 2000) included representation of the Hookeriales in studies primarily aimed at reconstructing the phylogeny of the Hypnales. Buck *et al.* (2000) studied *trnL-trnF* and *rps4*, and included eight taxa of Hookeriales *s.str.*, plus *Hypopterygium*, *Ptychomnion*, *Glyphothecium* and *Garovaglia*. De Luna *et al.* (2000) sequenced *trnL-trnF*, *rps4* and *rbcL*, but included only *Hookeria*, *Lepidopilum*, *Hypopterygium* and *Ptychomnion*. Both reports indicated a close relationship of the Ptychomniaceae with the Hookeriales and the inclusion of *Hypopterygium* in the same general relationship. In Buck *et al.* (2000), *Hypopterygium* was sister to the Hookeriales and the Ptychomniaceae/Garovagliaceae were embedded within the order. De Luna *et al.* (2000), with smaller taxon representation, also placed *Hypopterygium* sister to the rest of the order and *Ptychomnion* sister to the Hookeriales *s.str.*

The current study was undertaken with four objectives in mind, (1) to understand the relationships of the major orders of pleurocarpous mosses, (2) to test the circumscription of the Hookeriales as traditionally defined, (3) to better resolve the relationships of the Hypopterygiaceae, Ptychomniaceae, Garovagliaceae, as well as the genera and families more commonly included in the Hookeriales and (4) to focus on the evolution of morphological characters that are traditionally used to diagnose the Hookeriales.

Materials and methods

Taxon and DNA sampling

Eighty-nine taxa were sampled from the Hookeriales and five taxa from the Hypnales. In addition, five taxa were chosen as outgroups following Cox *et al.* (2004). Table 1 presents the taxa sequenced and GenBank accession numbers of the sequences used in the analyses. Classification here follows Buck & Goffinet (2000). Species identifications were confirmed by the authors. Four DNA regions were selected for analysis: partial 26S ribosomal RNA gene sequences (26S), mitochondrial intron sequences from NADH protein-coding subunit 5 (*nad5*), chloroplast ribosomal small protein 4 (*rps4*) and the *trnL* (UAA) 5' exon – *trnF* (GAA) region (*trnL-trnF*).

Molecular protocols

Total genomic DNA was extracted using a standard CTAB procedure (Doyle & Doyle, 1990), with subsequent cleaning using the Wizard DNA Clean-up Kit (Promega) and elution in 50 μ l of nanopure water. Double-stranded DNA templates were prepared by polymerase chain reaction (PCR), employing 30 cycles of 1 min at 97 °C, 1 min at 52 °C and 3 min at 72 °C, preceded by an initial melting step at 97 °C and followed by a final extension period of 7 min at 72 °C. The annealing temperature was lowered to 45 °C when amplification failed at the higher temperature. Amplification and sequencing primers for *rps4* and *trnL* are described in Buck *et al.* (2000 — *rps4* and *trnL-trnF*) and Shaw (2000 — 26S). The *nad5* region was amplified with 4F (GAAGGAGTAGGTCTCGCTTCA) and 3R (AAAACGCCTGCTGTTACCAT) and sequenced with the same primers plus Ki (Beckert *et al.*, 1999). Amplification was achieved using 1.25 units *Taq* polymerase (Perkin Elmer) in a 50 μ l reaction volume (1 \times thermostable buffer, 2.5 mM MgCl₂, 200 mM dNTPs, 300 mM primer). Fragments were cleaned on a QIAquick (Qiagen) PCR purification spin column and sequenced using each amplification primer in conjunction with the ABI Prism Dye Terminator Cycle Sequencing Ready Reaction Kit (P. E. Applied Biosystems). Sequencing products were resolved on an ABI (model 3700) automated sequencer.

DNA sequence editing and alignment

For each taxon and sequenced DNA region, forward (5'–3') and reverse (3'–5') sequences were assembled and checked for inaccurate base calling using Sequencher (vers. 4.1, Gene Codes Corp.). Consensus sequences were aligned manually using Se-AL (vers. 2, <http://evolve.zoo.ox.ac.uk/software/Se-AL/main.html>) and regions of ambiguous alignment and incomplete data (*e.g.* at the beginning and end of sequences) were identified and excluded from subsequent analyses.

Morphological characters

Morphological characters were chosen that traditionally either have been used in segregating taxa within the Hookeriales, or more widely in pleurocarpous mosses (see Table 2). As many such characters as possible were chosen with discrete character states. The following characters were used.

1. Capsule presentation: exserted vs. immersed. This character is a reflection of seta length in comparison to the length of perichaetial leaves. Immersed capsules in pleurocarpous mosses are often associated with an epiphytic habit.
2. Capsule surface: smooth vs. furrowed. Furrowed capsules are diagnostic for the traditional Ptychomniaceae, but otherwise are uncommon within the pleurocarps.
3. Exostome teeth: with zig-zag centre line vs. furrowed. Most moss exostome teeth have a zig-zag centre line. However, furrowed exostome teeth occur in several, seemingly unrelated lineages, sometimes in association with epiphytism.
4. Annulus: differentiated vs. not differentiated. Cells around the mouth of the capsule that aid in dehiscence of the

Taxon	Voucher	rps4	trnL	nad5	26S
Outgroup taxa:					
<i>Aulacomnium turgidum</i>	Hedderson 6385 (RNG)	AF023809	AF023728	AY312869	AY330427
<i>Bescherellia brevifolia</i>	Streimann 38462 (RNG)	AJ251313	AF215903	AY452322	AY452402
<i>Braithwaitea sulcata</i>	Streimann 38403 (RNG)	AF023820	AF023745	AY452323	AY452403
<i>Orthodontium lineare</i>	Hedderson s.n (RNG)	AF023800	AF023768	AY312881	AY330443
<i>Pyrrhobryum vallis-gratiae</i>	Hedderson 11755 (RNG)	AF023825	AF023754	AY312885	AY330448
Ingroup					
<i>Achrophyllum dentatum</i>	Australia, Streimann 61075	AY306853	AY306687	AY452315	AY452396
<i>Achrophyllum quadrifarium</i>	New Zealand, Streimann 51258	AY449660		AY452316	
<i>Actinodontium sprucei</i>	French Guiana, Buck 37977	AY306855	AY306689	AY452317	AY452397
<i>Adelothecium bogotense</i>	Brazil, Vital & Buck 19649	AY306856	AY306690	AY452318	AY452398
<i>Ancistrodes genuflexa</i>	Chile, Holz & Franzaring CH 00-154	AY306863	AY306697	AY452319	AY452399
<i>Arbusculohypopterygium arbusculum</i>	Chile, Holz & Franzaring CH 00-80	AY449665	AY449671	AY452366	AY452445
<i>Beeveria distichophylloides</i>	New Zealand, Fife 11150	AY306867	AY306701	AY452320	AY452400
<i>Benitotania elimbata</i>	Malaysia, Akiyama & Suleiman, 2002	AY449661	AY449669	AY452321	AY452401
<i>Brachythecium salebrosum</i>	Goffinet 4723 (DUKE)	AF143027	AF161120	AY312871	AY330429
<i>Brymela tutezona</i>	Panama, Salazar et al. 13656	AY449662			AY452404
<i>Brymela websteri</i>	Dominica, Schäfer-Verwimp 17861	AY306868	AY306702	AY452324	AY452405
<i>Bryobrothera crenulata</i>	Australia, Streimann 57716	AY306869	AY306703	AY452325	AY452406
<i>Callicostella colombica</i>	French Guiana, Buck 18797	AY449663			AY452407
<i>Callicostella diatomophila</i>	Cuba, Buck 23312	AY306870	AY306704	AY452326	AY452408
<i>Callicostella pallida</i>	French Guiana, Holz FG 00-14	AY306872	AY306706	AY452328	AY452410
<i>Callicostellopsis meridensis</i>	Venezuela, Griffin PV-898	AY306871	AY306705	AY452327	AY452409
<i>Calypstrochaeta brownii</i>	Australia, Streimann 60613	AY306873	AY306707	AY452329	AY452411
<i>Calypstrochaeta japonica</i>	China, Redfearn 35826	AY306874	AY306708	AY452330	AY452412
<i>Canalohypopterygium tamariscinum</i>	New Zealand, Frey & Pfeiffer 98-T10C (CHR)	AY306878	AY306712	AY452331	AY452413
<i>Catharomnion ciliatum</i>	New Zealand, Streimann 51423	AY306879	AY306713	AY452332	AY452414
<i>Chaetomitrium borneense</i>	Brunei Temburong, Tan 95-1116	A306880	AY306714	AY452333	AY452415
<i>Chaetomitrium dusenii</i>	Equatorial Guinea, Heras 499/94	AY306881	AY306715	AY452334	AY452416
<i>Cladomnion ericoides</i>	New Zealand, Streimann 51478	AY306884	AY306718	AY452336	AY452418
<i>Cladomniopsis crenato-obtusa</i>	Chile, Buck 41360	AY306883	AY306717	AY452335	AY452417
<i>Crosbya straminea</i>	New Zealand, Fife 10379	AY306887	AY306721		AY452421
<i>Crossomitrium epiphyllum</i>	French Guiana, Buck 33259	AY306885	AY306719	AY452337	AY452419
<i>Crossomitrium rotundifolium</i>	French Guiana, Buck 33042	AY306886	AY306720	AY452338	AY452420

Table 1 Voucher information and GenBank accession numbers for samples included in the molecular analyses. All specimens are deposited at NY unless otherwise indicated.

Taxon	Voucher	rps4	trnL	nad5	26S
<i>Cyathophorella hookeriana</i>	Thailand, Akiyama Th-39	AY306890	AY306724	AY452340	AY452423
<i>Cyathophorum adiantum</i>	Japan, Yamaguchi (Bryophytes of Asia, fasc. 6: #128)	AY306891	AY306725	AY452341	AY452424
<i>Cyathophorum bulbosum</i>	Australia, Streimann 55638	AY306889	AY306763	AY452339	AY452422
<i>Cyclodictyon albicans</i>	Colombia, Churchill <i>et al.</i> 18795	AY306892	AY306726	AY452342	AY452425
<i>Cyclodictyon roridum</i>	Ecuador, Buck 39563	AY306893	AY306727	AY452343	AY452426
<i>Daltonia gracilis</i>	Ecuador, Buck 39508A	AY306895	AY306728	AY452344	AY452427
<i>Daltonia longifolia</i>	Ecuador, Buck 39508	AY306895	AY306729	AY452345	AY452428
<i>Dendroclyathophorum decolyi</i>	Japan, Matsui 7264	AY306896	AY306730	AY452346	AY452429
<i>Dichelodontium nitidum</i>	New Zealand, Macmillan BH 99/14 (CHR)	AY449664	AY449670	AY452347	
<i>Dimorphocladon borneense</i>	BruneiTemburong, Tan 95-1060	AY306898	AY306732	AY452348	AY452430
<i>Diploneuron connivens</i>	Jamaica, Crosby 13732	AY306899	AY306733	AY452431	
<i>Distichophyllidium nymanianum</i>	Malaya, Mohamed & Damanhuri 1118 Musci Malaysiani Exsiccati, fasc. 2: #29	AY306901	AY306735	AY452350	
<i>Distichophyllum freycinetii</i>	U.S.A., Hawaii, Flynn 5151	AY306900	AY306734	AY452349	AY452432
<i>Distichophyllum pulchellum</i>	New Zealand, Streimann 51380	AY306902	AY306736	AY452351	AY452433
<i>Ephemeropsis trentepohlioides</i>	New Zealand, Macmillan 95/94	AY306906	AY306740		
<i>Euptychium robustum</i>	Australia, Streimann 56137	AY306907	AY306741	AY452352	AY452434
<i>Euptychium setigerum</i>	Australia, Streimann 45332	AY306908	AY306742	AY452353	
<i>Euptychium vitiense</i>	Fiji, Buck 7255	AY306909	AY306743		AY452435
<i>Garovaglia binsteadii varmirabilis</i>	Papua New Guinea, Iserentant B-73	AY306913	AY306747	AY452354	AY452436
<i>Garovaglia compressa</i>	Seram, Akiyama C-16340	AY306914	AY306748	AY452355	
<i>Garovaglia elegans</i>	Papua New Guinea, Hoffman 89-476	AY306915	AY306748	AY452356	AY452437
<i>Garovaglia powellii varbrevifolia</i>	Papua New Guinea, Iserentant B-81	AY306916	AY306750	AY452357	
<i>Garovaglia subelegans</i>	Papua New Guinea, Hoffmann 89-505	AY306918	AY306752	AY452358	AY452438
<i>Glyphothecium sciuroides</i>	Australia, Streimann 59969	AY306919	AY306753	AY452359	
<i>Hampeella alaris</i>	New Zealand, Buck 6865	AY306920	AY306754		
<i>Hampeella pallens</i>	Australia, Streimann 44664	AY306921	AY306755	AY452360	AY452439
<i>Hemiragis aurea</i>	Costa Rica, Dauphin 2949	AY306922	AY306756	AY452361	AY452440
<i>Hookeria acutifolia</i>	Ecuador, Buck 39558	AY306929	AY306764	AY452362	AY452441
<i>Hookeria lucens</i>	U.S.A., Buck 37714	AY306930	AY306764	AY452363	AY452442
<i>Hypnella diversifolia</i>	Ecuador, Buck 39277	AY306931	AY306765	AY452364	AY452443
<i>Hypnella pallescens</i>	French Guiana, Buck 37840	AY306932	AY306766	AY452365	AY452444
<i>Hypopterygium tamarisci</i>	Mexico, Buck 35314	AY449666	AY449672	AY452367	AY452446
<i>Lepidopilidium laevisetum</i>	Brazil, Schäfer-Verwimp 9237	AY306937	AY306771		

<i>Lepidopilidium portoricense</i>	French Guiana, <i>Buck</i> 37825	AY306939	AY306773	AY452369	AY452448
<i>Lepidopilum polytrichoides</i>	French Guiana, <i>Buck</i> 33307	AY306938	AY306772	AY452368	AY452447
<i>Lepidopilum scabrisetum</i>	Ecuador, <i>Buck</i> 39436	AY306940	AY306774	AY452370	AY452449
<i>Leskeodon auratus</i>	Puerto Rico, <i>Buck</i> 18286	AY306906	AY306776	AY452371	AY452450
<i>Leucomium steerei</i>	Venezuela, <i>Buck & Brewer</i> 15592		AY449673		AY452451
<i>Leucomium strumosum</i>	French Guiana, <i>Holz FG</i> 00-268	AY306943	AY306777	AY452372	AY452452
<i>Lopidium concinnum</i>	Australia, <i>Streimann</i> 43706	AY306945	AY306779	AY452373	AY452453
<i>Lopidium concinnum</i>	Chile, <i>Holz & Franzaring CH</i> 00-135	AY306946	AY306780	AY452374	AY452454
<i>Lopidium plumarium</i>	Brazil, <i>Vital & Buck</i> 20001	AY306947	AY306781	AY452375	AY452455
<i>Philophyllum tenuifolium</i>	Brazil, <i>Schäfer-Verwimp</i> 14548	AY306973	AY306807	AY452376	AY452456
<i>Pilotrichidium antillarum</i>	Puerto Rico, <i>Buck</i> 16127	AY306975	AY306809	AY452377	AY452458
<i>Pilotrichidium callicostatum</i>	Colombia, <i>Betancur et al.</i> 4725	AY306977	AY306811		AY452460
<i>Pilotrichum andersonii</i>	Trinidad, <i>Djan-Chékar</i> 94-678	AY306974	AY306808		AY452457
<i>Pilotrichum bipinnatum</i>	French Guiana, <i>Holz FG</i> 00-33	AY306976	AY306810	AY452378	AY452459
<i>Pilotrichum procerum</i>	Dominica, <i>Schäfer-Verwimp</i> 17941	AY306978	AY306812	AY452379	
<i>Ptychomnion aciculare</i>	Australia, <i>Streimann</i> 43623	AY306983	AY306817	AY452380	
<i>Ptychomnion cygnisetum</i>	Chile, <i>Holz & Franzaring CH</i> 00-72	AY306984	AY306818	AY452381	AY452461
<i>Ptychomnion ptychocarpon</i>	Chile, <i>Holz & Franzaring CH</i> 00-53	AY306985	AY306819	AY452382	
<i>Rhynchostegiopsis flexuosa</i>	Belize, <i>Allen</i> 18710	AY449667		AY452383	AY452462
<i>Rhynchostegiopsis tunguraguana</i>	Colombia, <i>Ramírez</i> P7690	AY306986	AY306820		AY452463
<i>Sauloma tenella</i>	Australia, <i>Streimann</i> 59726	AY306987	AY306821	AY452384	AY452464
<i>Schimperobryum splendissimum</i> var. <i>perdentatum</i>	Chile, <i>Holz & Franzaring Ch</i> 00-156 Bryotheca Göttingensis, fasc. 1: #20	AY306988	AY306822	AY452385	AY452465
<i>Stenodictyon pallidum</i>	Dominican Republic, <i>Buck</i> 7940	AY306997	AY306831		AY452466
<i>Stenodictyon wrightii</i>	Ecuador, <i>Buck</i> 10014	AY306998	AY306832	AY452386	AY452467
<i>Symphyodon imbricatifolius</i>	Brazil, <i>Schäfer-Verwimp</i> 14747	AY306999	AY306833	AY452387	AY452468
<i>Tetraphidopsis pusilla</i>	New Zealand, <i>Fife</i> 11592	AY307001	AY306835	AY452389	AY452470
<i>Tetrastichium fontanum</i>	Madeira, <i>Düll</i> Bryophyta Exsiccata Madeira #69	AY307000	AY306834	AY452388	AY452469
<i>Thamniopsis cruegeriana</i>	Trinidad, <i>Djan-Chékar</i> 94-652	AY307002	AY306836	AY452390	AY452471
<i>Thamniopsis incurva</i>	Trinidad, <i>Djan-Chékar</i> 94-667	AY449668	AY449674	AY452391	AY452472
<i>Thamniopsis pendula</i>	Colombia, <i>Churchill & Lineares</i> 18434	AY307003	AY306837	AY452392	AY452473
<i>Thamniopsis sinuate</i>	Colombia, <i>Callejas et al.</i> 2792	AY307004	AY306838	AY452393	AY452474
<i>Trachyxiphium drepanophyllum</i>	Brazil, <i>Vital & Buck</i> 20012	AY307005	AY306839	AY452394	AY452475
<i>Trachyxiphium guadalupense</i>	Trinidad, <i>Djan-Chékar</i> 94-670a				AY452476
<i>Trachyxiphium vagum</i>	Ecuador, <i>Buck</i> 39564	AY307006	AY306840	AY452395	AY452477

Table 1 Continued.

Taxon Outgroups	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Aulacomnium turgidum</i>	0	1	0	0	0	1	0	0	0	0	0	0	0
<i>Brachythecium salebrosum</i>	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Orthodontium lineare</i>	0	0	0	1	0	0	1	1	0	0	0	0	1
<i>Pyrrhobryum vallis-gratiae</i>	0	0	0	0	0	0	1	0	0	0	0	0	0
Taxon Ingroups													
<i>Achrophyllum dentatum</i>	0	0	0	0	1	1	1	0	1	1	0	0	0
<i>Achrophyllum quadrifarium</i>	0	0	0	0	1	1	1	0	1	1	0	0	0
<i>Actinodontium sprucei</i>	0	0	0	1	0	0	1	0	1	0	1	0	1
<i>Adelothecium bogotense</i>	0	0	0	0	1	0	1	1	1	0	0	0	0
<i>Ancistrodes genuflexa</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Beeveria distichophylloides</i>	0	0	0	0	1	0	1	0	1	1	0	0	0
<i>Benitotania elimbata</i>	?	?	0	?	1	0	1	?	?	?	0	0	0
<i>Bescherellea brevifolia</i>	0	0	0	1	0	0	0	1	0	0	0	0	0
<i>Braithwaitea sulcata</i>	0	1	0	1	0	0	0	0	0	0	0	0	1
<i>Brymela tutezona</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Brymela websteri</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Bryobrothera crenulata</i>	0	0	0	0	1	0	1	1	1	0	0	0	0
<i>Callicostella colombica</i>	0	0	0	0	1	0	1	1	1	1	1	0	0
<i>Callicostella diatomophila</i>	0	0	0	0	1	1	1	1	1	1	1	0	0
<i>Callicostella pallida</i>	0	0	0	0	1	1	1	1	1	1	1	0	0
<i>Callicostellopsis meridensis</i>	0	0	0	1	1	0	1	0	1	0	1	0	0
<i>Calyptrochaeta brownii</i>	0	0	1	0	1	0	1	1	1	1	1	0	0
<i>Calyptrochaeta japonica</i>	0	0	1	0	1	0	1	1	1	1	1	0	0
<i>Canalohypopterygium tamariscinum</i>	0	0	1	0	1	0	1	1	1	0	0	1	0
<i>Catharomnion ciliatum</i>	0	0	1	NA	1	0	1	0	1	NA	0	1	0
<i>Chaetomitrium borneense</i>	0	0	0	0	0	0	1	1	1	0	1	0	1
<i>Chaetomitrium dusenii</i>	0	0	0	0	0	0	1	?	0	0	1	0	1
<i>Cladomnion ericoides</i>	0	1	0	0	0	0	1	0	0	1	1	0	1
<i>Cladomniopsis crenato-obtusa</i>	0	1	0	0	0	1	0	0	0	1	1	0	1
<i>Crosbya straminea</i>	0	0	1	0	0	0	1	1	1	1	0	0	0
<i>Crossomitrium epiphyllum</i>	0	0	0	1	1	0	1	1	1	0	1	0	1
<i>Crossomitrium rotundifolium</i>	0	0	0	1	1	0	1	1	1	0	1	0	1
<i>Cyathophorum (Cyathophorella) hookerianum</i>	0	0	1	0	1	0	1	1	0/1	0	0	1	0
<i>Cyathophorum adiantum (Cyathophorella tonkinensis)</i>	0	0	1	0	1	0	1	1	1	0	0	1	0
<i>Cyathophorum bulbosum</i>	0	0	0	0	1	0	1	0	1	0	0	1	0
<i>Cyclodictyon albicans</i>	0	0	1	0	1	0	1	1	1	1	1	0	0
<i>Cyclodictyon roridum</i>	0	0	1	0	1	0	1	1	1	1	1	0	0
<i>Daltonia gracilis</i>	0	0	1	1	0	0	1	1	1	0	0	0	0
<i>Daltonia longifolia</i>	0	0	1	1	0	0	1	1	1	0	0	0	0
<i>Dendrocyathophorum decolyi</i>	0	0	1	0	1	0	1	1	0	0	1	1	0
<i>Dendrohypopterygium arbusculum</i>	0	0	1	0	1	0	1	0	0	0	0	1	0
<i>Dichelodontium nitidum</i>	0	1	0	1	0	1	0	1	0	0	1	0	1
<i>Dimorphocladon borneense</i>	0	0	?	?	1	0	0	?	?	?	1	0	1
<i>Diploneuron connivens</i>	0	0	0	0	0	0	1	1	1	1	1	0	0
<i>Distichophyllidium nymanianum</i>	0	0	1	1	1	0	1	1	1	0	0	0	0
<i>Distichophyllum freycinetii</i>	0	0	1	0	1	0	1	0	1	1	0	0	0
<i>Distichophyllum pulchellum</i>	0	0	1	0	1	0	1	0	1	1	0	0	0
<i>Ephemeropsis trentepohlioides</i>	0	0	0	0	0	0	1	0	1	1	1	0	0
<i>Euptychium (sect. Crassisubulata) setigerum</i>	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>Euptychium (sect. Euptychium) robustum</i>	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>Euptychium (sect. Euptychium) vitiense</i>	1	0	0	0	0	0	0	1	1	0	1	0	1
<i>Garovaglia (sect. Aristatae) subelegans</i>	1	0	0	1	0	0	0	1	0	0	1	0	1
<i>Garovaglia (sect. Baeuerlenia) binsteadii var. mirabilis</i>	1	0	0	1	0	0	0	1	1	0	1	0	1
<i>Garovaglia (sect. Compressa) compressa</i>	0	0	0	1	1	0	0	1	0	0	1	0	1
<i>Garovaglia (sect. Endotrichum) elegans</i>	0	0	0	1	0	0	0	1	0	0	1	0	1
<i>Garovaglia (sect. Garovaglia) powellii var. brevifolia</i>	1	0	0	1	0	0	0	1	1	0	1	0	1

Table 2 Morphological data matrix

Characters 1–13, with their character states, are listed following the table, in two cases (in character 9), the character state is variable. In several cases no adequate material (or literature) is available to determine the character state and a question mark (?) is used. In *Catharomnion ciliatum* the peristome is endostomial only and so the exostome characters are not applicable.

Taxon Ingroups (cont.)	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Glyphothecium sciuroides</i>	0	1	0	0	0	0	0	1	0	0	1	0	1
<i>Hampeella alaris</i>	0	1	0	0	0	0	0	1	0	0	1	0	1
<i>Hampeella pallens</i>	0	1	0	0	1	0	0	0	0	1	1	0	1
<i>Hemiragis aurea</i>	0	0	0	0	0	0	1	1	1	1	1	0	1
<i>Hookeria acutifolia</i>	0	0	0	0	1	0	1	0	1	0	1	0	0
<i>Hookeria lucens</i>	0	0	0	0	1	1	1	0	1	0	1	0	0
<i>Hookeriopsis luteo-rufescens</i>	0	0	0	0	0	0	1	1	1	1	1	0	1
<i>Hypnella diversifolia</i>	0	0	0	0	0	0	1	1	1	0	1	0	1
<i>Hypnella pallescens</i>	0	0	0	0	1	1	1	1	1	1	1	0	1
<i>Hypopterygium tamarisci</i>	0	0	1	0	1	0	1	1	0	0	0	1	0
<i>Lepidopilidium laevisetum</i>	0	0	0	0	1	0	1	1	1	1	1	0	1
<i>Lepidopilidium portoricense</i>	0	0	0	0	1	0	1	1	1	1	1	0	1
<i>Lepidopilidium polytrichoides</i>	0	0	1	1	1	0	1	0	1	0	1	0	0
<i>Lepidopilidium scabrisetum</i>	0	0	0	1	1	0	1	0	1	0	1	0	1
<i>Leskeodon auratus</i>	0	0	1	1	1	0	1	1	1	0	0	0	0
<i>Leucomium steerei</i>	0	0	0	0	1	0	1	0	0	1	1	0	1
<i>Leucomium strumosum</i>	0	0	0	0	1	0	1	0	0	1	1	0	1
<i>Lopidium concinnum</i>	0	0	1	0	1	0	1	1	0	0	0	1	0
<i>Lopidium concinnum</i>	0	0	1	0	1	0	1	1	0	0	0	1	0
<i>Lopidium plumarium</i>	0	0	1	0	1	0	1	1	0	0	0	1	0
<i>Philophyllum tenuifolium</i>	0	0	0	0	1	0	1	0	0/1	1	1	0	1
<i>Pilotrichidium antillarum</i>	0	0	0	0	0	1	1	0	1	1	1	0	0
<i>Pilotrichidium callicostatum</i>	0	0	0	0	1	1	1	0	1	1	1	0	0
<i>Pilotrichum andersonii</i>	0	0	0	1	0	0	1	0	1	0	1	0	0
<i>Pilotrichum bipinnatum</i>	0	0	0	1	0	0	1	0	1	0	1	0	0
<i>Pilotrichum procerum</i>	0	0	0	1	0	0	1	0	1	0	1	0	0
<i>Ptychomnion aciculare</i>	0	1	0	0	0	0	1	0	0	1	1	0	1
<i>Ptychomnion cygnisetum</i>	0	1	0	0	0	0	1	0	0	1	1	0	1
<i>Ptychomnion ptychocarpon</i>	0	1	0	0	0	0	1	0	0	1	1	0	1
<i>Rhynchostegiopsis flexuosa</i>	0	0	0	0	1	0	1	0	0	1	1	0	1
<i>Rhynchostegiopsis tunguraguana</i>	0	0	0	0	1	0	1	0	0	1	1	0	1
<i>Sauloma tenella</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Schimperobryum splendissimum</i> var. <i>perdentatum</i>	0	0	0	0	1	0	1	0	1	0	1	0	1
<i>Stenodictyon pallidum</i>	0	0	0	0	0	0	1	1	1	1	1	0	1
<i>Stenodictyon wrightii</i>	0	0	0	0	0	0	1	1	1	1	1	0	1
<i>Symphiodon imbricatifolius</i>	0	0	0	1	1	0	0	0	0	0	1	0	1
<i>Tetraphidopsis pusilla</i>	0	1	0	1	0	0	0	0	0	0	1	0	1
<i>Tetrastichium fontanum</i>	0	0	0	0	1	0	1	?	1	1	1	0	0
<i>Thamniopsis cruegeriana</i>	0	0	0	0	1	0	1	0	1	1	1	0	1
<i>Thamniopsis incurva</i>	0	0	0	0	1	1	1	0	1	1	1	0	0
<i>Thamniopsis pendula</i>	0	0	0	0	1	0	1	0	1	1	1	0	1
<i>Thamniopsis sinuata</i>	0	0	0	0	1	0	1	0	1	1	1	0	1
<i>Trachyxiphium drepanophyllum</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Trachyxiphium guadalupense</i>	0	0	0	0	0	0	1	0	1	1	1	0	1
<i>Trachyxiphium vagum</i>	0	0	0	0	1	0	1	0	1	1	1	0	1

Characters:

1. Capsule exserted vs. immersed – 0: exserted. 1: immersed.
2. Capsule smooth vs. furrowed – 0: smooth (or sulcate). 1: furrowed.
3. Laminal limbium absent or present – 0: absent. 1: present.
4. Exostome striolate vs. smooth/papillose – 0: striolate. 1: smooth/papillose.
5. Plants terete vs. complanate – 0: terete. 1: complanate.
6. Leaves acute to acuminate vs. obtuse – 0: acute/acuminate. 1: obtuse.
7. Alar cells differentiated or not – 0: differentiated. 1: not differentiated.
8. Annulus differentiated or not – 0: differentiated. 1: not differentiated.
9. Calyptra cucullate vs. mitrate – 0: cucullate. 1: mitrate.
10. Exostome teeth with zig-zag centre line vs. furrowed – 0: zig-zag. 1: furrowed.
11. Costa single vs. double (short or long) – 0: single. 1: double.
12. Amphigymnia differentiated or not – 0: not differentiated. 1: differentiated.
13. Laminal cells short (1–3:1) vs. long (>3:1) – 0: short. 1: long.

Table 2 Continued.

- operculum, usually through swelling from water absorption, are differentiated in some mosses and not others.
5. Exostome: striolate vs. smooth/papillose. Exostome teeth within the pleurocarps may be cross-striolate, smooth, or variously papillose. Empirically, both smooth and papillose exostome teeth are grades along a single reduction series and thus considered a single character state. A response to epiphytism often is the shift from striolate exostome teeth to papillose or smooth ones.
 6. Calyptra: cucullate vs. mitrate. A calyptra that either splits up one side (cucullate) or one more like a small cap (mitrate) are the two character-state options. Often this character is stable at higher levels of classification. Typically, the Hookeriales, unlike most Hypnales, are characterized by mitrate calyptrae.
 7. Alar cells: differentiated vs. not differentiated. One of the standard morphological characters of the Hookeriales *s.str.* is the lack of alar cell differentiation. However, most Hypnales have some degree of differentiation of these cells in the basalmost leaf angles at the insertion, as do most Garovagliaceae/Ptychomniaceae.
 8. Laminal limbidium: absent vs. present. Leaves with elongate cells along the margins (and shorter cells within) are present throughout the Hookeriales in various lineages.
 9. Costa: single vs. double (short or long). A single costa seems to be plesiomorphic for pleurocarps (because of the acrocarpous origins of the group), but double costae occur in a number of seemingly unrelated taxa. Separation of short and double vs. long and double was not attempted because of the numerous intermediates found within the Hookeriales. A lack of costa was coded as double.
 10. Laminal cell length: short (1–3:1) vs. long (> 3:1). Laminal cells within pleurocarps range from isodiametric (or oblate) to elongate. Although a complete range of lengths can be found, most pleurocarpous mosses are either short-celled or long-celled.
 11. Plant axis: terete vs. complanate. This character is a reflection of the leaf orientation around the stem, resulting either in all leaves being similar (and thus terete plants) or having the dorsal and ventral leaves differentiated (sometimes subtly) from the lateral leaves (and thus complanate plants).
 12. Leaf apex: acute to acuminate vs. obtuse. Obtuse leaves are not common among mosses in general and especially in pleurocarps. However, plants in aquatic habitats (such as *Cladomniopsis*) not uncommonly are characterized by obtuse leaf apices.
 13. Amphigyminia: differentiated vs. not differentiated. The Hypopterygiaceae are characterized by small, ventral leaves (amphigyminia). Otherwise, they are very rare in pleurocarps. This character may be an extreme expression of character 11 (plants terete vs. complanate), but intermediates are not obvious.

Phylogenetic analyses

Phylogenetic analyses employing parsimony and maximum likelihood optimality criteria were conducted using the

software PAUP 4.0b8–10 (Swofford, 2001). Bayesian inference procedures used MrBayes (vers. 3.0), written by J.P. Huelsenbeck & F. Ronquist (<http://morphbank.ebc.uu.se/mrbayes3/>), and P4 (vers. 0.73), written by P. Foster (<http://www.nhm.ac.uk/zoology/external/foster/p4man/>), and were performed on the same computing architecture.

Non-parametric bootstrap analyses under parsimony were conducted for each data partition (DNA region) and, in order to most directly compare support levels, included only those taxa for which all partitions were present in the combined data set, using 300 replicates, each with two random-addition replicates, saving no more than 20 trees per replicate. See Table 1 for the taxa and the genes successfully sequenced from each. Taxonomic congruence among data partitions was investigated by visually inspecting bootstrap consensus trees for conflicting nodes supported at greater than 70%.

A hierarchical likelihood ratio test was used to select the appropriate likelihood model using MrModeltest-1.1b (Nylander, 2002). The chosen model (GTR+I+G — general time-reversible model (Rodriguez *et al.*, 1990) plus a proportion of invariable characters, with other site rates modelled by a discrete gamma distribution) and its estimated parameters were fixed (i.e. were not free to vary) in subsequent likelihood analyses. In addition, a likelihood ratio test of the molecular clock was conducted using the optimal model parameters. Optimal trees under the maximum likelihood criterion were sought using 10 replicates of random taxon-additions to the starting tree with tree bisection-reconnection branch-swapping.

Homogeneous Bayesian phylogenetic analyses were performed using MrBayes with six runs, each with 2 000 000 generations and four chains. Model parameters were sampled every 100 generations under a general time-reversible (GTR) model of DNA substitution, with substitution transition rates, base composition and shape of the gamma distribution of among-site rate heterogeneity estimated during the Markov Chain Monte Carlo (mcmc). The number of trees needed to reach stationarity (i.e. the ‘burnin’) in the mcmc chain was estimated by visual inspection of the plot of the tree -ln likelihood score versus number of generations using the graphing program GnuPlot-3.7.1 (Williams & Kelley, 1999). The trees of the burnin for each run were excluded from the tree set and the remaining trees from each run were combined to form the full sample of trees assumed to be representative of the posterior probability distribution. Nodes with significant posterior probabilities were found by constructing a 95% majority-rule consensus tree in PAUP.

Heterogeneous Bayesian analyses were performed using MrBayes with seven partitions: one for each of *trnL-trnF*, 26S, and *nad5*, plus an individual partition for each codon position of the *rps4* gene and a separate partition for the non-coding region of *rps4*. Each partition was subjected to analysis by MrModeltest to identify the appropriate model for each partition (*trnL-trnF*: GTR + I + G; 26S: GTR + I + G; *nad5*: GTR + G; *rps4* 1st positions: GTR + I + G; *rps4* 2nd and 3rd positions: GTR + I + G; and *rps4* non-coding: GTR). Six independent runs were performed each with 2 000 000 generations, four chains and sampling all model parameters every 100th

generation. Trees within the posterior distribution were analysed as described previously for homogeneous analyses.

To assess the goodness-of-fit of a seven partition heterogeneous model and the homogeneous model, both models were optimized using P4 on the ML tree and compared using a likelihood ratio test statistic.

Morphological character reconstructions

The following taxa were pruned from the optimal maximum likelihood tree, after consideration of morphological character-state distributions, to ensure the tree was fully bifurcating (as required by Discrete 4.0): *Garovaglia powellii*, *Callicostellopsis meridensis*, *Lopidium concinnum* (one of two accessions), *Trachyxiphium vagum* and *Thamniopsis pendula*. In addition, *Euptychium vitiense* and *Ephemeropsis trentepohlioides* were removed due to their very high rates of molecular evolution: branch lengths were 0.069 and 0.079, respectively. The model and model parameters were recalculated for the pruned ML tree using MrModeltest. Due to the rejection of the molecular clock for the pruned data set, branch lengths of the ML tree were rescaled using r8s (Sanderson, 2003). We attributed the rejection of the molecular clock to variation in intrinsic rates of molecular evolution among lineages rather than to variation in organismal generation times and hence we sought to scale the phylogeny to relative timings of cladogenesis under the assumption of auto-correlation of molecular rates among lineages. Branch rescaling was achieved using the non-parametric rate smoothing (NPRS) algorithm with a gamma distribution of rates (the value of the shape parameter was re-estimated on the pruned tree in PAUP with optimal parameters as described above except the proportion of invariant characters was set to zero because of the requirements of r8s; $\alpha = 0.2553$), with *Orthodontium lineare* designated as the root taxon and the age of the ingroup set to 100. Optimization of branch lengths was conducted with 20 random starts each with 10 perturbations. Optimization of the root branch necessitated the removal of *Orthodontium lineare* from the resulting tree. For each individual morphological character reconstruction, taxa were removed from the analyses when the morphological character-state was coded as unknown or inapplicable. Branch lengths in the ancestral and descendant branches of the tree were adjusted when removing nodes (i.e. taxa). A branch length table was obtained in PAUP based on the pruned optimal tree for each character and the branch length table and morphological character states were converted to Pagel formatted trees (Pagel, 2002).

The evolution of morphological characters were reconstructed on the rescaled trees under maximum likelihood using Mesquite 0.996 (Maddison & Maddison, 2003) and Discrete 4.0 (Pagel, 1994, 2002). For each character, a likelihood ratio test ($LRT = -2\ln(L^1/L_2)$) was conducted between a one-parameter (likelihood of a single rate for forward and reverse transitions – L1) and an asymmetric two-parameter model (likelihood of separate rates for forward and reverse transitions – L2) and a χ^2 approximation with 0.05 level of confidence and one degree of freedom to test for a significant departure from the null hypothesis. If the asymmetric two-parameter model was not a significantly better fit to the data than the single transition model, the single transition rate model

was used in ancestral state reconstructions. Proportional likelihoods for ancestral state reconstructions were recorded for each node and cross-validated using Discrete ('local' calculations; Pagel, 2002) with model and rate(s) constrained to the optimal values obtained from Mesquite. ML character reconstructions at nodes were considered significant when the ratio of the two character-state likelihoods exceeded 7:1 (Schulter *et al.*, 1997). Discrete (Pagel, 2002) cannot handle multistate characters, but only binary ones. Although this is unfortunate, given the advantages of being able to use information contained in branch lengths and to assess the probability of ancestral character-state reconstruction, we believe that reconstruction of binary state characters under Maximum Likelihood is a worthy pursuit.

Results and discussion

Data characteristics

The combined data set of 99 taxa included 3952 sites, of which 741 were excluded due to ambiguous alignment or incomplete data at the beginning and end of sequence regions. Of the remaining sites, 601 were from *rps4* (224 parsimony informative: 69 1st positions, 43 2nd positions, 102 3rd positions, 10 non-coding sites), 331 were from *trnL-trnF* (62 parsimony informative), 1210 were *nad5* (262 parsimony informative) and 1069 were from 26S rDNA (143 parsimony informative). No conflict among partitions was found when accessed by parsimony bootstrap (> 70%), hence all partitions were considered to reflect the same underlying phylogenetic history.

Phylogenetic analyses

The likelihood ratio test ($LRT = 2(-\ln null - -\ln alternative)$) of the homogeneous ($-\ln 21428.57274$) versus the heterogeneous seven partition ML analysis ($-\ln 20957.5869384$) indicated that the seven partition analysis was a significantly better fit to the data than was the homogeneous model (941.97 d.f. = 249; $P \ll 0.001$).

The single optimal tree for all 99 taxa found under the maximum likelihood criterion, with heterogeneous Bayesian posterior probabilities (bpp) for nodes (>95%), is presented in Figure 1. ($-\ln 21428.57274$: base frequencies – A: 0.3222, C: 0.1846, G: 0.2107, T: 0.2825, substitution matrix – A<>C: 1.3982, A<>G: 4.6444, A<>T: 0.2888, C<>G: 1.0153, C<>T: 5.1767, G<>T: 1.0, gamma distribution shape parameter – α : 0.6645, proportion of invariant characters: pinvar: 0.4721). The first dichotomy of the ingroup splits the pleurocarpous mosses into two well-supported lineages (both 100% bpp), namely, the Ptychomniales and the Hypnales plus Hookeriales. Within the Ptychomniales clade, the Ptychomniaceae (incl. *Hampeella*, *Ptychomnion*, *Tetraphidopsis*, *Cladomniopsis* and *Cladomnion*) form a grade from which the Garovagliaceae are derived. *Dichelodontium nitidum*, classified by Buck & Goffinet (2000) in the Hypnalean family Lepydontaceae, is also part of the Ptychomniaceae grade. The Garovagliaceae form a well-supported monophyletic group (100% bpp); however, *Euptychium setigerum* is more closely related to *Garovaglia* spp. than to other *Euptychium* spp.

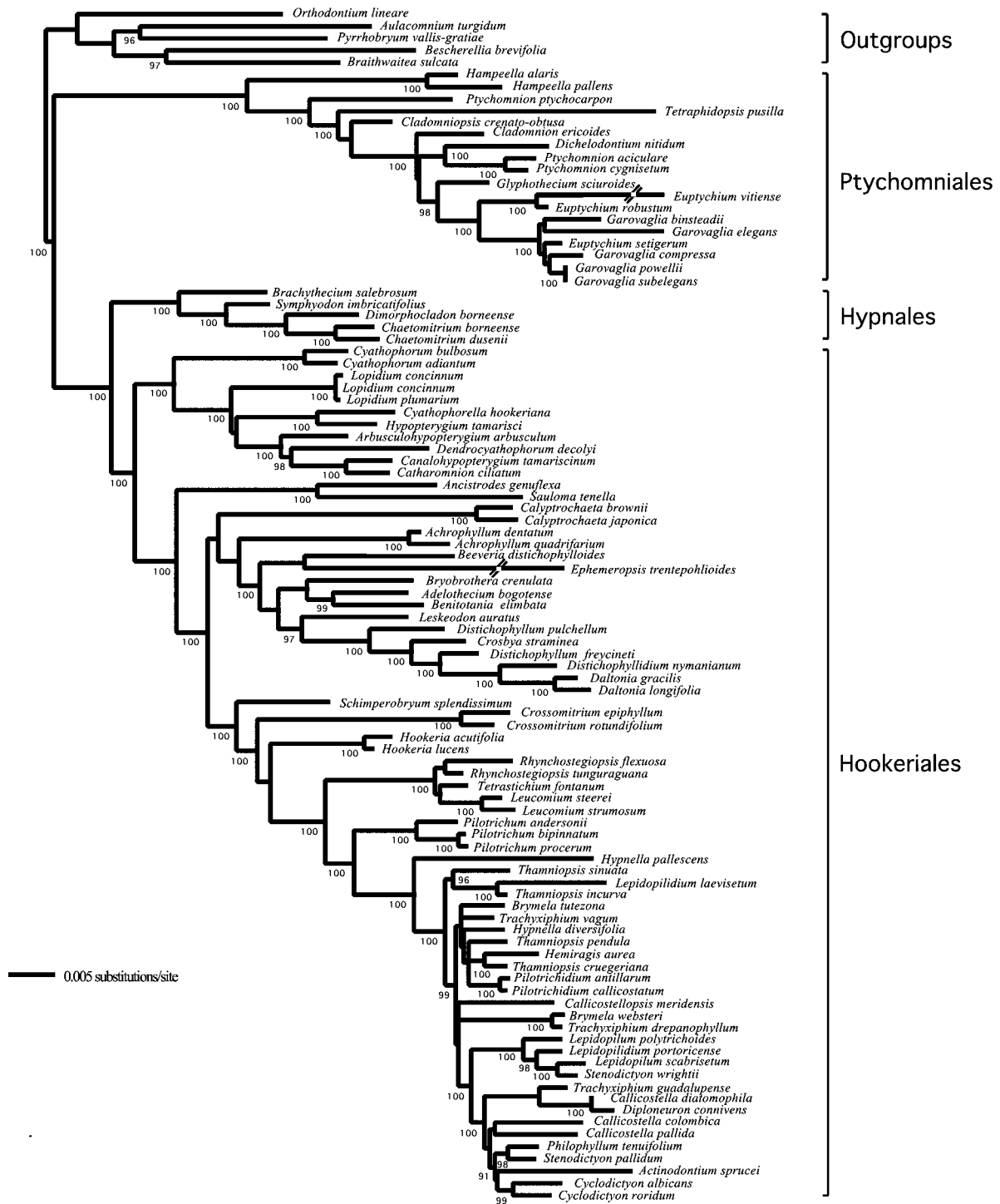


Figure 1 Phylogram of the optimal maximum likelihood tree ($-\ln$ likelihood = 21428.57274) found during ten random taxon-addition searches with tree bisection-reconnection branch swapping under a general time-reversible substitution model with among site rate heterogeneity modelled by a proportion of invariant characters (pinvar) with the remainder gamma distributed among four rate classes each averaged by the mean. Branches were collapsed if the branch length was less than or equal to $1e-08$. Model parameters were fixed at the following values for the duration of the search: base frequencies: A = 0.3222, C = 0.1846, G = 0.2107, T = 0.2825; GTR: A-C = 1.3982, A-G = 4.6444, A-T = 0.2888, C-G = 1.0153, C-T = 5.1767, G-T = 1.000; pinvar = 0.4721; shape = 0.6645. Numbers to the right of nodes or below branches indicate Bayesian posterior probabilities ($> 95\%$) under a heterogeneous model with seven partitions based on 96 000 trees sampled from the posterior distribution under a four partition heterogeneous model (see text for details), with all parameters estimated during the Markov Chain Monte Carlo. To aid graphical representation, the branches leading to *Euptychium vitiense* and *Ephemeropsis trentepohlioides* have been arbitrarily shortened: their actual values (in expected number of substitutions/per site) are 0.069 and 0.079, respectively. Classification follows Buck & Goffinet (2000), except for the proposed classification and circumscription of Ptychomniales and Hookeriales.

The Hypnales and Hookeriales are placed as well-supported (100% bpp) sister-groups. The first dichotomy within the Hookeriales splits the Hypopterygiaceae plus some members of the Hookeriaceae from the remaining taxa. Within the former clade, two hookeriaceous taxa, *Cyathophorum bulbosum* and *Cyathophorum adiantum* (100% bpp), form the sister group to the remainder of the Hypopterygiaceae (100% bpp), the latter also containing the hookeriaceous taxa *Cyathophorella hookeriana* and *Dendrocyathophorum decolyi*. *Ancistrodes genuflexa* (Meteroriaceae, Hypnales) and *Sauloma tenella* (Pilotrichaceae, Hookeriales) form the sister group to the remaining hookeriaceous taxa (100% bpp). Within the latter, two clades are discernible. The first clade includes members of the Daltoniaceae, Adelotheciaceae, *Beeveria* (Pilotrichaceae) and *Achrophyllum* (Hookeriaceae). Both *Calyptrochaeta* (Daltoniaceae) and *Achrophyllum* are not well supported as members of the clade (< 95% bpp). The second clade and sister group to this mostly daltoniaceous clade, is well supported (100% bpp) and includes members of the Hookeriaceae, Leucomiaceae and Pilotrichaceae. *Schimperobryum* (Hookeriaceae), *Crossomitrium* (Pilotrichaceae) and *Hookeria* (Hookeriaceae) form the next three successive splits from the group. The Leucomiaceae (minus *Philophyllum*) plus *Tetrastichium fontanum* (Pilotrichaceae) form a well-supported clade (100% bpp) that is itself the sister group to the remaining Pilotrichaceae (100% bpp). Within the Pilotrichaceae, *Pilotrichum* (100% bpp) forms the sister group to the remaining members of the family. *Hypnella pallescens* and a clade composed of *Thamniopsis sinuata*, *T. incurva* and *Lepidopilidium laevisetum*, form the next two successive splits from the Pilotrichaceae. The remaining taxa form a well-supported monophyletic lineage (99% bpp). The genera *Lepidopilum*, *Lepidopilidium*, *Stenodictyon*, *Trachyxiphium*, *Brymela*, *Hypnella*, *Thamniopsis* and *Calliostella* are not well supported as monophyletic genera. However, precise relationships among species of these taxa are not discernible with confidence. *Philophyllum tenuifolium* (Leucomiaceae) is well supported as a member of the Pilotrichaceae and forms a clade with *Stenodictyon pallidum* (98% bpp).

Significant (> 95%) support for two nodes differed between homogeneous and heterogeneous Bayesian analyses. Posterior probability for the node uniting *Thamniopsis sinuata*, *T. incurva* and *Lepidopilidium laevisetum* was 89% in homogeneous analyses and 96% in heterogeneous analyses. In contrast, the posterior probability of the node uniting *Brymela tutezona*, *Hypnella diversifolia*, *Hemiragis aurea*, *Thamniopsis cruegeriana*, *T. pendula*, *Pilotrichidium antillarum*, *P. calliostatatum* and *Trachyxiphium vagum* was significant (96%) in the homogeneous analyses, but non-significant (90%) in the heterogeneous analyses.

Morphological character reconstructions

Reoptimization of the branch lengths and model parameters for the pruned (93 taxon) data set resulted in a tree with likelihood $-\ln 20381.95260$ (base frequencies – A: 0.3212, C: 0.1879, G: 0.2100, T: 0.2809, substitution matrix – A<>C: 1.3734, A<>G: 4.7440, A<>T: 0.2991, C<>G: 0.9272, C<>T: 5.1521, G<>T: 1.0, gamma distribution shape parameter – α :

Character	Mk1 (–log L)	AsymmMk (–log L)	LRT statistic	P
1	17.068	9.962	14.22	< 0.001
2	16.163	11.457	8.811	0.003
3	46.287	42.495	4.25	0.007
4	55.197	54.859	0.68	0.410
5	46.224	43.849	4.77	0.029
6	34.581	31.847	2.73	0.098
7	24.040	17.452	24.04	< 0.001
8	26.761	26.332	0.858	0.354
9	21.643	19.382	4.52	0.036
10	45.596	40.842	9.52	0.002
11	58.074	57.857	0.434	0.051
12	34.950	32.787	4.326	0.038
13	6.715	6.589	0.252	0.616

Table 3 Likelihoods of morphological characters under a Markov k-state 1 parameter (Mk1) model and asymmetric Markov k-state 2 parameter (AsymmMk) model and the likelihood ratio test (LRT) statistic and probability (P), between the two models.

0.7014, proportion of invariant characters: pinvar: 0.4944). Enforcement of a molecular clock under the same model resulted in a tree with $-\ln$ likelihood 20586.48804, hence the molecular clock was rejected by the likelihood ratio test ($2(20586.48804 - 20381.95260) = 409.071$, d.f. = 91, $P \ll 0.001$).

Table 2 is the morphological data matrix. Table 3 presents model likelihoods, character transition rates and likelihood ratio statistics for each morphological character. The reconstructed histories of five characters, namely, exostome centre line form (char. 3), annulus differentiation (char. 4), plant axis (char. 11), leaf apex shape (char. 12) and presence of amphigymnia (char. 13) were ambiguous at the root node and throughout much of their respective character trees. These reconstructions do not provide sufficient confidence in character-state transitions and therefore diagnoses of synapomorphies for clades and hence are not described in further detail.

Figures 2–9 show ML character reconstructions of selected morphological characters on the NPRS tree. Statistically significant ancestral character-state reconstructions at nodes are indicated by the branch colours (grey vs. black). Pie-charts at nodes indicate proportions of the likelihood associated with each character-state when ancestral character-state reconstruction is ambiguous. Capsule presentation (char. 1: Fig. 2) is reconstructed as equivocal throughout much of the ‘backbone’ of the phylogeny even though the only four taxa possessing immersed capsules in the analysis are in the Garovagliaceae, which occurs at a relatively tip-ward position in the tree (A in Fig. 2). This seemingly counter-intuitive reconstruction is due to the difficulty of reconstructing the ‘root’ ancestral character-state under the ML criterion (see Pagel (2002) for a fuller explanation). Furrowed capsules (char. 2: Fig. 3) are reconstructed as plesiomorphic for the pleurocarpous mosses whereas smooth capsules represent a synapomorphy for the Hypnales plus Hookeriales clade (A in Fig. 3). A further reversal in

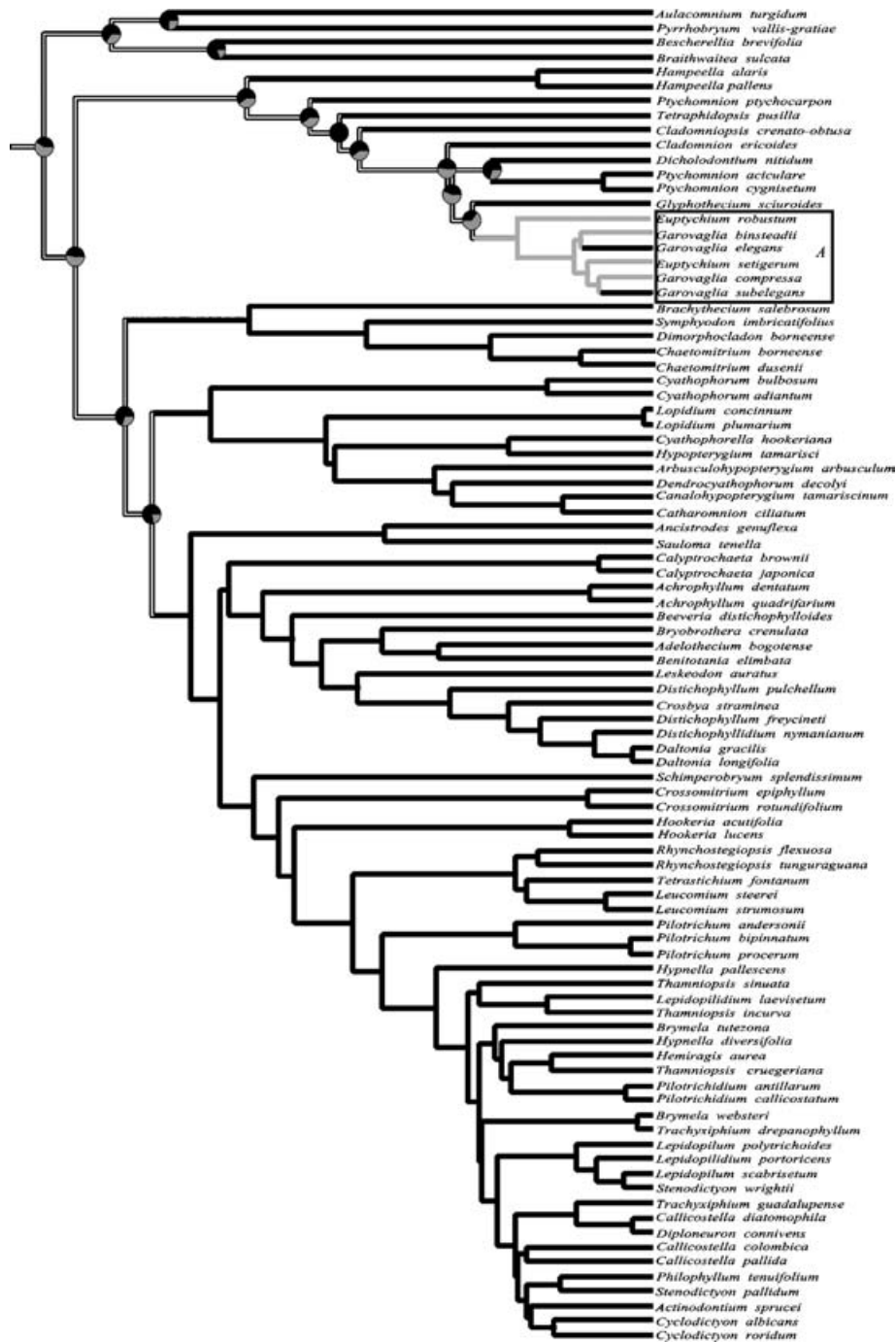


Figure 2 ML morphological character reconstructions for *capsule presentation*: black = exserted; grey = immersed (asymmetric 2-parameter transition model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

the Garovagliaceae is ambiguously reconstructed but may represent a synapomorphy for the family (B in Fig. 3).

Furrowed exostome teeth (char. 3: Fig. 4) is the ancestral character-state of the pleurocarpous mosses, however transitions to a zig-zag centre line are ambiguously reconstructed and may have arisen independently as many as 18 times. Mitrated calyptrae (char. 6: Fig. 5) have also arisen independently at least six times from ancestors with cucullate calyptrae. Mitrated calyptrae may represent a synapomorphy for the clade formed by

the Hookeriaceae (in part), Leucomiaceae and Pilotrichaceae (A in Fig. 5); however, the immediate ancestor to this clade is ambiguously reconstructed with 75% proportion of the likelihood suggesting a cucullate reconstruction at this node. The cucullate calyptra is a synapomorphy uniting the Leucomiaceae and *Tetrastichium*, with a further reversal to the mitrated form having arisen in *Tetrastichium* (B in Fig. 5).

The reconstruction of the differentiation of alar cells in the leaf lamina (char. 7: Fig. 6) indicates that differentiated alar

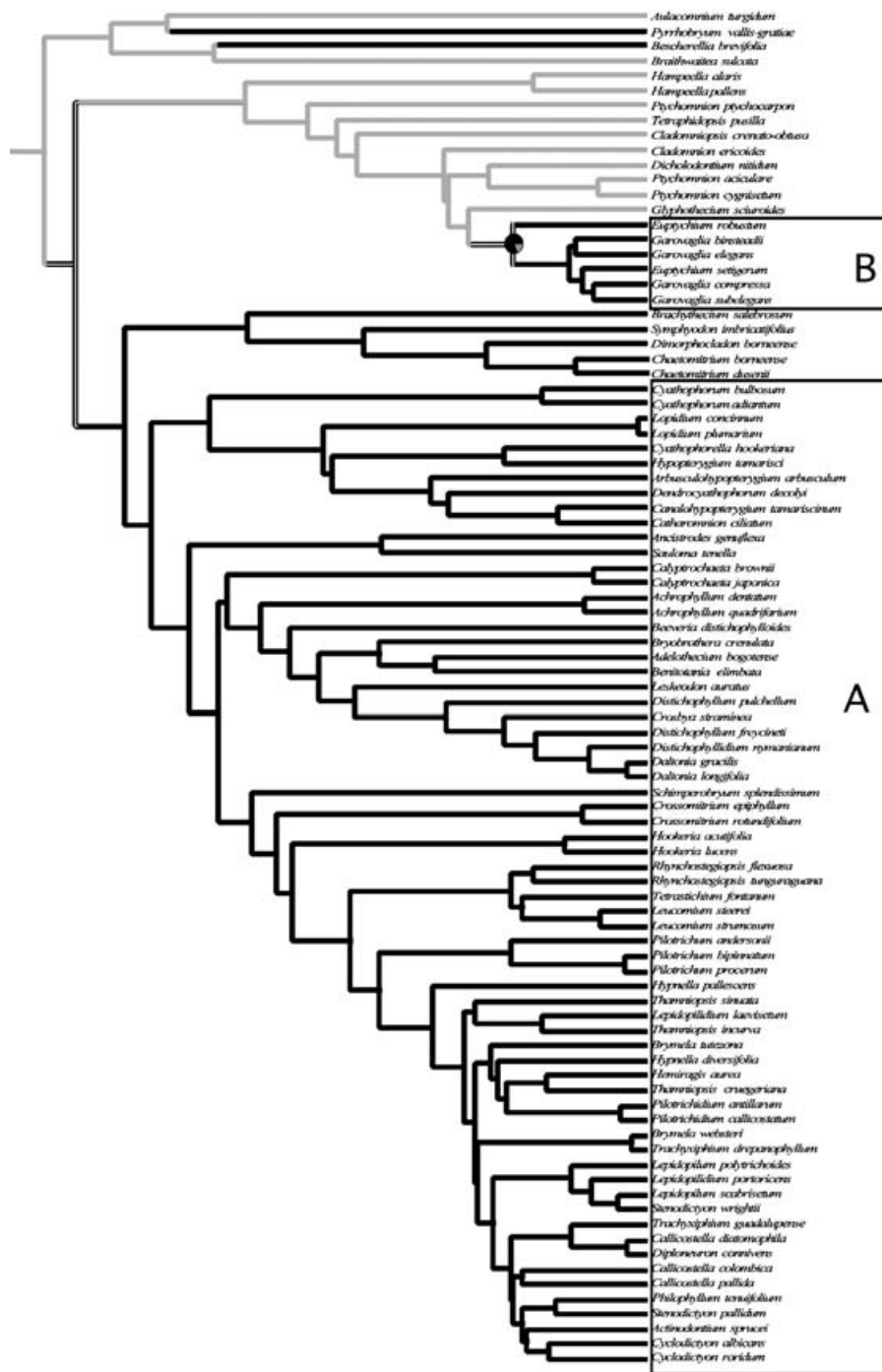


Figure 3 ML morphological character reconstructions for *capsule surface*: black = smooth; grey = furrowed (asymmetric 2-parameter transition model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

cells have been lost at least five times. Although not statistically significant, a lack of differentiated alar cells is most likely (85% proportion of likelihood) a synapomorphy for the Hookeriales (A in Fig. 6). The presence of a laminal limbidium (char. 8: Fig. 7) as the ancestral character-state of the Hypopterygiaceae (plus *Dendrocyathophorum*) (A in Fig. 7) is statistically significant. However, its presence may represent a plesiomorphy at this level due to ambiguous reconstruction at the node uniting

Cyathophorum bulbosum, *Cyathophorum adiantum* and the Hypopterygiaceae. Nevertheless, the higher proportion of the likelihood indicates that this is the least likely reconstruction. In contrast, the presence of a laminal limbidium in the Daltoniaceae (B in Fig. 7), although also ambiguously reconstructed, is most likely a synapomorphy as indicated by the proportion of the likelihood assigned to the character-state. A laminal limbidium has arisen by convergence in three additional lineages:

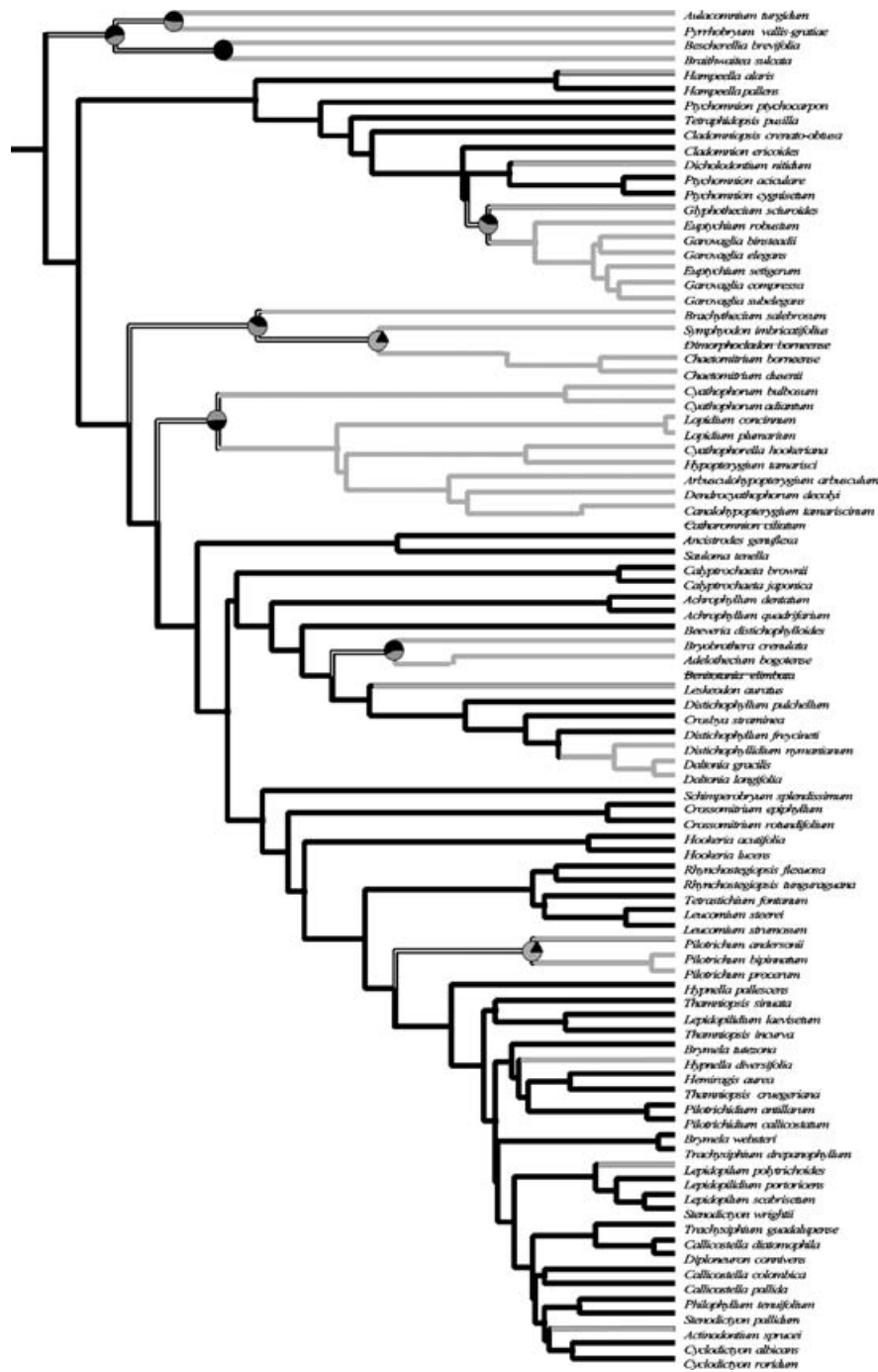


Figure 4 ML morphological character reconstructions for *exostome teeth*: black = furrowed centre line; grey = zig-zag centre line (asymmetric 2-parameter model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

Calyptrichaeta, *Cyclodictyon* and *Lepidopilum polytrichoides* (arrows in Fig. 7).

A double costa (char. 9: Fig. 8) is reconstructed as synapomorphic for the clades represented by the Ptychomniales (A in Fig. 8), *Chaetomitrium* and *Calyptrichaeta* and most likely (83% of the likelihood) for the clade uniting *Ancistrodes* and *Sauloma* and (87% of the likelihood) for the clade formed by Hookeriaceae (partially), Leucomiaceae and Pilotrichaceae (B

in Fig. 8). A double costa is also autapomorphic for *Symphodon imbricatifolius*. Long laminal cells (char. 10: Fig. 9) are plesiomorphic for the pleurocarpous mosses, with short laminal cells having been derived at least 11 times and maybe as many as 16 times. Short laminal cells in the Hookeriaceae are most likely synapomorphies for the hypopterygiaceous clade (58% of the likelihood) (A in Fig. 9) and the *Acrophyllum*, *Adelotheciaceae*, plus *Daltoniaceae* clade (77% of the likelihood)

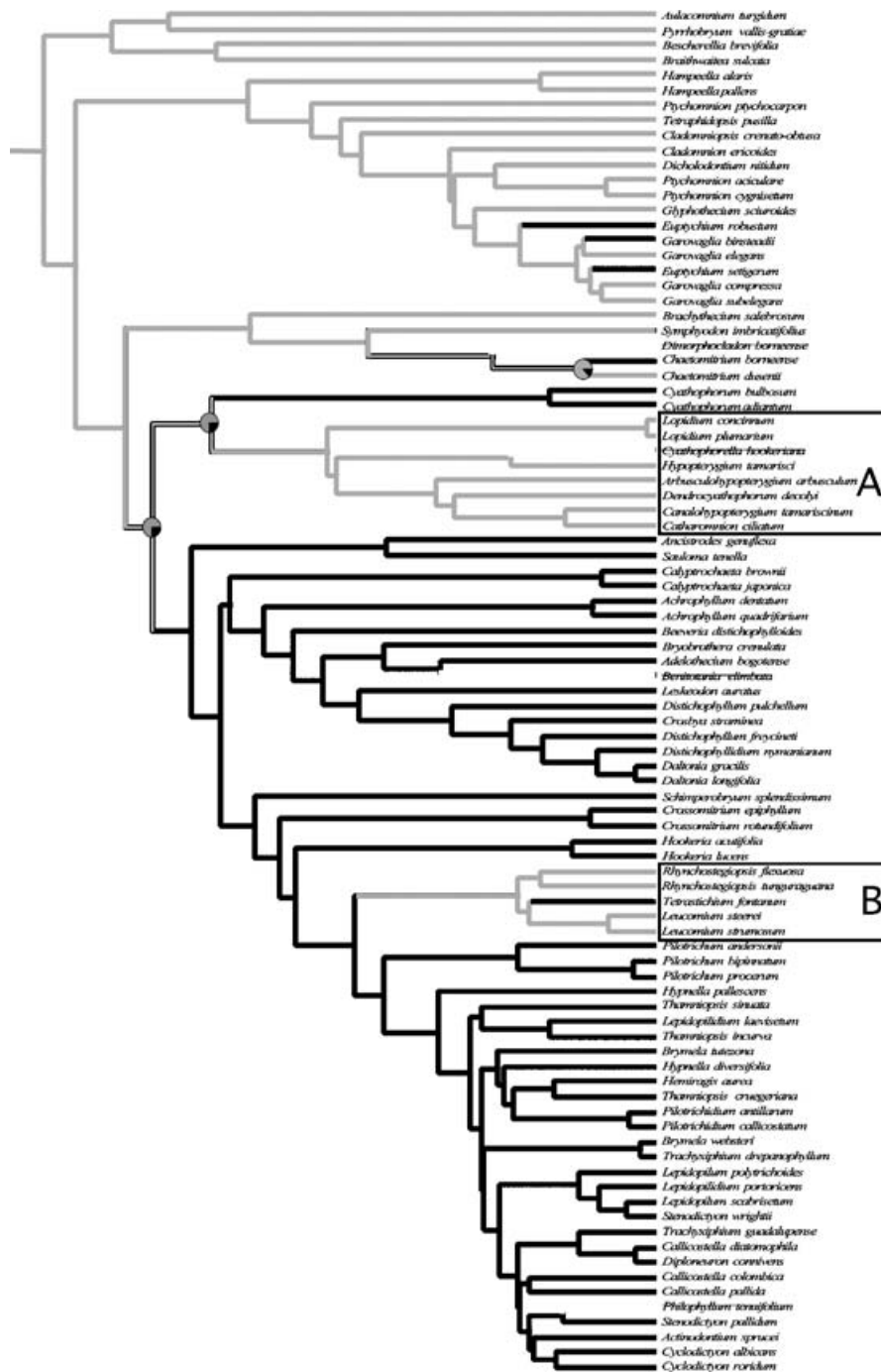


Figure 5 ML morphological character reconstructions for *calyptra*: black = mitrate; grey = cucculate (single parameter model (Mk₁). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

(B in Fig. 9), however the reconstructions are not statistically significant.

Systematics *Ptychomniaceae*

One of the more original findings that our analyses have revealed is that the Ptychomniales are sister to the remainder of the pleurocarpous mosses, i.e. the Hookeriales plus the Hypnales. In Buck & Goffinet (2000), the Ptychomniaceae and Garovagliaceae were placed in the Hookeriales suborder

Ptychomniaceae. In this classification, the Hookeriales were placed in the superorder Hypnanae. However, this relationship is no longer supported and thus the ptychomnioid mosses now need to be placed in their own monordinal superorder.

Ptychomniaceae W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **superord. nov.**

Plantae plerumque grandes turgidae vix ramosae saepe gemmis in axillis foliorum; folia costa brevi et duplici vel

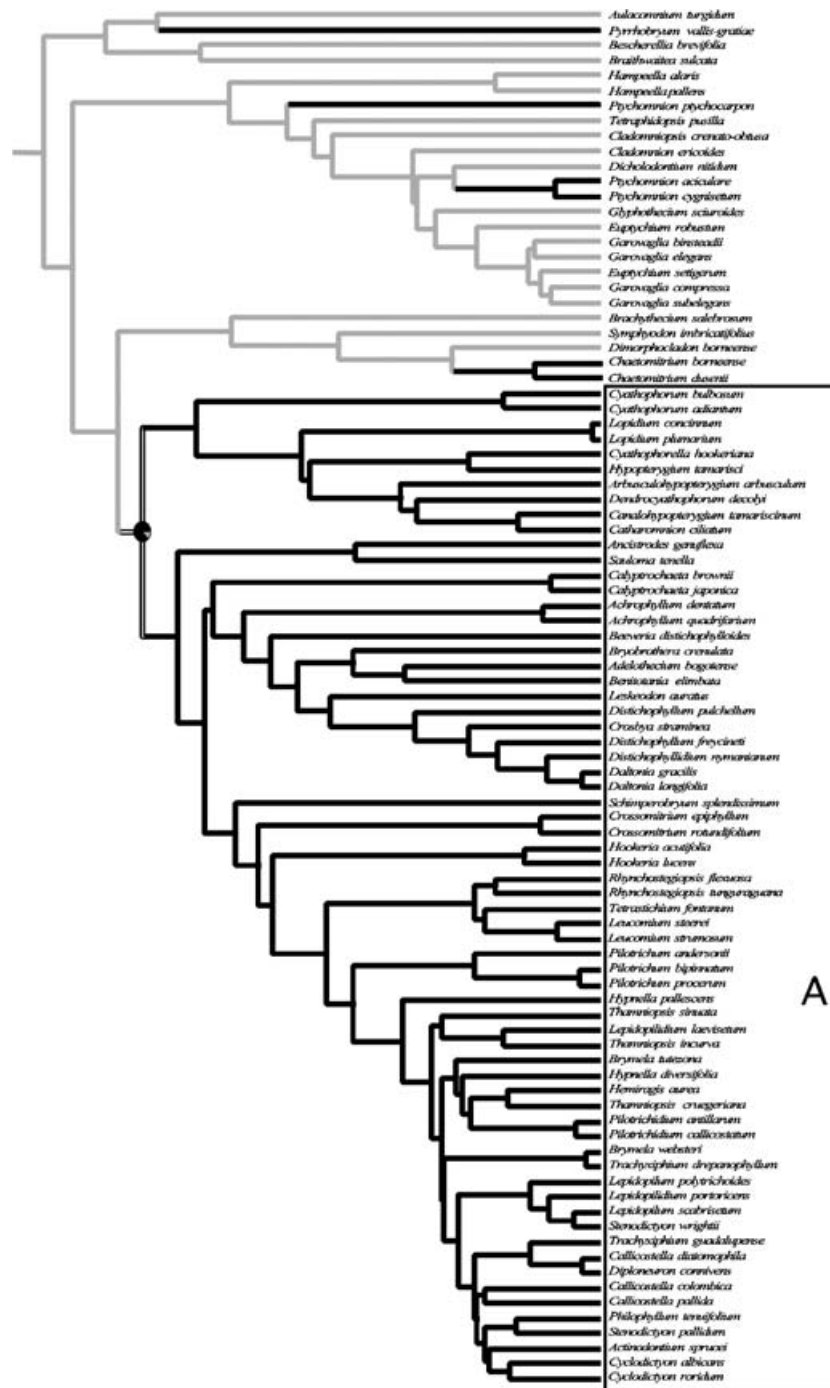


Figure 6 ML morphological character reconstructions for *alar cells*: black = non-differentiated; grey = differentiated (asymmetric 2-parameter model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

destituta; capsulae plerumque erectae aliquando sulcatae. Typus: Ptychomniales.

Ptychomniales

The genera of the Ptychomniaceae and Garovagliaceae form a well-supported clade. The traditionally recognized Garovagliaceae comprise a monophyletic group, but recognition of the family leaves the Ptychomniaceae paraphyletic. Thus, a single family, the Ptychomniaceae (with nomenclatural

priority), is recognized for the group after synonymy of the Garovagliaceae. This group of Gondwanan genera are the sister group to the remainder of the pleurocarps and is here recognized at the ordinal level.

Ptychomniales W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **ord. nov.**

Plantae in hemisphaerio australi crescenti plerumque grandes turgidae vix ramosae saepe gemmis in axillis foliorum; folia

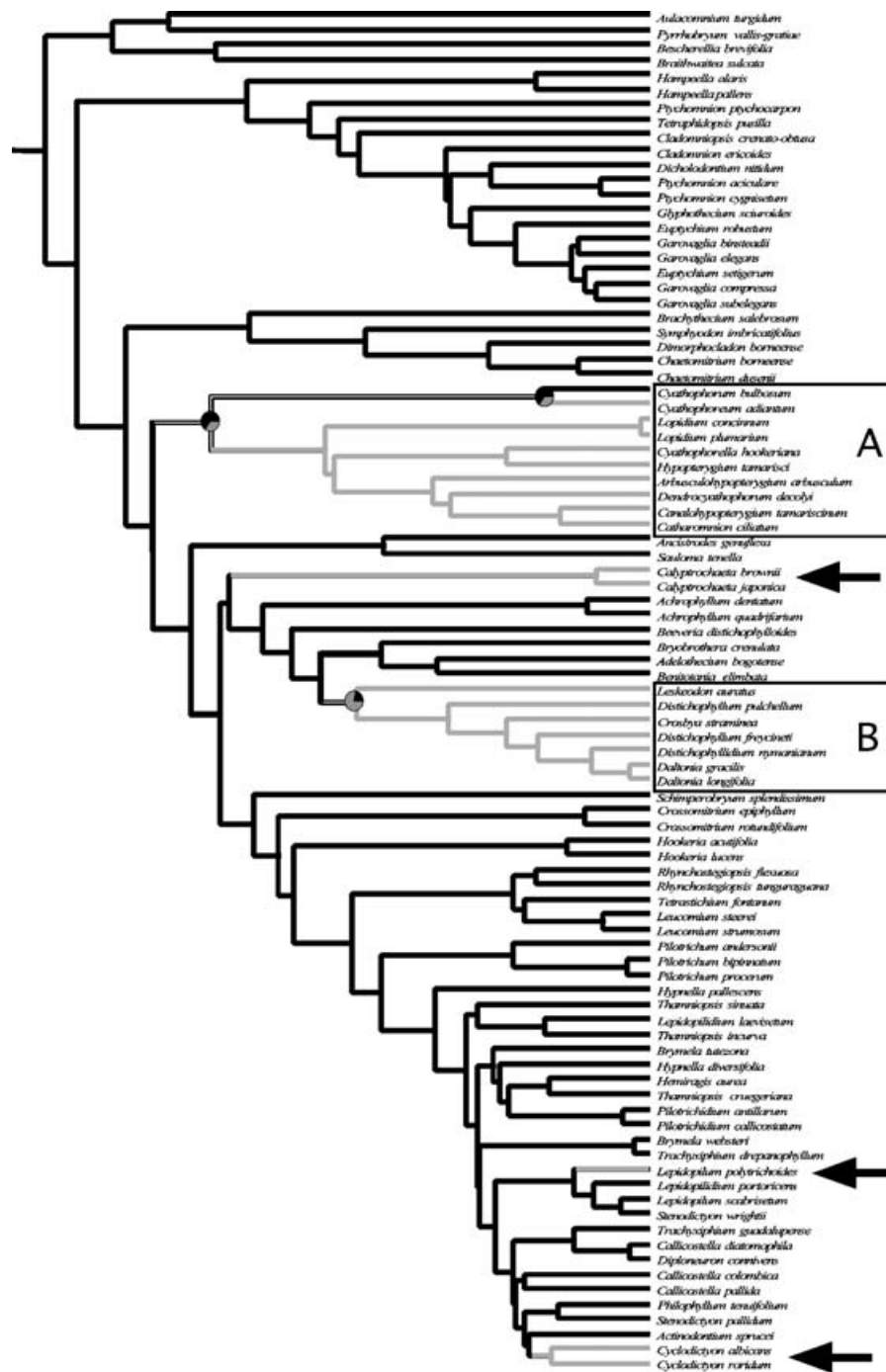


Figure 7 ML morphological character reconstructions for *laminal limbidium*: black – absent; grey – present (single parameter model (Mk1). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

aliquando plicata costa brevi et duplici vel destituta; capsulae plerumque erectae aliquando sulcatae. Typus: Ptychomniaceae M. Fleisch., *Musci Fl. Buitenzorg* 3: 656 (1908).

As indicated above, the Ptychomniales accommodate a single family, the Ptychomniaceae, which contains the Garovagliaceae (M. Fleisch.) W.R. Buck & Vitt in its synonymy. The double costa of the Ptychomniales is a synapomorphy for the order (A in Fig. 8), although the character has arisen independently in several other lineages of pleurocarps.

The earliest diverging genera within the order, *Hampeella*, *Ptychomniella* and *Tetraphidopsis* are relatively slender plants, but the trend has been toward more robust, turgid plants, often with infrequent branching. Within the order, uniseriate gemmae are common in leaf axils. The alar cells are usually differentiated as oblate, thick-walled, often coloured cells. Most genera of Ptychomniaceae *s.str.* tend to have weakly differentiated alar cells. The genus *Glyphothecium* has the most strongly differentiated alar cells and is the sister taxon

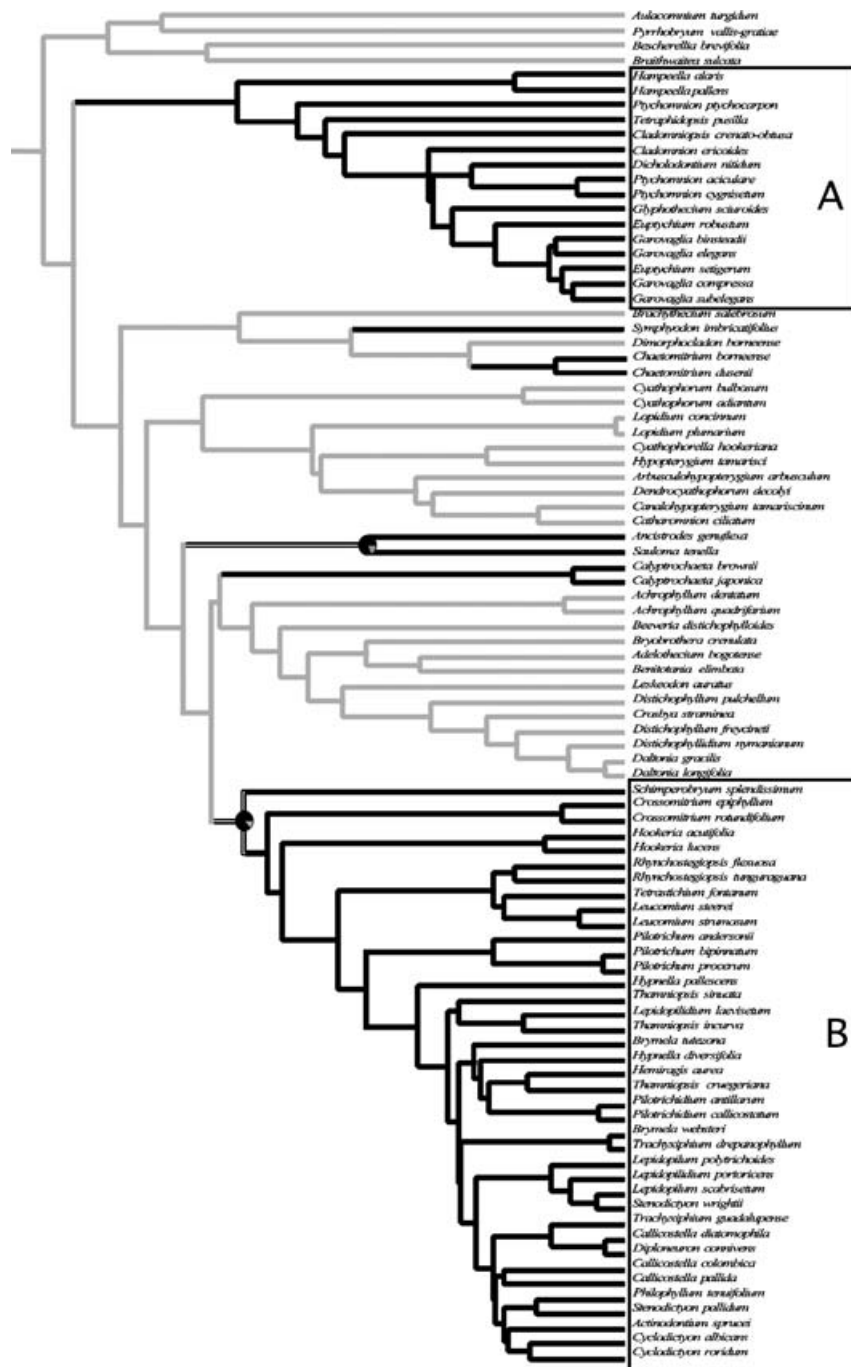


Figure 8 ML morphological character reconstructions for *costa*: black = double (or absent); grey = single (asymmetric 2-parameter model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

to the garovaglioid group which has mostly well-developed alar cells. The earliest diverging taxa traditionally assigned to the Ptychomniaceae *s.str.* have sporophytes that are long-exserted and the capsules are mostly furrowed. However, in the derived garovaglioid genera, the capsules are immersed (or emergent) and smooth; the former character-state is a synapomorphy for the group, although the latter is not significantly reconstructed (Figs 2A, 3B). Concurrent with this reduction in overall sporophyte morphology is a simplification of the peristome architecture from well developed with striolate

exostome teeth, a high basal membrane, well-developed segments and appendiculate cilia, as seen in *Ptychomnion* and *Cladomniopsis*, to papillose exostome teeth, no basal membrane, slender segments and no cilia. In the most extreme case, *Endotrichellopsis* During (not included in this study), the endostome is lacking altogether.

The Ptychomniaceae *s.str.* have traditionally (Brotherus, 1925) been subdivided into two subfamilies, the monogeneric Ptychomnioideae and the Cladomnioideae, containing the rest of the genera. The division was based solely on the

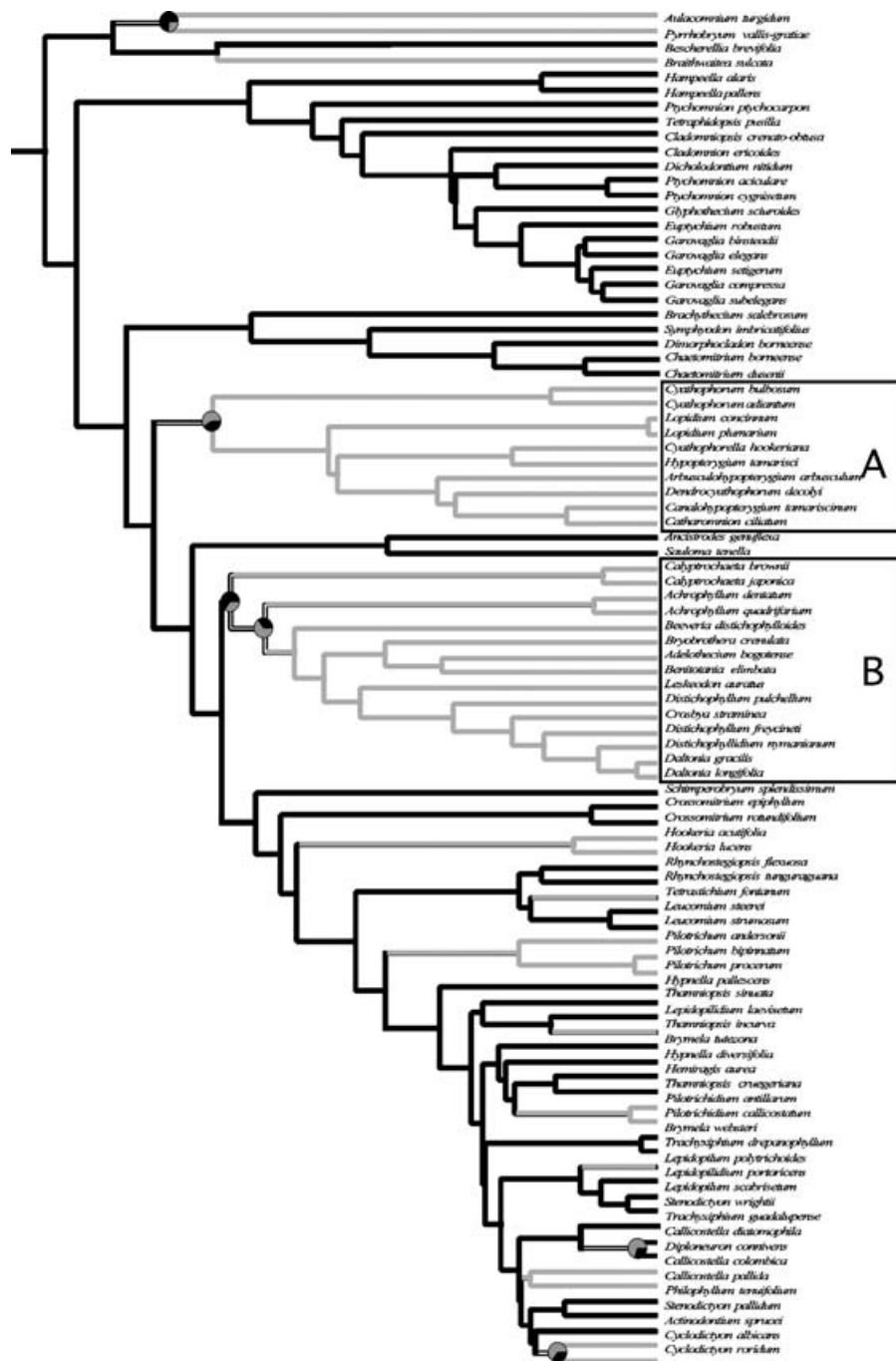


Figure 9 ML morphological character reconstructions for *laminal cell length*: black = long (> 3:1 length/width); grey = short (1–3:1 length/width) (asymmetric 2-parameter model). Non-significant (equivocal reconstructions) are indicated by a pie chart with proportions of the likelihood assigned to character states.

inclined, curved capsule of *Ptychomnion* and the erect capsules of the other genera. More recently, Hattaway (1984) emended the Ptychomnioideae to also contain *Cladomniopsis*. The emended Ptychomnioideae were circumscribed by terricolous plants with relatively elongate setae, striate exostome teeth, well-developed endostomial segments and absence of asexual propagula. However, our data indicate that *Ptychomnion* and *Cladomniopsis* are not sister taxa and not even *Ptychomnion* alone deserves infrafamilial recognition. Due to the polyphyly

of the Ptychomnioideae and Cladomnioideae, no infrafamilial taxa are here recognized within the newly circumscribed Ptychomniaceae.

A number of novel relationships within the Ptychomniaceae are revealed by the molecular data. Most of these have been previously recognized at some level, but often not at an appropriate one, thus necessitating nomenclatural changes. One of the earliest diverging taxa within the Ptychomniaceae and outside a clade containing other species of *Ptychomnion*, is

P. ptychocarpon. It is characterized by relatively slender plants, long-creeping stems with rhizoids scattered throughout (rather than only at the base of stems), thin-walled laminal cells, red (rather than black) setae and erect capsules with cryptoporous stomata. These differences led Brotherus (1909) to accommodate *P. ptychocarpon* in its own subgenus. Molecular data support the interpretation that *P. ptychocarpon* is phylogenetically isolated from its congeners. It is here recognized as a monospecific genus, *Ptychomniella*.

Ptychomniella (Broth.) W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **gen. et stat. nov.** *Ptychomnion* sect. *Ptychomniella* Broth. in Engl. & Prantl, *Nat. Pflanzenfam.* **1**(3): 1222 (1909).

Type and only species: **Ptychomniella ptychocarpa** (Schwägr.) W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **comb. nov.** *Hypnum ptychocarpon* Schwägr., *Linnaea* **18**: 561 (1844); *Stereodon ptychocarpon* (Schwägr.) Mitt., *J. Linn. Soc., Bot.* **4**: 89 (1859); *Ptychomnion ptychocarpon* (Schwägr.) Mitt., *J. Linn. Soc., Bot.* **12**: 536 (1869).

During (1977) included three genera in the Garovagliaceae (sub Pterobryaceae subfam. Garovaglioideae). We sampled species from *Euptychium* and *Garovaglia*. Recent material of *Endotrichellopsis* was not available. Of the six sections of *Garovaglia* that During (1977) recognized, we were able to obtain material from five: *G. binsteadii* (sect. *Baeuerlenia*), *G. elegans* (sect. *Endotrichum*), *G. compressa* (sect. *Compressae*), *G. powellii* (sect. *Garovaglia*) and *G. subelegans* (sect. *Aristatae*). During (1977) did not present a formal phylogeny, but rather provided a diagrammatic representation of phenetic relationships. Within this, two groups of sections were recognized, one with sects *Garovaglia*, *Baeuerlenia* and *Aristatae* and the other with sects *Endotrichum*, *Compressae* and *Angustifoliae* (the latter not sampled in this study). In our study, sects *Baeuerlenia* and *Endotrichum* constitute a clade that is sister to the remaining sections (plus *Euptychium setigerum*). In a second clade, sect. *Compressae* is sister to sects *Garovaglia* and *Aristatae*. During (1977) recognized two sections within *Euptychium*, sect. *Euptychium* for six species and sect. *Crassisubulata* for *E. setigerum*. *Euptychium setigerum* has flaccid leaves that are not seriatly arranged, a unique condition in *Euptychium* but typical of *Garovaglia*. In all species of *Euptychium*, except *E. setigerum*, the laminal cells are smooth, rather than abaxially prurulose. However, abaxial prurulose laminal cells are found in various species of *Garovaglia*. Additionally, the perichaetial leaves in *E. setigerum* are abruptly cuspidate, rather than gradually acuminate as in other species of *Euptychium*. In contrast, *Garovaglia* has perichaetial leaves that are typically abruptly tapered. *Euptychium* is traditionally separated from *Garovaglia* on the basis of striate (rather than papillose) exostome teeth and a high basal membrane with 16 keeled segments (rather than 32 filiform segments without a basal membrane). Nevertheless, the molecular data clearly indicate that *E. setigerum* belongs within *Garovaglia*. As in other circumstances, it appears as if gametophytic features are more reliable as indicators of relationships than sporophytic ones (Buck, 1991). Because of the unique peristomial features

(for *Garovaglia*) and the resolution presented here showing it sister to sects *Compressae*, *Garovaglia* and *Aristatae*, the sect. *Crassisubulata* is transferred to *Garovaglia*.

Garovaglia Endl. sect. **Crassisubulata** (During) W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **comb. nov.** *Euptychium* sect. *Crassisubulata* During, *Bryophyt. Biblioth.* **12**: 64 (1977).

Type and only species: *Garovaglia setigera* (Sull.) Mitt. in Seem., *Fl. Vit.* 396 (1873); *Pilotrichum setigerum* Sull., *Proc. Amer. Acad. Arts Sci.* **3**: 80 (1854); *Endotrichum setigerum* (Sull.) Sull., *U.S. Expl. Exped. Wilkes Musci* 20 (1859); *Meteorium setigerum* (Sull.) Mitt., *Bonplandia* **9**: 366 (1861); *Euptychium setigerum* (Sull.) Broth. in Engl. & Prantl, *Nat. Pflanzenfam.* **1**(3): 786 (1906).

The sole species of the section has been divided into two subspecies, one widespread and the other restricted to New Caledonia. The narrow endemic with longer leaf apices and more strongly prurulose laminal cells needs nomenclatural emendation.

Garovaglia setigera subsp. **austrocaledonica** (Besch.) W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **comb. nov.** *Garovaglia austrocaledonica* Besch., *Ann. Sci. Nat. Bot.* **V**, **18**: 226 (1873), “*austro-caledonica*”; *Endotrichum austrocaledonicum* (Besch.) A. Jaeger, *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* **1875–76**: 231 (1877); *Euptychium austrocaledonicum* (Besch.) Broth. in Engl. & Prantl, *Nat. Pflanzenfam.* **1**(3): 786 (1906); *Euptychium setigerum* subsp. *austrocaledonicum* (Besch.) During, *Bryophyt. Biblioth.* **12**: 71 (1977).

Our data clarify the placement of the New Zealand endemic, *Dichelodontium nitidum*. The monospecific genus has traditionally been placed in the Ptychomniaceae (Brotherus, 1925) and Hattaway (1984) provisionally retained it in the family but suggested a possible placement in the Pterobryaceae (Hypnales) as more appropriate. Most recently, Allen (1999), based on both gametophytic and sporophytic features, moved the genus to the Lepyrodonataceae (Hypnales). However, the molecular data incontrovertibly place the genus within the Ptychomniales, in a close relationship with the genus *Ptychomnion* itself.

Hypnanae

With the removal of the Ptychomniales from the circumscription of the Hypnanae, the superorder now contains the two orders Hookeriales and Hypnales. The superordinal taxon was first recognized by Buck & Goffinet (2000). However, they failed to validly publish the name and we take this opportunity to do so now.

Hypnanae W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **superord. nov.**

Plantae statura variabili plerumque non grandes nec turgidae raro gemmis in axillis foliorum; folia costa singulari vel longa et duplici vel destituta; capsulae plerumque inclinatae raro sulcatae. Typus: Hypnales.

Hookeriales

Based on our phylogenetic results, the Hookeriales can be classified into seven families, the Hypopterygiaceae, Saulomataceae, Daltoniaceae, Schimperobryaceae, Hookeriaceae, Leucomiaceae and Pilotrichaceae, the latter with two subfamilies. Undifferentiated alar cells are most likely a synapomorphy for the order, however support for the character state is not significant (Fig. 6).

The Hypopterygiaceae plus *Cyathophorum* (Hookeriaceae) are strongly supported (100%) as the sister group to the rest of the Hookeriales. This is in marked contrast to the taxonomic position suggested by Buck & Vitt (1986) and Buck (1998) who considered the family to be outside the circumscription of all other pleurocarps.

Buck (1988, 1998) diagnosed the Hookeriales (excluding the Hypopterygiaceae) by the architecture of the endostome: the segments are united by a crosswall across the keel, giving them the appearance of a miniature bamboo culm in longitudinal section. Most Hypopterygiaceae lack this feature, perhaps because of association with other peristomial reductions. However, in taxa with very well developed peristomes, such as *Arbusculohypopterygium arbusculum*, not only are the segmental crosswalls present, but even endostomial cilia are well developed. Thus, the morphology supports the inclusion of the Hypopterygiaceae in the Hookeriales even though many of the hypopterygioid genera have reduced peristomes. In the studies of Blöcher & Capesius (2002) and Stech *et al.* (2002), as well as the phylogeny presented here, *Cyathophorum* (Hookeriaceae) is sister to the Hypopterygiaceae and, therefore, the traditional Cyathophoroideae would be appropriate as a name for this clade. *Cyathophorum adiantum* had previously been placed in *Cyathophorella*, but Kruijjer (2002) synonymized that genus with *Cyathophorum*. However, the lectotype species of *Cyathophorella*, *C. hookeriana*, previously unsequenced, does not appear closely related to *Cyathophorum s.str.* *Cyathophorella hookeriana*, as well as *C. parvifolia*, have axillary hairs with short, swollen apical cells, a feature unique in the Hypopterygiaceae. Thus, it may be that *Cyathophorella* deserves either recognition but with a more restricted delimitation, or possibly synonymy with *Hypopterygium* (rather than *Cyathophorum*). Our results indicate that *Cyathophorella hookeriana* is strongly supported as the sister taxon to *Hypopterygium tamarisci*.

In contrast to the analyses of both Stech *et al.* (2002) and Blöcher & Capesius (2002), our phylogeny shows the pinnately branched *Lopidium* as sister to the palmately branched Hypopterygiaceae. In Stech *et al.* (2002), Kruijjer's *Dendrohypopterygium*, of only two species, was divided into two monospecific genera, based solely on *trnL* data, with weak bootstrap support. The type species of *Dendrohypopterygium*, *D. filiculiforme*, was not sampled here and therefore we are unable to assess the value of *Dendrohypopterygium*. However, our work does lend support to the recognition of *Hypopterygium arbusculum*, the type of *Arbusculohypopterygium* and the second species of Kruijjer's *Dendrohypopterygium*, as generically distinct from *Hypopterygium s.str.* Stech *et al.* (2002) suggested that *Arbusculohypopterygium* appears related to *Dendroclypeum*

and our work, as well as that of Blöcher and Capesius, shows a similar relationship.

One of the more surprising results of our study was the well-supported (100%) positioning of two genera, *Sauloma* and *Ancistrodes*, as sister to all other Hookeriales with the exception of the Hypopterygiaceae *s.lat.* The two genera are both south temperate with *Ancistrodes* being restricted to southern Chile. Although not sampled due to lack of recently collected material, *Vesiculariopsis* probably also belongs to this group, based on its similar laminal areolation to the other two genera. Because of this group's position, it is here described as a new family.

Saulomataceae W.R. Buck, C. Cox, A.J. Shaw & Goffinet, fam. nov.

Plantae caulibus flaccidis, caules cellulis corticis porosis in sectione transversali collenchymatosis; pili axillares 2-cellulares cellula basali 3–4:1 cellula apicali elongata ambobus hyalinis; folia costa brevi duplici; laminae cellulae elongatis; setae elongatae laeves; capsulae inclinatae exothecii cellulis collenchymatosis; exostomii dentes striolati aliquando exarati; endostomium bene evolutum ciliis destitutis.

Plants epiphytic, pale green. Stems flaccid, with cortical cells porose, in cross-section cells collenchymatous, central strand absent; axillary hairs 2-celled, the basal cell 3–4:1, the apical cell elongate, both cells hyaline. Leaves lanceolate to ovate-lanceolate, short- to long-acuminate; margins mostly entire, sometimes with recurved teeth in the acumen; costa short and double or absent; laminal cells elongate, thin- to firm-walled, not porose, smooth; alar cells not differentiated. Autoicous or dioicous. Setae elongate, smooth; capsules inclined, with collenchymatous exothecial cells; annulus well differentiated in *c.* 3 rows (not verified for *Vesiculariopsis*); exostome teeth striolate, sometimes furrowed; endostome well developed, with a high basal membrane, segments keeled, with baffle-like cross-walls, sometimes perforate, lacking cilia. Calyptrae mitrate or cucullate.

Type: *Sauloma* (Hook. & Wilson) Mitt. Other included genera: *Ancistrodes* Hampe, *Vesiculariopsis* Broth.

A short, double costa is most likely a synapomorphy of the Saulomataceae, although the likelihood of the character reconstruction is less than significant at the ancestral node of the family (C in Fig. 8). Although not reconstructed here because of the large number of possible character states, the shape of the laminal cells in the Saulomataceae is distinctive. They are long-oval and firm-walled, unlike any others seen in the order.

The Daltoniaceae as currently circumscribed (Buck & Goffinet, 2000) are a polyphyletic assemblage. In the most likely tree (Fig. 1), *Calyptrochaeta* (Daltoniaceae) is the sister taxon to a clade of single-costate taxa that includes *Achrophyllum* (Hookeriaceae) and members of the Adelotheciaceae and Daltoniaceae. In some of the non-optimal trees, *Calyptrochaeta* is resolved with the double-costate group of genera (B in Fig. 8) and indeed the genus has a short, double costa. Nevertheless, Buck (1988) previously included the genus in the Daltoniaceae because of a number of other characters, including bordered leaves, 3–4-celled hyaline axillary hairs and fringed calyptrae. The molecular data tentatively

support the placement of *Calyptrochaeta* in a re-circumscribed Daltoniaceae.

Beeveria was segregated from *Achrophyllum* (Fife, 1992) because of plants pale when dry (vs. brown or black), fusi-form gemmae on stem apices (vs. L- or T-shaped gemmae on leaves), narrower exostomial furrow and lower endostomial basal membrane. Our results support the recognition of *Beeveria* as separate from *Achrophyllum*, thus making *Achrophyllum* monophyletic rather than polyphyletic. *Beeveria* is resolved as sister to *Ephemeropsis*, but without significant support. *Ephemeropsis* is the morphologically most reduced member of the Hookeriales and probably the most reduced of all pleurocarpous mosses. The plants are little more than persistent protonemata that form sex organs from which the sporophytes develop. For this reason, it has often been recognized in its own monogeneric family (Brotherus, 1925; Miller, 1971). However, Buck (1988), based on sporophytic and calyptral characters, placed the genus in the Daltoniaceae.

A recent publication (Akiyama *et al.*, 2003) places the newly described *Benitotania* as sister to *Adelothecium* and those two genera as sister to *Bryobrothera*, but the authors chose to recognize the genus as placed in a broadly interpreted Daltoniaceae (as we do here). Their *rbcL* molecular data give the same internal relationships in this group as does our more extensive genomic sampling.

Another conclusion, ultimately requiring nomenclatural alteration, is the situation involving *Distichophyllum*, *Distichophyllidium*, *Crosbya* and *Daltonia*. Although few of the species belonging to these genera were sampled, *Distichophyllum* is clearly not monophyletic. Ultimately, generic recognition within the *Distichophyllum*–*Daltonia* clade may require either all generic names to be synonymized with *Daltonia* (the oldest generic name in the complex), or possibly the description of some new genera. However, *Distichophyllum* has *c.* 103 recognized species, *Daltonia* *c.* 60 species, *Distichophyllidium* 5 species and *Crosbya* 2 species (Crosby *et al.*, 2000) and therefore our limited sampling does not permit definitive conclusions. Typification of the current generic names may resolve some problems. *Distichophyllum* Dozy & Molk. has not been typified, although only three species were included in the original description, *D. cuspidatum* (Dozy & Molk.) Dozy & Molk., *D. spathulatum* (Dozy & Molk.) Dozy & Molk. and *D. cristatum* (Hedw.) Dozy & Molk. The last name is now placed in *Calyptrochaeta* and thus is not a good choice for a lectotype. Because of its obtuse leaf apices (which most species in the genus have) and the common occurrence of the species in South-East Asia (Mohamed & Robinson, 1991), we here designate *Distichophyllum spathulatum* as the lectotype of the genus.

The use of the name *Distichophyllum* sect. *Mniadelphus* Mitt. has a confused history. *Mniadelphus* was originally used as a generic name by Carl Müller (1848), but he included the name *Distichophyllum* (Dozy & Molkenboer, 1846) in synonymy and *Mniadelphus* is therefore illegitimate. Mitten (1869) treated *Mniadelphus* as a section within *Distichophyllum*, providing a description but also citing “*Mniadelphus*, C. Müll. Syn. ii. 20, ex parte.” All eight species included by Mitten in the section are now placed in *Leskeodon*, thus making

Distichophyllum sect. *Mniadelphus* a synonym of that genus and not available for use at the sectional level in *Distichophyllum*. To formalize this interpretation, *Distichophyllum auratum* (Müll. Hal.) Mitt. (*Mniadelphus auratus* Müll. Hal., *Leskeodon auratus* (Müll. Hal.) Broth.) is here designated as lectotype of *Distichophyllum* sect. *Mniadelphus* Mitt. Therefore, the current concept of this sectional name in *Distichophyllum*, for example, Tan & Robinson (1990), as large species with leaves more than 3 mm long and scabrous to papillose setae, will need a new name. Until the generic boundaries are better clarified in the *Daltonia*–*Distichophyllum* complex, it seems premature to offer such a name.

The earliest diverging taxa in the *Distichophyllum*–*Daltonia* clade are relatively large plants, typically either growing on soil or bases of trees. Additional sampling of *Distichophyllidium* species may indicate whether they compose a monophyletic unit or whether the reduction from a single to a short and double costa has occurred repeatedly in *Distichophyllum* *s.lat.* In *Daltonia*, the plants are relatively small and often restricted to growing on branches or twigs of trees, often in areas of high humidity.

Schimperobryum is sister to the bulk of the bicostate Hookeriales. It is restricted to southernmost South America. It is distinctive by the large plants with a short, double costa and long-hexagonal, porose laminal cells. The seta is very short (*c.* 2 mm), unlike that in many of its most closely related genera. By recognition of *Schimperobryum* at the familial level, most of the other families of the Hookeriales recognized by Buck & Goffinet (2000), with minimal rearrangement of generic inclusions, can be recognized.

Schimperobryaceae W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **fam. nov.**

A Hookeriaceis *s.str.* cellulis folii longihexagonis parietibus tenuibus porosis, propagulio asexuali insidens caulibus non apicibus vel axillis foliorum exorientibus, et seta brevissima differt.

Plants terrestrial, pale green. Stems flaccid, with cortical cells firm- to thick-walled, central strand absent; axillary hairs 3–4-celled, the basal cell quadrate, brown, the apical cells elongate, thick-walled, hyaline. Leaves ovate, short-acuminate; margins mostly entire; costa short and double or absent; laminal cells long-hexagonal, thin-walled, porose, smooth; alar cells not differentiated. Asexual propagula stem-borne. Dioicous. Setae short, smooth; capsules erect, with collenchymatous exothecial cells; annulus well differentiated; exostome teeth striolate, not furrowed; endostome well developed, with a low basal membrane, segments keeled, with baffle-like cross-walls, not perforate, cilia single, rudimentary to *c.* 1/3 the segment length. Calyptrae mitrate.

Type and only genus: *Schimperobryum* Margad.

The Hookeriaceae *s.str.*, as resolved in this study, can be construed to include only *Hookeria* itself. A more traditional circumscription, including *Hookeria* and *Crossomitrium*, is here shown as a grade rather than a clade, but without significant support. Buck’s (1988, 1998) definition was considerably different, also including genera which in this study are included in the Daltoniaceae and Hypopterygiaceae and excluding

Crossomitrium. Following Allen (1990), *Crossomitrium* has been considered to be closely related to *Lepidopilum*. *Hookeria* grows on humus or soil, whereas *Crossomitrium* is primarily epiphyllous, although some species are more common as twig epiphytes. Both are composed of species with strongly complanate foliation, large, lax laminal cells and scant costal development. Both genera have asexual propagula arising from leaves (the leaf apex in *Hookeria* and leaf axils in *Crossomitrium*). The setae are elongate. This is in contrast to the stem-borne propagula and short setae of *Schimperobryum*. It may well be, with increased data, that the position of *Crossomitrium* will be confirmed with statistical support and hence will also deserve familial status. However, with the present data, we prefer to retain the genus in the Hookeriaceae.

The Leucomiaceae, containing *Leucomium*, *Rhynchostegiopsis* and *Tetrastichium*, but not *Philophyllum*, form a monophyletic group with cucullate calytra being synapomorphic for the family (B in Fig. 5). *Philophyllum*, placed by Buck (1992) in the Leucomiaceae because of the undifferentiated stem anatomy and the cucullate calytrae, is shown here to be more closely related to *Stenodictyon pallidum* in the Pilotrichaceae.

The residue of the genera of the Hookeriales falls within a broadly circumscribed Pilotrichaceae. These genera all have double costae and a strong tendency to have a hyalodermis. Like elsewhere in the order, peristomial reduction has occurred, often with pairs of traditional genera separated only by striate vs. papillose exostome teeth. Our data suggest such genera are often at best paraphyletic. The family can be divided into two subfamilies. The monogeneric Pilotrichoideae are distinguished by creeping primary stems and a stipitate habit. The rest of the genera are provisionally placed in the Hypnelloideae Broth. These are all non-stipitate plants, although a few taxa do grow erect rather than prostrate. Most genera have very strong double costae but there are at least four clades with short double costae, presumably a result of reduction. For the most part, resolution below this level is not possible, either due to insignificant resolution or limited sampling in larger genera. A few exceptions are discussed below.

Two species of *Hypnella* were sampled, *H. pallescens* and *H. diversifolia*. *Hypnella pallescens* is a member of *Hypnella s.str.*, as typified by *H. leptorrhyncha* and has a very strong, double costa, extending much of the leaf length. This taxon is sister to all other Pilotrichaceae subfam. Hypnelloideae. However, *Hypnella diversifolia*, the type of the sometimes-segregated genus, *Neohypnella*, seems to be more closely related to *Pilotrichidium*. Therefore, we would suggest that *Neohypnella* once again be recognized for this species with a relatively short costa. The two species had previously been placed in the same genus because of the seriatly pluripapillose laminal cells. However, it is noteworthy that this condition is probably a convergence and the close relationship between *Neohypnella* and *Pilotrichidium* might be indicated by the fact that one of the species of *Pilotrichidium*, *P. callicostatum*, also has pluripapillose laminal cells, although the papillae are not seriatly arranged.

A close relationship exists between *Lepidopilum*, *Lepidopilidium* and *Stenodictyon*. *Lepidopilum* is tradition-

ally separated from *Lepidopilidium* by the papillose, non-furrowed exostome teeth, as opposed to cross-striolate, furrowed teeth. Gametophytically the two are inseparable. *Stenodictyon* has a peristome similar to that of *Lepidopilidium*, but the plants are terete rather than complanate-foliate. In our analysis, *Lepidopilidium portoricense*, a Caribbean and northern South American plant, is sister to a clade formed by *Lepidopilum scabrisetum* and *Stenodictyon wrightii* and with these taxa form the sister group to *Lepidopilum polytrichoides*, indicating that at least some species of *Lepidopilidium* should be merged into *Lepidopilum*. However, a second species of *Lepidopilidium*, *L. laevisetum*, from southeastern Brazil, is most closely related to species of *Thamniopsis*. This latter genus has similar peristomes as well as a stem hyalodermis. As in *Lepidopilidium*, the two species of *Stenodictyon* sampled, *S. wrightii* and *S. pallidum*, appear not to be closely related. *Stenodictyon wrightii* is part of the *Lepidopilum* clade while *S. pallidum* is related to *Philophyllum* and *Cyclodictyon*. However, until the *Lepidopilum*-*Lepidopilidium* generic definition is resolved, it is premature to transfer *Stenodictyon wrightii* because it has the peristome traditionally associated with *Lepidopilidium*, but is here resolved within *Lepidopilum*.

Callicostella diatomophila has the same sequence data as the postulated ancestor of the monospecific *Diploneuron* and not at all like those of the other species of *Callicostella*. *Diploneuron* has been recognized because the strong double costa has each of its forks in the upper part of the leaf becoming marginal (and thus more or less limbial) and fusing in the leaf apex. *Callicostella diatomophila* does not have such a costa, but the costa is very strong and ends near the leaf apex. Both taxa are strong calciphiles and restricted to the Greater Antilles. As an alternative to describing a new genus for *C. diatomophila*, we transfer it into *Diploneuron*.

Diploneuron diatomophilum (Müll. Hal.) W.R. Buck, C. Cox, A.J. Shaw & Goffinet, **comb. nov.** *Hookeria diatomophila* Müll. Hal., *Hedwigia* **37**: 247 (1898); *Callicostella diatomophila* (Müll. Hal.) M. Fleisch., *Hedwigia* **63**: 216 (1922); *Pilotrichidium diatomophilum* (Müll. Hal.) Crosby, *Ann. Missouri Bot. Gard.* **57**: 257 (1970); *Schizomitrium diatomophilum* (Müll. Hal.) B. H. Allen & Crosby, *J. Hattori Bot. Lab.* **61**: 56 (1986).

A synopsis of the classification proposed here is presented in Table 4.

Excluded taxa

In addition to the genera treated above, samples from a number of genera were sequenced because the genera were traditionally placed either in the Hookeriaceae itself (*Chaetomitrium* and *Dimorphocladon*) or in the Hookeriales (*Symphiodon*). Buck & Goffinet (2000) transferred these genera to the Symphyodontaceae and placed the family in the Hypnales (along with *Chaetomitriopsis*, not sampled here). In a previous study (Buck *et al.*, 2000), an extensive array of Hypnanean mosses were sequenced. However, for this study, only a limited sample was included in the analyses. Nevertheless,

Order	Family	Genera
Ptychomniales	Ptychomniaceae (Garovagliaceae)	Cladomnion, Cladomniopsis, Dichelodontium, Euptychium, Garovaglia, Glyphothecium, Hampeella, Ptychomniella, Ptychomnion, Tetraphidopsis
Hookeriales	Hypopterygiaceae	Arbusculohypopterygium, Canalohypopterygium, Catharomnion, Cyathophorella (t), Cyathophorum, Dendrocyathophorum, Dendrohypopterygium, Hypopterygium, Lopidium
	Saulomataceae	Ancistrodes, Sauloma, Vesiculariopsis
	Daltoniaceae	Achrophyllum, Adelotheicum, Beeveria, Benitotania, Bryobrothera, Calyptrochaeta (t), Crosbya, Daltonia, Distichophyllidium, Distichophyllum, Ephemeropsis, Leskeodon, Leskeodontopsis, Metadistichophyllum
	Schimperobryaceae	Schimperobryum
	Hookeriaceae	Crossomitrium (t), Hookeria
	Leucomiaceae	Leucomium, Rhynchostegiopsis, Tetrastichium
	Pilotrichaceae subfam. Pilotrichoideae	Pilotrichum
	Pilotrichaceae subfam. Hypnelloideae	Actinodontium, Amblyotropis, Brymela, Callicostella, Callicostellopsis, Cyclodictyon, Diploneuron, Helicoblepharum, Hemiragis, Hookeriopsis, Hypnella, Lepidopilidium, Lepidopilum, Neohypnella, Philophyllum, Pilotrichidium, Stenodesmus, Stenodictyon, Thamniopsis, Trachyxiphium

Table 4 Synopsis of proposed classification for Ptychomniales and Hookeriales. (t) = tentative placement.

Chaetomitrium, *Dimorphocladon* and *Symphiodon* all cluster with the Hypnales, indicating a relationship there rather than with the Hookeriales.

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