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The Hypnales are the largest order of mosses comprising approximately 4200 species. Phylogenetic reconstruction within the group has proven to be difficult due to rapid radiation at an early stage of evolution and, consequently, relationships among clades have remained poorly resolved. We compiled data from four sequence regions, namely, nuclear ITS1–5.8S–ITS2, plastid *trn*L–F and *rps*4, and mitochondrial *nad*5, for 122 hypnalean species and 34 species from closely related groups. Tree topologies from both Bayesian and parsimony analyses resolve the order as monophyletic. Although inferences were made from fast-evolving genes, and despite strong phylogenetic signal in the nuclear ITS1–5.8S–ITS2 data, monophyly, as well as backbone nodes within the Hypnales, remains rather poorly supported except under Bayesian inferences. Ancestral distribution based on Bayesian dispersal-vicariance analysis supports a Gondwanan origin of the Hypnales and subsequent geographical radiation in the area of the former Laurasian supercontinent. Reconstruction of historical biogeography is congruent with mainly tropical and Gondwanan distributions in the sister groups Hypnodendrales, Ptychomniales, and Hookeriales, and with the dating for the oldest pleurocarp and hypnalean fossils. We contrast groupings in the phylogenetic tree with recent classifications and other phylogenetic inferences based on molecular data, and summarise current knowledge on the evolutionary history of, and relationships among, the Hypnales.

Keywords: Biogeography, Molecular systematics, Phylogeny, Pleurocarpous mosses, Taxonomy

Introduction

The Hypnales, together with the Hypnodendrales, Ptychomniales, and Hookeriales, belong to a monophyletic group called the 'core pleurocarps' within which practically all species are exclusively pleurocarpous (Bell *et al.*, 2007; Frey & Stech, 2009). The order Hypnales can be distinguished from other pleurocarp orders by tendency to have differentiated alar cells and smooth capsules (Buck *et al.*, 2005; Goffinet *et al.*, 2008). The order contains approximately 4200 species, and comprises one-third of all mosses (Bryophyta; Frey & Stech, 2009; Goffinet *et al.*, 2008). Despite significant research effort (Table 1), a well-supported phylogeny based on extensive taxon sampling is still unavailable for the Hypnales. Phylogenetic reconstruction is hampered by low molecular diversity and exceptionally short branch lengths resulting from a rapid diversification at an early stage of evolution (Shaw *et al.*, 2003, 2005; Newton *et al.*, 2007). The deep lineages that diversified during the early stages of

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hypnalean evolution have very low statistical support in current molecular phylogenies. The absence of a well-supported phylogenetic tree for the Hypnales has prevented a reliable evaluation of the order of diversification events and therefore biogeographical, ecological, and morphological trends within the group have not been explored or have remained speculative (Goffinet *et al.*, 2008).

The first studies applying phylogenetic and/or molecular systematic methods to the Hypnales attempted to explore the origin of the pleurocarpous growth habit as well as relationships among pleurocarps (Hedenäs, 1995; Tsubota *et al.*, 1999; Buck *et al.*, 2000a,b; De Luna *et al.*, 2000; Newton *et al.*, 2000). These early molecular phylogenies had fairly limited taxon sampling, but it was nevertheless sufficient to resolve ordinal relationships between pleurocarpous mosses (Tsubota *et al.*, 1999; Buck *et al.*, 2000a; De Luna *et al.*, 2000; Newton *et al.*, 2000). Their most important finding was that the traditional division of pleurocarps into three orders, the Hookeriales, Leucodontales (=Isobryales), and Hypnales was artificial, and the results led to extensive changes in the delimitation of the Hypnales (Buck *et al.*, 2000a). These results were congruent with the first phylogenetic inferences from morphological data, which had already suggested that ordinal divisions might not reflect natural relationships (Hedenäs, 1995). Traditionally, the Hypnales (Hypnobryales Fleisch. in Brotherus, 1925) included only pleurocarpous mosses that had hypnobryoid peristomes, while species with reduced, isobryoid peristomes were assumed to form a distinct lineage including two orders, the Leucodontales and the Hookeriales (Buck & Vitt, 1986). Buck and Vitt (1986) defined the Hypnales by a single synapomorphy: the 'shouldered exostome', referring to the exostome teeth that are sharply contracted above the lower half the tooth length. Inferences from molecular data confirmed that isobryoid, reduced peristomes have evolved several times independently within pleurocarps and that the Leucodontales comprise a polyphyletic group of taxa with reduced peristomes within the Hypnales (Cox & Hedderson, 1999; Buck *et al.*, 2000a,b; De Luna *et al.*, 2000; Newton *et al.*, 2000; Tsubota *et al.*, 1999, 2002). Consequently, the two orders were merged to form the Hypnales *s.l.* In addition to their systematic implications, the phylogenetic inferences supported the hypothesis that sporophytic characters are labile and that reduction in Isobryalean peristomes may be a consequence of shifts to xerophytic and epiphytic habitats (Buck & Vitt, 1986; Buck, 1991).

After the initial focus on large-scale relationships among pleurocarpous mosses, phylogenetic reconstructions aimed at identifying the sister-group of the Hypnales and testing hypotheses about their diversification. Shaw *et al.* (2003) explored the diversification of the Hypnales, which has resulted in striking differences in the levels of molecular divergence and branch lengths between the sister orders Hypnales and Hookeriales (see also Cox *et al.*, 2010). The results suggested that most of the major lineages appeared within the first 20% of the history of Hypnales (Shaw *et al.*, 2003). Estimates of divergence times suggested that the lineage radiated during the late Jurassic or early Cretaceous, between 157–123 mya (Newton *et al.*, 2007). Although the rapid radiation has often been connected to adaptive changes, and, for example, the evolution of epiphytic species with angiosperms as a substrate, or diversification in the new sheltered habitats found on angiosperm forest floors (Buck, 1991; Buck & Vitt, 1986; Shaw *et al.*, 2003), molecular dating suggested that early diversification was not connected to exploitation of new microhabitats in angiosperm forests (Newton *et al.*, 2007). The factors that led to the rapid diversification of the group thus remain unknown.

Table 1 Summary of earlier phylogenetic treatments aiming at the Hypnales

Year	Authors	DNA regions	No. of taxa	Reference	Main aim
2000	Buck *et al.*	cp: *trn*L–F, *rps*4	86	Mol. Phyl. Evol. 16: 180–198	Delimitation of pleurocarp orders
2000	De Luna *et al.*	cp: *trn*L–F, *rps*4, *rbc*L	38	Bryologist 103: 242–256	Relationships of pleurocarp orders
2002	Tsubota *et al.*	cp: *rbc*L	181	Hikobia 13: 645–665	Relationships among pleurocarps
2003	Shaw *et al.*	cp: *trn*L–F, *rps*4	241	Evolution 57: 2226–2241	Biodiversity and diversification of Hypnales + Hookeriales
2004	Tsubota *et al.*	cp: *rbc*L	193	Hikobia 14: 149–170	Relationships among mosses
2007	Troitsky *et al.*	cp: *trn*L–F n: ITS1–5.8S–ITS2	214	Biochemistry (Moscow) 72: 1368–1376	Relationships among Hypnales
2007	Newton *et al.*	cp: *rbc*L, *rps*4	160 (27)	Syst. Ass. Spec. Vol. Series 71: 337–366	Dating diversification of pleurocarpous mosses;
2007	Ignatov *et al.*	cp: *trn*L–F n: ITS1–5.8S–ITS2	135 (144)	Syst. Ass. Spec. Vol. Series 71: 321–336	Relationships among Hypnales, position of Leskeaceae
2010	Cox *et al.*	cp: *trn*L–F, *rps*4 mt: *nad*5 n: partial 26S	657 (269)	Phytotaxa 9: 175–195	Phylogenetic relationships and molecular diversity among mosses
2010	Merget & Wolf	n: ITS2	1634	BMC Res Notes 3: 320	Utility of ITS2 and its secondary structure in Hypnales phylogeny reconstruction

In this paper, we attempt to resolve phylogenetic relationships within the Hypnales based on inferences from an exhaustive sampling of available sequences for four loci obtained from previous studies (Table 1). The data, which are derived from multiple exemplars of hypnalean families, are complemented here with new sequences, and used to test hypotheses on the origin, diversification and relationships within the Hypnales. Since the history of pleurocarp classification prior to the molecular systematic era has recently been thoroughly reviewed by Buck (2007), we shall here concentrate on findings concerning the evolutionary history of the Hypnales at the family level and above that have been made during the last 20 years using molecular systematic approaches. The new phylogeny will be used for establishing historical biogeographical and morphological trends within the group, and for discussing the origin and diversification of the Hypnales. In addition, we will discuss problems and weaknesses with the methods used in recent studies, including the present one, as well as possible future approaches to reconstructing the phylogeny of the Hypnales.

Material and methods

Taxon sampling and molecular data

The original data set included 156 taxa (Appendix), with 122 belonging to the Hypnales, 23 to the Hookeriales, five to the Ptychomniales, four to the Hypnodendrales, and two to outgroup species from groups that are closely related to the core pleurocarps (Bell *et al.*, 2007; Frey & Stech, 2009). Within the Hypnales we aimed to sample 2–4 representatives from all families. Frey & Stech (2009) recognise 46 families within the Hypnales, whereas Goffinet *et al.* (2008) accept 42. Our sampling includes species belonging to 43 families that are recognised in these classifications, one undescribed taxon which represents a family level operational taxonomic unit (the OPP-clade; Appendix, Quandt *et al.*, 2009) and one recently described family, the Acrocladiaceae (Tangney *et al.*, 2010).

We sequenced four genomic regions: the nuclear ITS1–5.8S–ITS2, the plastid *rps*4 and *trn*L–F, and the mitochondrial *nad*5. The majority of the *rps*4, *trn*L–F, and *nad*5 sequences were publicly available, and missing entries were mostly sequenced from the same DNA extractions and/or voucher specimens from which previously existing sequences were derived (Budyakova *et al.*, 2003; Shaw *et al.*, 2003, 2005, 2008; Gardiner *et al.*, 2005; Bell *et al.*, 2007; Olsson *et al.*, 2009a; Tangney *et al.*, 2010; Cox *et al.*, 2010; Pokorny *et al.*, 2012). Voucher specimens and sequence accession numbers are listed in the Appendix. Laboratory work for all newly produced sequences was performed in the Laboratory of Molecular Systematics (The Swedish Museum of Natural History, Stockholm, Sweden), the Institute of Botany, Dresden University of Technology, or the A. N. Belozersky Research Institute of Physico-Chemical Biology (Lomonosov Moscow State University, Moscow, Russia). Protocols for DNA extractions, PCR amplifications, including primer sequences and sequencing, are described in our earlier publications (Huttunen *et al.*, 2008; Olsson *et al.*, 2009a).

Phylogenetic reconstruction

Sequences were aligned manually with PhyDE® ver. 1 (Müller *et al.*, 2005) using an alignment of Buchbender *et al.* (2006) as a scaffold. The indel data were included in the phylogenetic analyses by coding indel events into a separate data matrix with SeqState (Müller, 2005) using the simple indel coding (SIC) method developed by Simmons & Ochoterena (2000). In the ITS1–5.8S–ITS2 alignment 2390 positions (1985 positions in ITS1 and 405 positions in ITS2), and in the *trn*L–F alignment 28 positions were excluded as mutational hotspots leading to ambiguity in assessing homology between sequences. The previously reported eight base-long inversion in the *trn*L–F spacer (Quandt & Stech, 2004) was included as reverse complement (Quandt *et al.*, 2003). Gaps were treated as missing data.

Phylogenetic reconstruction was performed using Bayesian and parsimony methods with the programmes MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Altekar *et al.*, 2004) and TNT (Goloboff *et al.*, 2008). For Bayesian analyses, we used a parallel version of MrBayes running on four processors in the Bioportal resources of the University of Oslo (http://www.bioportal.uio.no). The data were divided into seven partitions: six DNA loci (ITS1, 5.8S, ITS2, *nad*5, *rps*4, and *trn*L–F) and the binary coded indels. Evolutionary models for DNA sequence data were tested for the partitions (ITS1–5.8S–ITS2, *nad*5, *rps*4, and *trn*L–F) with the programme MrModeltest2.3 (Nylander, 2004) in conjunction with PAUP 4.0 (Swofford, 1998). The Akaike Information Criterion served for the model selection. A discrete model employing identical rates of forward and backward transitions (Lewis, 2001) was applied to the indel matrix. Two simultaneous runs of Metropolis Coupled Markov Chain Monte Carlo (MC^3), both with one cold and seven heated chains, were run for 10^9 generations. Posterior probabilities for trees and parameters were saved every 500 generations and parameters for each data partition were sampled independently from each other. To avoid MC^3 chains becoming trapped in regions of the tree space representing topologies with unrealistically long branch lengths, we set an exponential prior on branch lengths with a mean value of 0.01 (Brown *et al.*, 2010).

The burn-in phase for chains was determined using plots of likelihood against generation number provided by the Bioportal server. Trees sampled prior to the stationarity phase were excluded.

Bayesian inference was performed on six data sets: two combined data sets, one including all sequence partitions but without the indel matrix and the other including indels, and separate analyses for each of the four DNA sequence regions, ITS1–5.8S–ITS2, *nad*5, *trn*L–F, and *rps*4. Independent analyses of sequence partitions served to explore possible conflicting phylogenetic signal between the data partitions. Trees resulting from these analyses were compared, and taxa with a conflicting placement supported by >0.95 posterior probability or >80% jackknife support in trees based on different DNA sequence data sets were excluded.

The parsimony analyses were performed with TNT v.1.1 (Goloboff *et al.*, 2008) for the two combined data sets. We used the option 'New Technology Search' (NTS) in which four methods, namely sectorial searches, ratchet, drift, and tree fusing, are alternated during the analysis to ensure thorough exploration of tree space. Default settings were applied for NTS and starting trees for the analysis rounds were obtained from 100 rounds of random addition sequence. Trees for jackknifing were obtained from 1000 random addition rounds similar to the original analyses.

TreeGraph 2 (Stöver & Müller, 2010) was used to summarise the topology and support from different analyses (Figures 1 and 2). When referring to Figure 1 in the text, support for branches is stated, unless otherwise indicated, for all four combined analyses in the following order: posterior probability from Bayesian analysis without indel coding (PP), posterior probability with indels (PP SIC), parsimony jackknife support without indel coding (PJ), and parsimony jackknife with indels (PJ SIC).

Assessing the phylogenetic structure of the data partitions

Statistical robustness, or 'phylogenetic structure' (*R*), was compared for five data partitions: the four DNA-sequence partitions, ITS1–5.8S–ITS2, *nad*5, *trn*L–F, and *rps*4, and a partition including indels from all four sequenced regions (compare Quandt *et al.*, 2003; Müller *et al.*, 2006). Indels in the analysis of DNA sequence partitions were treated as missing data and did not contribute to the phylogenetic structure of these partitions. Indel positions from all four sequence regions were merged into a single partition because the small number of indels in all loci other than the ITS1–5.8S–ITS2 region prevented meaningful independent analysis. Comparisons are based on differences in *R* between data partitions in mean support across nodes (Tables 4 and 5). When *R* is 1, all branches are maximally supported by the chosen support statistic, while *R* is 0 in a completely unresolved 50% majority rule consensus tree (a detailed definition of *R* is provided by Müller *et al.*, 2006). We used bootstrap proportions as a measure of support in the parsimony analyses and a simple significance test to test for differences in phylogenetic structure between different markers or character sets. All analyses were automated using Perl scripts within the Linux operating system. The analysis flow is described in detail by Müller *et al.* (2006), although for the present study, the original script by Müller *et al.* (2006) was modified to better account for strongly staggered alignments, comparing the same number of nucleotides per sample rather than the same number of alignment positions (Krug *et al.*, 2012, unpublished data).

Phylogenetic diversity

Phylogenetic diversity (PD; Faith, 1992, 1994) indicates the proportional length of a subtree in the total minimum-spanning tree. PD was calculated using combined sequence data (ITS1–5.8S–ITS2, *trn*L-F, *rps*4, and *nad*5) for three groups: a Hypnales clade, a Hypnales grade and a Hypnales crown clade (Figure 1). The 50% consensus tree from the Bayesian SIC analysis (Figure 1) was used for PD calculations. For proper comparison of PDs between groups, taxon sampling should be proportional to the number of species in each clade (Table 2). The Hypnales is, however, much less densely sampled than the other orders due to its size, and therefore, PD most likely underestimates phylogenetic diversity within the group.

Reconstruction of ancestral distribution areas

We used Bayesian dispersal-vicariance analysis (BayesDIVA; Ronquist, 1997; Nylander *et al.*, 2008) as implemented in the programme S-DIVA (Yu *et al.*, 2010) to explore historical biogeography and ancestral distribution areas. Due to a limitation for size of data sets in S-DIVA (a maximum of 125 terminals), taxon sampling was reduced, and only five outgroup species, together with all 120 Hypnales species that were resolved within a monophyletic Hypnales clade (Figure 1), were included in the analysis. A sample of 10 000 Bayesian trees from the analysis of the combined sequence and indel data was used for the S-DIVA inferences. A fully resolved tree, which is required as an output tree for presenting the results from S-DIVA, was reconstructed by compiling a majority rule consensus tree from the Bayesian tree sampling (Figure 2). The S-DIVA analysis was performed on a set of 10 000 trees using the default settings. Only ancestral distributions that were supported by >0.95 probability are shown in Figure 2.

Geographical distribution for all species was coded using two areas, Gondwanan (A) and Laurasian (B) (Figure 2), mainly following the plant geographic boundaries presented by Wijk *et al.* (1967), but with some adjustments to reflect more closely the break-up of landmasses into two supercontinents: Gondwana and Laurasia, in the Jurassic and Cretaceous. Species occurring in both areas were coded as AB. Adjustments to the geographic boundaries of Wijk *et al.* (1967) were made for four areas: As3, As4, As5, and Afr1. In As5, species occurring only in Turkey, Iran, and Afghanistan were coded as B (Laurasian distribution), and those only in the Arabian Peninsula as A (Gondwanan distribution); in As4 New Guinea was treated as part of the former Gondwanan supercontinent (A), while the rest of the area was Laurasian (B); in As3, species occurring only in the Indian subcontinent (India, Pakistan, Bangladesh, and Sri Lanka) were coded as Gondwanan (A) and those in the rest of As3 (Thailand, Myanmar, and Laos) as Laurasian; and North Africa north of the Sahara (Afr1 in Wijk *et al.*, 1967) was included in B. Species occurring primarily in northern cool climatic areas but extending into high altitude regions of the Himalayas in the northern part of the Indian subcontinent were coded as B. Exceptions in Afr1 and the northern parts of the Indian subcontinent can be justified due to close geographical connections between areas belonging to the former Gondwanan and Laurasian supercontinents, which blur biogeographical distinctions between the areas. The presence of Laurasian species in the Himalayas or in North Africa is here assumed to result from recent dispersal from Laurasia. In North Africa, the Sahara acts as a strong dispersal barrier between southern and northern Africa and therefore, the bryophyte flora in North Africa has stronger affinities to the European flora than to that of other parts of Africa (Hedenäs, 2007a; Ros *et al.*, 1999; see also Sanmartín & Ronquist, 2004).

Results

DNA sequence data and phylogeny

After exclusion of hypervariable DNA regions, the aligned lengths of the DNA regions included in the phylogenetic analysis were 3091 sites for ITS1–5.8S–ITS2, 1283 sites for *nad*5, 699 sites for *rps*4, and 871 sites for the *trn*L–F region (Table 3). The matrix including indels had 1609 sites. The majority of these indel events came from ITS1–5.8S–ITS2 (1303 characters in the indel matrix). Gaps in the *rps*4 alignment added 35 characters to the indel matrix, and *nad*5 and *trn*L–F 100 and 171 characters, respectively. MrModel test favoured a general time-reversible model of nucleotide substitution with gamma distributed rates for substitutions among sites and a proportion of invariable sites (GTR + γ + I) for all four tested data partitions (ITS1–5.8S–ITS2, *nad*5, *trn*L–F, and *rps*4).

After independent analysis of the four sequence regions, one species, *Rhynchostegium conostomus*, was omitted from the data set due to significant conflict in the resolution of its affinities based on individual data partitions. Mitochondrial *nad*5 and plastid *rps*4 resolved *R. conostomus* with high support within the Amblystegiaceae clade, whereas ITS1–5.8S–ITS2 and *trn*L–F placed it with high support in the Brachytheciaceae. The final combined analysis thus included 155 species (Appendix, Figures 1 and 2).

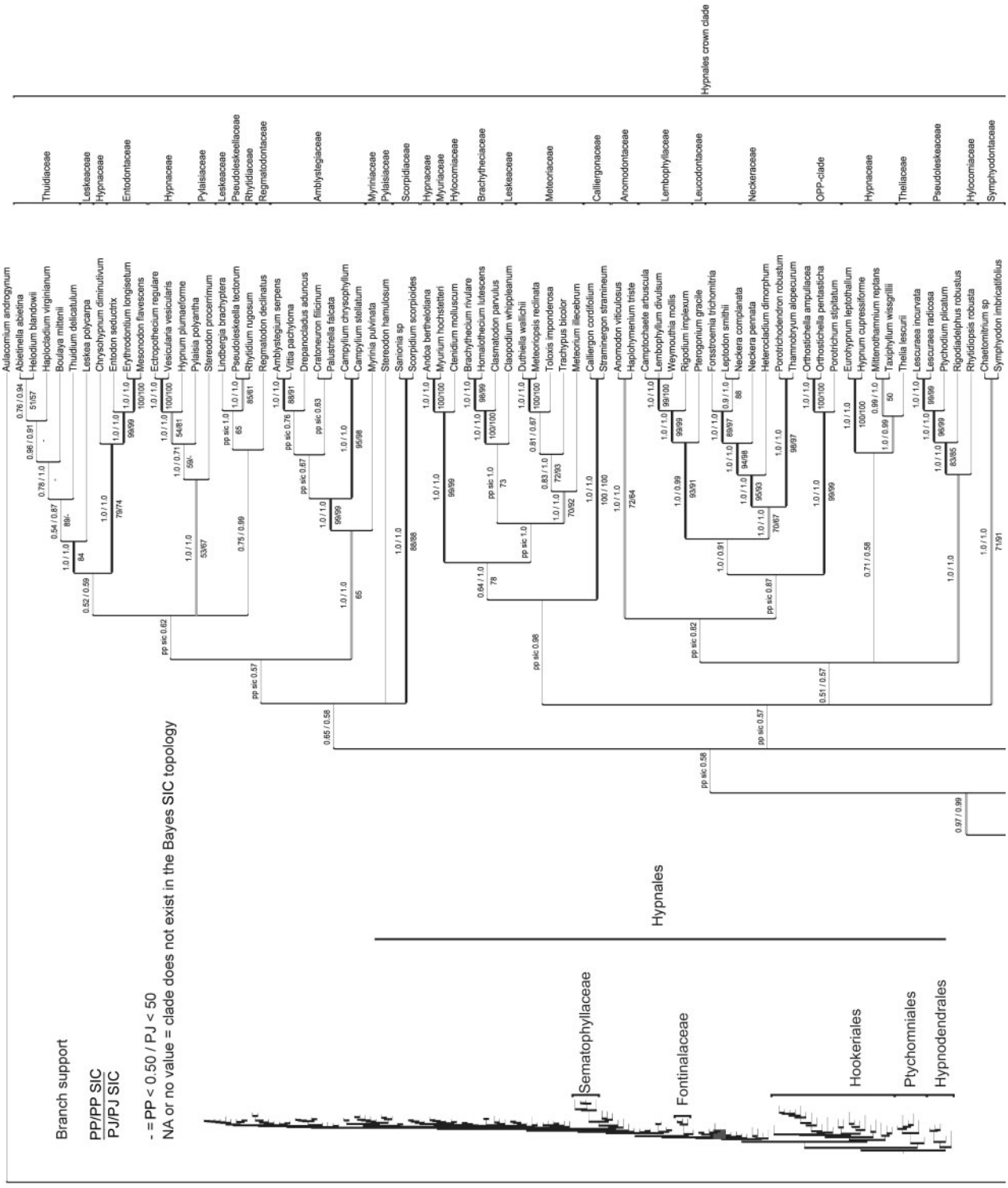
The two MC^3 chains sampled 40 000 trees in all Bayesian analyses: the two combined data sets and the four analyses of individual data sequence regions. In the Bayesian analysis of the combined data without indels, 32 812 trees were retained after exclusion of trees sampled during the burn-in phase and these were summarised in a majority-rule consensus tree. When indel data were included, 30 715 trees were sampled after stationarity and these were also used to construct a majority-rule consensus tree (Figure 1).

Parsimony analysis of combined data without indels found 59 most parsimonious trees with a length of 6958. When the matrix including indel information was added, the set of most parsimonious trees comprised 74 trees of length 9640 steps.

Phylogenetic relationships

Parsimony analysis including indels (MP SIC), and Bayesian analyses both with (Bayes SIC) and without indels (Bayes), yielded congruent results, although the topology from the parsimony analysis was considerably less resolved within the Hypnales (Figure 1). The phylogeny inferred under parsimony from sequence data alone (i.e. without indels; MP) differed from the previously mentioned ones in the branching order of groups, but none of these differences were supported by >50% jackknife frequencies (results not shown). In Figure 1, only support for branches that are shared with other analyses is provided. The major differences between the MP topology and the other analysis were that (1) the Hypnales were not resolved as monophyletic, due to the nested position of the Hookeriales among the early-diverging hypnalean lineages; and (2) relationships below family level within the Hypnales crown clade were mostly unresolved.

In the other three analyses (MP SIC, Bayes, and Bayes SIC), the Hypnales were resolved as monophyletic but received high support only from Bayesian inferences (Figure 1; PP 1.0/PP SIC 1.0/PJ and PJ SIC). One hypnalean family, the Orthorrhynchiaceae, was consistently resolved with very high support (1.0/1.0/99/100) as sister to the Ptychomniales. The Hypopterygiaceae composed a robust monophyletic group (1.0/1.0/98/99) that was inferred to share a


Hypnales crown clade
Thuidiaceae
Leskeaceae
Hypnaceae
Entodontaceae
Hypnaceae
Pylaisiaceae
Leskeaceae
Pseudoleskeellaceae
Rhytidiaceae
Regmatodontaceae
Amblystegiaceae
Myriniaceae
Pylaisiaceae
Scorpidiaceae
Hypnaceae
Myuriaceae
Hylocomiaceae
Brachytheciaceae
Leskeaceae
Meteoriaceae
Calliergonaceae
Anomodontaceae
Lembophyllaceae
Leucodontaceae
Neckeraceae
OPP-clade
Hypnaceae
Theliaceae
Pseudoleskeaceae
Hylocomiaceae
Symphyodontaceae
Aulacomnium androgynum
Abietinella abietina
Helodium blandowii
Haplocladium virginianum
Boulaya mittenii
Thuidium delicatulum
Leskea polycarpa
Chrysohypnum diminutivum
Entodon seductrix
Erythrodontium longisetum
Mesonodon flavescens
Ectropothecium regulare
Vesicularia vesicularis
Hypnum plumaeforme
Pylaisia polyantha
Stereodon procerrimum
Lindbergia brachyptera
Pseudoleskeella tectorum
Rhytidium rugosum
Regmatodon declinatus
Amblystegium serpens
Vitiia pachyloma
Drepanocladus aduncus
Cratoneuron filicinum
Palustriella falcata
Campylium chrysophyllum
Campylium stellatum
Myrinia pulvinata
Stereodon hamulosum
Sanionia sp
Scorpidium scorpioides
Andoa berthelotiana
Myurium hochstetteri
Ctenidium molluscum
Brachythecium rivulare
Homalothecium lutescens
Clasmatodon parvulus
Claopodium whippleanum
Duthiella wallichii
Meteoriopsis reclinata
Toloxis imponderosa
Trachypus bicolor
Meteorium illecebrum
Calliergon cordifolium
Straminergon stramineum
Anomodon viticulosus
Haplohymenium triste
Camptochaete arbuscula
Lembophyllum divulsum
Weymouthia mollis
Rigodium implexum
Pterogonium gracile
Forsstroemia trichomitria
Leptodon smithii
Neckera complanata
Neckera pennata
Heterocladium dimorphum
Porotrichodendron robustum
Thamnobryum alopecurum
Orthostichella ampullacea
Orthostichella pentasticha
Porotrichum stipitatum
Eurohypnum leptothallum
Hypnum cupressiforme
Mittenothamnium reptans
Taxiphyllum wissgrillii
Thelia lescurii
Lescuraea incurvata
Lescuraea radicosa
Ptychodium plicatum
Rigodiadelphus robustus
Rhytidiopsis robusta
Chaetomithrium sp
Symphyodon imbricatifolius
Sematophyllaceae
Fontinalaceae
Hypnales
Hookeriales
Ptychomniales
Hypnodendrales
Branch support
PP/PP SIC
PJ/PJ SIC
- = PP < 0.50 / PJ < 50
NA or no value = clade does not exist in the Bayes SIC topology

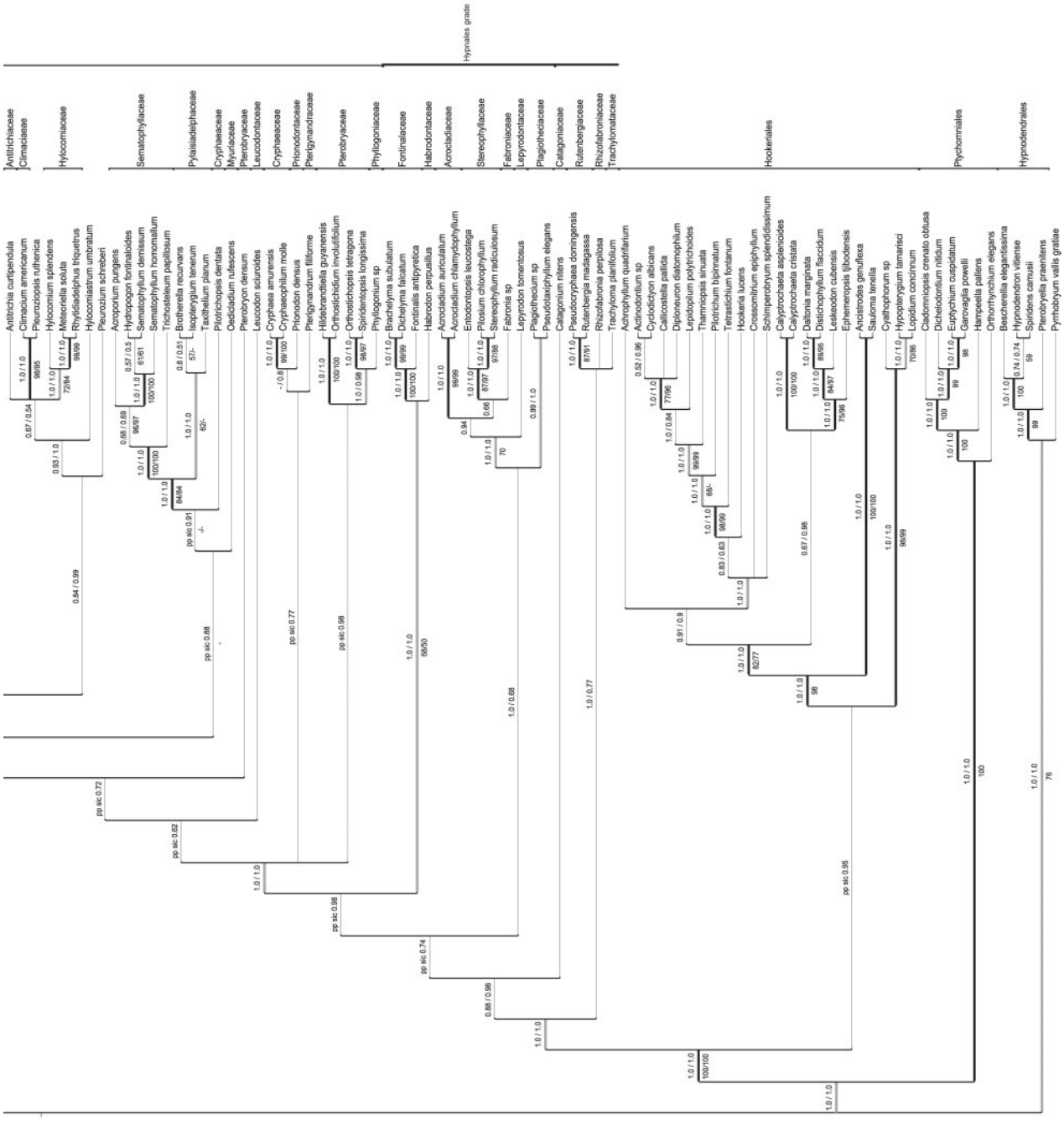
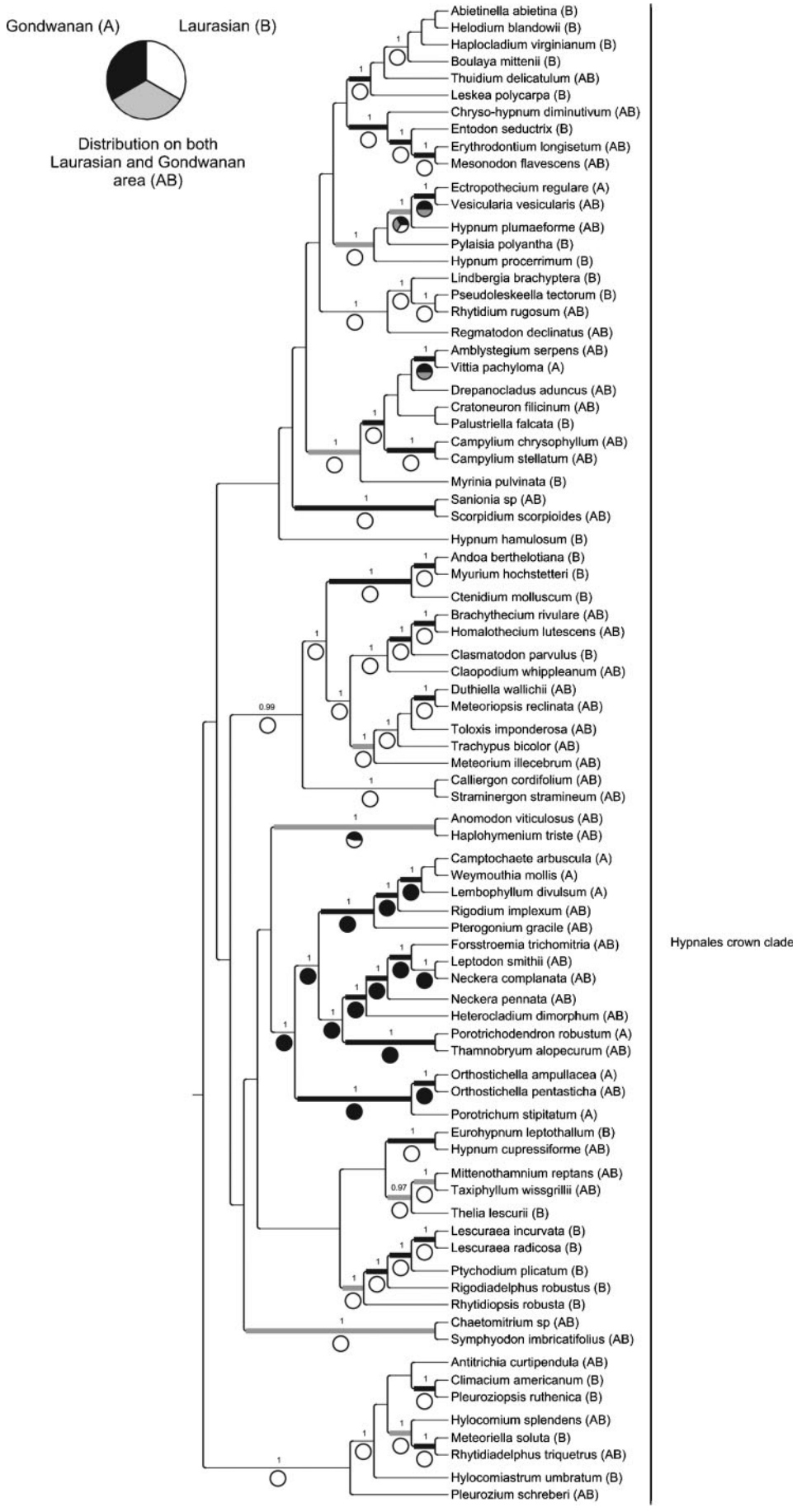


Figure 1 Phylogenetic relationships of the Hypnales based on nuclear ITS1–5.8S–ITS2, plastid *trn*L–F and *rps4*, and mitochondrial *nad5* sequence data. The topology is based on a Bayesian inference using a combined matrix composed of sequence data and a binary coded indel matrix. Bayesian posterior probability (PP) for clades is indicated above and parsimony jackknife frequences (PJ) below branches. Values before the slash (/) indicates support from Bayesian inference without indel data, whereas values after the slash are based on the analysis including indels. PJ and PP support $<50\%$ is indicated with a dash (-), while nodes that are not resolved in parsimony analysis only PP support is given. Branches well supported in all analyses (PP$\geqslant$0.95 and PJ$\geqslant$75) are in bold with black highlighting and those well supported only in Bayesian analysis (PP$\geqslant$0.95) are in bold with grey highlighting.


Gondwanan (A)
Laurasian (B)
Distribution on both Laurasian and Gondwanan area (AB)
Abietinella abietina (B)
Helodium blandowii (B)
Haplocladium virginianum (B)
Boulaya mittenii (B)
Thuidium delicatulum (AB)
Leskea polycarpa (B)
Chryso-hypnum diminutivum (AB)
Entodon seductrix (B)
Erythrodontium longisetum (AB)
Mesonodon flavescens (AB)
Ectropothecium regulare (A)
Vesicularia vesicularis (AB)
Hypnum plumaeforme (AB)
Pylaisia polyantha (B)
Hypnum procerrimum (B)
Lindbergia brachyptera (B)
Pseudoleskeella tectorum (B)
Rhytidium rugosum (AB)
Regmatodon declinatus (AB)
Amblystegium serpens (AB)
Vittia pachyloma (A)
Drepanocladus aduncus (AB)
Cratoneuron filicinum (AB)
Palustriella falcata (B)
Campylium chrysophyllum (AB)
Campylium stellatum (AB)
Myrinia pulvinata (B)
Sanionia sp (AB)
Scorpidium scorpioides (AB)
Hypnum hamulosum (B)
Andoa berthelotiana (B)
Myurium hochstetteri (B)
Ctenidium molluscum (B)
Brachythecium rivulare (AB)
Homalothecium lutescens (AB)
Clasmatodon parvulus (B)
Claopodium whippleanum (AB)
Duthiella wallichii (AB)
Meteoriopsis reclinata (AB)
Toloxis imponderosa (AB)
Trachypus bicolor (AB)
Meteorium illecebrum (AB)
Calliergon cordifolium (AB)
Straminergon stramineum (AB)
Anomodon viticulosus (AB)
Haplohymenium triste (AB)
Camptochaete arbuscula (A)
Weymouthia mollis (A)
Lembophyllum divulsum (A)
Rigodium implexum (AB)
Pterogonium gracile (AB)
Forsstroemia trichomitria (AB)
Leptodon smithii (AB)
Neckera complanata (AB)
Neckera pennata (AB)
Heterocladium dimorphum (AB)
Porotrichodendron robustum (A)
Thamnobryum alopecurum (AB)
Orthostichella ampullacea (A)
Orthostichella pentasticha (AB)
Porotrichum stipitatum (A)
Eurohypnum leptothallum (B)
Hypnum cupressiforme (AB)
Mittenothamnium reptans (AB)
Taxiphyllum wissgrillii (AB)
Thelia lescurii (B)
Lescuraea incurvata (B)
Lescuraea radicosa (B)
Ptychodium plicatum (B)
Rigodiadelphus robustus (B)
Rhytidiopsis robusta (B)
Chaetomitrium sp (AB)
Symphyodon imbricatifolius (AB)
Antitrichia curtipendula (AB)
Climacium americanum (B)
Pleuroziopsis ruthenica (B)
Hylocomium splendens (AB)
Meteoriella soluta (B)
Rhytidiadelphus triquetrus (AB)
Hylocomiastrum umbratum (B)
Pleurozium schreberi (AB)
0.99
0.97
Hypnales crown clade

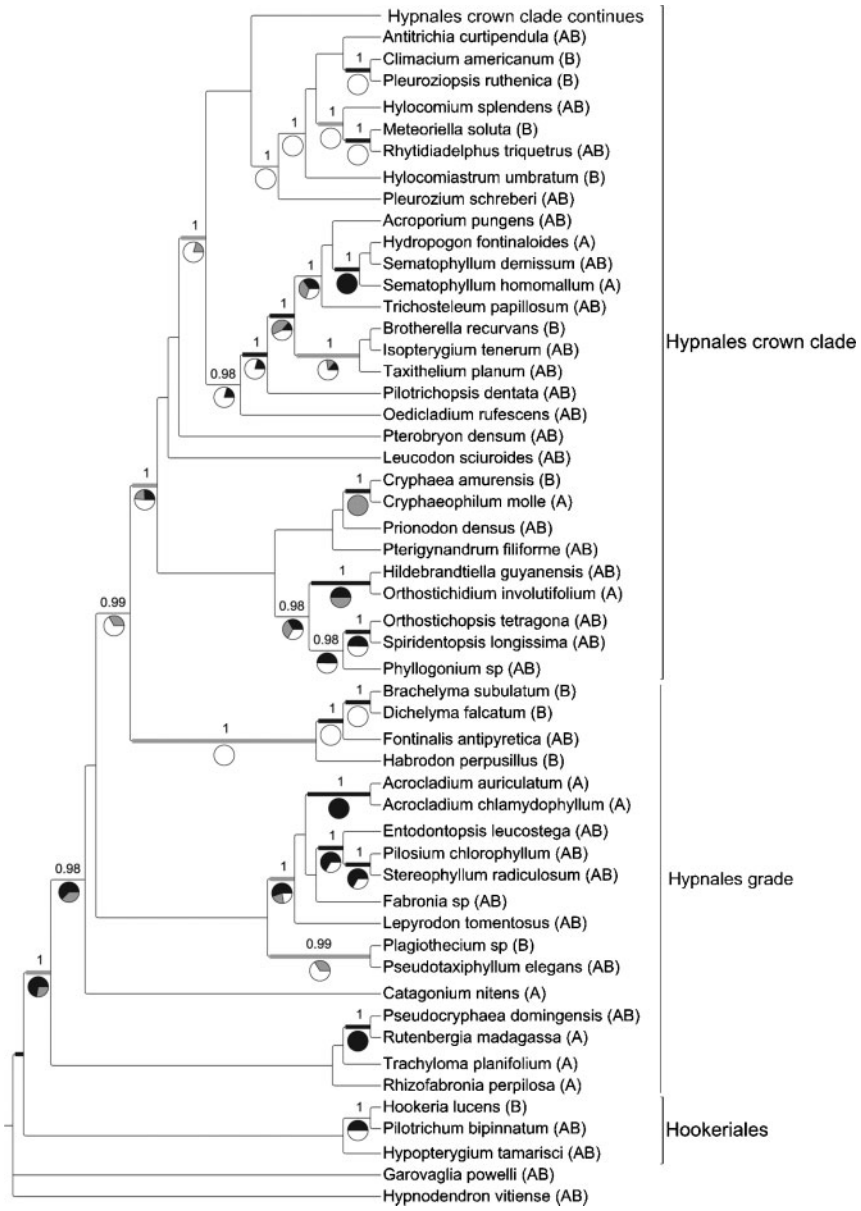


Figure 2 Ancestral distribution of Hypnales taxa according Bayes-DIVA analysis based on 10 000 trees sampled from Bayesian analysis of nuclear ITS1–5.8S–ITS2, plastid *trn*L–F, and *rps*4, and mitochondrial *nad*5 sequence data. Indels were included as a separate presence/absence matrix. Coding for each terminal is given in parenthesis after species name (A=modern distribution in area of former Gondwanan supercontinent; B=modern distribution in area of former Laurasian supercontinent; AB=distribution in both areas). Pie diagrams show probabilities for states A/B/AB at each node where the probability of an obtained ancestral distribution at a given node taking into account phylogenetic uncertainty is ⩾0.95. These probabilities are indicated numerically above branches. Support for branches from phylogenetic analysis is indicated by branch shading. Branches well supported in all analyses (PP⩾0.95 and J⩾75) are in bold with black highlighting and those well supported only in Bayesian analysis (PP⩾0.95) are in bold with grey highlighting.

unique ancestor with the sister group comprising the remaining Hookeriales only in the Bayes SIC analysis (pp 0.95). In all other analyses, the Hypopterygiaceae was the sister group to the Hypnales and Hookeriales *s.str.* The Hookeriales *s.str.* (i.e. excluding the Hypopterygiaceae) are recovered as monophyletic with high support in all analyses (1.0/1.0/97/98), and hence formed the sister group to the Hypnales, except as mentioned above in the Bayes SIC analysis. The monophyly of the remaining pleurocarpous orders was always well supported: the Ptychomniales (1.0/1.0/99/100) and the Hypnodendrales (1.0/1.0/99/99).

Relationships within the Hookeriales were well-resolved and highly supported. By contrast, successive cladogenic events in the Hypnales, especially those associated with early diversification, were poorly supported except in the Bayes SIC analysis. Two nodes in the Hypnales backbone gained full support from both Bayesian analyses: the shared ancestry of all Hypnales and that of a hypnalean crown clade (Figure 1). The earliest diverging families within the Hypnales clade are mainly tropical and Southern Hemisphere taxa representing rather few species, whereas the crown clade comprises species-rich

Table 2 Numbers of genera in each of the 'core pleurocarp' orders (% of total number of genera in core pleurocarps, or within Hypnales, % of total number of genera in the order: see Bell *et al.*, 2007; Frey & Stech, 2009), number of genera included in this study (% of total number of genera in the group) and phylogenetic diversity (PD) of clades within the Hypnales compared to entire tree and to Hypnales clade. PDs are calculated by contrasting the total tree length (=5.46) with the minimum spanning tree length of the clade in question

	No. of genera (Frey & Stech, 2009)	No. of sampled genera	PD (% of total tree)	PD (% of Hypnales clade)	Length of min. spanning tree
Hypnodendrales	14 (2.9%)	4 (28.6%)			
Ptychomniales	13 (2.7%)	5 (38.5%)			
Hookeriales	52 (10.7%)	22 (42.3%)			
Hypnales	406 (83.7%)	116 (28.6%)	57.5	100.0	3.14
Basal grade	32 (7.9%)	17 (53.1%)			
Crown clade	374 (92.1%)	99 (26.5%)	45.6	79.3	2.49
The apical group sister to *Pterobryon densum*	327 (80.5%)	88 (26.9%)	39.6	68.8	2.16

Northern Hemisphere families (Figure 1). Despite their almost exclusively Northern Hemisphere distributions, the Fontinalaceae and Plagiotheciaceae are resolved within the grade of lineages that branched off earliest within the Hypnales.

Within the Hypnales crown clade in the Bayesian analysis (Figure 1), a well-supported node (PP 0.97/ PP SIC 0.99) separates the clade containing the most apical hypnalean families, such as the Amblystegiaceae, Brachytheciaceae, Lembophyllaceae, Neckeraceae, Sematophyllaceae and Thuidiaceae, from the Phyllogoniaceae, Pterobryaceae, Prionodontaceae, Cryphaeaceae, Leucodontaceae, and Pterigynandraceae, as well as from taxa in the grade subtending the Hypnales crown clade in the Bayesian analysis (Figure 1). The MP SIC analysis also resolves this grouping but without support. Branching order differed in poorly supported (PP and PP SIC <0.95) parts of the tree. For example, the sequence of clades composing the grade subtending the Hypnales crown clade differed after the inclusion of indel data. The divergence order of groups among the most apical Hypnales families also varied between analyses and the relationships between these families remain unclear.

Phylogenetic structure of data partitions

Analysis of phylogenetic structure in each data partition revealed that base substitutions in the ITS1–5.8S–ITS2 region had both a higher information content and a stronger phylogenetic signal compared to the other DNA sequence partitions and the indel data (Tables 4 and 5). Information content and signal in the indel data partition were clearly lower than in any of the four DNA sequence data partitions. Variation in information content in tested sequence partitions followed DNA sequence divergence; the partition with the highest divergence (ITS1–5.8S–ITS2) had the highest information content while the least divergent had the lowest (*nad*5) (Tables 3 and 4). The quality of the phylogenetic signal (measured in a comparison of

Table 3 Information on sequenced DNA regions

Region	Aligned length (bp)	% variable sites	% PI sites	% divergence	Ranking all sites	Ranking PI sites only
ITS1–5.8S–ITS2	3091	24.3	12.8	10.69	1	1
*trn*L–F	871	29.6	18.0	5.31	2	3
*rps*4	699	44.6	27.0	4.53	3	4
*nad*5	1283	34.0	17.7	2.19	3	2
indels	1609	100	37.9	5.16	4	5

Table 4 Comparison of phylogenetic structure (*R*) for all sites between data partitions used in phylogenetic analysis. Four data partitions, ITS1–5.8S–ITS2, *trn*L–F, *rps*4, and *nad*5, contained DNA sequence data where gaps were treated as missing data, while the fifth consisted of combined indel information from all four DNA regions. A statistically insignificant difference in *R* statistics is indicated by *ns*

Comparison	Winning partition	Mean difference in *R*	SE	95% confidence interval	
ITS versus *nad*5	ITS	0.0610	0.0018	0.0575	0.0645
ITS versus *rps*4	ITS	0.0502	0.0009	0.0484	0.0521
ITS versus indels	ITS	0.0633	0.0010	0.0613	0.0653
*trn*L–F versus ITS	ITS	−0.0268	0.0015	−0.0298	−0.0238
*trn*L–F versus *nad*5	*ns*	0.0024	0.0022	−0.0020	0.0068
*trn*L–F versus *rps*4	*trn*L–F	0.0293	0.0014	0.0265	0.0320
*trn*L–F versus indels	*trn*L–F	0.0296	0.0011	0.0274	0.0318
*rps*4 versus *nad*5	*ns*	0.0030	0.0018	−0.0006	0.0066
*rps*4 versus indels	*rps*4	0.0164	0.0012	0.0141	0.0187
indels versus *nad*5	*nad*5	−0.0059	0.0010	−0.0079	−0.0039

parsimony informative [PI] sites), however, showed a different pattern. For example, despite low divergences in *nad*5 sequences, PI positions in *nad*5 had a stronger phylogenetic signal compared to those in the more variable *trn*L–F and *rps*4 regions (Tables 3 and 5).

Phylogenetic diversity

Although the number of genera in the Hypnales is significantly greater than in the three other core pleurocarp orders combined, the Hypnales contain only 57.5% of the total phylogenetic diversity (Table 2). This may be biased by scarcer taxon sampling; only 28.6% of genera in the Hypnales are sampled, while the proportion of sampled genera is clearly higher in the Ptychomniales (38.5%) and Hookeriales (42.3%). Within the Hypnales, the earliest diverging lineages comprising the Hypnales grade (Figure 1) are much better sampled compared to the large number of genera in the Hypnales crown clade (Table 2). Genera in the Hypnales grade comprise 7.9% of the total number of genera in the Hypnales, while the Hypnales crown clade comprise 92.1% and the apical Hypnales group 80.5%. Phylogenetic diversity in the Hypnales crown clade and in the apical Hypnales group is 45.6% and 39.6%, respectively, of the total diversity in the tree, and 79.3% and 68.8% of the diversity in the Hypnales clade.

Ancestral distribution areas and historical biogeography

Dispersal-vicariance analysis suggested a Gondwanan distribution for the ancestor of the Hypnales (Figure 2). A shift to Laurasian distributions is indicated at the base of the Hypnales crown clade (Figure 2), although several recent dispersals to (and subsequent radiations in) former areas of the Gondwanan supercontinent are also indicated within the Hypnales crown clade, e.g. within the Lembophyllaceae–Neckeraceae clade and the Sematophyllaceae. A shift from the Gondwanan distribution that characterises the grade of lineages branching off first within the Hypnales to a Laurasian distribution in the most apical hypnalean groups manifests as a gradual transition through a series of tropical and warm temperate families, i.e. the earliest diverging lineages in the Hypnales crown clade. The families that have radiated most extensively in cool climates in fragments of the former Laurasian supercontinent occur within the apical clade of the Hypnales crown clade. Although Gondwanan distributions are otherwise in the majority in the grade subtending the Hypnales crown clade, the Fontinalaceae and Plagiotheciaceae lineages represent shifts to Laurasian distributions. Owing to low support for the Hypnales backbone nodes, probabilities of ancestral distributions remain low (<0.95).

Discussion

Overview of phylogenetic relationships within the Hypnales inferred from sequence data

The Hypnales are resolved as monophyletic, but only Bayesian analyses provide strong support for the clade (Figure 1). Other than in the inferences of Buck *et al.* (2000a,b), the Hypnales *s.l.* have almost invariably been resolved as a clade with either low (Tsubota *et al.*, 2002, 2004; Olsson *et al.*, 2009a), or strong support (Buck *et al.*, 2005; Stech *et al.*, 2008), but their unique ancestry has recently been questioned (Cox *et al.*, 2010). A sister-group relationship with the Hookeriales is recovered here, as in most earlier studies (Figure 1; Tsubota *et al.*, 2002, 2004; Buck *et al.*, 2005). The core Hookeriales form a robust lineage (Figure 1; Tsubota *et al.*, 2002; Buck *et al.*, 2005), but the affinity of the group to the Hypopterygiaceae is controversial. While the monophyly of the Hypopterygiaceae is well-supported (Figure 1; Shaw *et al.*, 2008), topologies indicating relationships with the Hookeriales *s.str.* and the Hypnales typically lack strong support (Figure 1; Buck *et al.*, 2000b), and the family has even been resolved within the Hypnales (Cox *et al.*, 2010). However, recent analyses using sequence data from all three genomes infer the Hypopterygiaceae as the first branching lineage among the Hookeriales with significant support (Pokorny *et al.*, 2012).

The molecular tree suggests that the family Orthorrhynchiaceae may need to be excluded from the Hypnales and transferred to the Ptychomniales. The

Table 5 Comparison of phylogenetic structure (*R*) for parsimony informative sites between data partitions used in phylogenetic analysis. Analyses were performed for four DNA sequence data partitions, ITS1–5.8S–ITS2, *trn*L–F, *rps*4, and *nad*5, and a partition including combined indel information from all four DNA regions. A statistically insignificant difference in *R* statistics is indicated by *ns*

Comparison	Winning partition	Mean difference in R	SE	95% confidence interval	
ITS versus indels	ITS	0.0757	0.0010	0.0737	0.0777
*nad*5 versus ITS	ITS	−0.0312	0.0011	−0.0334	−0.0290
*nad*5 versus indels	*nad*5	0.0541	0.0012	0.0518	0.0565
*trn*L–F versus ITS	*ns*	0.0028	0.0014	−0.0000	0.0055
*trn*L–F versus *nad*5	*nad*5	−0.0125	0.0015	−0.0155	−0.0095
*trn*L–F versus *rps*4	*trn*L–F	0.0242	0.0013	0.0216	0.0268
*trn*L–F versus indels	*trn*L–F	0.0432	0.0011	0.0410	0.0454
*rps*4 versus ITS	ITS	−0.0297	0.0015	−0.0327	−0.0266
*rps*4 versus *nad*5	*nad*5	−0.0253	0.0015	−0.0283	−0.0224
*rps*4 versus indels	*rps*4	0.0308	0.0012	0.0285	0.0332

family was established by Lin (1983) to accommodate the single genus *Orthorrhyncium* Reichardt. The genus was previously placed in the Phyllogoniaceae (Hypnales), while recent classifications (Goffinet *et al.*, 2008; Frey & Stech, 2009) have followed Lin's (1984) original placement among the Hypnales. The molecular data, however, surprisingly resolves it with high support as sister to the Ptychomniales (Figure 1). Morphological characters, such as the absence of pseudoparaphyllia and the presence of axillary rhizoids in the *Orthorrhynchiaceae*, contrast with the leaf-like pseudoparaphyllia and rhizoids on stems just below the costa insertion found in Phyllogoniaceae species. These characters certainly support a distant relationship between the families. Although further studies are required to confirm the relationship of the Orthorrhynchiaceae to the Ptychomniales, it should be noted that both have axillary rhizoids.

The families in the Hypnales can be segregated into two groups: a Hypnales crown clade and a series of taxa forming a Hypnales grade (Figure 1). Ten families, the Trachylomataceae, Rutenbergiaceae, Stereodontaceae, Catagoniaceae, Plagiotheciaceae, Lepyrodontaceae, Fabroniaceae, Acrocladiaceae, Habrodontaceae, and Fontinalaceae comprise the Hypnales grade (Figure 1). These families typically contain few taxa and have predominantly tropical and Southern Hemisphere distributions (Figure 1). The only exceptions are the Plagiotheciaeae (approximately 100 species; Pedersen & Hedenäs, 2002) and the Fontinalaceae (27 species), which occur predominantly in the Northern Hemisphere. Morphological characters that are frequent among taxa in the Hypnales grade include naked branch primordia (i.e. a lack of pseudoparaphyllia) and axillary rhizoids (Hedenäs, 1995). The absence of pseudoparaphyllia is shared with the Hookeriales and may represent a plesiomorphic character state in pleurocarpous mosses.

The families comprising the Hypnales grade are recovered among lineages branching off earliest within the Hypnales in various studies, although always without significant support unless gaps are treated as a fifth character state in the phylogeny reconstruction (Buck *et al.*, 2000a; Tsubota *et al.*, 2004; Ignatov *et al.*, 2007; Troitsky *et al.*, 2007; Cox *et al.*, 2010; Merget & Wolf, 2010). Family delimitation has been tested using molecular systematic methods for at least four families in the Hypnales grade: the Acrocladiaceae, Fontinalaceae, Habrodontaceae, and Plagiotheciaceae (Shaw & Allen, 2000; Pedersen & Hedenäs, 2002; Budyakova *et al.*, 2003; Tangney *et al.*, 2010). Delimitation of the Plagiotheciaceae has remained controversial as support for the first diverging lineages in the family is low (Pedersen & Hedenäs, 2002). Our results support a broad family circumscription as suggested by Pedersen and Hedenäs (2002), although *Acrocladium*, *Rhizofabronia*, and *Catagonium* are not resolved within the family (Figure 1; Tangney *et al.*, 2010). As in earlier molecular analyses, the Acrocladiaceae, Fontinalaceae, and Habrodontaceae are resolved here as monophyletic with high support and thus warrant recognition as independent families (Figure 1; Shaw & Allen, 2000; Pedersen & Hedenäs, 2002; Budyakova *et al.*, 2003; Troitsky *et al.*, 2007; Tangney *et al.*, 2010). Even if more detailed familial studies are still lacking, well-supported core-groups also exist for the Stereophyllaceae and Rutenbergiaceae (Figure 1; Tangney *et al.*, 2010).

Within the Hypnales crown clade, relationships between the six earliest diverging lineages (i.e. the Phyllogoniaceae, Pterobryaceae, Prionodontaceae, Cryphaeaceae, Leucodontaceae, and Pterigynandraceae) are poorly supported and the topology is sensitive to small changes in the data such as additions of data partitions (Figure 1). These families are relatively small in terms of species numbers (Figure 1) and are distributed in tropical and warm temperate areas with only a few species occurring in areas with cool temperate to arctic climates. Although all of these families contain an unambiguous small core of taxa, precise delimitation, especially for the Cryphaeaceae, Pterobryaceae, and Leucodontaceae, awaits confirmation (Figure 1; Maeda *et al.*, 2000; Quandt *et al.*, 2004; Stech *et al.*, 2011). A monogeneric Antitrichiaceae has already been segregated from the Leucodontaceae by Ignatov and Ignatova (2004; see also Ignatov *et al.*, 2007; Troitsky *et al.*, 2007; Frey & Stech, 2009) and its independent position is supported here (Figure 1).

Among the apical clade, the most species-rich hypnalean families, such as the Amblystegiaceae, Brachytheciaceae, Sematophyllaceae, and Pylaisiadelphaceae, have remained rather stable and well-supported across phylogenetic inferences and their monophyly are confirmed here (Figure 1; Cox *et al.*, 2010). The apical group, sister to *Pterobryon densum* in Figure 1, contains 80.5% of the genera, but only 68.8% of the phylogenetic diversity in the Hypnales (Table 2), although the low value for phylogenetic diversity may be partially due to scattered taxon sampling as compared with, for example, the basal Hypnales grade. Buck *et al.* (2000b) presented a detailed discussion of relationships among pleurocarps, and compared to the knowledge of familial circumscriptions at that time our results and other recent molecular inferences represent significant progress, especially in family delimitations of the Amblystegiaceae (Vanderpoorten *et al.*, 2002a,b, 2003), Brachytheciaceae (Ignatov & Huttunen, 2002; Huttunen & Ignatov, 2004; Huttunen *et al.*, 2004, 2007), Entodontaceae (Tsubota *et al.*, 2001, 2002), Lembophyllaceae (Huttunen *et al.*, 2004; Quandt *et al.*, 2009), Meteoriaceae (Quandt & Huttunen, 2004;

Quandt *et al.*, 2004; Huttunen *et al.*, 2004; Huttunen & Quandt, 2007), Neckeraceae (Olsson *et al.*, 2009b, 2010, 2011), Pseudoleskeaceae (Gardiner *et al.*, 2005), and Sematophyllaceae (Tsubota *et al.*, 2001, 2002, 2004). Following some taxonomic revision, monophyly of these families is now well-supported. In molecular trees, a well-supported core group also exists for many other families, such as the Calliergonaceae, Hylocomiaceae, Pylaisiaceae, Scorpidiaceae, and Thuidiaceae (Figure 1). Although their delimitation has already been explored using molecular inferences, they are still in need of further revision (Chiang & Schaal, 2000; Gardiner *et al.*, 2005; Hedenäs, 2006; Ignatov *et al.*, 2007; Hedenäs & Vanderpoorten, 2007; Stech *et al.*, 2008; Garcia-Avila *et al.*, 2009; Cox *et al.*, 2010; Wang *et al.*, 2010).

The generic circumscription of less than one-third of hypnalean families has been tested against a criterion of monophyly based on molecular phylogenetic inference. The most species-rich family in the Hypnales, the Hypnaceae, is consistently recovered as polyphyletic and redefining the family and testing the affinities of its taxa is one of the most challenging tasks (Figure 1; Tsubota *et al.*, 2002, 2004; Ignatov *et al.*, 2007; Troitsky *et al.*, 2007; Olsson *et al.*, 2009a; Cox *et al.*, 2010). As the species currently placed in the Hypnaceae appear to be scattered in distant parts of the Hypnales phylogeny (Figure 1), any study aiming to clarify familial delimitation and taxonomy needs to include a very large number of species from across the entire Hypnales crown clade. The Leskeaceae are also still resolved as polyphyletic (Figure 1; Frey & Stech, 2009), although Ignatov and Ignatova (2004) have already divided it into three families, the Leskeaceae, Pseudoleskeellaceae, and Pseudoleskeaceae (Gardiner *et al.*, 2005). Unlike in the Ignatov *et al.* (2007) and Troitsky *et al.* (2007) topologies, the core Thuidiaceae (incl. Helodiaceae) appears here as sister to *Leskea*, a position which allows retention of the family name Leskeaceae. Although the Anomodontaceae in a very narrow sense appears here as monophyletic, the family was resolved as severely polyphyletic in earlier studies (Tsubota *et al.*, 2002; Olsson *et al.*, 2009a).

Morphological delimitation of higher-level taxonomic entities revealed by molecular inferences is often difficult. The taxonomic value of some characters that may be useful in family level delimitations, such as the structure and arrangement of pseudoparaphyllia, the colour, surface structure, position, and arrangement of rhizoids on shoots and presence of dwarf males, is still underexplored in the light of groupings revealed by molecular inferences (Iwatsuki, 1987; Hedenäs, 1987, 1989, 2007b; Ignatov & Hedenäs, 2007; Hedenäs & Bisang, 2011). Most morphological characters that have been considered to be taxonomically important in pleurocarpous mosses have evolved independently in several unrelated lineages. The results presented here add to the evidence for parallel evolution of, for example, sporophytic reductions, examples of which can be found in almost all larger hypnalean families; short, double costae (e.g. in the Hypnaceae and Plagiotheciaceae); complanate shoots (Neckeraceae, Plagiotheciaceae); short, rhombic cell shape (Pterigyandraceae, Leskeaceae, Cryphaeaceae *s.l.*); and pendent growth forms (Meteoriaceae, Brachytheciaceae, Lembophyllaceae, Cryphaeaceae) (Buck & Vitt, 1986; Vanderpoorten *et al.*, 2002a; Quandt & Huttunen, 2004; Huttunen *et al.*, 2004; Gardiner *et al.*, 2005; Olsson *et al.*, 2009b). Factors that could lead to lability and parallel evolution of morphologies are rapid evolutionary shifts between character states, for example due to simple genetic regulation, plasticity, and natural selection (Grout, 1908; Vitt, 1981; Vitt & Glime, 1984; Buck, 1991; Hedenäs, 2001; Vanderpoorten *et al.*, 2003; Huttunen *et al.*, 2004; Vanderpoorten & Jacquemart, 2004; Vanderpoorten & Goffinet, 2007; Olsson *et al.*, 2009c; Sotiaux *et al.*, 2009; Huttunen & Ignatov, 2010).

Origin and diversification of the Hypnales in the light of phylogeny, dispersal-vicariance analysis, and fossil data

Reconstruction of ancestral distributions favours a Gondwanan origin of the Hypnales followed by a radiation of the most species-rich families in Laurasia (Figure 2). A Gondwanan origin is also supported by the extant distributions of groups most closely related to the Hypnales. The majority of the Hypnodendrales, Ptychomniales, and Hookeriales occur in the Southern Hemisphere and in tropical areas. Based on the shared distributions of these three orders, Bell *et al.* (2007) proposed that the common ancestor of the Hypnales arose in the Southern Hemisphere. Such a transition from an ancestral Gondwanan to a Laurasian distribution also characterises the evolutionary history of the Sphagnales (Shaw *et al.*, 2010).

Fossil data for early pleurocarps are very scanty and provides no evidence for a Gondwanan origin. The first moss fossils similar to pleurocarps, the genera *Uskatia* Neub. and *Rhizinigerites* Meyen, are from the Upper Permian (260–251 mya) deposits in Angaraland and Subangaraland, areas that are today situtated in North Eastern European Russia and North Asia (Neuburg, 1960; Gomankov & Meyen, 1986; Ignatov, 1990; Ignatov & Shcherbakov, 2007). Hence, the origin of the pleurocarpous growth habit predates the breakup of Pangea, which began in the

early Jurassic, *ca* 190 mya (Sahabi *et al.*, 2004; Labails *et al.*, 2010), although the location of these fossils does not support a Gondwanan origin. However, due to the unique morphological characters of the fossils, such as leaves attached to shoots only by the costa (*Uskatia* Neub.) and leafless axes supporting clusters of rhizoids (*Rhizinigerites* Meyen), these Permian pleurocarps cannot be assigned to any modern lineages, and they may even represent an extinct lineage of pleurocarps (Newton *et al.*, 2007). Their relationships to modern pleurocarpous mosses and significance in estimating the timing of the origin of the Hypnales remains dubious.

Extinct lineages that are morphologically closer to modern Hypnales appear later in the fossil record, in the Mesozoic era. *Palaeodichelyma sinitzae* Ignatov & Shcherbakov from the late Jurassic closely resembles modern hypnalean mosses, and in the protologue was placed close to *Dichelyma* (Fontinalaceae; Ignatov & Shcherbakov, 2007). Some putative members of the Hookeriales that are dated to the late Jurassic and early Cretaceous have also recently been found in many localities in the Transbaical area of Siberia and in Mongolia (Ignatov, 1992; Ignatov & Shcherbakov, 2011; Ignatov *et al.*, 2011). Molecular dating suggests that at the time these fossil taxa were extant, rapid radiation was underway among hypnalean mosses (the Jurassic, *ca* 157–198 mya; Newton *et al.*, 2007). The former Gondwanan and Laurasian supercontinents were gradually separating and Laurasia was further fragmented and divided by the widening Atlantic and epicontinental seas (Cox, 1974; Sanmartín *et al.*, 2001 and references therein). The rapid radiation may thus have occurred in the area of the Laurasian supercontinent (Figure 2; Newton *et al.*, 2007) and, therefore, climatic and geological changes in the Northern Hemisphere could have been important factors behind the diversification. For example, during the same time period, the evolution of woody vegetation in Gondwana and in Laurasia followed different patterns. Conifer forests in Laurasia were more diverse and had more endemic species than in Gondwana, while, for example, the Pinaceae diversified during the early Cretaceous in the Northern Hemisphere with no equivalent radiation taking place in the Southern Hemisphere (Philippe *et al.*, 2004). This could have been due to the fragmentation of Laurasia into several disjunct provinces, while a smaller number of more widespread vegetation zones were present in Gondwana (Philippe *et al.*, 2004).

Emerging cool climates, the origin of the boreal biome during the Cenozoic in the Northern Hemisphere (Taggart & Cross, 2009), and complex geological events in areas of the former Laurasian supercontinent may have favoured diversification within some hypnalean families (Figure 2; Krassilov & Schuster, 1984). Almost all large families with high levels of extant species diversity in cool climate areas are resolved within the Laurasian apical Hypnales group. In contrast with the postulated antiquity of the ancestors of the pleurocarps, the relatively recent radiation within the crown group is consistent with the short branch lengths that characterise its internal relationships (Figure 1), lower phylogenetic diversity in the Hypnales crown clade than in the basal grade (Table 2), and young age estimates for some of the most species-rich families (e.g. a *ca* 65 my age for the Brachytheciaceae, node 96 in Newton *et al.*, 2007). Buck & Vitt (1986) considered the Hypnales (excluding the Leucodontales) to be the only pleurocarpous order that successfully diversified in northern temperate regions. The young age of the boreal flora as a whole may also explain the similarity of boreal floras on different continents (Hedenäs, 2007a). Recent radiation in cool Laurasian climates may also explain differences in radiation patterns and branch lengths between the tropical Hookeriales and the Hypnales. An interesting exception within the Hypnales crown clade is the tropical Sematophyllaceae, in which branch lengths are clearly longer than in other families (Figure 1).

Problems within phylogenetic reconstruction in the Hypnales: limitations due to sampling, markers, and phylogenetic signal

Although some well-supported clades have been resolved within the Hypnales, published phylogenies have yet to reliably identify deep diversification events defining the evolutionary history of the group. This could be explained by (1) reliance on single DNA sequence regions; (2) scarce taxon sampling and poor selection of outgroups; and 3) limited phylogenetic information content in the data.

Early attempts at reconstructing evolutionary histories relied on inferences from single loci and focused on deeper taxon sampling (e.g. the plastid *rbc*L gene; Tsubota *et al.*, 1999, 2002, 2004). Very recently, Merget and Wolf (2011) tested the utility of the nuclear ITS2 region for phylogeny reconstruction in the Hypnales, although they concentrated on showing the value of combining primary and secondary structure information in phylogenetic reconstruction rather than on exploring relationships among the Hypnales. Although some groupings in these single gene phylogenies deviate from each other and from the other published studies, well-supported families, such as the Sematophyllaceae, are resolved as monophyletic. Merget and Wolf (2011) resolved only 11 out of 35 included hypnalean families as clades and many families that are monophyletic in

most other phylogenies, such as the Brachytheciaceae (Figure 1), were polyphyletic. In both *rbc*L and ITS2 trees branch support, especially at deep nodes, is low or missing (Tsubota *et al.*, 1999, 2002, 2004; Merget & Wolf, 2011). In addition, possible deviations from organismal phylogeny reduce the utility of these studies, for example, in revising taxonomy or further exploring the evolution of the Hypnales.

Early phylogenies were limited by the time and expense involved in collecting data, hence typically only a few taxa were sampled (Table 1). In family-level studies, taxon selection often suffers from limited outgroup sampling, partly due to poor understanding of large-scale relationships among the Hypnales. When results from these familial studies are compared with large-scale ordinal level studies (Figure 1; Tsubota *et al.*, 2004; Ignatov *et al.*, 2007; Troitsky *et al.*, 2007; Cox *et al.*, 2010), it is apparent that in many of them, taxon selection is clearly insufficient to properly evaluate monophyly at the family level. Even in some of the published large-scale phylogenies of the Hypnales, difficulties in selecting appropriate outgroups hampers evaluation of relationships and evolutionary trends among the oldest members of the order (e.g. Merget & Wolf, 2011).

Owing to awareness of low molecular diversity within the Hypnales, many recent projects have attempted to overcome problems with sequence variation by using the fastest evolving DNA regions, especially the nuclear ITS1–5.8S–ITS2 and plastid *trn*L–F regions (Troitsky *et al.*, 2007; Ignatov *et al.*, 2007; Olsson *et al.*, 2009a). Results from analysis of phylogenetic structure in the data partitions show that phylogenetic signal per PI position in the ITS1–5.8S–ITS2 region is very strong compared to less divergent sequence regions (Tables 3–5). This result is in line with the comparison of plastid regions by Müller *et al.* (2006), and supports the view that some qualitative differences exist in phylogenetic signal from slowly and rapidly evolving genes. Because the majority of the positions in the indel data matrix were from the ITS1–5.8S–ITS2 region, strong phylogenetic signal from substitution events in ITS1–5.8S–ITS2 (i.e. the ITS sequence partition) compared to that from the indel partition indicates that substitutions and indel events differ in their utility for phylogeny reconstruction (Tables 3 and 5). However, high sequence length variation and variation in repeat structures between species, which is typical for ITS1–5.8S–ITS2, also hampers alignment. Strict guidelines that make use of data on molecular evolution and secondary structure are needed for alignment, and exclusion of ambiguous regions, such as mutational hotspots for which no positional homology exists, is necessary due to dissimilar repeat structures between terminals (Kelchner, 2000; Borsch *et al.*, 2003; Quandt *et al.*, 2003; Quandt & Stech, 2004, 2005). Methods that rely on the treatment of gaps as a fifth character state in phylogenetic analysis, may, however, be overly optimistic for analyses of fast evolving sequence regions due to heavy overweighting of long indel events (Quandt *et al.*, 2004).

Future challenges in phylogenetic reconstruction of the Hypnales

Despite increasing quantities of data being used in phylogenetic analyses of the Hypnales, we are still lacking a well-supported phylogeny which can be used for exploring the relationships and diversification of the group. The data set analysed here is the largest for the order Hypnales in terms of numbers of sequenced bases. Even if it is able to cast new light on some aspects of evolution of the order, phylogenetic signal is not strong enough to resolve family level relationships. Although we also aimed here to maximise the phylogenetic information content in the data by using the most rapidly evolving DNA regions in combination with some relatively slowly evolving ones (Stech & Quandt, 2010), alignment of highly divergent ITS sequences is a challenging and time-consuming task. The best solution to these problems would be to use a large number of both nuclear and plastid loci from coding or other moderately divergent genomic regions. This alternative has only recently become realistic as a result of the development of Next Generation Sequencing techniques, which will hopefully have an important role to play in the future in helping to resolve the Hypnales backbone.

Many hypnalean families have yet to be revised using modern phylogenetic methods in combination with a thorough re-assessment of morphological characters. Recent work on higher-level taxonomic relationships provides valuable information for taxon selection in future studies as well as tools for planning projects on some of the most severely polyphyletic families, such as the Hypnaceae and Leskeaceae. Ancestral distributions at deep hypnalean nodes and information from fossil data suggest that radiation at an early stage of hypnalean evolution within the order may have been influenced by major environmental and climatic changes between the early Permian and mid-Cretaceous. This hypothesis could be tested by molecular dating of diversification events in the Hypnales phylogeny, but due to weak support at backbone nodes, such studies must await improvements in data and phylogenetic inferences.

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Appendix

Voucher specimens and EMBL/GenBank accession numbers for sequenced taxa. Classification is after Frey and Stech (2009), except for families for which a literature reference is given in the table.

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Aulacomnium androgynum (Hedw.) Schwägr.	FM161077	AY857795	AJ291564	AF023811	Bell 1299 (BM)
Pyrrhobryum vallis-gratiae (Hampe ex Müll.Hal.) Manuel	HE659996	AF023754	AY631230	AY631167	Hedderson 13347 (BM)
Hypnodendrales					
Bescherellia elegantissima Duby	…	AY524500	AY608578	AY524472	Bell 364 (BM)
Hypnodendron vitiense Mitt.	FM161142	AY524499	AY524526	AY524471	Bell 480 (BM)
Pterobryella praenitens Müll.Hal.	…	AF509536	AY524539	AY524483	Streimann 55850 (CBG)
Spiridens camusii Thér.	HQ443771	AY524503	AY524530	AY524475	Bell 416 (BM)
Ptychomniales					
Cladomniopsis crenato-obtusa M.Fleisch.	HE659998	AY306717	AY452335	AY306883	ITS — Bell 2139 (H); *trn*L–F, *nad*5, *rps*4 — Buck 41360 (NY)
Dichelodontium nitidum (Hook.f. & Wilson) Broth.	HE659997	AY449670	AY452347	AY449664	Macmillan BH 99/14 (CHR)
Euptychium cuspidatum (Mitt.) Mitt.	HQ443747	DQ194209	DQ200890	AY631144	Newton 5373 (BM)
Garovaglia powellii Mitt.	HQ443748	DQ194217	DQ200894	DQ296008	Newton 6496 (BM)
Hampeella pallens (Sande Lac.) M.Fleisch.	HE659999	DQ194224	DQ200899	DQ186844	Newton 5407 (BM)
Hookeriales					
Achrophyllum quadrifarium (Sm.) Vitt & Crosby	HQ443707	HQ443850	AY452316	AY449660	Streimann 51258 (NY)
Actinodontium sp.	HQ443708	AY306689	AY908451	AY306855	ITS — *A. ascendens* Schwägr., Frahm 2006401 (BONN); *nad*5, *trn*L–F, *rps*4 — *A. sprucei* (Mitt.) A.Jaeger, Buck 37977 (NY)
Ancistrodes genuflexa (Müll.Hal.) Crosby	GU568687	AY101380	AY452319	AY631138	ITS, *trn*L–F — Blöcher 34 (pers. *herb.*); *nad*5 — Holz & Franzaring CH 00-154 (NY); *rps*4 — Bell 1253 (BM)
Callicostella pallida (Hornsch.) Ångström	HQ443715	AY306706	AY452328	AY306872	Holz FG 00-14 (NY)
Calyptrochaeta asplenioides (Brid.) Crosby	HQ398634	HQ398635	HQ443786	HQ443818	ITS, *nad*5, *rps*4 — Pócs (NY); *trn*L–F — Pócs 9612/M (EGR)
Calyptrochaeta cristata (Hedw.) Desv.	HQ443719	HQ443856	HQ443787	HQ443819	Frahm 1–11 (BONN)
Crossomitrium epiphyllum (Mitt.) Müll.Hal.	HQ443724	AY306719	AY452337	AY306885	Buck 33259 (NY)
Cyathophorum sp.	EF680787	AY306723	AY631214	AY631143	ITS — *C. adiantum* (Griff.) Mitt., Yamaguchi Bryophytes of Asia, fasc. 6 (NY); *trn*L–F — *C. bulbosum* (Hedw.) Müll.Hal., Streimann 55638 (NY); *nad*5, *rps*4 — *C. bulbosum*, Bell 476 (BM)
Cyclodictyon albicans (Hedw.) Kuntze	HQ443727	AY306726	AY452342	AY306892	Churchill *et al.* 18795 (NY)
Daltonia marginata Griff.	GQ905920	GQ906140	HQ443795	HQ443828	Schäfer-Verwimp 9492 (NY)
Diploneuron diatomophilum (Müll.Hal.) W.R.Buck, C.J.Cox, A.J.Shaw & Goffinet	HQ443733	AY306704	AY452326	AY306870	Buck 23312 (NY)
Distichophyllum flaccidum (Hook.f. & Wilson) Mitt.	HQ443737	HQ443866	HQ443799	HQ443833	Buck 46275 (NY)
Ephemeropsis tjibodensis K.I.Goebel	HQ443745	HQ443873	HQ443806	HQ443840	Bisang & Hedenäs s.n. (S; B57686)
Hookeria lucens (Hedw.) Sm.	FM161138	GU570196	FM161289	AY306930	ITS, *trn*L–F, *nad*5 — Buchbender 466 (pers. *herb.*); *rps*4 — Buck 37714 (NY)
Hypopterygium tamarisci (Sw.) Brid. ex Müll.Hal.	HE660000	AY449672	AY452367	AY449666	ITS - Kruijer 2007.03.001 (L); *trn*L–F, *nad*5, *rps*4 — Buck 35314 (NY)
Leskeodon cubensis (Mitt.) Thér.	HQ443759	HQ443879	HQ443808	HQ443845	Djan-Chekar 94–340 (NY)
Lopidium concinnum (Hook.) Wilson	EF680800	AY306779	AY452373	AY306945	Streimann 43706 (NY)
Sauloma tenella (Hook.f. & Wilson) Mitt.	HQ443770	AY306821	AY452384	AY306987	Streimann 59726 (NY)
Schimperobryum splendidissimum (Mont.) Margad.	EF680807	AY306822	AY452385	AY306988	Holz & Franzaring Ch 00-156 Bryotheca Gottingensis fasc. 1 #20 (NY)
Tetrastichium fontanum (Mitt.) Cardot	…	AY306834	AY452388	AY307000	Düll, Bryophyta Exsiccata Madeira 69 (NY)
Thamniopsis sp.	HQ443779	AY306838	HQ443778	AY307004	ITS, *trn*L–F, *rps*4 — *T. sinuata* (Mitt.) W.R.Buck, Callejas *et al.* 2792 (NY); *nad*5 — *T. secunda* (Griff.) W.R.Buck, Long 36213 (E)
Pilotrichum sp.	HQ443766	AY306810	AY452378	AY306976	ITS — *P. procerum* Mitt., Schäfer-Verwimp 17941 (NY; BBH50); *trn*L–F, *nad*5, *rps*4 — *P. bipinnatum* (Schwägr.) Brid., Holz FG 00-33 (NY)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Lepidopilum polytrichoides (Hedw.) Brid.	HQ443754	AY306772	AY452368	AY306938	ITS — Frahm *et al.* 185 (BONN); *trn*L–F, *nad*5, *rps*4 — Buck 33307 (NY)
Acrocladiaceae (Tangney *et al.*, 2010)					
Acrocladium auriculatum (Mont.) Mitt.	AF543550	AF543546	GU568681	AJ862338	Blöcher s.n. (BONN)
Acrocladium chlamydophyllum (Hook.f. & Wilson) Müll.Hal. & Broth.	AF509863	AF509543	GU568682	AJ862339	Frey 98-T154 (B)
Amblystegiaceae					
Amblystegium serpens (Hedw.) Schimp.	AF464987	AF397836	AY908685	AY908237	ITS — Vanderpoorten 4630 (DUKE); *trn*L–F — Huttunen 1416 (H); *nad*5, *rps*4 - Newton 4714 (pers. *herb.*)
Campylium stellatum (Hedw.) C.E.O.Jensen	AF403609 (only ITS2)	AF397821	HE717028	HE717067	Pykälä 7033 (H)
Campylium chrysophyllum (Brid.) Lange	AF168150	AY009831	AY908418	AF143048	ITS, *trn*L–F — Anderson 26799 (DUKE); *nad*5, *rps*4 — Buck 32532 (NY)
Cratoneuron filicinum (Hedw.) Spruce	AF168155	AY009817	AY908425	AY908250	ITS, *trn*L–F — Lewis 87262 (DUKE); *nad*5, *rps*4 — Smith 3618 (MO)
Drepanocladus aduncus (Hedw.) Warnst.	AF180949	AY009828	AY908422	AY908241	ITS, *trn*L–F — Schofield 104541 (DUKE); *nad*5, *rps*4 — Shevock 17088 (MO)
Palustriella falcata (Brid.) Hedenäs	AF168158	AY626006	AY908421	AY908243	ITS — Schofield & Godfrey 97864 (DUKE); *trn*L–F — Hedenäs & Kooijman (S; B1094); *nad*5, *rps*4 — Shevock 18521 (MO)
Vittia pachyloma (Mont.) Ochyra	AY062886	AY062889	AY908463	AY908240	Goffinet 5605 (DUKE)
Anomodontaceae					
Anomodon viticulosus (Hedw.) Hook. & Taylor	FM161076	AM990343	FM161241	HE717066	Buchbender 449 (pers. *herb.*)
Haplohymenium triste (Ces.) Kindb.	AM990374	FM161113	FM161269	AY908202	Enroth 63154 (H)
Antitrichiaceae					
Antitrichia curtipendula (Timm ex Hedw.) Brid.	HE660002	HE717045	HE717027	AY908570	Buchbender 525 (pers. *herb.*)
Brachytheciaceae					
Brachythecium rivulare Schimp.	FM161081	AF397866	FM161245	AM990348	Parnela s.n., 19. May 1996 (H);
Clasmatodon parvulus (Hampe) Sull.	DQ200082/AF403614	AF397813	AY908519	AY663329	ITS, *trn*L–F — Redfearn & Allen 23. Apr. 1992 (H); *nad*5 — Buck 33446 (NY); *rps*4 — Goffinet 3871 (CONN)
Rhynchostegium conostomus (Mont.) Huttunen & Ignatov	DQ336903	DQ336926	AY908684	AY908239	ITS, *trn*L–F — Larrain 288 (NY); *nad*5, *rps*4 — Mahu 21497 (MO)
Homalothecium lutescens (Hedw.) H.Rob.	EF617558	HE717052	HE717033	HE717071	Een s.n., 9 June 1995 (S)
Calliergonaceae					
Calliergon cordifolium (Hedw.) Kindb.	AY625984	AY626003	AY908710	AF469844	Hedenäs s.n., 8 Jun 2003 (S; B81133)
Straminergon stramineum (Dicks. ex Brid.) Hedenäs	AM946398	AM946396	FM161330	AM990351	Müller s.n., 22 Oct. 2005 (DR028753)
Catagoniaceae					
Catagonium nitens (Brid.) Cardot	GU568688	AF472449	AY908473	AF469810	Goffinet 5459 (DUKE)
Climaciaeae					
Climacium americanum Brid.	HE660004	HE717048	AY908646	AY908573	ITS, *trn*L–F — Anderson 26227 (S); *nad*5, *rps*4 — Newton 5000 (pers. *herb.*)
Pleuroziopsis ruthenica (Weinm.) Kindb. ex E.Britton	AY999170	DQ019930	AY908647	AY908571	Schofield 111104 (DUKE)
Cryphaeceae					
Cryphaea amurensis Ignatov	FM161090	AM990355	FM161251	AM990355	Ignatov 97-269 (J. Enroth pers. *herb.*)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Cryphaeophilum molle (Dusén) M.Fleisch.	AF509840	AF509544	HE717030	HE717068	Blöcher 42 (pers. *herb.*)
Pilotrichopsis dentata (Mitt.) Besch.	HE660003	HE717059	AY908715	AY908599	ITS, *trn*L–F — Mizutani 13658 (S); *nad*5, *rps*4 — Buck 23843 (NY)
Entodontaceae					
Entodon seductrix (Hedw.) Müll.Hal.	JN896314	HE717051	HE717032	HE717070	Tan 92–129 (MHA)
Erythrodontium longisetum (Hook.) Paris	AY255497	AY255484	AY908527	AY908256	ITS, *nad*5, *rps*4 — Newton 4282 (pers. *herb.*); *trn*L–F GenBank
Mesonodon flavescens (Hook.) W.R.Buck	AY255502	AY255483	AY908529	AY908255	ITS, *nad*5, *rps*4 — Kolema 132 (NY); *trn*L–F — GenBank
Fabroniaceae					
Fabronia sp.	AY528883	AY527128	AY908754	AY908199	ITS, *trn*L–F — *F. ciliaris* (Brid.) Brid., Bezgodov 268 (MHA); *nad*5, *rps*4 — *F. pusilla* Raddi, Hedderson 9230 (RNG)
Rhizofabronia perpilosa (Broth.) Broth.	GU568693	AF472476	GU568686	AF469837	Pócs *et al.* 88122/C (S; B53343)
Fontinalaceae					
Brachelyma subulatum (P.Beauv.) Cardot	AF192094	AF191503	AY908492	AF306998	ITS, *trn*L–F, *nad*5 — Allen Exs. 87 (DUKE); *rps*4 — Allen Exs. 86 (DUKE)
Dichelyma falcatum (Hedw.) Myrin	AF192097	AF191505 (AF191506)	AY908493	AY908318	Allen Exs. 92 (DUKE)
Fontinalis antipyretica Hedw.	AF192107	AF023771	AY908494	AF023817	ITS — Allen Exs. 101 (DUKE); *trn*L–F, *nad*5, *rps*4 — Hedderson 11849 (RNG)
Habrodontaceae					
Habrodon perpusillus (De Not.) Lindb.	AY528880	AY527126	AY908683	AY908293	ITS, *trn*L–F — M. & E. Ignatov s.n., 9 Aug 2002 (MHA); *nad*5, *rps*4 — Hedderson 9443 (RNG)
Helodiaceae					
Helodium blandowii (F.Weber & D.Mohr) Warnst.	AY009803	AY009852	AY908393	AY908339	ITS, *trn*L–F — Schofield 108637 (DUKE); *nad*5, *rps*4 — Shevock 18635 (MO)
Hylocomiaceae					
Ctenidium molluscum (Hedw.) Mitt.	AF230989/AF403632	HE717049	AY908440	AY907954	ITS1 — Stech B880103.2 (L); ITS2 — Pykälä 8706 & Nurmi (H; H4043455); *trn*L–F — Pedersen 12/04 (BM); *nad*5, *rps*4 — Newton 4717 (pers. *herb.*)
Hylocomiastrum umbratum (Ehrh. ex Hedw.) M.Fleisch.	FM161141	AM990396	FM161291	AM990396	Ignatov & Bezgodov 81 (MHA, H)
Hylocomium splendens (Hedw.) Schimp.	HE660006/AF403610	AF397840	AY908447	AY908280	ITS, *trn*L–F — Huttunen 1441 (H); *nad*5, *rps*4 — Schofield 98369 (DUKE)
Meteoriella soluta (Mitt.) S.Okamura	AF403606 (only ITS2)	AY306784	AY908637	AY306950	Koponen *et al.* 49610 (H)
Pleurozium schreberi (Willd. ex Brid.) Mitt.	AJ288349/AJ288563	HE717060	AY908642	AY908281	ITS — GenBank; *trn*L-F — Quandt s.n. (BONN); *nad*5, *rps*4 — Thornton 35 (DUKE)
Rhytidiadelphus triquetrus (Hedw.) Warnst.	HE660005/AF403631	AF397811	AY908636	AM990396	ITS, *trn*L–F — Huttunen 1440 (H); *nad*5, *rps*4 — Thornton 20a (DUKE)
Rhytidiopsis robusta (Hook.) Broth.	HE660007	AY683574	AY908465	AY908574	ITS, *trn*L-F — Vitt 35999 (MHA); *nad*5, *rps*4 — Goffinet 7874 (UCONN)
Hypnaceae					
Andoa berthelotiana (Mont.) Ochyra	FM161074	FM161239	FM161239	FM161239	Hedenäs s.n., 4. June 1990 (S; B8333)
Chryso-hypnum diminutivum (Hampe) W.R.Buck	HE660008	HE717047	HE717029	AY908345	ITS, *nad*5 — Hedenäs ME95-88 (S); *trn*L–F — Hedenäs ME95–108 (S); *rps*4 — Churchill *et al.* 20423 (MO)
Ectropothecium regulare (Brid.) A.Jaeger	HE660009	HE717050	HE717031	HE717069	Pócs 881 07/c
Eurohypnum leptothallum (Müll.Hal.) Ando	AY695733/AY695786	AY683563	AY908443	AY908203	ITS, *trn*L–F — Ignatov 34/129 (MHA); *nad*5, *rps*4 — Yamaguchi 132 (MO)
Hypnum cupressiforme Hedw.	FM161143	AM990398	FM161292	AM990398	Quandt s.n., 26 Dec. 2005 (pers. *herb.*)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Hypnum plumaeforme Wilson	AY695743/AY695768	AY683604	HE717035	-	ITS, *trn*L–F — Li s.n., 2003 (MHA); *nad*5 — Frahm 1627 (MHA, *Herb.* Frahm)
Mittenothamnium reptans (Hedw.) Cardot	HE660010	HE717055	AY908627	AY908346	ITS, *trn*L–F — Hedenäs s.n. (S; B15195); *nad*5, *rps*4 — Allen 18674 (MO)
Taxiphyllum wissgrillii (Garov.) Wijk & Margad.	AY999168	AF472481	HE717043	AF469842	ITS — Ignatova 11/81 (H ex MHA); *trn*L–F, *nad*5, *rps*4 — Hedenäs s.n. (S; B3645)
Vesicularia vesicularis (Schwägr.) Broth.	HE660011	HE717065	AY908406	AY908559	Majestyk 4104 (BONN)
Lembophyllaceae					
Camptochaete arbuscula (Sm.) Reichardt	FM161087	AY306768	AY908658	AY908330	Streimann 51408 (H)
Lembophyllum divulsum (Hook.f. & Wilson) Lindb.	FM161146	AY306769	AY908656	AY306935	Frahm 8–25 (pers. *herb.*)
Rigodium implexum Kunze ex Schwägr.	FM161209	AF543547	FM161327	AM990436	Quandt A10008 (pers. *herb.*)
Weymouthia mollis (Hedw.) Broth.	FM161237	AY306847	AY908659	AY307013	ITS — ID 99-Mo2 (CHR, Quandt pers. *herb.*); *trn*L–F, *nad*5, *rps*4 — Streimann 58249 (H)
Lepyrodontaceae					
Lepyrodon tomentosus (Hook.) Mitt.	AJ862688/AF509839	AF509541	AY908748	AY908585	ITS, *trn*L–F — Blöcher 74 (BONN); *nad*5, *rps*4 — De Luna & Keller 2246 (pers. *herb.*)
Leskeaceae					
Claopodium whippleanum (Sull.) Renauld & Cardot	AY173458	AY683584	AY908746	AY908294	ITS — Ros & Werner 10278 (MUB); *trn*L–F — Düll 22C4/2 (H); *nad*5, *rps*4 — Shevock 19289 (DUKE)
Leskea polycarpa Ehrh. ex Hedw.	AY528881	AF397810	AJ291576	HE717074	ITS, *trn*–F — Ignatov s.n., 18 June 1996 (MHA); *nad*5 — Muhle 231197-1 (ULM); *rps*4 — Pykälä 10872 (H)
Lindbergia brachyptera (Mitt.) Kindb.	FM161151	AM990407	FM161300	AM990407	H3194519 (H)
Leucodontaceae					
Leucodon sciuroides (Hedw.) Schwägr.	FM161149	AM990405	AY908716*	AY908186	Buchbender 293 (pers. *herb.*)
Pterogonium gracile (Hedw.) Sm.	HE660012	HE717062	HE717041	AY907970	Buchbender 348 (pers. *herb.*)
Meteoriaceae					
Duthiella wallichii (Mitt.) Müll.Hal.	HE660013/AF403612	AF397782	AY908728	AY908286	ITS, *trn*L–F — Koponen *et al.* 54168 (H); *nad*5, *rps*4 — Redfearn 35722 (MO)
Meteoriopsis reclinata (Müll.Hal.) M.Fleisch.	HE660014/AF403666	AY306782	AY908726	AY306948	ITS — Koponen *et al.* 55437 (H); *trn*L–F — Allen 6695 (MO); *nad*5 - Shevock 17996 (MO); *rps*4 — Allen 6695 (MO)
Meteorium illecebrum Sull.	HE660015/AF188046	AF187241/AF187257	AY908733	AY908187	ITS, *trn*L–F — Cardenas MEXU 5441 (BONN); *nad*5, *rps*4 — Newton 4288 (pers. *herb.*)
Toloxis imponderosa (Taylor) W.R.Buck	FM161232/AF395631	AY044067	AY908732	AY908289	ITS, *trn*L–F — Norris 90418 (H); *nad*5, *rps*4 — Buck 39522 (DUKE)
Trachypus bicolor Reinw. & Hornsch.	DQ200118/AF395624	AY044060	AY908446	AY908290	ITS, *trn*L–F — Koponen *et al.* 50721 (H); *nad*5, *rps*4 — Koponen 32098 (RNG)
Myriniaceae					
Myrinia pulvinata (Wahlenb.) Schimp.	AY528886/AY528887	AY527127	HE717036	HE717075	Ignatov s.n., 29 Sept. 1999 (MHA)
Myuriaceae					
Myurium hochstetteri (Schimp.) Kindb.	HE660026/AF509861	AF509542	AY908439	AY908180	ITS — Frahm Mh26; *trn*L–F — Quandt E10017 (pers. *herb.*); *nad*5, *rps*4 — Rumsey 17/7 (pers. *herb.*)
Oedicladium rufescens (Reinw. & Hornsch.) Mitt.	HE660016	JQ815890	HE717039	HE717076	Koponen *et al.* 50934 (H)
Neckeraceae					
Alleniella complanata (Hedw.) S.Olsson, Enroth & D.Quandt	FM161158	AM990413	FM161305	AM990413	Buchbender 204 (pers. *herb.*)
Forsstroemia trichomitria (Hedw.) Lindb.	FM161103	AM990365	FM161260	AY908263	ITS, *trn*L–F, *nad*5 — Streimann & Pócs 65120A (Buchbender pers. *herb.*); *rps*4 — Anderson 27401 (DUKE)
Heterocladium dimorphum (Brid.) Schimp.	AY695757/AY695771	AY683586	AY908640	AY908259	Norris 101992 (H; H3212307)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Leptodon smithii (Hedw.) F.Weber & D.Mohr	FM161147	AM990403	FM161297	AY908261	ITS, *trn*L–F, *nad*5 — De Sloover 44851 (B); *rps*4 — Rumsey s.n. (pers. *herb.*)
Neckera pennata Hedw.	AY009809	AF315072	AY908652	AY908265	Schofield *et al.* 97354 (H; H3203794)
Porotrichodendron robustum Broth.	FM161197	AM990426	FM161318	AM990426	Lewis 88-1390 (B; B264620)
Thamnobryum alopecurum (Hedw.) Nieuwl. ex Gangulee	FM161218	AM990444	FM161334	AF023834	Brohbachdal s.n., 11 July 2003 (Buchbender pers. *herb.*)
'OPP-clade'(Quandt *et al.*, 2009)					
Porotrichum stipitatum (Mitt.) W.R.Buck.	HE660018	HE717061	HE717040	JQ815892	Hedenäs s.n., 4 Oct. 1998 (S; B104830)
Orthostichella pentasticha (Brid.) W.R.Buck	HE660017/AY429502	AY429496	AY908655	AY907962	ITS, *trn*L–F — MA-Musci 26093 (MA); *nad*5, *rps*4 — Cardenas 5891 (MO)
Orthostichella rigida (Müll.Hal.) B.H.Allen & Magill	FM161185	AF508315	FM161312	AM990422	ITS, *trn*L–F, *nad*5 — Hedenäs s.n. (S; B48305); *rps*4 — Quandt A10001 (pers. *herb.*)
Orthorrhynchiaceae					
Orthorrhynchium elegans (Hook.f. & Wilson) Reichardt	…	…	AY908766	AY908612	*nad*5, *rps*4 — Streimann 53758 (NY)
Phyllogoniaceae					
Phyllogonium sp.	AY908193	HE717058	AY908709	AY908193	ITS — *P. fulgens* (Hedw.) Brid., Holst 4336 (BONN); *trn*L–F, *nad*5, *rps*4 — Newton 4854 (pers. *herb.*);
Plagiotheciaceae (Pedersen & Hedenäs 2002)					
Pseudotaxiphyllum elegans (Brid.) Z.Iwats.	GU568692	AF472473	AY908753	AF469834	Schofield 107922 (DUKE)
Plagiothecium sp.	GU568690	AF472466	AY908763	AF469827	ITS, *trn*L–F, *rps*4 — *P. curvifolium* Schlieph. ex Limpr., Buck 16262 (DUKE); *nad*5 — *P. cavifolium* (Brid.) Z.Iwats., Buck 32520 (NY)
Prionodontaceae					
Prionodon densus (Sw. ex Hedw.) Müll.Hal.	HE660019	AF161169	AY908718	AF143076	ITS — Churchill *et al.* s.n. (H; H3121817); *trn*L–F, *nad*5, *rps*4 - Churchill *et al.* 19068 (NY)
Pseudoleskeaceae					
Lescuraea incurvata (Hedw.) E.Lawton	AY693661	AY683595	…	…	Ignatov 394 (MHA)
Lescuraea radicosa (Mitt.) Mönk.	AF516169/AF516147	AY683570	AY908737	AY908326	ITS — Ignatov s.n., 21 Aug. 1999 (MHA); *trn*L–F — Ignatov 34204(MHA); *nad*5, *rps*4 — Whittemore 5372 (NY)
Ptychodium plicatum (Schleich. ex F.Weber & D.Mohr) Schimp.	AY695740/AY695765	AY683596	AY908735	AY908327	ITS, *trn*L–F — Musa Bol. Exc. 1162, Odyu(?) 318/90; *nad*5, *rps*4 — Paton 2723 (E)
Rigodiadelphus robustus (Lindb.) Nog.	AF516166/AF516156	AY762373	AY908736	AY908569	Deguchi s.n., 8 Aug 1998 (MHA)
Pseudoleskeellaceae					
Pseudoleskeella tectorum (Funck ex Brid.) Kindb. ex Broth.	AF516168/AY695776	AY683579	AY908416	AY907950	Ignatov 32/30 (MHA)
Pterigynandraceae					
Pterigynandrum filiforme Hedw.	AY528890/AY528891	AY526198	AY908757	AY908189	ITS, *trn*L—F — Ignatov s.n., 4 July 1991 (MHA); *nad*5, *rps*4 — Schofield & Belland 92748 (MO)
Pterobryaceae					
Hildebrandtiella guyanensis (Mont.) W.R.Buck	FM161119	AF509559	FM161275	AY306927	ITS, *trn*L–F, *nad*5 — Drehwald 4425 (pers. *herb.*); *rps*4 — Allen 17684 (MO)
Orthostichidium involutifolium (Mitt.) Broth.	…	AY306792	AY908700	AY908195	Magill & Crosby 8387 (MO)
Orthostichopsis tetragona (Sw. ex Hedw.) Broth.	HE660020	HE717057	AY908689	AY908192	ITS, *trn*L–F — Churchill *et al.* s.n. (H; H3194625); *nad*5, *rps*4 — Newton 4616 (pers. *herb.*)
Pterobryon densum Hornsch.	HQ443767	AF397838	AY908693	HE717078	ITS, *rps*4 — Pd9 (BONN); *trn*L–F — Allen 12532 (BM); *nad*5 - Linares & Churchill 3649 (NY)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Spiridentopsis longissima (Raddi) Broth.	…	HE717064	AY908690	AY908564	*trn*L–F — Schäfer-Verwimp & Verwimp s.n., 21 July 1987 (S; B97329); *nad*5, *rps*4 — Schäfer-Verwimp 13185 (MO)
Pylaisiaceae					
Pylaisia polyantha (Hedw.) Schimp.	AY528881	AY527137	AY908408	AY907960	ITS, *trn*L–F — Ignatov s.n., 10 July 2003 (MHA); *nad*5, *rps*4 — Stebel & Stebel 600/95 (MO)
Stereodon procerrimus (Molendo) Baumgartner	AY695755/AY695780	AY683590	HE717037	HE717073	Ignatov 01-439 (MHA)
Stereodon hamulosus (Schimp.) Lindb.	HE660027	HE717054	HE717034	HE717072	Ignatov 28/53 (MHA)
Pylaisiadelphaceae					
Brotherella recurvans (Michx.) M.Fleisch.	…	HE717046	AY908470	AY908227	*trn*L–F, *nad*5, *rps*4 — Buck 31506 (NY)
Isopterygium tenerum (Sw.) Mitt.	HE660021 (only ITS2)	AF161130	HE717038	AF143037	ITS — Merrill 13306 (BONN); *trn*L–F, *nad*5, *rps*4 — Buck 33462 (NY)
Taxithelium planum (Brid.) Mitt.	…	AF161147	AY908549	AY908231	Schäfer-Verwimp, Verwimp 9722 (S; B97363)
Regmatodontaceae					
Regmatodon declinatus (Hook.) Brid.	…	…	AY908413	AY908191	Magill *et al.* 7689 (MO)
Rhytidiaceae					
Rhytidium rugosum (Ehrh. ex Hedw.) Kindb.	AY009801	AF264046	AY908415	AY907951	ITS — Schofield & Godfrey 98103 (DUKE); *trn*L–F — Stech B930910.1 (L); *nad*5, *rps*4 — Rumsey 229 (pers. *herb.*)
Rutenbergiaceae					
Rutenbergia madagassa Geh. & Hampe	GU568694	AY524514	AY524542	AY524486	Fisher 33 (BM)
Pseudocryphaea domingensis (Spreng.) W.R.Buck	GU568691	GU568674	GU568685	AY908188	ITS, *trn*L–F, *nad*5 — Allen 12901 (S); *rps*4 — Newton 4542 (pers. *herb.*)
Scorpidiaceae					
Sanionia sp.	AF168148	AY009860	AY908436	AY908253	ITS, *trn*L–F — *S. uncinata* (Hedw.) Loeske, Schofield 95255 (DUKE) *nad*5, *rps*4 — *S. orthothecioidese* (Lindb.) Loeske, Schofield & Talbot 111743 (MO)
Scorpidium scorpioides (Hedw.) Limpr.	AY625995	AY626014	AY908435	AY908584	Hedenäs s.n., 2 Oct. 2009 (S; B164615)
Sematophyllaceae					
Acroporium pungens (Hedw.) Broth.	HE660023	HE717044	AY908539	AY908207	ITS, *trn*L–F — Churchill *et al.* s.n., 17. March 1990 (S); *nad*5, *rps*4 — Buck 33028 (NY)
Hydropogon fontinaloides (Hook.) Brid.	HE660024	HE717053	AY908535	AY908216	ITS, *trn*L–F — Solomon s.n., 2. June 1987 (S); *nad*5, *rps*4 — Allen Exs. 54 (DUKE)
Sematophyllum homomallum (Hampe) Broth.	HE660022/AF509838	AF509540	HE717042	JQ815891	Streimann 54149 (BONN)
Sematophyllum demissum (Wilson) Mitt.	…	AF161148	AY908479	AY908214	Buck 2425915 (NY)
Trichosteleum papillosum (Hornsch.) A.Jaeger	…	AF161149	AY908541	AF143056	Buck 33002 (NY)
Stereophyllaceae					
Entodontopsis leucostega (Brid.) W.R.Buck & Ireland	AY999175	AF161153	AY908501	AY908295	ITS — Sastre-De Jesus *et al.* 1440 (H, ex NY); *trn*L–F — Djan-Chékar 94–726 (NY); *nad*5, *rps*4 — Newton 4583 (pers. *herb.*)
Pilosium chlorophyllum (Hornsch.) Müll.Hal.	GU568689	GU568673	AY908749	AF143059	ITS, *trn*L–F — Schäfer-Verwimp & Verwimp s.n. (S; B97842); *nad*5, *rps*4 — Buck 32979 (NY)
Stereophyllum radiculosum (Hook.) Mitt.	AY999176	AF472484	AY908750	AF469846	ITS — Streimann 52160 (H); *trn*L–F, *nad*5, *rps*4 — Zardini 7102 (DUKE; 0017438)

Appendix Continued

	ITS1–5.8S–ITS2	*trn*L–F	*nad*5	*rps*4	Voucher specimen
Symphyodontaceae					
Chaetomitrium sp.	HE660025	AY306715	AY452334	AY306881	ITS — *C. setosum* Broth. ex Dixon., Tan 95–1115 (MHA); *trn*L–F, *nad*5 — *C. dusenii* Müll.Hal. ex Broth., Heras 499/94 (NY)
Symphyodon imbricatifolius (Mitt.) S.P.Churchill	FM161214	AY306833	AY452387	AY306999	Schäfer-Verwimp 13309 (H; H3202267)
Theliaceae					
Thelia lescurii Sull.	AJ288411/AJ277223	AF161117	AY908745	AF143024	Buck 32864 (NY)
Thuidiaceae					
Abietinella abietina (Hedw.) M.Fleisch.	AY009802	AY009850	AY908386	AY907953	ITS, *trn*L–F — Allen 19816 (DUKE); *nad*5, *rps*4 — Schofield 103458 (DUKE)
Boulaya mittenii (Broth.) Cardot	FM161080	AM990347	AY908395	AY908338	ITS, *trn*L–F — Tanaka 7308 (HIRO); *nad*5, *rps*4 — Shevock 16392 (MO)
Haplocladium virginianum (Brid.) Broth.	AF168160	AF161133	AY908401	AF143040	Buck 32482 (NY)
Thuidium delicatulum (Hedw.) Schimp.	AF176278	AF161132	AY908398	AF143039	Buck 32594 (NY)
Trachylomataceae					
Trachyloma planifolium (Hedw.) Brid.	FM161234	AM990449	FM161338	AM990449	Frahm 3–12 (BONN)