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Cleaning a taxonomic dustbin: placing the European *Hypnum* species in a phylogenetic context!

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Abstract

The pleurocarpous moss genus *Hypnum* s.l. is a species-rich (> 40 species) cosmopolitan genus, of which 21 taxa occur in Europe. Although several of these species show high morphological resemblance there are strong indications that the genus is highly paraphyletic, which may be masked by convergent morphological evolution. Using molecular information, we analyse whether the morphological similarity of gametophytes of the European *Hypnum* taxa is explained by common ancestry or convergence. We provide a phylogenetic reconstruction of the relationships of the currently recognized European *Hypnum* taxa in a broad pleurocarpous moss context (192 taxa) using the nuclear ITS1-5.8S-ITS2, the plastid *rps*4 gene and *trn*L-F, and the mitochondrial *nad*5 intron. Bayesian tree topologies show that the genus is polyphyletic, and we retain only the *Hypnum cupressiforme* complex within *Hypnum*. The genus originally represented half of the moss species diversity, as it accommodated basically all pleurocarpous mosses; here we retain only seven species and one variety. The remainder of the species where resolved either within the three families Amblystegiaceae, Entodontaceae, and Pylaisiaceae, or in an independent clade that we describe as the new family Stereodontaceae. The Stereodontaceae includes five European species, all in the genus *Stereodon*, where they were already placed in the 18th century. In addition, we describe the four new genera *Aquilonium*, *Insomniella*, *Jochenia*, and *Lignocariosa*, and make new combinations for several *Hypnum* species.

Keywords: Amblystegiaceae, Entodontaceae, Pylaisiaceae, Stereodontaceae, *Aquilonium*, *Insomniella*, *Jochenia*, *Lignocariosa*

Introduction

The pleurocarpous moss genus *Hypnum* Hedw. represents a species-rich cosmopolitan genus that has a long history of changing species composition. This actually started with Linnaeus' "Species Plantarum" where all more or less creeping and branched, or pleurocarpous mosses were included in *Hypnum* (Linnaeus 1753). According to Linnaeus', nearly half of the moss diversity belonged in one genus. Since then, botanists have tried to sort this ecologically important but often neglected diversity (Ando 1972). Hedwig (1801), at the starting point of moss (excluding *Sphagnum*) nomenclature, distributed the pleurocarpous mosses among four genera. However, *Hypnum* still contained the vast majority of pleurocarpous species. The treatments by Bruch, Schimper, and Gümbel (1851), Fleischer (1906–1908, 1915–1923) and Brotherus (1908, 1925) introduced the family Hypnaceae Schimp. and reduced the number of *Hypnum* species to a more realistic number of 60 taxa, a number approaching the present understanding. The name *Hypnum* comes from Hypnos (sleep), probably since various pleurocarps (not only *Hypnum* as presently understood) were used as filling of pillows and mattresses. The German name "Schlafmoos" for *Hypnum* is thus likely just what remains from this wider use of pleurocarps in earlier times. While one can report a constant erosion in species number within *Hypnum* and the Hypnaceae, a definite taxonomic treatment of the family and its type genus due to morphological characters could so-far not be achieved (Nishimura 1999).

Molecular phylogenetic studies solved taxonomic issues in many other pleurocarpous families (Huttunen & Ignatov 2004; Huttunen *et al.* 2013; Ho *et al.* 2012; Olsson *et al.* 2009a, 2009b, 2010, 2011; Pokorny *et al.* 2012) but have so-far been insufficient to provide a solid taxonomic concept for *Hypnum* or the Hypnaceae due to low levels of information in the used markers (Arikawa *et al.* 2008; Gardiner *et al.* 2005; Spagnuolo *et al.* 2008; Terracciano *et al.* 2012). However, they indicated the paraphyletic nature of the family and instigated regrouping of, for example, the

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Pylaisiaceae Schimp. (Arikawa *et al.* 2008; Câmara *et al.* 2018; Huttunen *et al.* 2012; Gardiner *et al.* 2005; Ignatov *et al.* 2007; Olsson *et al.* 2009b). Although different genetic regions have been tested to resolve taxonomic uncertainties, inter- and intraspecific relationships within *Hypnum* remain unresolved. Especially the *H. cupressiforme* complex (comprising *Hypnum andoi* A.J.E. Sm., *Hypnum cupressiforme* Hedw., *Hypnum heseleri* Ando & Higuchi, *Hypnum jutlandicum* Holmen & Warncke, *Hypnum lacunosum* (Brid.) Hoffm. ex Brid., *Hypnum resupinatum* Taylor, *Hypnum subjulaceum* Besch. and *Hypnum uncinulatum* Jur.) has been a matter of discussion until now (Spagnuolo *et al.* 2008; Terracciano *et al.* 2012). In addition to low genetic variation, the morphological discrimination of species in the *H. cupressiforme* complex is difficult due to high phenotypic plasticity (Ando 1972; Frahm 2009), ultimately leading to a controversial debate about the number of taxa within the complex (Smith 1997 and references therein).

Today, 43 taxa remain in the genus (Frey & Stech 2009) and out of these, 21 occur in Europe. The genus in its current sense is characterised as pleurocarpous with creeping to erect, often flattened stems with often more or less complanate or subcomplanate leaf arrangement. Both stem and branch leaves are usually falcate-secund to circinate, ovate to elongate-lanceolate, acuminate to aristate, concave, and occasionally wrinkled. The leaves have a short double costa, which is rarely completely lacking. The differentiated alar cells are few or numerous, transversely rectangular, quadrate or especially near insertion rectangular, thick-walled and coloured or thin-walled and hyaline. The median leaf lamina cells are linear or shortly so, smooth or, in some species, dorsally and distally prorate. Pseudoparaphyllia are present and vary from suborbicular to narrowly lanceolate, and are sometimes branched. So-far, sporophyte characteristics have not been considered for the genus' delimitation (Sauer 2001).

The genus *Hypnum* as well as the family Hypnaceae have remained an assortment of species that superficially share similar morphological character states, and have succinctly been termed a "bryological dustbin" (Olsson *et al.* 2009b). Here, we aim to resolve the relationship especially of the 21 European taxa that have been referred to *Hypnum*, within a broad phylogenetic context using four molecular markers from all three genomes.

Materials and methods

Taxon sampling. We aimed to include at least two exemplars from different geographic regions, for each of the 21 European *Hypnum* taxa, plus *H. plumaeforme* and *H. fauriei.* This sampling was embedded in a recent analysis on the origin and diversification of the moss order Hypnales (Huttunen *et al.* 2012) but was slightly enlarged with taxa that showed affinities with the different species in earlier analyses (Appendix 1). Following Huttunen *et al.* (2012), *Eriodon* was not included in the analyses.

Molecular data. Huttunen *et al.* (2012) provided a molecular data set spanning four regions: the nuclear ITS1-5.8S-ITS2 (ITS), the plastid *rps*4 gene, including the *trn*S-*rps*4 intergenic spacer (IGS) (*rps*4) and *trn*L-F (*trn*L group I intron and the *trn*L-F IGS), and the mitochondrial *nad*5 intron (*nad*5) which were obtained for the taxon sampling above. Protocols for DNA extractions, PCR amplifications, including primer sequences and sequencing are described in Olsson *et al.* (2009b). Voucher specimens and sequence accession numbers are listed in Appendix 1 for the 189 newly generated sequences; the remainder are available in Huttunen *et al.* (2012).

Contig assembly, alignment and phylogenetic reconstructions. Consensus sequences of the newly generated pherograms were assembled in PhyDE-1 (Müller *et al*., 2005, available at phyde.de; accessed 2018-01-01) and manually aligned using the alignments of Huttunen *et al.* (2012) as a scaffold. The indel data was 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 accordance with Huttunen *et al.* (2012) we slightly enlarged and modified the defined mutational hotspots as a result of the newly incorporated sequences (Table 1). The hotspots were excluded prior phylogenetic analyses. Similarly, the previously reported inversion in the *trn*L-F IGS (Quandt & Stech 2004) as well as a newly observed inversion in the *trn*L-F IGS of *Cladomniopsis crenato-obtusa* M. Fleisch. were included as reverse complement (Borsch & Quandt 2009; Quandt *et al.* 2003). Gaps were treated as missing data. Phylogenetic reconstructions were performed using a parallel version of MrBayes v3.2.6 on XSEDE on CIPRES with 16 processors (Altekar *et al.* 2004; Miller *et al.* 2010; Ronquist *et al.* 2012). The data were divided in four partitions: three DNA loci with one partition for each genome (1: ITS, 2: *nad*5, 3: *rps*4 & *trn*L-F,) and the binary coded indels. For each DNA partition an independent GTR+Γ+I model (unlinked) was applied while the indel matrix followed the restriction site model implemented in MrBayes. Two simultaneous runs of Metropolis Coupled Markov Chain Monte Carlo (MC3), both with one cold and seven heated chains, were run for 10^8 generations. Posterior probabilities for trees and parameters were saved at every 1000 generations and parameters for each data partition were sampled independently from each other. The program Tracer v1.7 (Rambaut *et al.* 2018) was used to examine the log likelihoods as well as the effective sampling size and to determine stationarity of the MCMC search. Calculations of the consensus tree and of the posterior probability of clades were performed based upon the trees sampled after the chains converged (>25 %). Two independent Bayesian inferences were performed, one based solely on the combined nucleotide data set with all sequence partitions and a second with the indel matrix appended. In addition, maximum likelihood analyses were run on both concatenated matrices as well as the individual nucleotide partitions, using RAxML v8.2.10 (Stamatakis 2014) on the CIPRES servers (Miller *et al.* 2010) with the GTRCAT model for the nucleotide partitions and the included binary model for the indels in effect. Bootstrap replicates were set to 1000. The original data matrix was thoroughly tested for congruence (Huttunen *et al.* 2012) that lead to the exclusion of *Eriodon* which we followed here. Nevertheless, likelihood tree topologies of the taxonomically extended individual data sets were checked for significant incongruence prior concatenation.

TABLE 1. Location (i.e., absolute position in the combined data set) and corresponding region of mutational hotspots (HS), including the observed inversions (I). The location of the inversion is given with respect to the corrected and analysed matrix (i.e., the inversion is included as reverse complement).

No.	Position	Region (nuclear)	No.	Position	Region (plastid))
HS1	72–495	ITS1	I1	6840–6847	*trn*L-*trn*F IGS
HS2	770–1350	ITS1	I2	6863–6867	*trn*L-*trn*F IGS
HS3	1925–2983	ITS1			
HS4	3434–3441	ITS1			
HS5	3662–3675	ITS2			
HS6	4159–4743	ITS2			
HS7	5589–5600	ITS2			
HS8	5656–5840	ITS2			

TreeGraph 2 (Stöver & Müller 2010) was used to summarize the topology and support from the different analyses (Figure 1). In Figure 1, support for branches is given on the branches, unless otherwise indicated, for all four combined analyses in the following order: posterior probability from Bayesian analysis without indel coding (pp), pp with indels (pp sic), Maximum likelihood support without indel coding (ML), and ML with indels (ML sic).

Results

DNA sequence data and phylogeny. The total length of the combined and aligned dataset adds up to 8895 nucleotides. After excluding the eight identified hotspots (Table 1) and reverse complementing both observed inversions, 5942 bp remained (Table 2). The nuclear partition made up the biggest part of the cleaned dataset with 3078 bp, followed by the plastid partition (1575 bp) and the mitochondrial region (1289 bp), compare Table 2.

TABLE 2. Sequence length, divergence and proportional contribution of the different regions to the data matrix as well as ti/tv ratios, number and distribution of indels. Number of characters, p-distance (p-dist.), transition/transversion ratio (ti/tv), variable sites, parsimony informative sites (p.i.) and number of indels are presented based on the data set with the hotspots excluded, whereas the length range together with the mean and the standard deviation (S.D.) are provided from the original alignment.

Character set	No. chars.	**Length range [nt]**	**Mean [nt]**	**S.D.**	**p-dist. [%]**	**Ti/tv**	**Variable sites [%]**	**p.i. sites [%]**	**No. indels**
ITS	3078	325–1475	651,828	179,394	9,688	1,413	22,807	13,223	1278
*trn*L-F	873	265–456	371,395	56,197	4,56	2,56	28,981	18,442	184
*rps*4	702	539–607	566,191	104,165	3,701	4,985	48,148	32,479	34
*nad*5	1289	1011–1122	1081,856	129,371	1,846	6,128	38,092	23,429	103

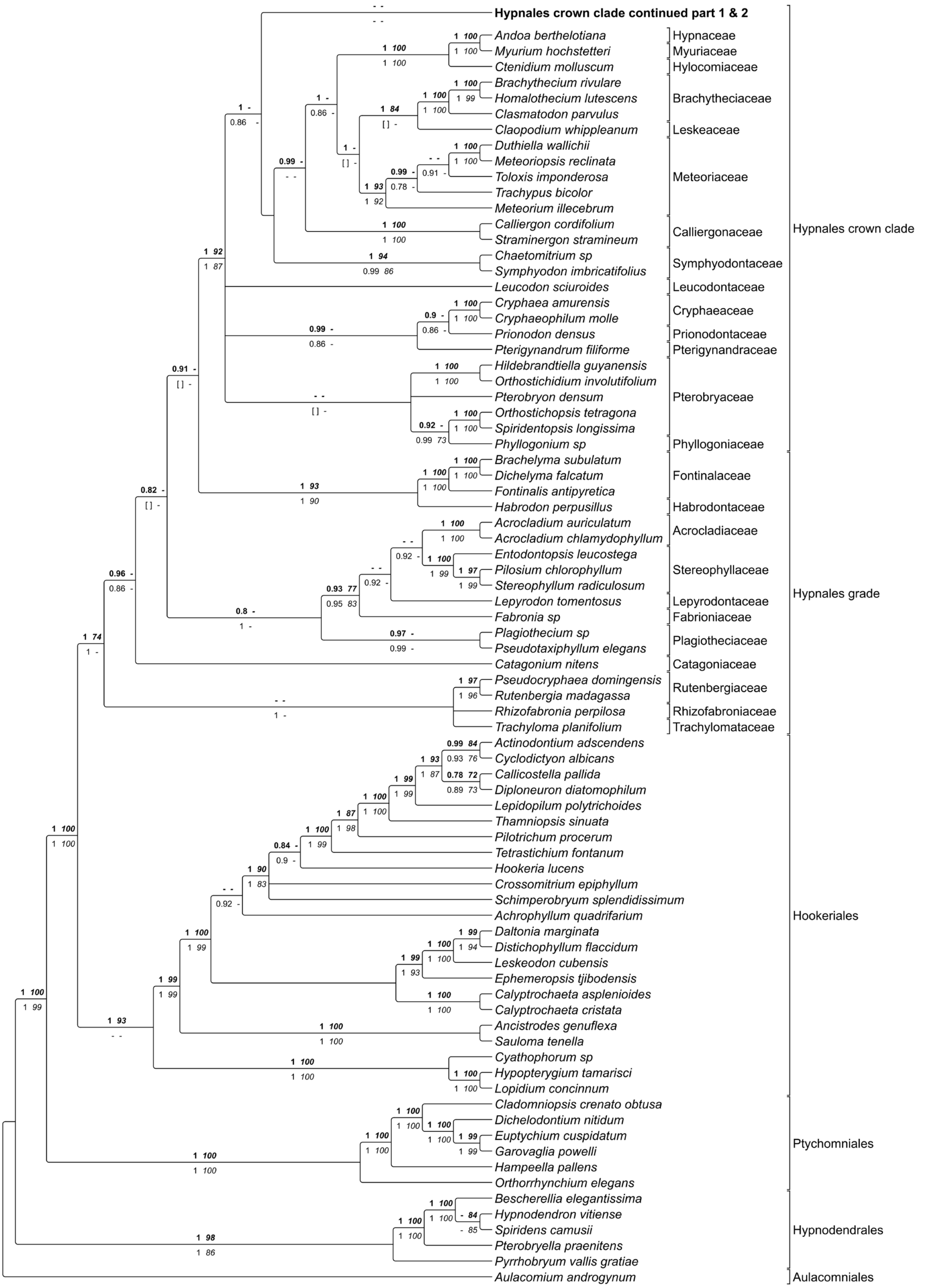

FIGURE 1. Phylogram of the Bayesian inference based on the concatenated nucleotide data (cp: *trn*L-F, *rps*4, mt: *nad*5, nr: ITS) and the appended SIC-indel matrix (SIC: simple indel coding). The posterior probabilities of the Bayesian inference and the maximum likelihood bootstrap support values are depicted along the branches. Bold support values show SIC results, support values in italics display the likelihood results. Values below 0.8 (PP) / 70 (BS) were excluded from the graphical representation. Square brackets below the branches indicate that the phylogenetic reconstruction without indel coding resulted at these nodes in a different branching pattern but without significant support. Otherwise the alternative values are given. The tree is separated into three consecutive parts.

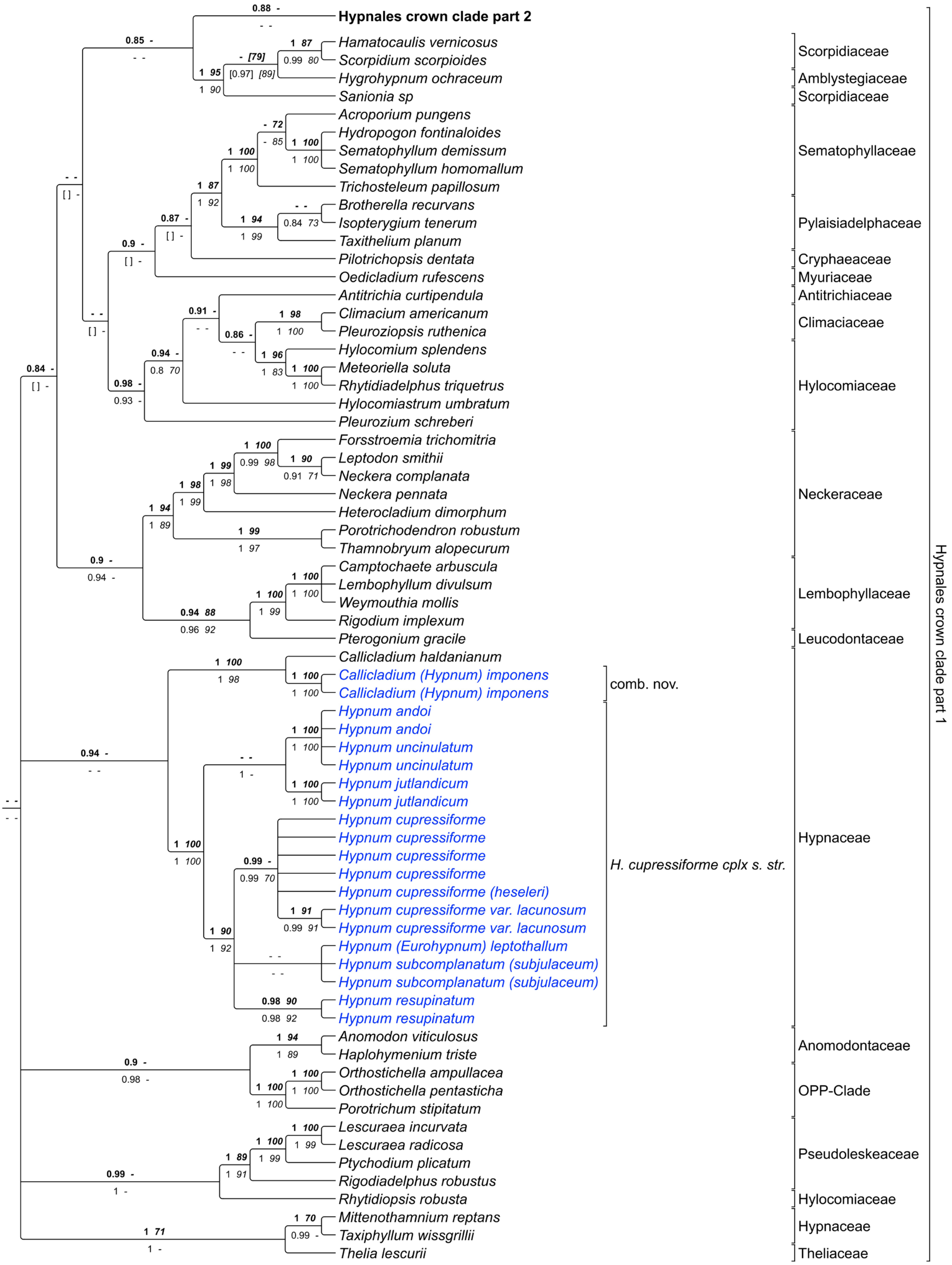

FIGURE 1 (continued). Hypnales crown clade part 1.

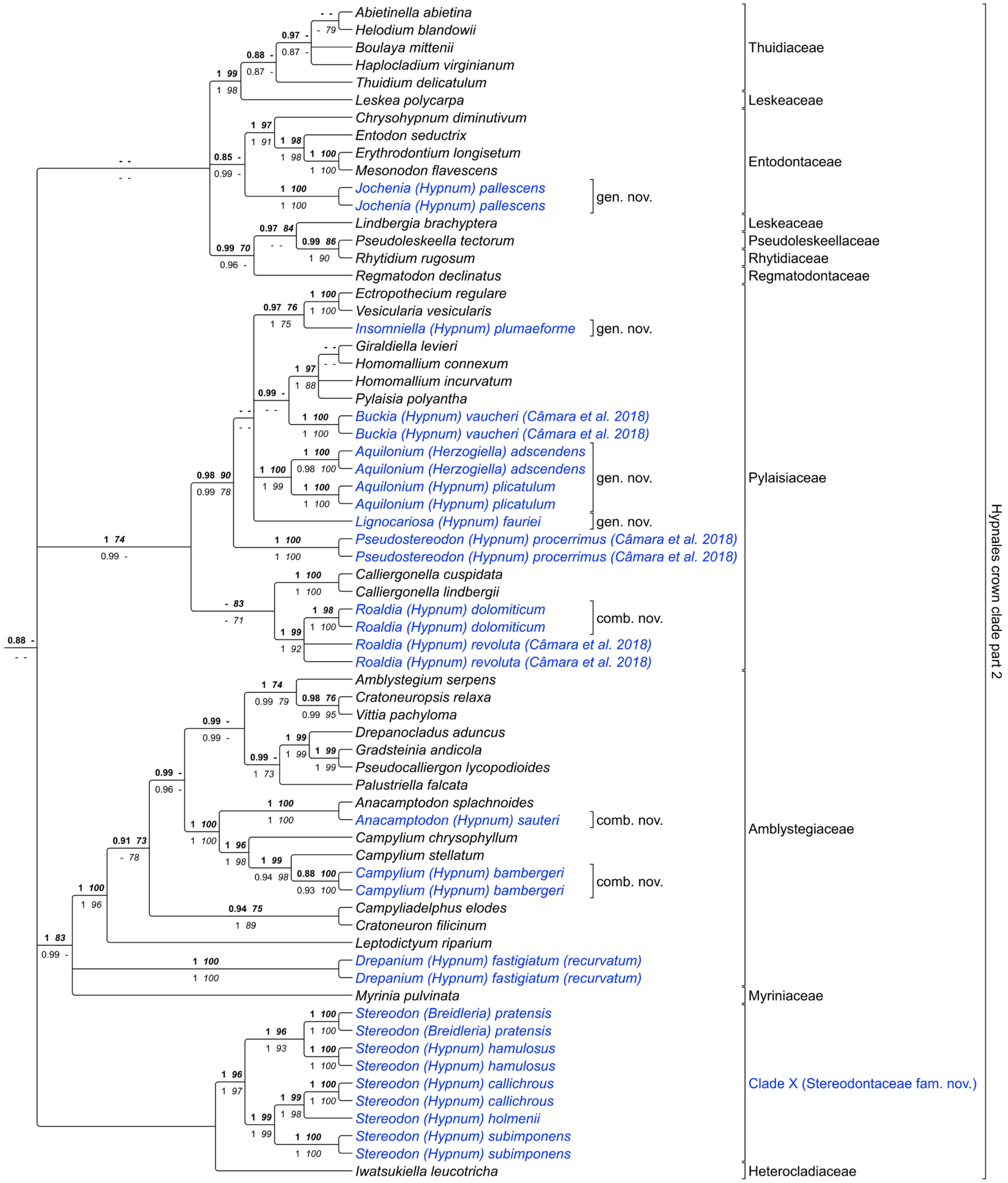

FIGURE 1 (continued). Hypnales crown clade part 2.

Phylogenetic relationships. No significant incongruence of the taxonomically extended individual data sets could be detected. The overall recovered phylogeny matches the results of Huttunen *et al.* (2012), thus we refrain from reporting the backbone phylogeny in detail and concentrate on the placement of the included *Hypnum* and related species (compare Appendix 1). Species of the genus *Hypnum* are distributed along five different clades including the Amblystegiaceae Kindb., Entodontaceae Kindb., Hypnaceae, Pylaisiaceae and a so far unknown clade (Clade X, Figure 1). The other species cluster into their respective families according to Frey & Stech (2009). The unknown clade X is significantly supported by all of our analyses [pp 1, pp sic 1, ML 97, ML sic 96]. Within this clade *B. pratensis* and *H. hamulosum* cluster together as sister species [pp 1, pp sic 1, ML 96, ML sic 93], next to a clade consisting of *H. callichroum*, *H. holmenii* and *H. subimponens* [pp 1, pp sic 1, ML 99, ML sic 99]. *Drepanium fastigiatum* (Hampe) C.E.O. Jensen*, H. bambergeri* as well as *H. sauteri* cluster within the Amblystegiaceae. *H. bambergeri* [pp 0.93, pp sic 0.88, ML 100, ML sic 100], is nested within *Campylium* (Sull.) Mitt. [pp 1, pp sic 1, ML 98, ML sic 96], whereas *H. sauteri* clusters in a clade with *Anacamptodon* Brid. [pp 1, pp sic 1, ML 100, ML sic 100]. The recently revised species *Buckia (Hypnum) vaucheri* (Lesq.) D.Ríos, M.T.Gallego & J.Guerra, *Roaldia revoluta* (Mitt.) P.E.A.S.Câmara & M.Carvalho-Silva and *Pseudostereodon procerrimus* (Molendo) M.Fleisch. (compare Câmara *et al.* 2018) cluster together with *Hypnum plumaeforme* Wilson, *H. dolomiticum* and *H, fauriei* Cardot into the well supported Pylaisiaceae [pp 0.99, pp sic 1, ML -, ML sic 74]. *H. dolomiticum* clusters in a clade with *Roaldia* P.E.A.S. Câmara & Carv.-Silva [pp 1, pp sic 1, ML 92, ML sic 99]. *H. plumaeforme* forms the sister taxon to *Ectropothecium* Mitt. and *Vesicularia* (Müll. Hal.) Müll. Hal. [pp 1, pp sic 0,97, ML 75, ML sic 76]. Hy*pnum plicatulum* (Lindb.) A. Jaeger clusters together with *Hypnum adscendens* (Lindb.) A. Jaeger [pp 1, pp sic 1, ML 99, ML sic 100]. All in all, the clade of the Pylaisiaceae is highly supported by our molecular data and contains seven *Hypnum* species or species formerly placed in *Hypnum*.

The only *Hypnum* species clustering into the Entodontaceae is *Hypnum pallescens* (Hedw.) P. Beauv. However, the support values are insignificant in three out of four analyses [pp 0.99, pp sic 0.85, ML -, ML sic -].

Only 8 out of the 21 European *Hypnum* taxa cluster into one clade with *H. cupressiforme* (*H. andoi*, *H. heseleri*, *H. imponens, H. jutlandicum*, *H. lacunosum* (i.e. *H. cupressiforme var. lacunosum*)*, H. resupinatum*, *H. subjulaceum* (i.e. *H. subcomplanatum*) and *H. uncinulatum*) plus *Callicladium haldanianum* (Grev.) and *Eurohypnum leptothallum* (Müll. Hal.) Ando. *Callicladium haldanianum* and *H. imponens* form a distinct clade sister to the remaining species of the *H. cupressiforme* complex, which is supported by maximal support values in most analyses [pp 1, pp sic 1, ML 98, ML sic 100]. Within the remainder of the complex, the relationships are in most cases resolved. *H. andoi*, *H. uncinulatum* and *H. jutlandicum* cluster into one clade, while *H. cupressiforme*, *H. heseleri*, *H. lacunosum* (i.e. *cupressiforme var. lacunosum*), *H. resupinatum, H. subjulaceum* (i.e. *H. subcomplanatum*) and *Eurohypnum leptothallum* form a significantly supported sister clade [pp 1, pp sic 1, ML 92, ML sic 90]. Within the *H. jutlandicum* clade, *H. andoi* and *H. uncinulatum* cannot be differentiated by the molecular markers we used, forming polytomy. Within the sister clade, *H. cupressiforme* forms an unresolved cluster with *H. heseleri*. *Hypnum cupressiforme var. lacunosum* however is resolved as a clearly supported clade by our molecular data. In turn *H. resupinatum* clusters into another separate clade. *H. cupressiforme var. subjulaceum* joins *E. leptothallum* in an unsupported clade.

Discussion

Our results support former phylogenetic analyses in that *Hypnum* is polyphyletic (Arikawa *et al.* 2008; Câmara *et al.* 2018; Gardiner *et al.* 2005; Huttunen *et al.* 2012; Ignatov *et al.* 2007). As supposed by Hedenäs' morphological studies on pleurocarpous mosses in 1989 the species of *Hypnum* sensu lato are scattered across the crown hypnalean taxa outside the *H. cupressiforme* complex (Hedenäs 1989). Furthermore, our data suggest recognition of several new genera, new combinations, as well as the introduction of a new family, and support the taxonomic changes already implemented for *Buckia (Hypum) vaucheri, Pseudostereodon (Hypnum) procerrimus* and *Roaldia (Hypnum) revoluta* (Câmara *et al.* 2018).

As pointed out by Câmara *et al.* (2018), the taxonomic placement of *Callergionella* has been ambiguous in the past. While Cox *et al.* (2010) resolve the genus within the Pylaisiaceae, it receives a sister group relationship to the Pylaisiaceae, or if included in the family represent the first branching lineage such as in Arikawa *et al.* (2008) as well as Ignatov *et al.* (2007). Although we used more marker regions, we were not able to resolve the position of the genus inside the Pylaisiaceae. However, we corroborate the results of Câmara *et al.* (2018) and retain *Callergionella* within the Pylaisiaceae as potential sister group to *Roaldia*. In addition we recommend including *Hypnum dolomiticum* in *Roaldia*. Even though Ando proposed that *H. dolomiticum* is morphologically not well enough defined to merit species rank, our molecular data show a clear circumscription of *H. dolomiticum* (Ando 1973). Furthermore, we suggest extending the Pylaisiaceae by several genera, to accommodate the species *H. plumaeforme*, *H. plicatulum* and *H. fauriei*. Along Câmara *et al.* (2018) analysis we suggest to allocate *H. fauriei* into a separate genus that we name *Lignocariosa* and to re-establish the genus *Pseudostereodon* (Broth.) M. Fleisch. for *H. procerrimum*. However, the placement of *H. fauriei* within the Pylaisiaceae remains unclear. Although Arikawa *et al.* (2008) excluded *H. plicatulum* and *H. callichroum* from the Pylaisiaceae, Câmara *et al.* (2018) stated that this should be reconsidered, since *H. plicatulum* clusters together with *Herzogiella adscendens*, within the Pylaisiaceae, whereas *Hypnum callichroum* clusters together with *H. hamulosum* outside the Pylaisiaceae (Arikawa *et al.* 2008; Câmara *et al.* 2018). Our results support the exclusion of *H. callichroum* from the Pylaisiaceae and the inclusion of *H. plicatulum* and *Herzogiella adscendens*. Like nearly all *Hypnum* taxa, both species have previously been included in *Stereodon* (Brid.) Rchb. Some authors even synonymized *Stereodon* with *Hypnum* (Gardiner et *al.* 2005). *Stereodon* was later lectotypified by Ignatov & Ignatova (2004) with the type species *Stereodon callichrous (Brid.) Lindb* (= *Hypnum callichroum*), placed within the Pylaisiaceae. In previous studies as well as in the present study *H. callichroum* clusters into a separate clade, consequently *H. plicatulum* and *Herzogiella adescens* cannot be included in *Stereodon* and *Stereodon* itself has to be placed into a new family. We propose to establish a new genus for these species, *Aquilonium*, with *Aquilonium adscendens* (Lindb.) Hedenäs, Schlesak, D. Quandt as its type species. These two species have a stem with a hyalodermis and pseudoparaphyllia that are triangular or broadly irregular but are otherwise difficult to differentiate from many earlier *Hypnum* species by morphology. Additionally, we propose the establishment of a new family named Stereodontaceae Hedenäs, Schlesak, D. Quandt to legitimate the high statistical support for the clade including *Stereodon* (Clade X, Figure 1), with, i.a., *Hypnum callichroum*. This clade further comprises *H. hamulosum*, *H. holmenii*, *H. subimponens* and *Breidleria pratensis*.

Alongside these changes, we suggest an addition to the genera within the Ambylstegiaceae by including *Drepanium* (Schimp.) C.E.O. Jensen, which clusters as one of the most basal genera of the family. Additionally, the present study suggests, with high statistical support an inclusion of *Hypnum bambergeri* in *Campylium*. This association was found already in earlier studies (Ignatov *et al.* 2007; Gardiner *et al.* 2005). Furthermore, *H. sauteri* should be included into *Anacamptodon*. Similarly, *Hypnum pallescens* clusters within the family Entodontaceae and, as already suggested by Gardiner *et al.* (2005), a new genus needs to be established to accommodate this species.

Hypnum cupressiforme, the type species of *Hypnum*, includes a wide morphological diversity. Because the same is true for other taxa within the *H. cupressiforme* complex, this has frequently lead to discussions regarding the recognition of taxa, and at which level they should be accepted (Smith 1997). Even though the number of taxa included in the complex has decreased, phylogenetic studies using molecular markers such as ITS and *trn*L-F were unable to resolve the taxonomic issues (Spagnuolo *et al.* 2008; Terracciano *et al.* 2012). Despite the low genetic diversity found within the complex by Spagnuolo *et al.* (2008), another study - though on a rather limited sampling - with a wider geographical scale and the inclusion of several outgroup species carried out by Terranciano *et al.* (2012) indicated that *H. imponens* and *H. jutlandicum* are distinct taxa (but see Hedenäs 2012). Some molecular studies even suggested a paraphyly of the *H. cupressiforme* complex (Arikawa *et al.* 2008; Terracciano *et al.* 2012). This hypothesis is supported by our results, which implicates the enlargement of the monotypic genus *Callicladium* by *Hypnum imponens* and a reintegration of *Eurohypnum leptothallum* into *Hypnum*, as already suggested by Arikawa *et al.* (2008). In addition, our results show four independent clusters within the *H. cupressiforme* complex. *H. jutlandicum*, *H. andoi* and *H. uncinulatum* cluster together with *H. uncinulatum* representing the first branching lineage. *H. andoi* and *H. uncinulatum* are indistinguishable by our molecular analyses; however, mixed occurrences indicate genetic differentiation (Smith 1997). *Hypnum resupinatum* and *H. subjulaceum* (i.e. *H. subcomplanatum*) separate into two separate clusters from the *H. cupressiforme*. Hence, they cannot be considered variants of *H. cupressiforme*, which is further supported by frequent mixed occurrences. Even though *H. lacunosum* (i.e. *H. cupressiforme var. lacunosum*) is rarely found in mixed occurrences with *H. cupressiforme* (Hedenäs 2012) and forms a separate entity, it is nested within *H. cupressiforme*, and thus cannot be circumscribed as a separate species. The same accounts for *H. heseleri* Ando & Higuchi.

After more than 200 years of studies, the species of *Hypnum* can now be comfortably distributed among nine morphologically and molecularly well-defined genera. Although it has lost the throne of being the most speciose moss genus, its fame is still captured on an ordinal level, the Hypnales W.R. Buck & Vitt. The Hypnales, which originated in the upper Cretaceous (Krug 2017) and thereafter experienced a rapid radiation (Krug 2017; Shaw *et al.* 2003) still represent half of the moss diversity. Obviously, convergent evolution has led to similar gross morphology in quite unrelated lineages although, with some exceptions (Huttunen *et al.* 2008; Olsson *et al*. 2009b, 2011; Quandt *et al.* 2009), we do at present not understand exactly which environmental factors are crucial to explain various plant habits. We are left with the question why the falcate-secund leaves of *Hypnum* s.str. and other pleurocarpous moss species are such a successful evolutionary “invention” that they developed numerous times in different pleurocarpous moss lineages? The present study further underlines that the falcate-secund leaves and many other so-called “key characters” that were traditionally used to circumscribe moss taxa, need careful evaluation before they are applied for such purposes.

Taxonomic treatment

Hypnaceae

Hypnum Hedw., Species Muscorum Frondosorum 236. 1801 (*nom. cons.*).

Type species: *Hypnum cupressiforme* Hedw., Species Muscorum Frondosorum 291. 1801 (*typ. cons.*) = syn. *Hypnum heseleri* Ando & Higuchi, Journal of the Hattori Botanical Laboratory 75: 98. 1994.

Other treated taxa: *Hypnum andoi* A.J.E. Sm., Journal of Bryology 11: 606. 1981 [1982]. *Hypnum cupressiforme* var. *lacunosum* Brid., Muscologia Recentiorum 2(2): 136. 1801. *Hypnum jutlandicum* Holmen & E. Warncke, in Damsholt *et al.*, Botanisk Tidsskrift 65: 179. 1969. *Hypnum leptothallum* (Müll. Hal.) Paris, Index Bryologicus Supplementum Primum 204. 1900 ≡ *Eurohypnum leptothallum* (Müll. Hal.) Ando, Botanical Magazine, Tokyo 79: 761. 1966. *Hypnum resupinatum* Taylor, in Spruce, Annals and Magazine of Natural History, ser. 2, 3: 280. 1849. ***Hypnum subcomplanatum*** Hedenäs, Schlesak, D. Quandt, nom. et stat. nov. ≡ (basionym) *Hypnum cupressiforme* var. *subjulaceum* Molendo, *Bericht des Naturhistorischen Vereins in Augsburg* 18: 183. 1865 (*Hypnum subjulaceum* Besch., in Paris, Index Bryologicus 1263. 1898, *nom. nud.*). *Hypnum uncinulatum* Jur., Botanische Zeitung (Berlin) 24: 21. 1866.

Callicladium H.A. Crum, Bryologist 74: 167. 1971.

Type species: *Callicladium haldanianum* (Grev.) H.A. Crum, Bryologist 74: 167. 1971.

Other treated taxon: ***Callicladium imponens*** (Hedw.) Hedenäs, Schlesak, D. Quandt ≡ (basionym) *Hypnum imponens* Hedw., Species Muscorum Frondosorum 290, pl. 77, f. 1–5. 1801.

Stereodontaceae, fam. nov.

Diagnosis: Species similar to *Hypnum* s.str., but with dwarf male plants, a stem with hyalodermis, and leaves with few or numerous inflated, thin-walled alar cells.

Type genus: *Stereodon* (Brid.) Rchb., Conspectus Regni Vegetabilis 33. 1828.

Stereodon (Brid.) Rchb., Conspectus Regni Vegetabilis 33. 1828.

Type species: *Stereodon callichrous* (Brid.) Lindb., Acta Societatis Scientiarum Fennicae 10: 255. 1872 (Lectotype, Ignatov & Ignatova (2004))

Other treated taxa: *Stereodon hamulosus* (Schimp.) Lindb., Acta Societatis Scientiarum Fennicae 10: 255. 1872. *Stereodon holmenii* (Ando) Ignatov & Ignatova, Arctoa, a Journal of Bryology 11 (Supplement 2): 855. 2004. *Stereodon pratensis* (W.D.J. Koch ex Spruce) Warnst., Kryptogamenflora der Mark Brandenburg, Laubmoose (Band 2, Heft V) 964. 1906 ≡ *Breidleria pratensis* (W.D.J. Koch ex Spruce) Loeske, Studien zur Vergleichenden Morphologie und Phylogenetischen Systematik der Laubmoose 172. 1910. *Stereodon subimponens* (Lesq.) Broth., Die Natürlichen Pflanzenfamilien I (3, Lieferung 232–233): 1072. 1908.

Hypnum erectiusculum Sull. & Lesq. most likely also belongs in *Stereodon* (cf., Hedenäs 1992), but since we did not include this species in our molecular sampling, we refrain from making the formal combination here.

Amblystegiaceae

Drepanium (Schimp.) C.E.O. Jensen, in Lange & Jensen, Meddelelser om Grønland 3: 326. 1887.

Type species: *Drepanium fastigiatum* (Hampe) C.E.O. Jensen, in Lange & Jensen, Meddelelser om Grønland 3: 326. 1887. (lectotype, Ignatov & Ignatova (2004)) = *D. recurvatum* (Lindb. & Arnell) G. Roth, Die Europäischen Laubmoose 2 (Lieferung 10): 613. 55 f. 24. 1904 (cf., Ando 1973).

Anacamptodon Brid., Muscologiae Recentiorum Supplementum 4: 136, pl. 2, f. 11. 1819 [1818]

Type species: *Anacamptodon splachnoides* (Froel. ex Brid.) Brid., Muscologiae Recentiorum Supplementum 4: 136. 1819 [1818].

Other treated taxon: ***Anacamptodon sauteri*** (Schimp.) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Hypnum sauteri* Schimp., in Sauter, Flora 33: 445. 1850.

Campylium (Sull.) Mitt., Journal of the Linnean Society, Botany 12: 631. 1869 ≡ *Hypnum* sect. *Campylium* Sull., Manual of the Botany of the Northern United States. Second Edition 677. 1856.

Type species: *Hypnum stellatum* Hedw., Species Muscorum Frondosorum 280. 1801 ≡ *Campylium stellatum* (Hedw.) C.E.O. Jensen, in Lange & Jensen, Meddelelser om Grønland 3: 328. 1887 (lectotype, Pfeiffer (1871–1875), cf., Isoviita & Hedenäs (1997)).

Other treated taxon: ***Campylium bambergeri*** (Schimp.) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Hypnum bambergeri* Schimp., Synopsis Muscorum Europaeorum 698. 1860.

Pylaisiaceae

Pseudostereodon (Broth.) M. Fleisch., Die Musci der Flora von Buitenzorg 4: 1376. 1923.

Type species: *Pseudostereodon procerrimus* (Molendo) M. Fleisch., in Brotherus, Die natürlichen Pflanzenfamilien, Zweite Auflage 11: 455. 1925.

Roaldia P.E.A.S. Câmara & Carv.-Silva, in Câmara *et al.*, Journal of Bryology 40: 257. 2018.

Type species: *Roaldia revoluta* (Mitt.) P.E.A.S. Câmara & Carv.-Silva, in Câmara *et al.*, Journal of Bryology 40: 257. 2018 ≡ *Hypnum revolutum* (Mitt.) Lindb., Öfversigt af Förhandlingar: Kongl. Svenska Vetenskaps-Akademien 23(10): 542. 1866 [1867].

Other treated taxon: ***Roaldia dolomitica*** (Milde) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Hypnum dolomiticum* Milde, Botanische Zeitung (Berlin) 22 (19, Beil.): 21. 1864.

Buckia D. Ríos, M.T. Gallego & J. Guerra, in Câmara *et al.*, Journal of Bryology 40: 258. 2018.

Type species: *Buckia vaucheri* (Lesq.) D. Ríos, M.T. Gallego & J. Guerra, in Câmara *et al.*, Journal of Bryology 40: 258. 2018 ≡ *Hypnum vaucheri* Lesq., Mémoires de la Société des Sciences Naturelles de Neuchâtel 3(3): 48. 1846.

Lignocariosa Hedenäs, Schlesak, D. Quandt, gen. nov.

Diagnosis: Plants autoicous, medium-sized, stems up to 7 cm long and stem leaves to 2.2 x 0.7 mm, stem lacking a well-developed hyalodermis, alar groups well developed, with basal cells inflated, thin-walled and hyaline, spore capsules (1.5)2.0–3.0 mm long, spores (14)16–22(24) µm.

Etymology: From combining the words *lignum* (wood) and *cariosum* (rotten). The species typically grows on rotten wood (Ando & Schofield 1999)

Type species: ***Lignocariosa fauriei*** (Cardot) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Hypnum fauriei* Cardot, Beihefte zum Botanischen Centralblatt 17(1): 41, f. 26. 1904.

Aquilonium Hedenäs, Schlesak, D. Quandt, gen. nov.

Diagnosis: Similar to *Hypnum* s.str., but stem with hyalodermis and pseudoparaphyllia triangular or broadly irregular.

Type species: ***Aquilonium adscendens*** (Lindb.) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Stereodon adscendens* Lindb., Acta Societatis Scientiarum Fennicae 10: 255. 1872 [1873] ≡ *Hypnum adscendens* (Lindb.) A. Jaeger, in Jaeger & Sauerbeck, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1877–78: 328 (Gen. Sp. Musc. 2: 592). 1880 ≡ *Herzogiella adscendens* (Lindb.) Z. Iwats & W.B. Schofield, Journal of the Hattori Botanical Laboratory 37: 609. 1973.

Other treated taxon: ***Aquilonium plicatulum*** (Lindb.) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Stereodon plicatulus* Lindb., Acta Societatis Scientiarum Fennicae 10: 254. 1872 [1873] ≡ *Hypnum plicatulum* (Lindb.) A. Jaeger, Bericht über die Thätigkeit der St. Gallischen Naturwissenschaftlichen Gesellschaft 1877–1878: 316. 1880.

Insomniella Hedenäs, Schlesak, D. Quandt, gen. nov.

Diagnosis: Plants robust, with shoots up to >10 cm long and stem leaves to 3.0 x 1.0 mm, leaves base varying around cordate, leaf lamina cells short, especially in relation to leaf length, 40–82 µm long.

Type species: ***Insomiella plumaeforme*** (Wilson) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Hypnum plumaeforme* Wilson, London Journal of Botany 7: 277. pl. 10: d. 1848.

Entodontaceae

Jochenia Hedenäs, Schlesak, D. Quandt, gen. nov.

Diagnosis: Differs from *Drepanium* or *Roaldia* species with recurved leaf margins by having branches less or hardly complanate, leaves strongly denticulate, and operculum rostrate.

Etymology: Named after Prof. Jochen Heinrichs (1969–2018), distinguished German botanist specialised in bryophytes.

Type species: ***Jochenia pallescens*** (Hedw.) Hedenäs, Schlesak, D. Quandt, comb. nov. ≡ (basionym) *Leskea pallescens* Hedw., Species Muscorum Frondosorum 219, pl. 55, f. 1–6. 1801 ≡ *Hypnum pallescens* (Hedw.) P. Beauv., Prodrome des Cinquième et Sixième Familles de l'Aethéogamie 67. 1805.

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APPENDIX 1. Voucher specimens and EMBL/GenBank accession numbers for additionally included taxa in dataset of Huttunen *et al.* (2012). Classification is after Frey & Stech (2009).

Taxon	ITS 1 & 2	*trn*L-F	*nad*5	*rps*4	Herbarium: voucher number
Amblystegiaceae					
Anacamptodon splachnoides (Froel. ex Brid.) Brid.	AY009810	AY009816	AY908419	AF143031	
Anacamptodon (*Hypnum*) *sauteri* (Schimp.) Hedenäs, Schlesak, D. Quandt	MK211872	MK211921	MK211970	MK212015	STU: 21695
Campyliadelphus elodes (Lindb.) Kanda	MK211837	MK211885	MK211935	N.A.	STU: 47697
Campylium (*Hypnum*) *bambergeri* (Schimp.) Hedenäs, Schlesak, D. Quandt	MK211844	MK211892	MK211941	MK211987	TUR: 7.8.2002 Kimmo Syrjänen, Roosa Leimu, Henry Väre, Heidi Kaipiainen
Campylium (*Hypnum*) *bambergeri* (Schimp.) Hedenäs, Schlesak, D. Quandt	MK211845	MK211893	MK211942	MK211988	STU: MP03293
Cratoneuropsis relaxa (Hook. f. & Wilson) M. Fleisch.	FJ535787	AY429494	AY908427	AY908244	
Drepanium fastigiatum (Hampe) C.E.O. Jensen	MK211867	MK211915	MK211964	MK212009	TUR: 3.8.1997 Kimmo Syrjänen
Drepanium fastigiatum (Hampe) C.E.O. Jensen	MK211868	MK211916	MK211965	MK212010	TUR: 20.VII.2011 Kimmo Syrjänen
Gradsteinia andicola Ochyra	HQ443749	HQ443874	AY908420	AY908246	
Hygrohypnum ochraceum (Turner ex Wilson) Loeske	MK211841	MK211889	AJ291574	AJ291574	MK211841 & MK211889: STU: 50967
Leptodictyum riparium (Hedw.) Warnst.	MK211881	MK211930	AY908713	AY907967	MK211881 & MK211930: STU: 997
Pseudocalliergon lycopodioides (Brid.) Hedenäs	MK211882	MK211931	MK211979	N.A.	STU: 50859
Entodontaceae					
Jochenia (*Hypnum*) *pallescens* (Hedw.) Hedenäs, Schlesak, D. Quandt	MK211862	MK211910	MK211959	MK212004	TUR: 26.4.2001 Kimmo Syrjänen
Jochenia (*Hypnum*) *pallescens* (Hedw.) Hedenäs, Schlesak, D. Quandt	MK211863	MK211911	MK211960	MK212005	TUR: 11.4.2003 Teppo Häyhä
Heterocladiaceae					
Iwatsukiella leucotricha (Mitt.) W.R. Buck & H.A. Crum	AF516162 FJ572361	FJ572443	AY908740	AY908583	
Hypnaceae					
Callicladium haldanianum (Grev.) H.A. Crum	AY695761 AY695785	AY762372	AY908760	AY908561	
Callicladium (*Hypnum*) *imponens* (Hedw.) Hedenäs, Schlesak, D. Quandt	MK211856	MK211904	MK211953	MK211998	TUR: 19.8.2005 Ari Parnela

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APPENDIX 1. (Continued)

Taxon	**ITS 1 & 2**	***trn*L-F**	***nad*5**	***rps*4**	**Herbarium: voucher number**
Callicladium (*Hypnum*) *imponens* (Hedw.) Hedenäs, Schlesak, D. Quandt	MK211857	MK211905	MK211954	MK211999	NY: William R. Buck 55682
Hypnum andoi A.J.E. Sm.	MK211842	MK211890	MK211939	MK211985	E: No.29457
Hypnum andoi A.J.E. Sm.	MK211843	MK211891	MK211940	MK211986	STU: MP02593
Hypnum cupressiforme Hedw.	MK211848	MK211896	MK211945	MK211990	E: No.40579
Hypnum cupressiforme Hedw.	MK211849	MK211897	MK211946	MK211991	NY: ACC:B192615
Hypnum cupressiforme Hedw.	MK211850	MK211898	MK211947	MK211992	MHA: M-483
Hypnum cupressiforme var. *lacunosum* Brid.	MK211860	MK211908	MK211957	MK212002	TUR: 18.IX.2012 Sanna Huttunen
Hypnum cupressiforme var. *lacunosum* Brid.	MK211861	MK211909	MK211958	MK212003	STU: 12.04.2005, M.Koperski
Hypnum heseleri Ando & Higuchi	MK211854	MK211902	MK211951	MK211996	S: B172157
Hypnum jutlandicum Holmen & Warncke	MK211858	MK211906	MK211955	MK212000	E: No.40589
Hypnum jutlandicum Holmen & Warncke	MK211859	MK211907	MK211956	MK212001	NY: # AML003-18
Hypnum resupinatum Taylor	MK211869	MK211917	MK211966	MK212011	E: No.42291
Hypnum resupinatum Taylor	MK211870	MK211918	MK211967	MK212012	E: No.41874
Hypnum subcomplanatum Hedenäs, Schlesak, D. Quandt	MK211875	MK211924	MK211973	MK212018	S: B103723
Hypnum subcomplanatum Hedenäs, Schlesak, D. Quandt	MK211876	MK211925	MK211974	MK212019	BP: 173103
Hypnum uncinulatum Jur.	MK211877	MK211926	MK211975	MK212020	LG: A005
Hypnum uncinulatum Jur.	MK211878	MK211927	MK211976	MK212021	LG: A047
Pylaisiaceae					
Buckia vaucheri (Lesq.) D.Ríos, M.T.Gallego & J.Guerra	MK211879	MK211928	MK211977	MK212022	TUR: 25.7.2010 Kimmo Syrjänen
Buckia vaucheri (Lesq.) D.Ríos, M.T.Gallego & J.Guerra	MK211880	MK211929	MK211978	MK212023	MHA: 06-114
Calliergonella cuspidata (Hedw.) Loeske	AF168145	GQ428068	AY908403	AY908183	
Calliergonella lindbergii (Mitt.) Hedenäs	AY009813	AF315069	MK211934	MK211982	MK211934& MK211982: MA: 14182
Giraldiella levieri Müll. Hal.	FM161104	N.A.	FM161261	AM990366	
Homomallium connexum (Cardot) Broth.	JN896316	KF770511.1	N.A.	KF770565	
Homomallium incurvatum (Schrad. ex Brid.) Loeske	MK211840	MK211888	MK211938	N.A.	STU: 24352
Lignocariosa (*Hypnum*) *fauriei* (Cardot) Hedenäs, Schlesak, D. Quandt	JN896313	N.A.	N.A.	N.A.	
Pseudostereodon (*Hypnum*) *procerrimus* (Molendo) M.Fleisch.	MK211866	MK211914	MK211963	MK212008	STU: 16216

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APPENDIX 1. (Continued)

Taxon	**ITS 1 & 2**	***trn*L-F**	***nad*5**	***rps*4**	**Herbarium: voucher number**
Roaldia (*Hypnum*) *dolomitica* (Milde) Hedenäs, Schlesak, D. Quandt	MK211851	MK211899	MK211948	MK211993	S: B279051
Roaldia (*Hypnum*) *dolomitica* (Milde) Hedenäs, Schlesak, D. Quandt	MK211852	MK211900	MK211949	MK211994	S: B279058
Roaldia (*Hypnum*) *revoluta* (Mitt.) P.E.A.S.Câmara & M.Carvalho-Silva	MK211871	MK211919	MK211968	MK212013	TUR: 28.VII.2011 Kimmo Syrjänen
Roaldia (*Hypnum*) *revoluta* (Mitt.) P.E.A.S.Câmara & M.Carvalho-Silva	N.A.	MK211920	MK211969	MK212014	TUR: 13.7.2008 Kimmo Syrjänen
Aquilonium (Hypnum) adscendens (Lindb.) Hedenäs, Schlesak, D. Quandt	MK211838	MK211886	MK211936	MK211983	DUKE: Acc: B166576
Aquilonium (Hypnum) adscendens (Lindb.) Hedenäs, Schlesak, D. Quandt	MK211839	MK211887	MK211937	MK211984	DUKE: Acc: B210973
Aquilonium (Hypnum) plicatulus (Lindb.) Hedenäs, Schlesak, D. Quandt	MK211864	MK211912	MK211961	MK212006	S: B279049
Aquilonium (Hypnum) plicatulus (Lindb.) Hedenäs, Schlesak, D. Quandt	MK211865	MK211913	MK211962	MK212007	S: B279047
Scorpidiaceae					
Hamatocaulis vernicosus (Mitt.) Hedenäs	EF172716	EF172790.1	AY908434	AY908251	
Stereodontaceae					
Stereodon (*Hypnum*) *callichrous* (Brid.) Lindb.	MK211846	MK211894	MK211943	MK211989	E: No.34038
Stereodon (*Hypnum*) *callichrous* (Brid.) Lindb.	MK211847	MK211895	MK211944	N.A.	E: No. 41851
Stereodon (*Hypnum*) *hamulosus* (Schimp.) Lindb.	MK211853	MK211901	MK211950	MK211995	TUR: 19.7.2007 Kimmo Syrjänen
Stereodon (*Hypnum*) *holmenii* (Ando) Ignatov & Ignatova	MK211855	MK211903	MK211952	MK211997	S: B183268
Stereodon (*Hypnum*) *pratensis* (W.D.J. Koch ex Spruce) Warnst.	MK211835	MK211883	MK211932	MK211980	S: B183108
Stereodon (*Hypnum*) *pratensis* (W.D.J. Koch ex Spruce) Warnst.	MK211836	MK211884	MK211933	MK211981	S: B202151
Stereodon (*Hypnum*) *subimponens* (Lesq.) Broth.	MK211873	MK211922	MK211971	MK212016	S: B180110
Stereodon (*Hypnum*) *subimponens* (Lesq.) Broth.	MK211874	MK211923	MK211972	MK212017	LG: 4682