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A molecular phylogeny of the Sematophyllaceae s.l. (Hypnales) based on plastid, mitochondrial and nuclear markers, and its taxonomic implications

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Abstract The Sematophyllaceae s.l. (Sematophyllaceae+Pylaisiadelphaceae) is a family of pleurocarpous mosses that is widely distributed throughout the globe, with centers of diversity in tropical forests. The circumscriptions of the family and its genera have been unstable, due to reductions in morphological complexity and alternative weightings of discrete morphological traits. Based on a sample spanning much of the generic diversity of the family, we inferred the phylogenetic relationships within the Sematophyllaceae s.l. from the variation in eight molecular markers from all three genomes (nuclear, mitochondrial, chloroplast). The Sematophyllaceae s.l. was resolved as monophyletic, as was the Sematophyllaceae s.str.; whereas the Pylaisiadelphaceae was found to be paraphyletic, although its monophyly could not be rejected. The morphological definition of the Pylaisiadelphaceae remains dubious, in the absence of unambiguous synapomorphies. The relationships of the clades of Pylaisiadelphaceae and Sematophyllaceae are discussed with respect to the circumscription of morphogenera, with a focus on the Sematophyllaceae crown clade (*Aptychopsis*, *Chionostomum*, *Colobodontium*, *Donnellia*, *Macrohymenium*, *Paranapiacabaea*, *Pterogoniopsis*, *Rhaphidorrhynchium*, *Schroeterella*, *Sematophyllum*, *Warburgiella*). Most genera of Sematophyllaceae were resolved as polyphyletic (e.g., *Acroporium*, *Donnellia*, *Schroeterella*, *Sematophyllum*, *Trichosteleum*) indicative of severe homoplasy in their putative diagnostic traits. We propose 4 new genera (*Brittonodoxa*, *Microcalpe*, *Pocsia*, *Vitalia*) and 19 new combinations (*Aptychopsis cylindrothecia*, *A. estrellae*, *A. tequendamensis*, *Brittonodoxa allinckxiorum*, *B. cataractae*, *B. lithophila*, *B. squarrosa*, *B. steyermarkii*, *B. subpinnata*, *Microcalpe subsimplex*, *Pocsia matutina*, *Pterogoniopsis paulista*, *Schroeterella exigua*, *Trichosteleum amnigenum*, *T. lonchophyllum*, *Vitalia caespitosa*, *V. cuspidifera*, *V. esmeraldica*, *V. galipensis*).

Keywords *Brittonodoxa*; *Microcalpe*; morphology; phylogeny; *Pocsia*; Pylaisiadelphaceae; Sematophyllaceae; *Vitalia*

Supplementary Material Electronic Supplement (Figs. S1–S45) and DNA sequence alignment files are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

■ INTRODUCTION

Assessing family circumscriptions and relationships in Hypnales, the largest order of mosses (Bryophyta), is challenging. Obstacles encountered include low molecular diversity and short branch lengths, incongruence between molecular phylogenetic reconstructions and traditional family delimitations, and weak morphological characterizations due to few synapomorphies (e.g., Shaw & al., 2003; Gardiner & al., 2005; Ignatov & al., 2007; Newton & al., 2007; Frey & Stech, 2009; Goffinet &

al., 2009; Cox & al., 2010; Huttunen & al., 2012). Nevertheless, the large, taxonomically complex families of Hypnales, such as Sematophyllaceae, are in particular need of reassessment based on comprehensive molecular and morphological datasets.

The Sematophyllaceae has a predominantly pantropical distribution and is probably the most common moss family in the tropics, with centers of diversity in Southeast Asia and the Neotropics. The family is taxonomically complex and its circumscription has long been a matter of debate. In its current circumscription, the Sematophyllaceae (sensu Frey & Stech,

2009; Goffinet & al., 2009) comprises about 500 species in 28 genera. Its members are characterized morphologically by having typically golden-green plants, leaves often falcate, well-developed, frequently inflated, colored alar cells, costa absent or short double, capsules with collenchymatous exothecial cells, an obliquely long-rostrate operculum, and a peristome with often furrowed exostome teeth, cross-striolate.

The circumscription of Sematophyllaceae has changed considerably over time. The family was initially described by Mitten (1869) as tribus Sematophylleae, with four genera (*Meiothecium* Mitt., *Potamium* Mitt., *Sematophyllum* Mitt., *Taxithelium* Mitt.). Brotherus (1908) raised the tribe to family

rank and recognized 12 genera, but excluded *Taxithelium*. Fleischer (1923) divided the Sematophyllaceae into four sub-families (Clastobryeae, Heterophyllieae, Macrohymenieae, Sematophylleae), accommodating 34 genera (Table 1). Brotherus (1925) subsequently followed Fleischer (1923) and retained the four subfamilies, but expanded the number of genera to 37, adding *Allioniella* Broth., *Aptychella* (Broth.) Herzog, and *Pylaisiopsis* (Broth.) Broth. Grout (1932) and Andrews (1954) merged representatives of the Hypnaceae within the Sematophyllaceae, thereby obscuring its morphological circumscription. Reimers (1954) included 37 genera in the family, and Vitt (1984) recognized 50 genera.

Table 1. Taxonomic history of Sematophyllaceae.

Mitten (1869)	Brotherus (1908)	Fleischer (1923)
		<i>Acanthocladium</i> Mitt.
		<i>Acanthorrhynchium</i> M.Fleisch.
		<i>Acroporium</i> Mitt.
		<i>Aptychopsis</i> (Broth.) M.Fleisch.
		<i>Brotherella</i> M.Fleisch.
	<i>Chionostomum</i> Müll.Hal.	<i>Chionostomum</i>
		<i>Clastobryophilum</i> M.Fleisch.
		<i>Clastobryella</i> M.Fleisch.
		<i>Clastobryopsis</i> M.Fleisch.
		<i>Clastobryum</i> Dozy & Molk.
		<i>Gammiella</i> Broth.
		<i>Glossadelphus</i> M.Fleisch.
		<i>Hageniella</i> Broth.
		<i>Heterophyllum</i> (Schimp.) Kindb.
		<i>Macrohymenium</i> Müll.Hal.
		<i>Mastopoma</i> Cardot
	<i>Meiotheciopsis</i> Broth.	<i>Meiotheciopsis</i>
<i>Meiothecium</i> Mitt.	<i>Meiothecium</i>	<i>Meiothecium</i>
	<i>Piloecium</i> (Müll.Hal.) Broth.	
<i>Potamium</i> Mitt.	<i>Potamium</i>	<i>Potamium</i>
	<i>Pterogonidium</i> Müll.Hal.	<i>Pterogonidium</i>
	<i>Pterogoniopsis</i> Müll.Hal.	<i>Pterogoniopsis</i>
		<i>Pylaisiadelpha</i> Cardot
	<i>Rhaphidostegium</i> (Schimp.) De Not.	<i>Rhaphidostichum</i> M.Fleisch.
		<i>Rhaphidorrhynchium</i> M.Fleisch.
	<i>Schraderella</i> Müll.Hal.	<i>Schraderella</i>
		<i>Schraderobryum</i> M.Fleisch.
		<i>Schroeterella</i> Herzog
<i>Sematophyllum</i> Mitt.	<i>Sematophyllum</i>	<i>Sematophyllum</i>
		<i>Struckia</i> Müll.Hal.
		<i>Syringothecium</i> Mitt.
<i>Taxithelium</i> Mitt.		<i>Taxithelium</i>
	<i>Trichosteleum</i> Mitt.	<i>Trichosteleum</i>
		<i>Trismegistia</i> (Müll.Hal.) Müll.Hal.
	<i>Warburgiella</i> Müll.Hal.	<i>Warburgiella</i>

The inferences by Hedenäs & Buck (1999) from a cladistic approach using morphological traits yielded a monophyletic Sematophyllaceae divided into two subfamilies, Sematophylloideae and Wijkioidae, rather than the four proposed by Fleischer (1923); and suggested the polyphyly of some genera, including the type *Sematophyllum*. The first molecular phylogenetic analyses by Tsubota & al. (2001a, b) also resolved the family into two sister clades, the core sematophyllaceous taxa (e.g., *Acroporium* Mitt., *Sematophyllum*, *Trichosteleum* Mitt.), and a clade that included *Brotherella* M.Fleisch., *Isopterygium* Mitt., *Platygyrium* Schimp., *Pylaisiadelpha* Cardot, and *Taxithelium*, which Tsubota & al. (2001a) called “the *Brotherella* lineage”. The latter lacks most or all of the features considered typical of the Sematophyllaceae, and was consequently described as a new family, the Pylaisiadelphaceae, by Goffinet & Buck (2004). The Pylaisiadelphaceae is characterized by leaves usually not falcate, alar cells few and quadrate, exothelial cells not collenchymatous, opercula often straight-rostrate, and exostome teeth not furrowed. The corresponding circumscriptions of the Sematophyllaceae s.str. (28 genera) and Pylaisiadelphaceae (16 genera) were adopted in the most recent classification of mosses (Frey & Stech, 2009; Goffinet & al., 2009).

Despite considerable progress, the delimitation of Sematophyllaceae and Pylaisiadelphaceae as well as circumscriptions of genera within both families remains under debate. With supraspecific systematic concepts typically based on patterns of sporophytic trait variation (Fleischer, 1904; Brotherus, 1925; Crosby, 1974; Shaw & al., 1989), the placement of taxa with variously reduced sporophytic characters can be challenging and subject to interpretation or weighting of gametophytic traits. Substantial gametophytic congruencies have been ignored in order to accommodate some genera of questionable affinity in the family. Not surprisingly, the larger genera show wide morphological variation, and generic boundaries within the Sematophyllaceae are rather unstable. Revisionary studies may be hampered by insufficient studies of type collections and a high percentage of misidentified herbarium collections (Buck & Tan, 1989; Câmara & al., 2014), and so far have been mainly restricted to either Asia (e.g., Buck & Tan, 1989; Tan & Buck, 1989; Tan & Jia, 1999) or the Neotropics (Câmara, 2011a, b; Câmara & Carvalho-Silva, 2013; Câmara & Shaw, 2013; Akiyama & al., 2015; Câmara & al., 2015). At the molecular level, the studies by Tsubota & al. (2001a, b) were based on only one chloroplast locus (*rbcL*) and the sample consisted largely of Southeast Asian species and lacked many types. More recent phylogenetic reconstructions of mosses based on a larger number of markers, but still limited taxon samples, confirmed the monophyly of the Sematophyllaceae s.str. (Cox & al., 2010; Huttunen & al., 2012). Whereas Huttunen & al. (2012) resolved the Pylaisiadelphaceae as monophyletic and sister to the Sematophyllaceae, the phylogenetic reconstructions of Cox & al. (2010), but also Akiyama & al. (2011) and Carvalho-Silva & al. (2014) resolved the Sematophyllaceae within a paraphyletic Pylaisiadelphaceae. However, a comprehensive molecular analysis of the circumscriptions and relationships of the Sematophyllaceae s.str. and Pylaisiadelphaceae

based on samples from all genera or major lineages, and a dataset with multiple markers has been lacking.

The present contribution addresses the circumscription of Sematophyllaceae and Pylaisiadelphaceae, and genera within both families, based on the most comprehensive molecular dataset available to date, including multiple loci from all three genomes (nuclear, mitochondrial, chloroplast) and a morphologically and geographically broader taxon sample comprising 14 of the 16 genera of Pylaisiadelphaceae and 21 of the 28 genera of Sematophyllaceae. Specifically, this study aimed to (1) resolve the circumscription, including testing of alternative molecular topologies; (2) test the monophyly of genera across both families; (3) map the distribution of morphological characters onto the phylogenetic reconstructions in order to identify possible synapomorphies for the clades in Pylaisiadelphaceae and Sematophyllaceae; and (4) where possible, draw taxonomic conclusions based on the molecular phylogenetic reconstructions and morphological characters.

■ MATERIALS AND METHODS

Taxon sampling. — Specimens were selected from across the global distribution of the Sematophyllaceae s.l. (Sematophyllaceae s.str., Pylaisiadelphaceae). As far as possible, types of generic names, and in several cases more than one accession per species, were sampled. The total sample comprised 105 specimens representing 87 species from 37 genera of Sematophyllaceae s.l. We sampled 14 of 16 genera of Pylaisiadelphaceae (87.5%) and 21 of 28 genera of Sematophyllaceae (78%). We added representatives from three other genera not cited by Goffinet & al. (2009) or Frey & Stech (2009), viz. *Fauriella* Besch. (Pylaisiadelphaceae), *Rhacopilopsis* Renaud & Cardot and *Rhaphidorrhynchium* (Sematophyllaceae). Most of the genera not included in this study are known only from their type collections or are monospecific genera from remote regions, from which recent collections suitable for molecular analysis could not be obtained. The missing genera are *Allionellopsis* Ochyra (known only from a few collections from 1909), *Hydropogonella* Cardot, *Meiotheciella* B.C.Tan. & al. *Piloecium* (Müll.Hal.) Broth., *Schraderella* Müll.Hal. (known only from the type collection), *Taxitheliella* Dixon (presumed extinct), *Timotimius* W.R.Buck (known only from the type collection), *Trismegistia* (Müll.Hal.) Müll.Hal., and *Trolliella* Herzog (endemic in Darjeeling, India). Material was taken from fresh collections from Brazil and/or Southeast Asia and from herbarium collections for species from other regions. Voucher information is provided in Appendix 1.

Two datasets were assembled. Dataset 1 comprised sequences from three loci for 27 species of Pylaisadelphaceae, a subset of Sematophyllaceae s.str. with 34 species, 12 representatives of other families of the Hypnales crown clade (sensu Huttunen & al., 2012), and 2 species of Plagiotheciaceae (Hypnales grade sensu Huttunen & al., 2012) as outgroup representatives. Dataset 2 included a broader taxon sample for the crown group within Sematophyllaceae s.str., and included 43 species of the Sematophyllaceae crown clade with 8 other

Table 2. Number of changes of selected morphological characters in the Sematophyllaceae s.str. clade as inferred from ancestral reconstruction.

Morphological characters	Changes
Collenchymatous exothecial cells	1
Asexual propagula	1
Pseudoparaphyllia	2
Sexuality	2
Opercula long-rostrate	2
Opercula rostrum oblique	2
Leaf-type of alar cells	4
Leaf-papilosity of cell	4

Table 3. Number of changes of selected morphological characters in the Sematophyllaceae crown clade as inferred from ancestral reconstruction based on the molecular tree.

Morphological characters	Changes
Sexuality	1
Asexual propagula	2
Leaf-papilosity of cell	2
Perichaetia papilosity	2
Leaf-type of alar cells	2
Exostome curvature	2
Exostome furrowed	2
Opercula rostrum oblique	2
Rostrum of opercula	2
Similarity of stem and branch leaves	2
Spores papilosity	3
Exostome trabecula	3
Leaf-alar cells wall	4
Leaf-color of alar cells	4
Perichaetia leaf cell shape	4
Leaf-margin type	4
Seta ornamentation	4
Segments papilosity	5
Leaf curvature	5
Perichaetia leaf shape	5
Perichaetia alar cells development	6
Perichaetia porose cells	6
Capsule inclination	7
Endostome presence	7
Rhizoid	7
Endostome perforation	8
Capsule symmetric	8
Leaf-cell shape	9
Seta curvature	9
Basal membrane	9
Capsule constriction below the mouth	10
Collenchymatous exothecial cells	10
Perichaetia curvature	10
Perichaetia curvature leaf margin	10
Annulus	11
Leaf-porose cells	12
Seta twisted	12
Homomallous leaves	17
Leaf-curvature margin	17
Leaf shape	>17

species of Sematophyllaceae clades as outgroup representatives. The 43 sequenced species of the Sematophyllaceae crown clade are representative in terms of genus diversity. The second dataset was treated separately because of the lower degree of molecular variation in the Sematophyllaceae crown clade, which results in short branches that make it more difficult to infer phylogenetic relationships. To deal with this problem, we extended the marker sampling but limited it to the Sematophyllaceae crown clade.

DNA extraction, amplification and sequencing. — Total genomic DNA was extracted using the mini-CTAB protocol (Doyle & Doyle, 1987). Eight markers were amplified and sequenced, the plastid *trnL* intron and *trnL-trnF* intergenic spacer (*trnL-F* region), the *rps4* and *rbcl* genes, the mitochondrial genome *nad5* intron and *nad4-5* intergenic spacer, and the nuclear ribosomal ITS1, ITS2 and partial 26S regions (amplified separately). Amplification and sequencing primers were those published by Magombo & al. (2003) for *rbcl*, Nadot & al. (1994) for *rps4*, Taberlet & al. (1991) for *trnL-F*, Bell & Newton (2005) for *nad5*, Groth-Malonek & al. (2007) for *nad4-5*, Sawicki & al. (2009) for ITS1 and ITS2, and Cox & al. (2004) for 26S. Single amplicons were produced for all markers except *nad5*, which was amplified as two overlapping fragments (*nad5K-nad5Li* and *nad5L-nad5Ki*, Bell & Newton, 2005). The PCR amplification mixture had a total volume of 50 µl and contained 5 µl of 10× thermophilic buffer, 5 µl of 50 mM MgCl₂, 0.5 µl *Taq* (Promega, Madison, Wisconsin, U.S.A.), 2 µl of BSA (10 mg/ml), 4 µl of 1 mM dNTP, 2.5 µl of each primer (10 µM), and 2.0 µl of DNA. For amplification of ITS1 and ITS2, 1 µl of dimethyl sulfoxide (DMSO) or betaine was added when amplifications initially failed. The PCR profile for ITS1, ITS2, 26S, *trnL*, *rbcl*, *rps4*, *nad5-4* and *nad5* was: 94°C (1 min), 52°C–59°C (1 min), 72°C (1 min) for 35 cycles, always preceded by an initial melting step of 2 min at 94°C and with a final extension of 72°C for 7 min. Primer annealing temperatures were 52°C for ITS2, 26S, *trnL*, and *rps4*, and 59°C, 54°C, 56°C, and 54°C for ITS1, *rbcl*, *nad4-5*, and *nad5*, respectively.

PCR products were purified and bidirectionally sequenced by Macrogen (Seoul, Korea) using the amplification primers. Sequences were assembled using Geneious v.6.1.6 (Biomatters, 2010). GenBank accession numbers of all newly generated sequences (466 in total) are listed in Appendix 1.

Phylogenetic analyses. — All sequences were initially aligned using Clustal X (Higgins & Sharp, 1988), and manually adjusted. The alignments of protein-coding regions were checked at the amino acid level as well, using PhyDE v.0.995 (Müller & al., 2006). Phylogenetic inferences were made with maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Maximum parsimony analyses were carried out using PAUP* v.4.0b10 for Macintosh (Swofford, 2002). Heuristic searches were repeated 100 times with random addition and tree bisection-reconnection (TBR) branch-swapping, saving a maximum of 10,000 trees. All characters were unordered and equally weighted. Gaps were either treated as missing data or coded as informative with the simple indel coding (SIC) strategy (Simmons & Ochoterena, 2000) as implemented in SeqState v.1.4.1 (Müller, 2005). Maximum likelihood analyses were performed using RAxML v.8 (Stamatakis, 2006; Stamatakis & al., 2008). Best-fit models of evolution were inferred based on the Akaike information criterion using jModelTest v.2.1.1 (Guindon & Gascuel, 2003; Darriba & al., 2012). The optimal and further models were tested for each individual marker and for the combined matrix. Clade support under MP and ML was estimated using the non-parametric bootstrap method (Felsenstein, 1985) based on the majority-rule consensus trees from 1000 pseudo-replicates, respectively, saving 1000 trees per pseudo-replicate. For the BI two parallel Markov Chain Monte Carlo (MCMC) simulations were run for 5 million generations in MrBayes v.3.2.6 (Ronquist & al., 2012), sampling one tree every 1000 generations. Convergence was established by ensuring that the mean standard deviation of split frequency was <0.01. Also, the software Tracer v.1.5 (Rambaut & Drummond, 2013) was used to determine when the tree sampling stabilized. The first 25% of the trees were

discarded as “burn-in”. A majority-rule consensus tree was constructed from the resulting trees to estimate the posterior probabilities (PP). Analyses were first conducted on individual loci. As conflicts in the topologies of the trees were present only at nodes with very low support (<75 for BS and <0.95 for PP), whatever analytical method was used (Electr. Suppl.: Figs. S1–S3), the topologies were considered congruent. The data were combined into a single matrix for dataset 1 (*rps4*, *trnL-F*, *nad5*) and another single matrix for dataset 2 (*rps4*, *trnL*, *rbcl*, *nad5*, *nad4-5*, ITS1, ITS2, 26S). Since analyses with different models did not affect the results, we used a single best-fit model (GTR+ Γ) for the combined matrix 1 and for the combined matrix 2. Differences in sampling between the two datasets are due to differences in successful sequencing of markers for each taxon. Taxonomic groups were recognized based on the presence of traditional morphological characters that would unite them as well as on good to moderate support (≥ 75 for BS and ≥ 0.95 for PP) in the phylogenetic trees.

Character mapping. — To identify possible synapomorphies for the clades in Pylaisiadelphaceae and Sematophyllaceae, we scored the species for all characters that have been traditionally used for the classification of Sematophyllaceae and Pylaisiadelphaceae (Tables 2, 3), for a total of 42 morphological characters (8 for Sematophyllaceae and Pylaisiadelphaceae, and 40 for Sematophyllaceae s.str.). Traits were scored based on herbarium specimens, including type collections (Appendices 2, 3), or on published descriptions. Character states were optimized using Mesquite v.3.03 (Maddison & Maddison, 2015), with “Markov k-state 1 parameter” for ancestral state reconstruction.

Alternative hypothesis test. — We applied the Shimodaira-Hasegawa (SH) test (Shimodaira & Hasegawa, 1999; Goldman & al., 2000) to statistically compare topologies reflecting contrasting phylogenetic hypotheses wherein specific taxa are resolved as either monophyletic or polyphyletic. Constrained trees were constructed using Mesquite v.3.03 (Maddison & Maddison, 2015), then loaded into PAUP* and a maximum likelihood search was done in order to find the optimal tree given the constraint. The new and original likelihood scores were then compared using the SH test implemented in PAUP* (Swofford, 2002) using 10,000 replicates under the resampling estimated likelihood (RELL). Alternative hypotheses testing focused on taxa retrieved as non-monophyletic in the optimal trees: the Pylaisiadelphaceae and the genera *Acroporium*, *Donnellia* Austin, *Schroeterella* Herzog and *Sematophyllum*.

RESULTS

Information on alignment lengths, numbers of variable and parsimony-informative characters, and tree statistics for both datasets is summarized in Table 4. Trees from individual markers and trees from analyses treating gaps as missing data or coding them by simple indel coding (SIC) (Simmons & Ochoterena, 2000) differed only in the degree of resolution. Critical nodes in conflicting topologies were never robustly supported. Consequently, only the phylogeny reconstructed from the combined matrices with indels coded by SIC are presented (Figs 1, 2) and discussed.

The branches in the optimal trees were mostly very short (Figs. 1, 2) within the Sematophyllaceae s.l. clade and in the Sematophyllaceae crown clade, in particular in contrast to those within the Pylaisiadelphaceae and those of the taxa composing the grade subtending the Sematophyllaceae crown clade. Furthermore, the support from variable sites scattered among the loci sampled was low overall across the backbone of the Sematophyllaceae s.l. (Fig. 1) and within the Sematophyllaceae s.str. (Fig. 2).

The Sematophyllaceae s.l. (including Pylaisiadelphaceae and Sematophyllaceae s.str.) was resolved as monophyletic, although supported only by Bayesian posterior probabilities (PP) (i.e., 1; Fig. 1). The monophyly of the Sematophyllaceae s.str. was, in contrast, always highly supported (maximum-parsimony bootstrap support [MP-BS] 93%/maximum-likelihood bootstrap support [ML-BS] 99%/PP 1; Fig. 1). The Pylaisiadelphaceae were consistently recovered as a paraphyletic group (Fig. 1), but the data did not allow rejecting the hypothesis that they arose from a single common ancestor, based on the SH test (Table 5). Several genera within the Sematophyllaceae s.str. were also resolved as polyphyletic. Testing whether the data do not allow rejection of the monophyly of *Acroporium*, *Donnellia*, *Schroeterella*, and *Sematophyllum* suggested that the polyphyletic nature of these genera is robust. In the case of *Donnellia*, the monophyly could not be rejected if only *D. commutata* (Müll.Hal.) W.R.Buck and *D. lageniformis* (Müll.Hal.) W.R.Buck were included; *D. matutina* W.R.Buck is unlikely to share a single ancestor with both species (Table 5).

The Pylaisiadelphaceae was resolved in eight clades (clades I–VIII), plus two branches with one species each (i.e., *Heterophyllum affine* (Hook.) M.Fleisch. and *Wijkia trichocolea* (Müll.Hal.) H.A.Crum) as successive, although unsupported, sister lineages of the grade composed of clades

Table 4. Alignment characteristics and maximum parsimony tree statistics of both datasets.

	Dataset 1 without gaps	Dataset 1 with gaps	Dataset 2 without gaps	Dataset 2 with gaps
Alignment length	1848	1928	6998	7324
Variable sites	530	620	1211	1525
Parsimony-informative sites	315	340	668	802
Length of most parsimonious trees	1206	1393	2249	2324
Consistency index (CI)	0.519	0.471	0.606	0.616
Retention index (RI)	0.769	0.717	0.754	0.744

Fig. 1. Bayesian consensus tree inferred from *rps4*, *trnL* and *nad5* sequences. Numbers above branches are: Bootstrap support values $\geq 75\%$ from maximum parsimony and maximum likelihood as well as Bayesian posterior probabilities ≥ 0.95 , respectively. “Max.” indicates BS = 100 and PP = 1. Asterisk (*) indicates types of genus names, plus sign (+) indicates types of the names of new genera here described, hyphen (-) indicates no support.

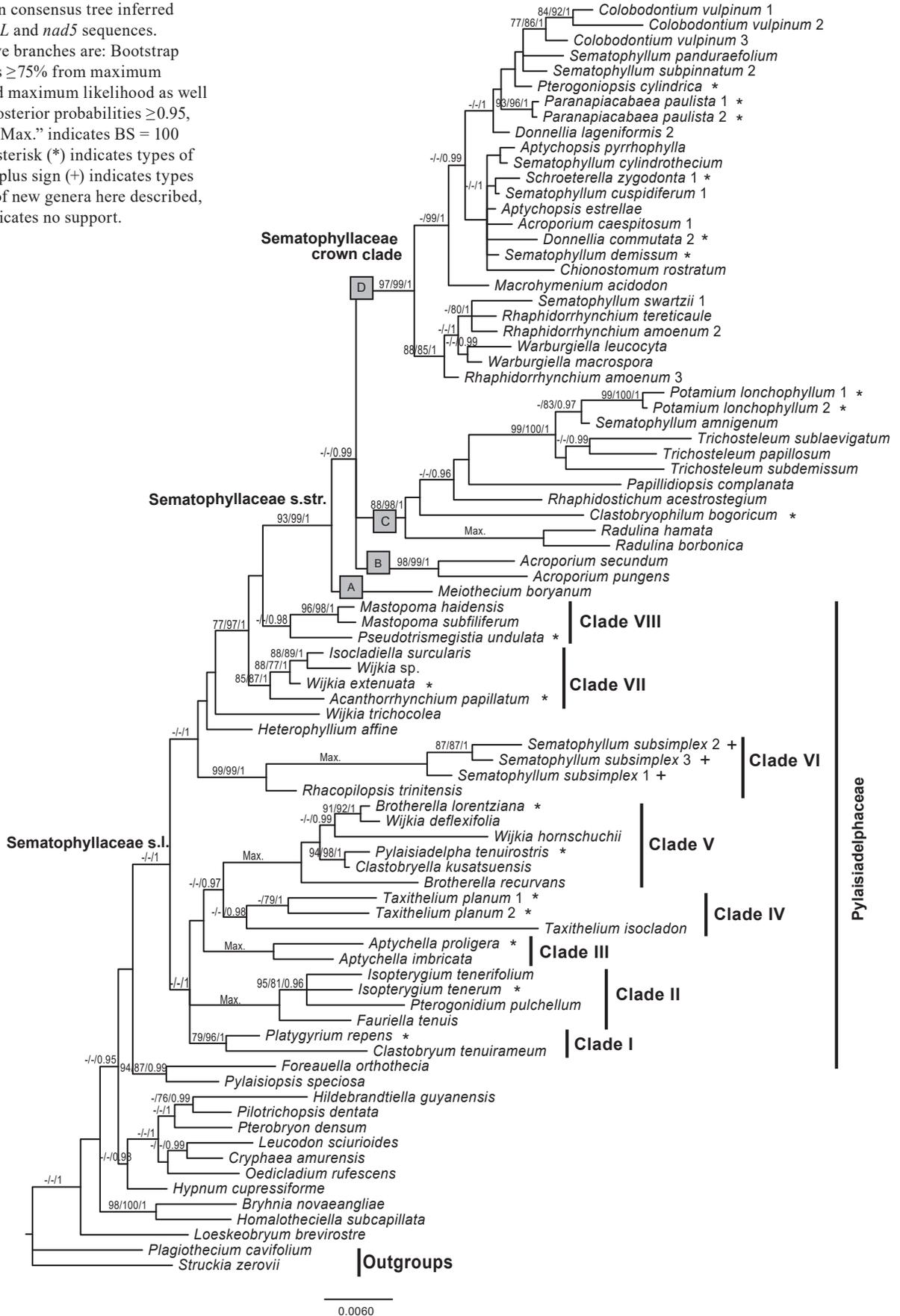


Fig. 2. Bayesian consensus tree inferred from *rps4*, *trnL*, *rbcL*, *nad4-5*, *nad5*, ITS1, ITS2 and 26S sequences. Numbers above branches are: Bootstrap support values $\geq 75\%$ from maximum parsimony and maximum likelihood as well as Bayesian posterior probabilities ≥ 0.95 , respectively. “Max.” indicates BS = 100 and PP = 1. Asterisk (*) indicates types of genus names, plus sign (+) indicates types of the names of new genera here described, hyphen (-) indicates no support.

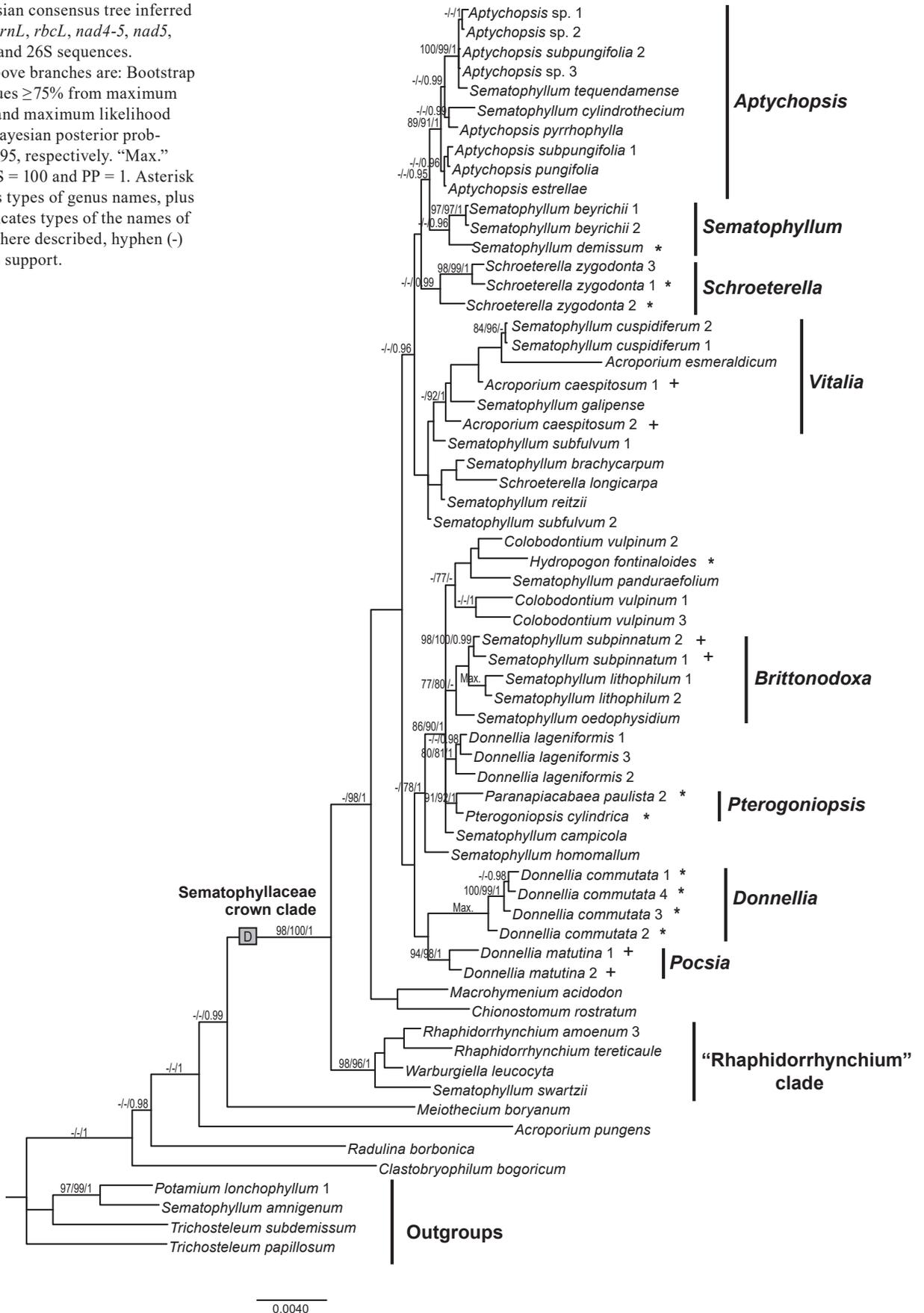


Table 5. Results from the Shimodaira-Hasegawa (SH) tests.

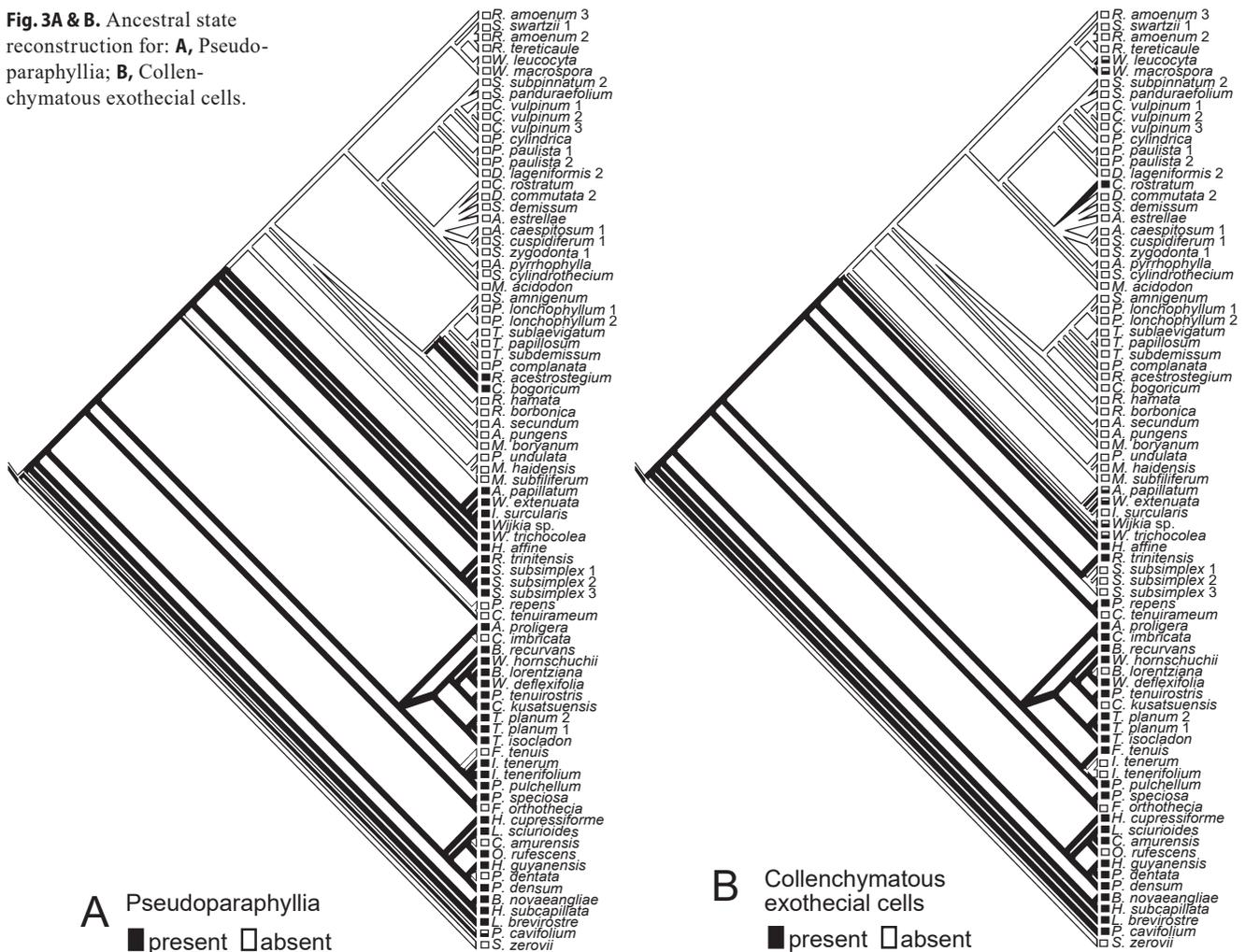
Constrained topology	Tree used	Diff-lnL	P
Monophyletic Pylaisiadelphaceae	Combined	57.52731	0.0540
Monophyletic <i>Acroporium</i>	Combined	399.94655	0.0000*
Monophyletic <i>Schroeterella</i>	Combined	96.68248	0.0117*
Monophyletic <i>Sematophyllum</i>	Combined	1403.25655	0.0000*
Monophyletic <i>Donnellia</i>	Combined	478.88263	0.0000*
<i>Donnellia commutata</i> + <i>D. lageniformis</i>	Combined	48.10096	0.0831

Statistically worse trees at $P < 0.05$ are marked with an asterisk (*).

VII and VIII. Clades I to V shared a single common ancestor although bootstrap support was lacking, whereas clades VI to VIII comprised a grade leading to the Sematophyllaceae s.str., with clade VIII sister to this family, albeit without support. Although a shared ancestry for clades VII and VIII and the Sematophyllaceae s.str. was rather robustly supported (Fig. 1), the alternative origin of the clades VII and VIII from an ancestor unique to the Pylaisiadelphaceae could not be rejected (Table 5).

Clade I included *Clastobryum* Dozy & Molk. and *Platygyrium* (79/96/1), clade II *Fauriella*, *Pterogonidium* Müll. Hal. and *Isopterygium* with maximum support, clade III *Aptychella* with maximum support, clade IV *Taxithelium* (PP 0.98), clade V *Pylaisiadelpha*, *Brotherella*, *Clastobryella* M.Fleisch., and *Wijkia* H.A.Crum p.p. with maximum support, clade VI *Sematophyllum subsimplex* (Hedw.) Mitt. and *Rhacopilopsis* (99/99/1), clade VII *Acanthorrhynchium* M.Fleisch., *Isoclatiella* Dixon and *Wijkia* p.p. (85/87/1),

Fig. 3A & B. Ancestral state reconstruction for: **A**, Pseudoparaphyllia; **B**, Collenchymatous exothecial cells.



and clade VIII *Mastopoma* Cardot and *Pseudotrismegistia* H.Akiyama & H.Tsubota (PP 0.98).

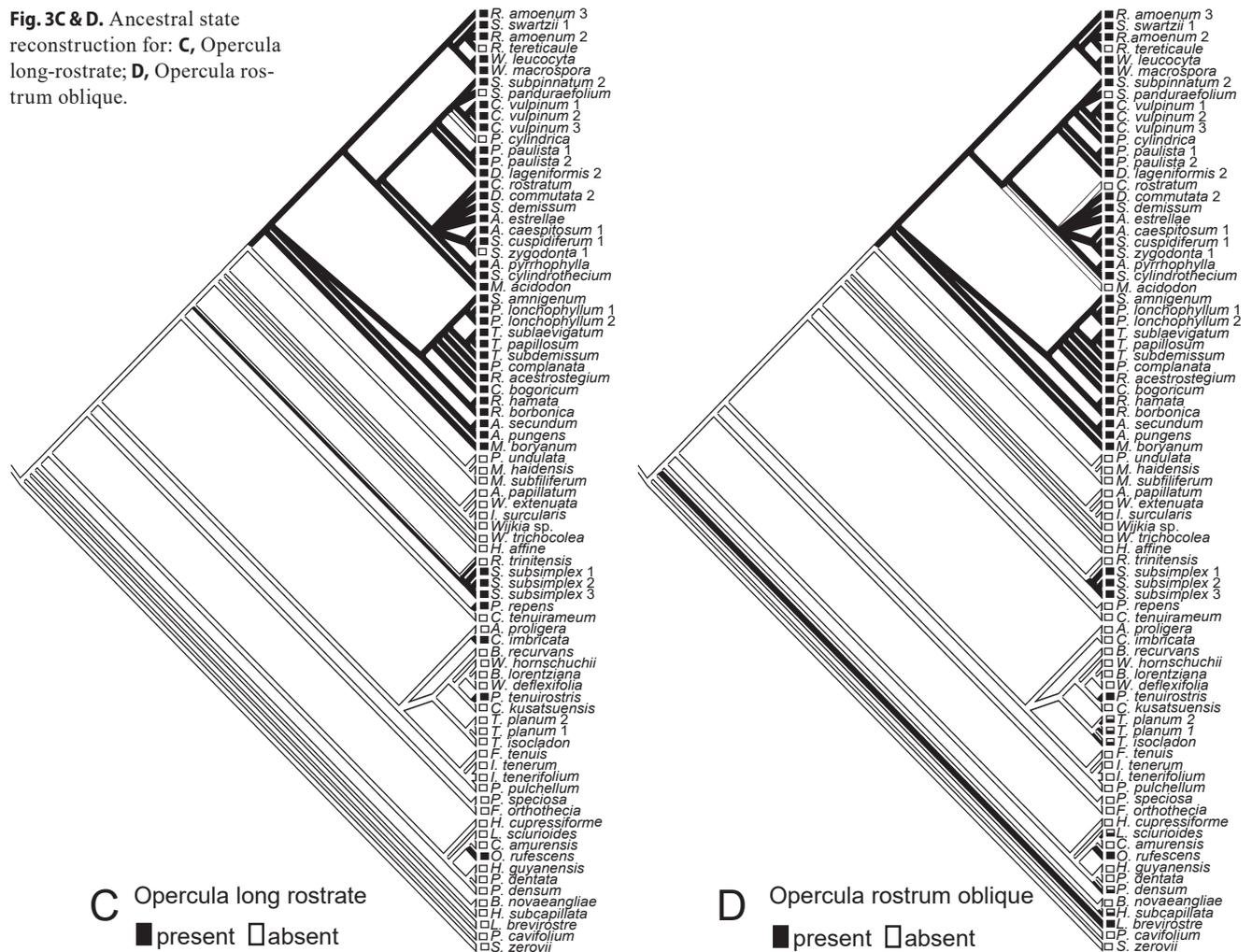
Within the Sematophyllaceae s.str., *Meiothecium boryanum* (Müll.Hal.) Mitt. was sister (PP 0.99) to all other species, which were resolved in three major clades. Clade B comprised *Acroporium pungens* (Hedw.) Broth. and *A. secundum* (Reinw. & Hornsch.) M.Fleisch. (98/99/1), clade C *Clastobryophilum* M.Fleisch., *Papillidiopsis* (Broth.) W.R.Buck & B.C.Tan, *Radulina* W.R.Buck & B.C.Tan, *Rhaphidostichum* M.Fleisch., and *Trichosteleum* as well as *Potamium* and *Sematophyllum amnigenum* (Broth.) Broth. (both nested in *Trichosteleum*) (88/98/1), and clade D (Sematophyllaceae crown clade) *Acroporium caespitosum* (Hedw.) W.R.Buck, *Aptychopsis* (Broth.) M.Fleisch., *Chionostomum* Müll.Hal., *Colobodontium* Herzog, *Donnellia*, *Macrohymenium* Müll.Hal., *Paranapiacabaea* W.R.Buck & D.M.Vital, *Pterogoniopsis* Müll.Hal., *Rhaphidorrhynchium*, *Schroeterella*, *Sematophyllum*, and *Warburgiella* Müll.Hal. (97/99/1).

Phylogenetic inferences from additional loci and focusing on the Sematophyllaceae crown clade (clade D; dataset 2), resolved nine clades with moderate or good support, which correspond to genera recognized in the present study (see

Discussion) (Fig. 2): 1, Rhaphidorrhynchium clade (98/96/1), including *Sematophyllum swartzii* (Schwägr.) W.H.Welch & H.A.Crum and *Warburgiella*, as sister to a clade containing all other representatives of clade D (–/98/1); 2, *Pocsia* (formerly *Donnellia matutina*, 94/98/1); 3, *Donnellia* s.str. (for *D. commutata*) with maximum support; 4, *Pterogoniopsis* (including *Paranapiacabaea*, 91/92/1); 5, *Brittonodoxa* (formerly *Sematophyllum* p.p., 77/80/–); 6, *Vitalia* (former *Acroporium* p.p. and *Sematophyllum* p.p., –/92/1); 7, *Schroeterella* s.str. (–/0.99); 8, *Sematophyllum* s.str. (PP 0.96); and 9, *Aptychopsis* including *Sematophyllum* p.p. (89/91/1). A clade comprising *Colobodontium*, *Hydropogon* Brid., and *Sematophyllum panduraefolium* (Broth.) Broth. was resolved, but was supported only in the ML analysis (ML-BS 77%). The relationships of these clades and clades containing *Donnellia lageniformis*, *Schroeterella longicarpa* P.E.A.S.Câmara & Carv.-Silva, other species of *Sematophyllum*, as well as the *Chionostomum*/*Macrohymenium* clade, are unresolved.

The morphological characters scored always revealed some degree of homoplasy within the Sematophyllaceae or Pylaisiadelphaceae (Figs. 3, 4; Electr. Suppl.: Figs. S4–S45). However, some characters are still useful to define Sematophyllaceae

Fig. 3C & D. Ancestral state reconstruction for: **C**, Opercula long-rostrate; **D**, Opercula rostrum oblique.



s.str. or clades within the family, viz. the absence of pseudoparaphyllia (Fig. 3A), the presence of collenchymatous exothecial cells (Fig. 3B), and the long-rostrate, oblique opercula (Fig. 3C, D). On the other hand, the enlarged and colored alar cells, frequently used to differentiate Sematophyllaceae from other families is a highly homoplastic character (Table 2; Electr. Suppl.: Fig. S23). The high level of homoplasy in many morphological characters, as well as the lack of morphological knowledge of the group suggest that much is still needed to understand the evolution of this group (Tables 2, 3).

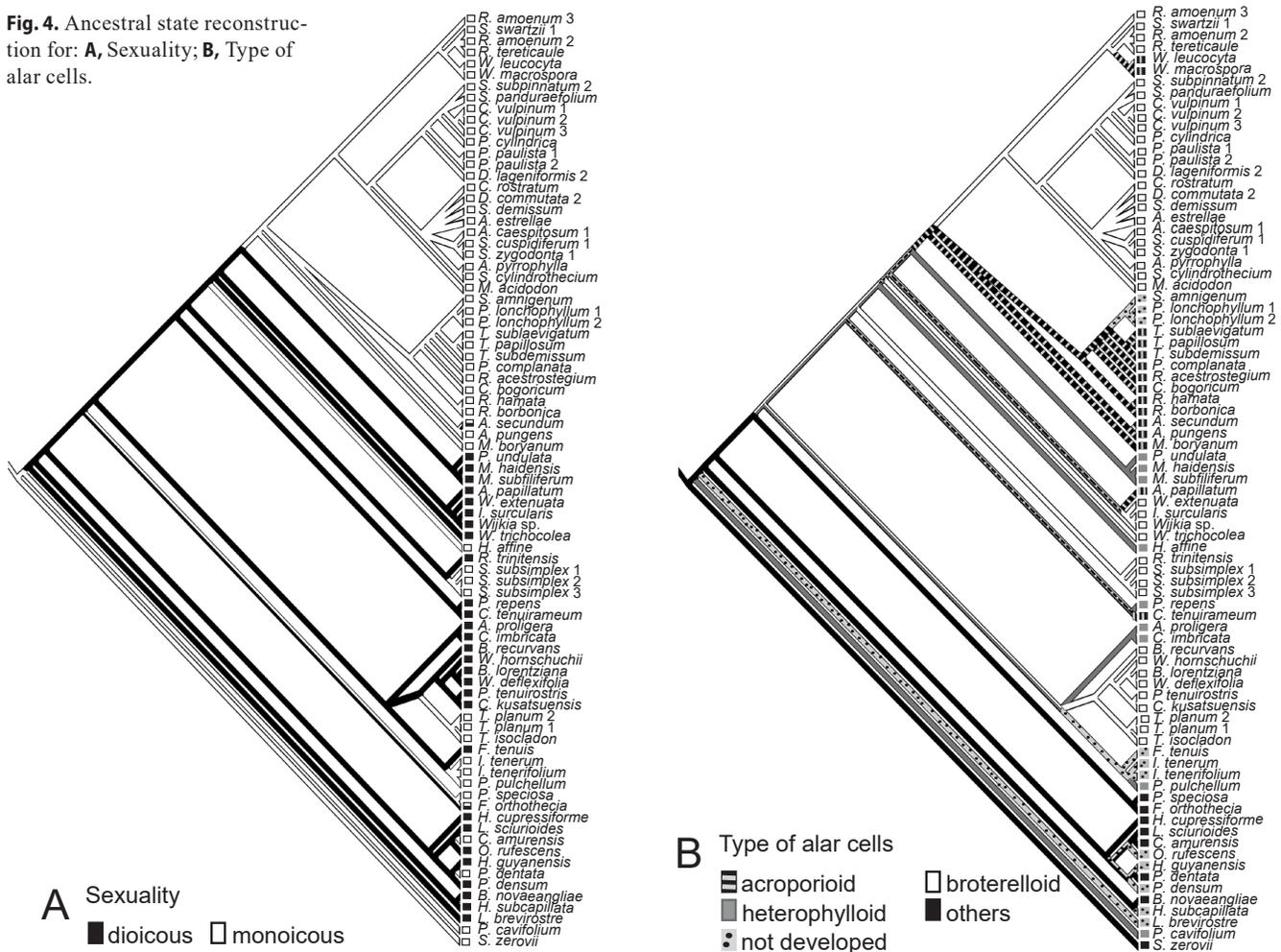
DISCUSSION

Circumscription of the Sematophyllaceae and Pylaisiadelphaceae. — The present results confirm the circumscription of the Sematophyllaceae s.str. sensu Frey & Stech (2009) and Goffinet & al. (2009) and the exclusion of *Acanthorrhynchium* (Akiyama & al., 2011). The clear molecular delimitation of Sematophyllaceae s.str. is in accordance with a suite of morphological characters (presence of pseudoparaphyllia, long-rostrate and oblique opercula, collenchymatous exothecial

cells (Fig. 3), and frequently autoicous sexual condition (except *Acroporium*) that characterize the family. However, these characters do not represent strict synapomorphies, since the respective states observed in Sematophyllaceae s.str. are either missing in a few taxa of the family, or are also present in some taxa of Pylaisiadelphaceae taxa as well, respectively (Fig. 3). Pseudoparaphyllia were thought to be filamentose in the Pylaisiadelphaceae but foliose in the Sematophyllaceae (Buck, 1998; Akiyama & al., 2011; Câmara & al., 2015). However, *Taxithelium* (Pylaisiadelphaceae) has both kinds of pseudoparaphyllia (Câmara, 2011b), and all reports of foliose pseudoparaphyllia in Sematophyllaceae s.str. (e.g., *Acroporium* in Câmara & al., 2015) were based on misinterpretation of leaf primordia. Consequently, pseudoparaphyllia are missing in Sematophyllaceae, except in *Clastobryophilum bogoricum* (Bosch & Sande Lac.) M.Fleisch. and *Rhaphidostichum acrostegium* (Sull.) W.R.Buck.

Pylaisiadelphaceae was resolved as paraphyletic in the present phylogenetic analyses, as inferred in previous studies (Tsubota, 2001a, b; Cox & al., 2010; Akiyama & al., 2011; Carvalho-Silva & al., 2014). However, the results of the SH tests show that the monophyly of Pylaisiadelphaceae

Fig. 4. Ancestral state reconstruction for: A, Sexuality; B, Type of alar cells.



based on the present data cannot be rejected. Although the Pylaisiadelphaceae lacks putative synapomorphies and is instead defined by the lack of “true Sematophyllaceous” features (cf. the original description by Goffinet & Buck, 2004), no morphological character is known that would support the extended family concept of the Sematophyllaceae s.l., comprising both the Pylaisiadelphaceae and Sematophyllaceae s.str. Consequently, we suggest to continue recognizing both families, Sematophyllaceae s.str. and Pylaisiadelphaceae.

In addition to the original circumscription of Pylaisiadelphaceae (Goffinet & Buck, 2004), one species of *Sematophyllum*, *S. subsimplex*, is nested in the Pylaisiadelphaceae clade VI together with *Rhacopilopsis trinitensis* (Müll.Hal.) E.Britton & Dixon (Fig. 1). *Sematophyllum subsimplex* was previously suggested to be distantly related to the remaining *Sematophyllum* species based on its color, alar cell development, and roughened calyptra (Buck, 1998). Based on the morphological and molecular differences, we accommodate *S. subsimplex* in a separate genus, *Microcalpe* Mitt., in Pylaisiadelphaceae (see taxonomy section). The species is widespread in the lowland American and African tropics. Several genera of the Pylaisiadelphaceae, such as *Brotherella*, *Gammiella* Broth., *Mastopoma*, and *Wijkia*, were not recovered as monophyletic (Akiyama & al., 2011; this study), but systematic changes will require further study, including obtaining DNA data for additional types.

Inferring suprageneric relationships in the Hypnales has been hampered by the low molecular diversity and short branch lengths resulting from a rapid diversification early in their history (e.g., Shaw & al., 2003; Newton & al., 2007; Huttunen & al., 2012). Huttunen & al. (2012) suggested that Sematophyllaceae was an exception within the Hypnales crown clade, with branch lengths clearly longer than in other families. The present data, however, show a more differentiated pattern, with comparably long branches in Pylaisiadelphaceae and the clades branching off first within Sematophyllaceae, but considerably shorter branches within the Sematophyllaceae crown clade (Fig. 1). Similar results were reported for other pantropical groups that have clades with long branches branching off first, and derived clades with short branches, e.g., Polygrammoid ferns (Schneider & al., 2004) or Annonaceae (Richardson & al., 2004).

In this contribution we have made our best attempts to recognize groups that are both monophyletic, and that have morphological characters that would distinguish them. We have recognized both new and old genera and avoided making assumptions about groups that either had poor or no support or were not supported by morphology. With this in mind, our data have confirmed the results of Cox & al. (2010), that the Pylaisiadelphaceae is not monophyletic.

One could argue in favor of the recognition of paraphyletic taxa, as an unavoidable consequence of evolution (Brummitt 2003); this matter has been much discussed in the past (see Brummitt, 1996, 2002, 2003; Brummitt & Sosef, 1998; Nelson & al., 2003), but it seemed to us that a monophyletic solution would be more desirable.

However, merging the two families (Sematophyllaceae s.str., Pylaisiadelphaceae) into one larger family Sematophyllaceae

would leave hardly any morphological trait or even a combination of traits that could morphologically support the existence of such a family, and consequently may as well be undesirable.

At this point, it seems more appropriate to recognize the two separate families Sematophyllaceae and Pylaisiadelphaceae, as the performed SH test could not reject the monophyly of the family Pylaisiadelphaceae (Table 5).

Over time, our understanding of morphology has progressed further with regard to the Sematophyllaceae rather than the Pylaisiadelphaceae, and additional investigation of the subject is much needed. It is still difficult to recognize good morphological synapomorphies (if they even exist) for Pylaisiadelphaceae, either because of the lack of investigation, or because their absence is an evolutionary fact.

Considerations on the Sematophyllaceae s.str. — Most genera of the Sematophyllaceae (e.g., *Acroporium*, *Donnellia*, *Schroeterella*, *Sematophyllum*) are not resolved as monophyletic (Fig. 2), but the relationships of the various species are weakly supported and in fact the data do not allow the hypothesis of the monophyly of these genera to be rejected (Table 5). These results reflect the long-known difficulties in defining generic boundaries in the family, since morphological features often overlap. The short branches with consequently low bootstrap support especially in the “Sematophyllaceae crown clade” (clade D in Figs. 1, 2) may suggest a rapid diversification, which may also be responsible for the few morphological differences among some clades and the resulting taxonomic confusion. The ancestral reconstruction of morphological characters has shown all the characters to be homoplastic (Table 3; Electr. Suppl.: Figs. S6–S43), except the sexuality of the plants (Fig. 4A). However, clades A to C, branching off first within Sematophyllaceae s.str., are characterized by alar cells of the acroporioid type, whereas the Sematophyllaceae crown clade displays alar cells of the brotherelloid type (Fig. 4B) (cf. Tan & Jia, 1999).

The type of *Acroporium* (*A. brevicuspdatum* Mitt.) has not been sequenced, but is morphologically very similar (e.g., furrowed exostome, alar cell arrangement) to *A. pungens* and *A. secundum* of clade B (Fig. 1), which we therefore consider to represent “true” *Acroporium*. The species in this clade are characterized by ovate to lanceolate and concave or tubulose leaves, a single row of inflated alar cells, supra-alar cells absent (acroporioid type alar cells; Tan & Jia, 1999), and a furrowed exostome (Câmara & al., 2015). The Asian representatives of *Acroporium* were shown to be monophyletic by Hedenäs & al. (2008).

Within clade C, *Trichosteleum* can be recognized by the presence of unipapillose laminal cells and brotherelloid alar cells (Tan & Jia, 1999). Although members of *Trichosteleum* have brotherelloid alar cells, the species used in this study all have acroporioid alar cells, as are present in all clade C species. *Sematophyllum amnigenum* and the monospecific *Potamium* form a sister clade to *Trichosteleum* (Fig. 1). Both species differ from *Trichosteleum* by their mostly smooth leaves, vestigial papillae, and lack of alar cells, and in addition *Potamium* has immersed capsules. These differences can be interpreted as adaptations to the aquatic habitat of both species. Species

within this clade also often have reduced perichaetia, small capsules and small spores. Since the type of *Sematophyllum* is placed in the Sematophyllaceae crown clade, and because *Trichosteleum* is an older name, this clade should be recognized as *Trichosteleum*. The necessary combinations for the species included in our molecular phylogeny are presented below.

Within the Sematophyllaceae crown clade (clade D), the *Rhaphidorrhynchium-Warburgiella* clade is characterized by small plants with circinate leaves, smooth, linear laminar cells, and an alar region of the acroporioid type, with colored and inflated alar cells. *Warburgiella* has been considered a paleotropical genus, but has proved to be quite common in the Neotropics as well, depending on its circumscription (Ramsay & al., 2004). *Rhaphidorrhynchium* is retained as a distinct genus because of its cucullate calyptra and smooth capsule neck, in contrast to the mitrate calyptra and warty capsule neck in *Warburgiella* s.l. Tan & al. (1998), may have over-expanded the boundaries of *Warburgiella* and some species recently placed in the genus (e.g., *W. leucocyta* (Müll.Hal.) B.C.Tan & al., which we sampled here) should possibly be returned to *Rhaphidorrhynchium* (Brotherus, 1925).

Donnellia is resolved as polyphyletic, with three clades (*D. commutata*, *D. lageniformis*, *D. matutina*). The SH tests rejected a monophyletic group with all three species together, but could not reject a monophyletic genus *Donnellia* with *D. commutata* and *D. lageniformis* only. Considering that we also could find no morphological differences to clearly separate the two species at genus level either, we are considering both as members of the same genus. *Donnellia* can be recognized by containing small plants with often homomalous, smooth leaves with the alar region poorly developed, a vase-shaped capsule with the exostome bone-white and a rudimentary, caducous endostome (often reported as absent). A detailed investigation of *Donnellia* will be published elsewhere (Carvalho-Silva, in prep.).

The third species, *D. matutina*, was described later; however it is quite different morphologically from other members of *Donnellia*. According to Buck (1993), *D. matutina* has a distinct, well-developed endostome with a high basal membrane and paired cilia, and the leaves with alar cells enlarged, inflated and colored, inclined at 45°, in a single row with about two rows of quadrate supra-alar cells. It also differs from the other members of *Donnellia* in having the exostome teeth on the front surface strongly trabeculate, with the central line impressed and leaves with alar cells poorly differentiated; and from *Chionostomum* in having leaves with cells that are shorter and porose. Based on the morphological and molecular differences, we accommodate *D. matutina* in a new genus, *Pocsia*.

The genera *Paranapiacabaea* and *Pterogoniopsis* were resolved as sister taxa and their gametophytes are similar in characters of leaf shape, size, and laminal cells. They are distinguished on the basis of sporophyte traits, such as the papillose exostome teeth in *Paranapiacabaea*, but they also share sporophyte features, such as the absence of trabeculae in the exostome. Consequently, we include *Paranapiacabaea paulista* W.R.Buck & Vital in *Pterogoniopsis*.

The *Brittonodoxa* clade comprises species previously placed in *Sematophyllum* or its synonym *Rhaphidostegium*, but which are molecularly separated from the generic type *S. demissum* (Wilson) Mitt. The clade has low to moderate bootstrap support and no Bayesian support; even so, it is quite distinct morphologically and is here recognized as a new genus, *Brittonodoxa*, accommodating species with homomalous, ovate and concave leaves with rhomboid, smooth apical cells, with an alar region of the brotherelloid type, having enlarged (but not inflated) and colored cells. The sporophytes are often erect, a frequent adaptation to the epiphytic habitat in mosses (Buck, 1980).

The *Vitalia* clade contains no type specimens of *Acroporium* or of *Sematophyllum*. As a consequence this clade has not previously been recognized at any taxonomic level and thus bears no name. Plants within this subclade are robust with galeate leaves and brotherelloid cells. Here we propose this clade to be recognized as a new genus, *Vitalia*, and provide new combinations.

Schroeterella zygodonta is monophyletic and consequently the respective clade is recognized. The other species of *Schroeterella*, *S. longicarpa*, has uncertain relationships and the SH test rejected the monophyly of the genus, therefore will be retained in this genus until further data are available. A full description of the genus was provided by Câmara & Carvalho-Silva (2013).

Finally, the *Aptychopsis* clade includes two species of *Sematophyllum*. Consequently, two new combinations for these species in *Aptychopsis* are proposed here. Plants in this clade can be recognized by their oblong to lanceolate leaves with the acroporioid (or less-often brotherelloid) type of alar cells, usually inflated, exceptionally thick-walled (often porose) and colored, and the presence of capsules with the endostome usually reduced (see also Câmara & Carvalho-Silva, 2013).

Due to the lack of resolution of some of the deep nodes, little can be inferred with respect to the geographic origin of Sematophyllaceae. The Pylaisiadelphaceae is a mostly Southeast Asian group, and only seven of the genera occur in the New World (*Aptychella*, *Isopterygium*, *Pterogonidium*, *Pylaisiadelpha*, *Sematophyllum subsimplex*, *Taxithelium*, *Wijkia*). Most of those genera have few species in the New World, e.g., *Aptychella*, and *Pylaisiadelpha* with one each, *Wijkia* with two, and *Taxithelium* with four; *Isopterygium* is particularly diverse in both regions and has eight species in the Americas. Those numbers are estimates, since most of these genera require taxonomic revision. *Sematophyllum subsimplex* occurs commonly in the New World, where it is abundant, but has also been reported from tropical Africa. On the other hand, taxa such as *Acanthorrhynchium*, *Brotherella*, *Clastobryum*, *Clastotobryella*, *Foreauella* Dixon & P.de la Varde, *Heterophyllum* Schimp. & Kindb., *Isocradiella*, *Mastopoma*, *Pseudotrismegistia*, and *Trismegistia* are restricted to Asia.

For Sematophyllaceae the situation is somewhat different, as only *Chionostomum*, *Clastobryophyllum*, *Macrohymenium*, *Papillidiopsis*, and *Radulina* are absent from the New World,

but entire genera (*Aptychopsis*, *Colobodontium*, *Donnellia*, *Paranapiacabaea*, *Pterogoniopsis*, *Schroeterella*) are endemic to the Americas. Most species of the Sematophyllaceae crown clade, including all species of the clades *Aptychopsis*, *Donnellia*, *Pterogoniopsis*, *Schroeterella*, and *Vitalia* are restricted to the New World, except for the clades *Brittonodoxa* and “Rhaphydorrhynchium” which have representatives in the Americas, Africa and Asia.

The non-endemic genus *Acroporium* seems to be an exception as only 2 species occur in the Americas, with likely more than 20 in Asia (Tan, 1994; Câmara & al., 2015). The genus *Sematophyllum*, the type of Sematophyllaceae, contains many species, most of them New World endemics.

Many of these genera are in need of taxonomic revision, but it appears that Sematophyllaceae has relatively high levels of endemism (with many New World endemics) compared with Pylaisiadelphaceae. Increased sampling and better resolution of some nodes will likely shed more light on the geographic patterns of both groups.

■ TAXONOMIC TREATMENT

Aptychopsis cylindrothecia (Broth.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** ≡ *Rhaphidostegium cylindrothecium* Broth. in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl. 83: 341. 1924 ≡ *Sematophyllum cylindrothecium* (Broth.) W.R.Buck & Schäf.-Verw. in J. Hattori Bot. Lab. 69: 162. 1991 – Holotype: Brazil, São Paulo, prope São Bernardo, *V.F. Schiffner 1846* (H-BR!; isotypes: NY barcode 01179095!, W!).

Aptychopsis estrellae (Müll.Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck in J. Bryol. 37: 289. 2015 ≡ *Hypnum estrellae* Müll.Hal., Syn. Musc. Frond. 2: 275. 1851 ≡ *Rhyncho-hypnum estrellae* (Müll.Hal.) Hampe in Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn, ser. 3, 2: 293. 1870 ≡ *Ectropothecium estrellae* (Müll.Hal.) Wijk & Margad. in Taxon 11: 221. 1962 ≡ *Acroporium estrellae* (Müll.Hal.) W.R.Buck & Schäf.-Verw. in Bol. Mus. Paraense Emilio Goeldi, N.S., Bot. 7: 646. 1993 (“1991”) – Holotype: Brazil, Serra d’Estrella, *H.C. Beyrich s.n.* (B, probably lost; isotype: BM!).

Aptychopsis tequendamensis (Hampe) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** ≡ *Hypnum tequendamense* Hampe in Linnaea 31: 529. 1862 ≡ *Sematophyllum tequendamense* (Hampe) Mitt. in J. Linn. Soc., Bot. 12: 491. 1869 ≡ *Rhaphidostegium tequendamense* (Hampe) A.Jaeger in Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 485 (Gen. Sp. Musc. 2: 749). 1878 – Holotype: Nova Grenada (Colombia), Tequendama, *A. Lindig 2153* (BM!; isotypes: FLAS barcode FLAS B48443, GOET barcodes GOET013664 & GOET013665, NY barcodes 01288687! & 01288688!, PC barcode PC0100762).

Distribution. – *Aptychopsis* is a New World endemic, common in montane and gallery forests.

Brittonodoxa W.R.Buck, P.E.A.S.Câmara & Carv.-Silva, **gen. nov.** – Type: *Brittonodoxa subpinnata* (Brid.) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva (≡ *Leskea subpinnata* Brid.).

Plants medium-sized, golden green, epiphytic. *Stems* creeping, freely branched, branches often ascending, central strand absent. *Pseudoparaphyllia* absent. *Leaves* of stem and branch similar, homomallous, ovate to oblong-ovate, 0.75–1.5 mm long, acute or short-acuminate, concave, margins entire; costa absent; cells long-rhomboidal, smooth, porose, firm- to thick-walled, shorter and mostly rhomboid in the acumen; alar cells enlarged, not or little inflated, colored. *Asexual propagula* not seen. *Autoicous*. *Perichaetial leaves* erect, oblong-ovate, 1–1.5 mm long, acuminate, plane, margins entire; costa absent; cells long-rhomboid, smooth; alar cells not differentiated. *Setae* elongate, smooth, 0.5–1 cm long; capsules erect to suberect, strongly constricted below mouth when dry; exothecial cells collenchymatous; annulus not differentiated; operculum long-rostrate; exostome with zig-zag center line, cross-striolate below, coarsely papillose above, trabeculate at back; endostome with high basal membrane, segments keeled, cilia absent. *Spores* spherical, finely papillose. *Calyptra* cucullate, naked, smooth.

Etymology. – The generic name honors Elizabeth Gertrude Knight Britton, one of the first female bryologists.

Distribution. – Members of *Brittonodoxa* occur in Mexico, Central and South America, and the West Indies, with some species in Africa.

Brittonodoxa allinckxiorum (W.R.Buck) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva, **comb. nov.** ≡ *Sematophyllum allinckxiorum* W.R.Buck in Mem. New York Bot. Gard. 76(3): 146, fig. 131a–g. 2003 – Holotype: French Guiana, Commune de Saül: Crique Saint-Éloi at Route de Bélizon, *W.R. Buck 33106* (NY barcode 799479!).

Brittonodoxa cataractae (W.R.Buck) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva, **comb. nov.** ≡ *Sematophyllum cataractae* W.R.Buck in Brittonia 35: 328. 1983 – Holotype: Brazil, Santa Catarina: Serra Geral, *E. Ule s.n.* (NY barcode 01178850!; isotypes: NY barcode 01178849!, R!, W!).

Brittonodoxa lithophila (Hornsch.) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva, **comb. nov.** ≡ *Hypnum lithophilum* Hornsch. in Martius, Fl. Bras. 1(2): 84. 1840 ≡ *Sematophyllum lithophilum* (Hornsch.) Ångström in Öfvers. Kongl. Vetensk.-Akad. Förh. 33(4): 42. 1876 ≡ *Sematophyllum loxense* var. *lithophilum* (Hornsch.) Lindb., Moss. Dillen. Hist. Musc.: 20. 1883, nom. illeg. ≡ *Rhaphidostegium lithophilum* (Hornsch.) Broth. in Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21, Afd. 3(3): 50. 1895 ≡ *Rhaphidostegium loxense* var. *lithophilum* (Hornsch.) Paris, Index Bryol.: 1099. 1898, nom. illeg. – Lectotype (designated by Buck in Nova Hedwigia 66: 243. 1998): Brazil, Serra dos Orgãos, *H.C. Beyrich s.n.* (BM!).

Brittonodoxa squarrosa (W.R.Buck) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva, **comb. nov.** ≡ *Sematophyllum*

squarrosus W.R.Buck in Mem. New York Bot. Gard. 76(3): 146, fig. 131h–m. 2003 – Holotype: French Guiana. Commune de Saül: ca. 1 km N of Eaux Claires on Route de Bélizon, *W.R. Buck 33051* (NY barcode 799480!).

Brittonodoxa steyermarkii (E.B.Bartram) W.R.Buck, P.E.A.S. Câmara & Carv.-Silva, **comb. nov.** ≡ *Sematophyllum steyermarkii* E.B.Bartram in Bryologist 49: 123. 1946 – Holotype: Guatemala. Dept. Izabal: along Río Frio, *J. Steyermark 39923* (FH!; isotypes: MICH barcode 526236, US barcode 2139305).

Brittonodoxa subpinnata (Brid.) W.R.Buck, P.E.A.S. Câmara & Carv.-Silva, **comb. nov.** ≡ *Leskea subpinnata* Brid., Muscol. Recent. Suppl. 2: 54. 1812 ≡ *Hypnum subpinnatum* (Brid.) Arn. in Mém. Soc. Linn. Paris 5: 302. 1827 ≡ *Rhaphidostegium subpinnatum* (Brid.) E.Britton in Bryologist 21: 28. 1918 ≡ *Sematophyllum subpinnatum* (Brid.) E.Britton in Bryologist 21: 28. 1918 – Holotype: In Hispaniola ad arbores habitant, *P.A. Poiteau s.n.* (B, probably lost; isotype: NY barcode 01178888!).

Microcalpe (Mitt.) W.R.Buck, **stat. nov.** ≡ *Sematophyllum* sect. *Microcalpe* Mitt. in J. Linn. Soc., Bot. 12: 477, 494. 1869 – Type: *Microcalpe subsimplex* (Hedw.) W.R.Buck. (≡ *Hypnum subsimplex* Hedw.).

Distribution. – Members of *Microcalpe* occur from Mexico and the Caribbean to northern South America and central Brazil, and in tropical Africa.

Microcalpe subsimplex (Hedw.) W.R.Buck, **comb. nov.** ≡ *Hypnum subsimplex* Hedw., Sp. Musc. Frond.: 270, fig. 11–14. 1801 ≡ *Isothecium subsimplex* (Hedw.) Brid., Bryol. Univ. 2: 357. 1827 ≡ *Stereodon subsimplex* (Hedw.) Mitt. in J. Proc. Linn. Soc., Bot., Suppl. 2: 114. 1859 ≡ *Microcalpe subsimplex* (Hedw.) Spruce, Cat. Musc.: 13. 1867 ≡ *Sematophyllum subsimplex* (Hedw.) Mitt. in J. Linn. Soc., Bot. 12: 494. 1869 ≡ *Plagiothecium subsimplex* (Hedw.) Besch. in Mém. Soc. Sci. Nat. Cherbourg 16: 251. 1872 ≡ *Rhaphidostegium subsimplex* (Hedw.) Besch. in Ann. Sci. Nat., Bot., sér. 6, 3: 254. 1878 ≡ *Rhaphidorrhynchium subsimplex* (Hedw.) Broth. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 11: 426. 1925 – Holotype: West Indies, *O. Swartz s.n.* (G!).

Pocsia Carv.-Silva, P.E.A.S. Câmara & W.R.Buck, **gen. nov.** – Type: *Pocsia matutina* (W.R.Buck) Carv.-Silva, P.E.A.S. Câmara & W.R.Buck. (≡ *Donnellia matutina* W.R.Buck).

Plants robust, golden green, epiphytic. *Stems* creeping, freely branched, branches often ascending, central strand absent. *Pseudoparaphyllia* absent. *Leaves* of stem and branch similar, homomallous, oblong-ovate or narrowly ovate, concave, 1.0–1.7 mm long; margins entire below, subserrulate above; costae short and double or absent; cells linear, smooth, porose; alar cells enlarged, inflated and colored, inclined at 45°, in a single row with about 2 rows of quadrate supra-alar cells. *Autoicous*. *Perichaetial leaves* erect, lanceolate to triangular,

1.5–2.2 mm long, acuminate, plane, margin entire; costae absent; cells linear, smooth; alar cells not differentiated. *Setae* elongate, smooth, about 1.5 cm long; capsules subarcuate when dry and suberect when moist, ovoid-cylindric, ca. 1 mm long, constricted below mouth when dry; exothecial cells weakly collenchymatous; annulus not differentiated; operculum long-rostrate; peristome double; exostome teeth bone-white, on front surface strongly trabeculate, toward base individual plates cross-striate with overlying papillae, but becoming smooth with age, with central line impressed, on back surface trabeculate, cross-walls papillose; endostome with high, papillose basal membrane, back surface smooth, segments not or scarcely keeled, cilia in pairs, stout. *Spores* spherical, strongly papillose. *Calyptrae* not seen.

Etymology. – The generic name is in honor of the great Hungarian collector and bryologist, Prof. Tamás Pócs.

Distribution. – *Pocsia* occurs in Africa (Rwanda, Democratic Republic of the Congo).

Pocsia matutina (W.R.Buck) Carv.-Silva, P.E.A.S. Câmara & W.R.Buck, **comb. nov.** ≡ *Donnellia matutina* W.R.Buck in Trop. Bryol. 8: 207. 1993 – Holotype: Rwanda, *T. Pócs 6060* (NY barcode 00289719; isotypes: G barcode G000114156, NY barcode 00114156!).

Pterogoniopsis paulista (W.R.Buck & Vital) Carv.-Silva, P.E.A.S. Câmara & W.R.Buck, **comb. nov.** ≡ *Paranapiacabaea paulista* W.R.Buck & Vital in Brittonia 44: 339. 1992 – Holotype: Brazil. São Paulo: Mun. Guapiara, Serra Paranapiacaba, Fazenda Intervales, slopes of Morro do Mirante, *D.M. Vital & W.R. Buck 20488* (SP!; isotypes: FH barcode 00220014, MO barcode MO-406543!, NY barcode 01179047!).

Distribution. – The genus occurs in Panama and South America, and this species is endemic to southeastern Brazil.

Schroeterella exigua (Broth.) P.E.A.S. Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** ≡ *Sematophyllum ulicinum* var. *exiguum* Broth. in Wettstein & Schiffner, Ergebn. Bot. Exp. Südbras. Musci: 345. 1924 ≡ *Schraderobryum ulicinum* var. *exiguum* (Broth.) Wijk & Margad. in Taxon 14: 198. 1965 ≡ *Acroporium exiguum* (Broth.) W.R.Buck & Schäfer-Verw. in Bol. Mus. Paraense Emílio Goeldi, N.S., Bot. 7: 651. 1993 (“1991”) – Holotype: Brazil, Minas Gerais, Serra dos Órgãos, *E. Ule 2081* (H-BR; isotype: NY!).

Distribution. – This species is endemic to Brazil, and the genus occurs in Ecuador, Bolivia and Brazil.

Trichosteleum amnigenum (Broth.) Carv.-Silva, P.E.A.S. Câmara & W.R.Buck, **comb. nov.** ≡ *Rhaphidostegium amnigenum* Broth. in Bih. Kongl. Svenska Vetensk.-Akad. Handl. 21, Afd. 3(3): 51. 1895 ≡ *Sematophyllum amnigenum* (Broth.) Broth. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 11: 433. 1925 – Holotype: Brazil, São Paulo, Santos, *C.W.H. Mosén 73* (H-BR!).

Distribution. – *Trichosteleum* is a widespread pantropical group.

Trichosteleum lonchophyllum (Mont.) Carv.-Silva, P.E.A.S. Câmara & W.R.Buck, **comb. nov.** = *Hypnum lonchophyllum* Mont., Syll. Gen. Sp. Crypt.: 10. 1856 = *Potamium lonchophyllum* (Mont.) Mitt. in J. Linn. Soc., Bot. 12: 473. 1869 = *Pterogoniella lonchophylla* (Mont.) A.Jaeger ex Paris, Index Bryol.: 1047. 1898 = *Sematophyllum lonchophyllum* (Mont.) J.Florsch. in Trop. Bryol. 3: 96. 1990 – Holotype: French Guiana, in aquis dulcibus fluitans prope Cayennan, F.M.R. Leprieur 1378 (PC barcode PC0130972!).

Vitalia P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **gen. nov.** – Type: *Vitalia caespitosa* (Hedw.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck (= *Leskea caespitosa* Hedw.).

Plants robust, golden green to dark green, epiphytic. *Stems* creeping, freely branched, central strand absent. *Pseudoparaphyllia* absent. Leaves of stem and branch similar, erect, never homomalous, galeate, oblong-ovate or ovate, concave, 1.5–2.2 mm long; margins entire, reflexed near midleaf; costae absent; cells linear, smooth; alar cells enlarged, inflated and colored. *Asexual propagula* absent. *Autoicous*. *Perichaetial leaves* erect, lanceolate to triangular, 1.5–2.2 mm long, acuminate, plane, margin entire; costae absent; cells linear, smooth; alar cells not differentiated. *Setae* elongate, smooth, 1–3 cm long; capsules suberect to pendent, ovoid-cylindric, ca. 1 mm long, constricted below mouth when dry; exothecial cells colenchymatous; annulus not differentiated; operculum long-rostrate; exostome with zig-zag center line, cross-striate below, coarsely papillose above, trabeculate at back; endostome with high basal membrane, segments keeled, cilia mostly in pairs. *Spores* spherical, finely papillose. *Calyptrae* cucullate, naked, smooth.

Etymology. – The name honors Daniel M. Vital, a famous Brazilian bryologist, one of the greatest naturalists in his country.

Distribution. – Members of *Vitalia* occur in Mexico and in South and Central America.

Vitalia caespitosa (Hedw.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** = *Leskea caespitosa* Hedw., Spec. Musc. Frond.: 233, pl. 49 fig. 1–5. 1801 = *Hypnum caespitosum* (Hedw.) Schrad. in J. Bot. (Schrad.) 1801(1): 200. 1803 = *Stereodon caespitosus* (Hedw.) Mitt. in J. Proc. Linn. Soc., Bot. Suppl. 2: 101. 1859 = *Rhaphidostegium caespitosum* (Hedw.) Besch. in Ann. Sci. Nat., Bot., sér. 6, 3: 247. 1876 = *Acroporium caespitosum* (Hedw.) W.R.Buck in Brittonia 35: 310. 1983 – Holotype: Locus Hispaniola, in ligno putrefacto, *O. Swartz s.n.* (G!; isotypes: BM!, NY barcode 01178869!).

Vitalia cuspidifera (Mitt.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** = *Sematophyllum cuspidiferum* Mitt. in J. Linn. Soc., Bot. 12: 480. 1869 = *Rhaphidostegium cuspidiferum* (Mitt.) A.Jaeger in Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 391 (Gen. Sp. Musc. 2: 460). 1878 – **Lectotype (designated here):** Ecuador. Andes Quitenses, Pallatanga (6000 ped.), *R. Spruce 999* (NY!; isoelectotypes: BM!, FLAS barcode FLAS B48444).

Vitalia esmeraldica (Müll.Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** = *Hypnum esmeraldicum* Müll. Hal., Syn. Musc. Frond. 2: 392. 1851 = *Rhaphidostegium esmeraldicum* (Müll.Hal.) Broth. in Engler & Prantl, Nat. Pflanzenfam. I(3): 1113. 1908 = *Sematophyllum esmeraldicum* (Müll.Hal.) Broth. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 11: 432. 1925 – Isotype: Ecuador, Esmeraldos, *W. Jameson s.n.* (NY barcode 01179029!).

Vitalia galipensis (Müll.Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck, **comb. nov.** = *Hypnum galipense* Müll.Hal. in Bot. Zeitung (Berlin) 6: 780. 1848 = *Sematophyllum galipense* (Müll.Hal.) Mitt. in J. Linn. Soc., Bot. 12: 480. 1869 = *Rhaphidostegium caespitosum* subsp. *galipense* (Müll. Hal.) Besch. in Ann. Sci. Nat., Bot., sér. 6, 3: 248. 1876 = *Rhaphidostegium galipense* (Müll.Hal.) Renaud & Cardot in Bull. Soc. Roy. Bot. Belgique 29(1): 183. 1890 – Holotype: Colombia, near Galipán, *N. Funck & L.J. Schlim 345* (B, probably lost; isotypes: BM!, G barcode G00114546, NY barcodes 01273710!, 01273711! & 01273712!, W!).

Note. – Although Galipán is located in Venezuela, the prologue cites it as in Colombia.

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Appendix 1. Voucher information and GenBank accession numbers in the order: Taxon, locality, collector and collector number, herbarium, GenBank accession numbers for *trnL-F*, *rps4*, *rbcl*, *nad4-5*, *nad5*, ITS1, ITS2 and 26S markers. New sequences are indicated with an asterisk (*). Sequences missing from the dataset are marked with hyphens (-).

Acanthorrhynchium papillatum (Harv.) M.Fleisch. – Thailand, *Kristoferson S006* (NY), *KU950800, AY908206, -, -, AY908468, -, -, *Acroporium caespitosum* (Hedw.) W.R.Buck 1 – Dominica, *Shäfer-Verwimp & Verwimp 17863* (NY), *KY039148, *KU936484, *KX130450, *KU996434, *KX130402, -, -, *KY050776; *Acroporium caespitosum* (Hedw.) W.R.Buck 2 – Brazil, *Câmara 2258* (UB), -, *KU936440, *KX130423, *KU996404, *KX130377, -, -, *KY050778; *Acroporium esmeraldicum* (Müll.Hal.) W.R.Buck – Brazil, *Faria 152* (UB), *KU950790, *KY419578, *KX130440, *KU996422, *KX130395, *KY050775, *KY050775, *KY050777; *Acroporium pungens* (Hedw.) Broth. – French Guiana, *Buck 33028* (NY), AF161121, AY908207, AF233572, -, AY908539, -, -, *KY419579; *Acroporium secundum* (Reinw. & Hornsch.) M.Fleisch. – China, *Liu & al. 3979*, GQ254047, GQ254028, GQ254037, -, GQ254023, -, GQ254057, GQ254057; *Aptychella prolifera* (Broth.) Herzog – Brazil, *Vital & Buck 19448* (NY), *KU950824, *KU936482, -, -, *KY078887, -, -, *Aptychopsis estrellae* (Müll.Hal.) P.E.A.S.Câmara, Carv.-Silva & W.R.Buck – Brazil, *Câmara 1913* (UB), *KU950765, *KU936435, *KX130418, *KU996397, *KX130370, *KX278689, *KX278689, *KX278689; *Aptychopsis pungifolia* (Hampe) Broth. – Brazil, *Câmara 2495* (UB), *KU950778, *KU936449, *KY078888, *KU996413, *KX130385, -, *KY419580, -, *Aptychopsis pyrrophylla* (Müll.Hal.) Wijk & Margad. – Brazil, *Câmara 2077* (UB), *KU950770, *KU936439, *KY078889, *KU996403, *KX130376, -, *KY419581, *KY419582; *Aptychopsis subpungifolia* (Broth.) Broth. 1 – Brazil, *Câmara 1935* (UB), *KU950767, *KU936436, *KX130419, *KU996399, *KX130372, *KX278698, *KX278698, *KX278698; *Aptychopsis subpungifolia* (Broth.) Broth. 2 – Brazil, *Câmara 2493* (UB), *KU950777, *KU936448, *KX130429, *KU996412, *KY419583, *KX278697, *KX278697, *KX278697; *Aptychopsis sp.* 1 – Brazil, *Câmara 1938A* (UB), -, *KY089046,

Appendix 1. Continued.

*KX130421, *KU996401, *KX130373, *KX278691, *KX278691, *KX278691; *Aptychopsis* sp. 2 – Brazil, *Câmara 1927* (UB), *KU950766, *KY089047, -, *KU996398, *KX130371, *KX278690, *KX278690, *KX278690; *Aptychopsis* sp. 3 – Brazil, *Souza 27* (UB), *KU950818, *KU936479, *KX130457, *KU996439, *KX130408, *KX278709, *KX278709, *KX278709; *Brotherella lorentziana* (Molendo ex Lorentz) Loeske – *De Sloover 17070*, *KU950814, *KY089048, -, -, *KY089049, -, -, *Brotherella recurvans* (Michx.) M.Fleisch. – United States of America, *Buck 31506* (NY), HE717046, AY908227, -, -, AY908470, -, -, *Bryhnia novaecangliae* (Sull. & Lesq.) Grout – United States of America, *Buck 32561* (NY), AF161122, AY908308, -, -, AY908523, -, -, *Chionostomum rostratum* (Griff.) Müll.Hal. – China, *Redfearn 33924* (NY), *KU950810, AY908210, *KX130448, *KU996432, AY908477, *KY089050, -, HM751377; *Clastobryella kusatsuensis* (Besch.) Z.Iwats. – Japan, *Buck 9611* (NY), *KU950752, AY908226, -, -, AY908460, -, -, *Clastobryophyllum bogoricum* (Bosch & Sande Lac.) M.Fleisch. – Philippines, *Tan 93-319* (NY), *KU950822, AY908202, -, -, AY908822, -, *KY089051, -, *Clastobryopsis imbricata* H.Akiyama, Y.Chang & B.C.Tan – Thailand, *Akiyama 31* (SING), LC059917, AB971899, -, -, AB971906, -, -, *Clastobryum tenuirameum* (Mitt.) Dixon – Nepal, *Miehe 14945* (NY), *KU950801, AY908230, -, -, AY908481, -, -, *Colobodontium vulpinum* (Mont.) S.P.Churchill & W.R.Buck 1 – Brazil, *Costa 5756* (RB), *KU950785, *KU936456, *KX130437, *KU996420, *KX130393, *KX278702, *KX278702, *KX278702; *Colobodontium vulpinum* (Mont.) S.P.Churchill & W.R.Buck 2 – Brazil, *Câmara 2326* (UB), *KU95500774, *KU936445, *KX130427, *KU996409, *KX130382, *KX278694, *KX278694; *Colobodontium vulpinum* (Mont.) S.P.Churchill & W.R.Buck 3 – Suriname, *Allen 25285* (MO), *KU950751, *KU936473, -, -, *KY089052, -, -, *Cryphaea amurensis* Ignatov – *Ignatov 97-269*, - AM990355, -, FM161251, FM161090, FM161090, FM161090; *Donnellia commutata* (Müll.Hal.) W.R.Buck 1 – Brazil, *Câmara 2455* (UB), *KU950776, *KU936447, *KY089053, *KU996411, *KX130384, *KX278696, *KX278696, *KX278696; *Donnellia commutata* (Müll.Hal.) W.R.Buck 2 – Brazil, *Soares 445* (UB), *KU950816, *KU936476, *KX130454, *KU996436, *KX130405, *KY078876, -, *KY078882; *Donnellia commutata* (Müll.Hal.) W.R.Buck 3 – Brazil, *Câmara 1877* (UB), *KU950763, *KU936434, *KX130416, *KU996395, *KX130368, *KY078879, -, *KY078885; *Donnellia commutata* (Müll.Hal.) W.R.Buck 4 – Brazil, *Soares 944* (UB), -, *KU936477, *KX130455, *KU996437, *KX130406, *KY078875, -, *KY078881; *Donnellia lageniformis* (Müll.Hal.) W.R.Buck 1 – Bolivia, *Catari 309* (MO), *KU950781, *KU936453, *KX130433, *KU996417, *KX130390, *KX278700, *KX278700, *KX278700; *Donnellia lageniformis* (Müll.Hal.) W.R.Buck 2 – Brazil, *Buck 26347* (NY), *KU950756, *KU936427, *KX130411, -, *KY089054, -, *KY078880, -, *Donnellia lageniformis* (Müll.Hal.) W.R.Buck 3 – Brazil, *Carvalho 95* (UB), -, *KU936451, *KX130431, *KU996415, *KX130388, *KY078878, -, -, *Donnellia matutina* W.R.Buck 1 – Zaire, *Pócs 7130* (NY), -, *KU936469, *KY419584, -, -, *KY078877, *KY419586; *Donnellia matutina* W.R.Buck 2 – Zaire, *Pócs 7771* (NY), *KU950808, *KU936470, *KX130447, *KX130401, -, *KY078874, *KY419587; *Fauriella tenuis* (Mitt.) Cardot – Japan, *Glime 4675* (NY), *KU950795, AY908233, -, -, AY908545, -, -, *Foreauella orthocheia* (Schwägr.) Dixon & P.de la Varde – China, *Redfearn 34244* (MO), *KU950809, AY908553, -, -, AY908461, -, -, *Heterophyllum affine* (Hook.) M.Fleisch. – United States of America, *Buck 21676* (NY), *KU950754, AY908577, -, -, AY908466, -, -, *Hildebrandtiella guyanensis* (Mont.) W.R.Buck – Honduras, *Allen 17684* (MO), AF509559, AY306927, -, -, -, -, *Homalotheciella subcapillata* (Hedw.) Broth. – United States of America, *Buck 32517* (NY), AF161154, AF143061, -, -, AY908510, -, -, *Hydrogopon fontinaloides* (Hook.) Brid. – *Solomon s.n.* (S) and *Allen 54* (DUKE) – -, AY908216 (*Allen 54*), -, -, AY908535 (*Allen 54*), HE660024 (*Solomon s.n.*), HE660024 (*Solomon s.n.*), HM751382 (*Allen 54*); *Hypnum cupressiforme* Hedw. – *Cox 599* (BM), AF472483, AF469815, -, -, AY908444, -, -, *Isocladia surcularis* (Dixon) B.C.Tan & Mohamed – Indonesia, *Shäfer-Verwimp & Verwimp 21005* (SW), *KU950812, AY908204, *KX130451, KC505385, AY908467, -, -, HM751385; *Isopterygium tenerifolium* Mitt. – Brazil, *Câmara 1978* (UB), *KU950768, -, *KY089055, *KY089056, *KX130374, -, -, *Isopterygium tenerum* (Sw.) Mitt. – Brazil, *Gama Neto 106* (UB), *KU950794, *KU936462, -, -, *KX011112, -, -, *Leucodon sciuroides* (Hedw.) Schwägr. – *Buchbender 293*, AM990405, AY908186, -, -, AY908716, -, -, *Loeskeobryum brevisrostre* (Brid.) M.Fleisch. – United States of America, *Buck 32522* (NY), AF161172, AY 908278, -, -, AY908635, -, -, *Mastopoma haidensis* W.B.Schofield – Canada, *Schofield 83989* (NY), -, *KU936472, -, -, *KY089057, -, -, *Mastopoma subfiliferum* Horik. & Ando – Thailand, *Akiyama Th-2* (NY), *KU950749, AY908224, AB071411, KC505391, AY908486, -, -, HM751389; *Macrohymenium acidodon* (Mont.) Dozy & Molk. – Madagascar, *Miller & Randrianasolo 4475* (MO), *KU950802, *KY089058, -, -, *KY089059, -, -, *Meiothecium boryanum* (Müll.Hal.) Mitt. – Trinidad, *Djan-Chékar 94-479* (NY), *KU950787, *KU936457, *KX130438, -, *KY089060, -, -, *KY078884; *Oediacidium rufescens* (Reinw. & Hornsch.) Mitt. – *Koponen & al. 50934* (H), JQ815890, HE717076, -, -, HE717039, -, -, *Papillidopsis complanata* (Dixon) W.R.Buck & B.C.Tan – Borneo, *Tan 95-1011* (MO), *KU950823, AY908220, -, -, AY908482, -, -, HM751715; *Paranapiacabaea paullista* W.R.Buck & D.M.Vital 1 – Brazil, *Vital & Buck 20614* (NY), *KY089061, AY908218, -, -, AY908480, -, -, *Paranapiacabaea paullista* W.R.Buck & D.M.Vital 2 – Brazil, *Câmara 2304* (UB), -, *KU936444, -, *KU996408, *KX130381, *KX278693, *KX278693, *KX278693; *Pilotrichopsis dentata* (Mitt.) Besch. – China, *Mizutani 13658* (S) and *Buck 23843* (NY), HE717059 (*Mizutani 13658*), AY908599 (*Buck 23843*), -, -, AY908715 (*Buck 23843*), -, -, *Plagiothecium cavifolium* (Brid.) Z.Iwats. – United States of America, *Buck 32520* (NY), AF161173, AY908321, -, -, AY908763, -, -, *Platygyrium repens* (Brid.) Schimp. – United States of America, *Buck 33448* (NY); AF161131, AY908234, -, -, AY908623, -, -, *Potamium lonchophyllum* (Mont.) Mitt. 1 – Brazil, *Peralta 12227* (SP), *KU950804, *KU936465, *KX130444, *KU996429, *KY859426, -, -, *Potamium lonchophyllum* (Mont.) Mitt. 2 – Colombia, *Churchill & al. 17636* (NY), -, AY908221, -, -, AY908540, -, -, *Pseudotrismegistia undulata* (Broth. & Yasuda) H.Akiyama & H.Tsubota – Thailand, *Akiyama TH-35* (NY), *KU950750, AY908618, -, -, AY908980, -, -, *Pterobryon densum* Hornsch. – *Allen 12532* & *Linarex & Churchill 3649* (NY), AF397838, AY908599, -, -, AY908715, -, -, *Pterogoniopsis pulchellum* (Hook.) Müll.Hal. – Trinidad, *Djan-Chékar 94-23* (NY), *KU950786, AY908232, -, -, AY908487, -, -, *Pterogoniopsis cylindrica* Müll.Hal. – Paraguay, *Buck 11943* (NY), *KU950753, AY908213, *KX130409, -, AY908537, *KX278686, *KX278686, HM751380; *Pylaisiadelpha tenuirostris* (Bruch & Schimp. ex Sull.) W.R.Buck – United States of America, *Buck 21744* (NY), *KU950755, *KU936426, *KX130410, *KY089062, KC505394, -, -, *Pylaisiopsis speciosa* (Mitt.) Broth. – Nepal, *Miehe 14071a* (NY), *KU950826, AY908555, -, -, AY908475, -, -, *Radulina borbonica* (Bél.) W.R.Buck – Equatorial Guinea, *Heras 515/94* (NY), *KU950797, AY908223, *KX130442, -, AY908485, -, -, *Radulina hamata* (Dozy & Molk) W.R.Buck & B.C.Tan – Australia, *Streimann 54122* (MO), *KU950821, *KU936481, -, -, *KY089063, -, -, *Rhacopilopsis trinitensis* (Müll.Hal.) E.Britton & Dixon – French Guiana, *Holz FG 00-257* (NY), *KU950798, AY908225, -, -, AY908543, -, -, *Rhaphidorrhynchium amoenum* (Hedw.) M.Fleisch. 1 – Australia, *Buck 58132* (NY), *KU950762, *KU936433, *KX130415, *KU996394, *KY859427, *KX278711, *KX278711, *KX278711; *Rhaphidorrhynchium amoenum* (Hedw.) M.Fleisch. 2 – Chile, *Ireland & Bellolio 34017* (NY), *KU950799, *KU936463, -, -, *KY089065, -, -, *Rhaphidorrhynchium amoenum* (Hedw.) M.Fleisch. 3 – Australia, *Buck 55483* (NY), *KU950761, *KU936432, -, -, *KY089064, -, -, *Rhaphidorrhynchium tereticaule* (Müll.Hal.) Broth. – Brazil, *Vital & Buck 19952* (NY), KU950825, KU936483, -, -, KY089066, -, -, *Rhaphidostichum acrostegium* (Sull.) W.R.Buck – Dominica, *Hill 27911* (NY), *KY089067, AY908222, -, -, AY908484, -, -, *Schroeterella longicarpa* P.E.A.S.Câmara & Carv.-Silva – Ecuador, *Buck 39478* (NY), AY908209, -, -, AY908478, -, -, HM751378; *Schroeterella zygodonta* Herzog 1 – Brazil, *Faria Jr. 2424* (UB), *KU950792, *KU936460, *KU996424, *KX130398, -, -, *KY078883; *Schroeterella zygodonta* Herzog 2 – Ecuador, *Buck 39276* (NY), -, *KU936430, *KY859425, *KU996393, *KX130367, -, -, *KY078886; *Schroeterella zygodonta* Herzog 3 – Brazil, *Souza 248* (UB), *KU950819, *KU936480, *KX130458, *KU996440, -, *KX278710, *KX278710, *KX278710; *Sematophyllum amnigenum* (Broth.) Broth. – Brazil, *Abdo 42* (UB), *KU950748, *KU936425, *KY089068, *KU996391, -, *KY078868, *KY078868, -, *Sematophyllum beyrichii* (Hornsch.) Broth. 1 – Brazil, *Câmara 2348* (UB), *KU950775, *KU936446, *KX130428, *KU996410, *KX130383, *KX278695, *KX278695, *KX278695; *Sematophyllum beyrichii* (Hornsch.) Broth. 2 – Brazil, *Carvalho-Silva 972* (UB), *KU950780, *KU936452, *KX130432, *KU996416, *KX130389, *KX278699, *KX278699, *KX278699; *Sematophyllum brachycarpum* (Hampe) Broth. – South Africa, *Phephu 66* (PRE), *KU950805, *KU936466, *KX130445, *KU996430, -, *KX278705, *KX278705, *KX278705; *Sematophyllum campicola* (Broth.) Broth. – Brazil, *Gama Neto 104* (UB), *KU950793, *KU936461, *KY859423, *KU996425, *KX130399, *KX278703, *KX278703, *KX278703; *Sematophyllum cuspidiferum* Mitt. 1 – Brazil, *Câmara 2284* (UB), *KU950772, *KU936442, *KX130425, *KU996406, *KX130379, *KY078865, -, *KY078872; *Sematophyllum cuspidiferum* Mitt. 2 – Brazil, *Câmara 2297* (UB), KU950773, KU936443, KX130426, KU996407, KX130380, KY078864, -, KY078871; *Sematophyllum cylindrothecium* (Broth.) W.R.Buck & Schäf.-Verw. – Brazil, *Buck 26694* (NY), *KU950757, *KU936428, *KX130412, *KU996392, *KY089069, *KX278687, *KX278687, *KX278687; *Sematophyllum decumbens* Mitt. – Colombia, *Churchill & al. 19059* (NY), *KU950782, *KU936454, *KX130434, *KU996418, -, -, -, *Sematophyllum demissum* (Wilson) Mitt. – United States of America, *Buck 36293* (NY), *KU950758, *KU936429, *KX130413, -, *KX130366, *KX278688, -

Appendix 1. Continued.

*KX278688, *KX278688; *Sematophyllum galipense* (Müll.Hal.) Mitt. – Brazil, *Câmara 2281* (UB), *KU950771, *KU936441, *KX130424, *KU996405, *KX130378, *KY078866, *KY078866, *KY078873; *Sematophyllum homomallum* (Hampe) Broth. – Australia, *Streitmann 54149*, HE717063, JQ815891, -, -, HE717042, HE660022, HE660022, -, *Sematophyllum lithophilum* (Hornsch.) Ångstr. 1 – Brazil, *Câmara 2012* (UB), *KU950769, *KU936438, *KX130422, *KU996402, *KX130375, *KX278692, *KX278692, *KX278692; *Sematophyllum lithophilum* (Hornsch.) Ångstr. 2 – Brazil, *Costa 5230* (RB), *KU950784, -, *KX130435, *KU996419, *KX130391, *KX278701, *KX278701, *KX278701; *Sematophyllum oedophysidium* W.R.Buck – Brazil, *Satori 147* (SP), *KU950811, *KU936471, *KX130449, *KU996433, *KY859428, *KX278706, *KX278706, *KX278706; *Sematophyllum panduraefolium* (Broth.) Broth. – Equatorial Guinea, *Heras 286/94* (NY), *KU950796, AY908217, *KY089070, *KU996426, AY908483, *KX278704, *KX278704, HM751379; *Sematophyllum reitzii* E.B.Bartram – Brazil, *Câmara 2556* (UB), -, -, *KX130430, -, *KX130386, *KY078863, -, -, *Sematophyllum subfulvum* (Broth.) Broth. 1 – Brazil, *Faria 183* (UB), *KU950791, *KY089071, *KX130441, *KU996423, *KX130397, -, *KY078862, *KY078869; *Sematophyllum subfulvum* (Broth.) Broth. 2 – Brazil, *Faria 170* (UB), -, -, *KU950827, *KX130396, -, -, *KY078869; *Sematophyllum subpinnatum* (Brid.) E.Britton 1 – Brazil, *Soares 433* (UB), *KU950815, *KU936475, *KX130453, *KU996435, *KX130404, *KX278707, *KX278707, *KX278707; *Sematophyllum subpinnatum* (Brid.) E.Britton 2 – Brazil, *Soares 1846* (UB), *KU950817, *KU936478, *KX130456, *KU996438, *KX130407, *KX278708, *KX278708, *KX278708; *Sematophyllum subsimplex* (Hedw.) Mitt. 1 – French Guiana, *Mori & Smith 25150* (NY), *KU950803, *KU936464, *KX130443, *KU996427, *KY089072, -, -, *Sematophyllum subsimplex* (Hedw.) Mitt. 2 – Brazil, *Pinheiro 137* (UB), *KU950806, *KU936467, *KX130446, *KU996431, *KX130400, -, -, *Sematophyllum subsimplex* (Hedw.) Mitt. 3 – Brazil, *Câmara 1896* (UB), *KU950764, *KY0889073, *KX130417, *KU996396, *KX130369, -, -, *Sematophyllum swartzii* (Schwägr.) W.H.Welch & H.A.Crum – Brazil, *Câmara 1938* (UB), -, *KU936437, *KX130420, *KU996400, -, *KY078867, -, -, *Sematophyllum tequendamense* (Hampe) Mitt. – Brazil, *Câmara 2835* (UB), *KU950779, *KU936450, *KY859424, *KU996414, *KX130387, -, *KY089074, *KY089075; *Struckia zerovii* (Laz.) Hedenäs – Russia, *Ignatov 34/49* (MHA), DQ836730, AF466939, -, -, JX081301, -, -, *Taxithelium isocladum* (Bosch & Sande Lac.) Renauld & Cardot – Malaysia, *Camara 974* (MO), KC840394, KC840394, -, -, KC505403, -, -, *Taxithelium planum* (Brid.) Mitt. 1 – *Newton 4641*, AF161147, AY908231, -, *KU996428, AY908549, -, -, HM751396; *Taxithelium planum* (Brid.) Mitt. 2 – *Cardenas 5904* (UB), KC840396, KC840396, -, -, KC505387, KC822118, -, -, *Trichosteleum papillosum* (Hornsch.) A. Jaeger – French Guiana, *Buck 33002* (NY), AF161149, AF143056, AF233574, -, AY908541, -, -, AY908209; *Trichosteleum sublaevigatum* Herzog – Brazil, *Silva Jr. 24* (UB), *KU950813, *KU936474, *KX130452, *KU996442, *KX130403, -, -, *Trichosteleum subdemissum* (Schimp. ex Besch.) A. Jaeger – Brazil, *Costa 5662* (RB), *KU950784, *KU936455, *KX130436, *KU996441, *KX130392, -, -, *Warburgiella leucocyta* (Müll.Hal.) B.C.Tan, W.B.Schofield & H.P.Ramsay – Australia, *Buck 52941* (NY), *KU950760, AY908219, *KX130414, -, AY908538, *KX278712, *KX278712, HM751385; *Warburgiella macrospora* (Dixon & Sainsbury) B.C.Tan, W.B.Schofield & H.P.Ramsay – Australia, Tasmania, *Buck 52799* (NY), *KU950759, *KU936431, -, -, *KY089076, -, -, *Wijkia deflexifolia* (Mitt. ex Renauld & Cardot) H.A.Crum – Japan, *Bryophytes of Asia Exc. 217*, *KU950788, *KU936458, -, -, *KY089077, -, -, *Wijkia extenuata* (Brid.) H.A.Crum – Australia, *Streimann 61180* (MO), *KU950820, AY908205, -, -, AY908542, -, -, *Wijkia hornschi* (M.Fleisch.) H.A.Crum – China, *1980 Sino-Amer. Exped. 2071D* (NY), *KU950789, *KU936459, -, -, *KY089078, -, -, *Wijkia trichocolea* (Müll.Hal.) H.A.Crum – Rwanda, *Pócs 6146* (NY), *KU950807, *KU936468, -, -, *KY089079, -, -, *Wijkia sp.* – Brazil, *Duarte-Silva 68* (UB), *KU936485, *KY859422, *KX130439, *KU996421, *KX130394, -, -, -.

Appendix 2. List of morphological characters and coding for Sematophyllaceae s.l.

1) Collenchymatous exothecial cells: (0) absent, (1) present. 2) Opercula rostrum oblique: (0) absent, (1) present. 3) Opercula long-rostrate: (0) absent, (1) present. 4) Asexual propagula: (0) absent, (1) present. 5) Sexuality: (0) monoicous, (1) dioicous. 6) Pseudoparaphyllia: (0) absent, (1) foliose, (2) filamentose. 7) Leaf-papilosity of cell: (0) smooth, (1) unipapillose, (2) pluripapillose. 8) Leaf-type of alar cells: (0) brotherelloid, (1) acroporioid, (2) heterophyllioid, (3) not developed, (4) others.

Species	1	2	3	4	5	6	7	8	Species	1	2	3	4	5	6	7	8
<i>Acanthorrhynchium papillatum</i>	0.1	0	0	0	1	1	1.2	1	<i>Fauriella tenuis</i>	0	0	0	0	1	0	2	3
<i>Acroporium caespitosum</i> l	1	1	1	0	0	0	0	0	<i>Foreauella orthothecia</i>	?	?	?	?	?	?	?	?
<i>Acroporium pungens</i>	1	1	1	0	0	0	0.1	1	<i>Heterophyllum affine</i>	0	0	0	0	0	2	0	2
<i>Acroporium secundum</i>	1	1	1	?	0.1	0	0	1	<i>Hildebrandtiella guyanensis</i>	0	0	0	1	1	1	0	3
<i>Aptychella imbricata</i>	0	0	1	1	1	0	0	2	<i>Homalotheciella subcapillata</i>	0	0.1	0	0	0	2	0	3
<i>Aptychella prolifera</i>	0	0	0	1	1	2	0	2	<i>Hypnum cupressiforme</i>	0	0	0	0	1	2	0	4
<i>Aptychopsis estrellae</i>	1	1	1	0	0	0	0	0	<i>Isocradiella surcularis</i>	1	0	0	0	1	1	0	?
<i>Aptychopsis pyrrophylla</i>	0.1	1	1	0	0	0	0	0	<i>Isopterygium tenerifolium</i>	1	0	0	?	0	1	0	3
<i>Brotherella lorentziana</i>	0	0	0	0	1	1	0	0	<i>Isopterygium tenerum</i>	1	0	0	1	0	1	0	3
<i>Brotherella recurvans</i>	0	0	0	0	1	1	0	0	<i>Leoskeobryum brevirostre</i>	0	1	0	0	1	2	0	3
<i>Bryhnia novaeangliae</i>	0	0	0	0	1	2	0	4	<i>Leucodon sciurioides</i>	0	0.1	0	0.1	1	1.2	0	4
<i>Chionostomum rostratum</i>	1	0	1	0	0	0	0	0	<i>Macrohymenium acidodon</i>	?	0	1	?	0	0	0	0
<i>Clastobryella kusatsuensis</i>	?	0	0	1	?	1	0	0	<i>Mastopoma haidensis</i>	?	0	0	0	1	?	?	2
<i>Clastobryophilum bogoricum</i>	1	1	1	0	0	0	1.2	1	<i>Mastopoma subfiliferum</i>	?	0	0	0	1	?	0	2
<i>Clastobryum tenuirameum</i>	?	0	0	1	1	?	0	1	<i>Meiothecium boryanum</i>	1	1	1	0	0	0	0	1
<i>Colobodontium vulpinum</i> 1	1	1	1	0	0	0	0	0	<i>Oedocladium rufescens</i>	?	1	1	1	1	2	0	3
<i>Colobodontium vulpinum</i> 2	1	1	1	0	0	0	0	0	<i>Papillidiopsis complanata</i>	1	1	1	0	0	0	1	1
<i>Colobodontium vulpinum</i> 3	1	1	1	0	0	0	0	0	<i>Paranapiacabaea paulista</i> 1	0.1	1	1	0	0	0	0	0
<i>Cryphea amurensis</i>	0	0	0	0	0	0	0	4	<i>Paranapiacabaea paulista</i> 2	0.1	1	1	0	0	0	0	0
<i>Donnellia commutata</i> 2	1	1	1	1	0	0	0	0	<i>Pilotrichopsis dentata</i>	0	0	0	0	0	0	0	4
<i>Donnellia lageniformes</i> 2	1	1	1	0	0	0	0	0	<i>Plagiothecium cavifolium</i>	0	0	0	1	0	0.2	0	2

Appendix 2. Continued.

Species	1	2	3	4	5	6	7	8	Species	1	2	3	4	5	6	7	8
<i>Platygyrium repens</i>	0	0	1	0	1	0	0	2	<i>Sematophyllum cylindrothecium</i>	0.1	1	1	0	0	0	0	0
<i>Potamium lonchophyllum</i> 1	1	1	1	0	0	0	0	3	<i>Sematophyllum demissum</i>	1	1	1	0	0	0	0	0
<i>Potamium lonchophyllum</i> 2	1	1	1	0	0	0	0	3	<i>Sematophyllum subpinnatum</i> 2	1	1	1	0	0	0	0	0
<i>Pseudotrismegistia undulata</i>	1	0	0	?	1	0	0	2	<i>Sematophyllum subsimplex</i> 1	1	1	1	0	0	2	0.1	0
<i>Pterobryon densum</i>	0	0.1	0	1	1	1	0	3	<i>Sematophyllum subsimplex</i> 2	1	1	1	0	0	2	0.1	0
<i>Pterogonidium pulchellum</i>	0	0	0	1	0	1.2	0	2	<i>Sematophyllum subsimplex</i> 3	1	1	1	0	0	2	0.1	0
<i>Pterogoniopsis cylindrica</i>	1	1	0	0	0	0	0	0	<i>Sematophyllum swartzii</i>	1	1	1	0	0	0	0	0
<i>Pylaisiadelpha tenuirostris</i>	0	1	1	1	1	1	0	0	<i>Struckia zerovii</i>	1	0	0	1	0	0	0	4
<i>Pylaisiopsis speciosa</i>	0	0	0	0	0	2	0	4	<i>Taxithelium isocladon</i>	0	0.1	0	0	0	1	2	0
<i>Radulina borbonica</i>	1	1	1	0	0	0	2	1	<i>Taxithelium planum</i> 1	0	0.1	0	0	0	2	2	0
<i>Radulina hamata</i>	1	1	1	0	0	0	2	0	<i>Taxithelium planum</i> 2	0	0.1	0	0	0	2	2	0
<i>Rhacopilopsis trinitensis</i>	0	0	?	0	1	1	0	0	<i>Trichosteleum papillosum</i>	1	1	1	0	0	0	1	1
<i>Rhaphidorrhynchium amoenum</i> 1	1	1	1	0	0	0	0	0	<i>Trichosteleum subdemissum</i>	1	1	1	0	0	0	1	1
<i>Rhaphidorrhynchium amoenum</i> 2	1	1	1	0	0	0	0	0	<i>Trichosteleum sublaevigatum</i>	1	1	1	0	0	0	1	1
<i>Rhaphidorrhynchium amoenum</i> 3	1	1	1	0	0	0	0	0	<i>Warburgiella leucocyta</i>	0.1	1	1	0	0	0	0	1
<i>Rhaphidorrhynchium tereticaule</i>	?	?	?	0	?	0	0	0	<i>Warburgiella macrospora</i>	0.1	1	1	1	0	0	1	1
<i>Rhaphidostichum acrostegium</i>	1	1	1	0	0	2	0	1	<i>Wijkia deflexifolia</i>	0	0	0	0	1	1	0	0
<i>Schroeterella zygodonta</i> 1	1	1	?	0	0	0	0	0	<i>Wijkia extenuata</i>	0.1	0	0	0	1	2	0.2	0
<i>Sematophyllum panduraefolium</i>	?	?	?	0	0	0	0	0	<i>Wijkia hornschuchii</i>	0	0	0	0	1	1	0	0
<i>Sematophyllum amnigenum</i>	1	1	1	0	0	0	0	3	<i>Wijkia</i> sp.	0.1	0	0	?	1	2	0	0
<i>Sematophyllum cuspidiferum</i> 1	1	1	1	0	0	0	0	0	<i>Wijkia trichocolea</i>	0.1	0	0	0	1	2	0	0

Appendix 3. List of morphological characters and coding for the Sematophyllaceae crown clade.

1) Collenchymatous exothecial cells: (0) slightly, (1) median, (2) strongly. 2) Opercula rostrum oblique: (0) absent, (1) present. 3) Rostrum of opercula: (0) short, (1) long. 4) Rhizoid: (0) clustered at base stem, (1) along the stem. 5) Asexual propagula: (0) absent, (1) present. 6) Sexuality: (0) monoic, (1) dioic. 7) Stem and branch leave: (0) similar, (1) differentiated. 8) Homomallous leaves: (0) absent, (1) present. 9) Leaf shape: (0) lanceolate to ovate, (1) oblong, (2) galeate, (3) elliptic, (4) obovate, (5) falcate secund. 10) Leaf-margin type: (0) entire, (1) not entire. 11) Leaf-curvature margin: (0) absent, (1) present. 12) Leaf curvature: (0) plane, (1) concave. 13) Leaf-porose cells: (0) absent, (1) present. 14) Leaf-cell shape: (0) rhombic, (1) linear flexuose. 15) Leaf-papillosity of cell: (0) smooth, (1) unipapillose, (2) pluripapillose. 16) Leaf-type of alar cells: (0) brotherelloid, (1) acroporioid, (2) heterophyllioid. 17) Leaf-color of alar cells: (0) colored, (1) not colored. 18) Leaf-alar cells wall: (0) thick, (1) thin. 19) Perichaetia curvature leaf margin: (0) plane, (1) curved. 20) Perichaetia leaf shape: (0) lanceolate, (1) oblong, (2) ovate. 21) Perichaetia alar cells development: (0) developed, (1) not developed. 22) Perichaetia curvature: (0) plane, (1) concave. 23) Perichaetia leaf cell shape: (0) rhombic, (1) linear flexuose. 24) Perichaetia papillosity: (0) absent, (1) present. 25) Perichaetia porose cells: (0) absent, (1) present. 26) Seta ornamentation: (0) smooth, (1) rugose. 27) Seta twisted: (0) present, (1) absent. 28) Seta curvature: (0) curved, (1) straight. 29) Capsule inclination: (0) erect, (1) inclined, (2) pendulous. 30) Capsule symmetric: (0) symmetric, (1) asymmetric. 31) Capsule constriction below the mouth: (0) absent, (1) present. 32) Annulus: (0) not developed, (1) developed. 33) Exostome curvature: (0) inflexed, (1) reflexed. 34) Exostome furrowed: (0) absent, (1) present. 35) Exostome trabecula: (0) present, (1) absent. 36) Endostome presence: (0) caducous, (1) persistent. 37) Endostome perforation: (0) absent, (1) present. 38) Basal membrane: (0) high, (1) median, (2) low. 39) Segments papillosity: (0) smooth, (1) papillose. 40) Spores papillosity: (0) smooth, (1) papillose or rugose.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Acroporium caespitosum</i> 1	2	1	1	1	0	0	0	1	1.3	0	1	1	1	1	0	0	0	0	1	2	1	1	1	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0
<i>Acroporium caespitosum</i> 2	2	1	1	1	0	0	0	1	1.3	0	1	1	1	1	0	0	0	0	1	2	1	1	1	0	1	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0
<i>Acroporium esmeraldicum</i>	2	1	1	1	0	0	0	1	2	0.1	1	1	1	1	0	0	0	0	1	2	1	1	1	0	1	0.1	1	0	1	1	1	0	0	0	0	1	1	0	1	1
<i>Acroporium pungens</i>	1	1	1	1	0	0	0	0	0	0	0	1	1	0.1	0.1	1	0	0	2	1	0	0.1	0	1	0.1	1	0	1	1	0	0	0	1	0	1	1	0	1	0	1.0
<i>Aptychopsis subpungifolia</i>	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	1	1	1	0	1	0	0	0	0.1	0	0	0	0	0	0	1	0	?	?	?	1
<i>Aptychopsis estrellae</i>	2	1	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	0	1	1	1	0	1	0	0	0.1	0	0	1	0	0	0	1	0	0	1	1	
<i>Aptychopsis pungifolia</i>	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	1	
<i>Aptychopsis pyrrophylla</i>	1.2	1	1	0	0	0	1	0.1	0	0	1	1	0.1	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	0	0	1	0	0	1	0	1	
<i>Aptychopsis</i> sp. 2	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	1
<i>Aptychopsis</i> sp. 1	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	?	1
<i>Aptychopsis</i> sp. 3	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Aptychopsis subpungifolia</i>	1.2	1	1	0	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	1	1	1	0	1	0	0	0	0.1	0	0	0	0	0	0	0	0	?	?	?	1
<i>Chionostomum rostratum</i>	2	0	1	0	0	0	1	0.1	1	1	1	0	1	0	0	0	0	0	?	?	1	?	?	0	?	0	?	1	1	?	?	?	0	?	0	1	?	0	1	

Appendix 3. Continued.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40		
<i>Clastrobryophyllum bogoricum</i>	1	1	1	1	0	0	0	1	0.1	1	1	1	1	1	2	1	0	0	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?
<i>Colobodontium vulpinum</i> 1	0	1	1	0	0	0	0	1	4	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0.1	0	0	0	0	0	0	0	0	1	1	2	1	1
<i>Colobodontium vulpinum</i> 2	0	1	1	0	0	0	0	1	4	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	0.1	0	0	0	0.1	0	0	0	0	0	0	0	0	1	0	2	1	1
<i>Colobodontium vulpinum</i> 3	0	1	1	0	0	0	0	1	4	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0	0.1	0	0	0	0	0	0	0	0	1	0	2	1	1	
<i>Donnellia commutata</i> 1	1	1	1	1	1	0	0	0	3.0	0	0.1	1	0	0	0	0	0	0	0.2	1	0	1	0	0	0	0	1	0.1	0	1	1	0	0	0	0	0	0	0	2	1	0.1	
<i>Donnellia commutata</i> 2	1	1	1	1	1	0	0	0	3.0	0	0.1	1	0	0	0	0	0	0	0.2	1	0	1	0	0	0	0	1	0.1	0	1	1	0	0	0	0	0	0	0	2	1	0.1	
<i>Donnellia commutata</i> 3	1	1	1	1	1	0	0	0	3.0	0	0.1	1	0	0	0	0	0	0	0.2	1	0	1	0	0	0	0	1	0.1	0	1	1	0	0	0	0	0	0	2	1	0.1		
<i>Donnellia commutata</i> 4	1	1	1	1	1	0	0	0	3.0	0	0.1	1	0	0	0	0	0	0	0.2	1	0	1	0	0	0	0	1	0.1	0	1	1	0	0	0	0	0	0	2	1	0.1		
<i>Donnellia lageniformes</i> 1	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0.1	1	1	1	0	0	0	1	0	2	1	1			
<i>Donnellia lageniformis</i> 2	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0.1	1	1	1	0	0	0	1	0	2	1	1			
<i>Donnellia lageniformis</i> 3	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0.1	1	1	1	0	0	0	1	0	2	1	1			
<i>Donnellia matutina</i> 1	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0.2	1	1	0	0	0	0	0	1	0.1	0	1	0	0	0	0	1	0	0	1	1			
<i>Donnellia matutina</i> 2	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0.2	1	1	0	0	0	0	0	1	0.1	0	1	0	0	0	0	1	0	0	1	1			
<i>Hydropogon fontinaloides</i>	?	?	?	?	?	?	?	1	1.0	1	1	0	0	1	0	2	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Macrohymenium acidodon</i>	2	0	1	1	0	0	1	1	0	0	1	1	1	0	0	0	0	1	?	?	?	?	?	?	?	0.1	0	1	1	?	1	?	?	0	1	0	1	?	?	?	?	
<i>Meiothecium boryanum</i>	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	?	?	?	?	
<i>Paranapiacabaea paulista</i> 2	1.2	1	1	1	0	0	0	1	1	0	1	1	1	0.1	0	0	0	1	0.1	0	1	1	1	0	0	0	0	0.1	0	1	0	0	0	0	0	0	1	0	1	0	1	
<i>Potamium lonchophyllum</i> 1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	0	2	1	1	0	0.2	1	0	0	1	0	0	1	0.1	1	1	1	0	1	0	1	1	0	1	0	1	0.1	
<i>Pterogoniopsis cylindrica</i>	1	1	0	1	0	0	0	0	0	0	0	0	0	0.1	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	0	1	1			
<i>Radulina borbonica</i>	2	1	1	0	0	0	0	1	5	1	0	1	1	0.1	2	1	0	1	1	0	1	1	0	1	0	0.1	0	0	1	1	0	0	0	1	0	1	1	0	1	1		
<i>Rhaphidorrhynchium amoenum</i> 3	2	1	1	0	0	0	0	1	5	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	2	1	1		
<i>Rhaphidorrhynchium tereticaule</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Schroeterella longicarpa</i>	1	1	?	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	?	1	1	0	2	1	?		
<i>Schroeterella zygodonta</i> 1	1	1	?	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	1	1		
<i>Schroeterella zygodonta</i> 2	1	1	?	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	1	1		
<i>Schroeterella zygodonta</i> 3	1	1	?	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	2	1	1		
<i>Sematophyllum panduraefolium</i>	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Sematophyllum amnigenum</i>	2	1	1	0	0	0	0	1	0	0	0	1	0	1	0	2	1	1	0	0	1	1	1	0	1	0	1	0.1	1	1	1	0	0	0	0	1	1	?	1	1		
<i>Sematophyllum beyrichi</i> 1	1	1	1	1	0	0	0	1	0.1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0		
<i>Sematophyllum beyrichi</i> 2	1	1	1	1	0	0	0	1	0.1	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0		
<i>Sematophyllum brachycarpum</i>	2	1	1	1	0	0	0	1	0	0	0.1	0	0	1	0	0	0	0	0.2	1	0	1	0	0	0	0	1	0	1	1	1	0	0	0	1	0	0	1	1			
<i>Sematophyllum campicola</i>	2	1	1	1	0	0	0	1	1.3	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1		
<i>Sematophyllum cuspidiferum</i> 1	2	1	1	1	0	0	0	1	2	0	0	1	0	1	0	0	0	0	1	2	0	1	1	0	1	0	1	0	1.2	1	1	1	0	0	0	1	0	0	1	1		
<i>Sematophyllum cuspidiferum</i> 2	2	1	1	1	0	0	0	1	2	0	0	1	0	1	0	0	0	0	1	2	0	1	1	0	1	0	1	0	1.2	1	1	1	0	0	0	1	0	0	1	1		
<i>Sematophyllum cylindrothecium</i>	1.2	1	1	0	0	0	0	0	0	0	1	1	0.1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0.1	0	0	0	0	0	0	0.1	?	0	1	1			
<i>Sematophyllum demissum</i>	2	1	1	0	0	0	0	1	0.1	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	?	1.2	?	1	?	?	?	?	?	?	?	?	?	?		
<i>Sematophyllum galipense</i>	2	1	1	1	0	0	0	2	0	1	1	1	1	0	0	0	0	0.2	0	1	1	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	1	1				
<i>Sematophyllum homomallum</i>	1	0.1	1	0	1	0	0	0.1	0	0.1	1	1	0.1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Sematophyllum lithophyllum</i> 1	2	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1			
<i>Sematophyllum lithophyllum</i> 2	2	1	1	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	1			
<i>Sematophyllum oedophysidium</i>	2	1	1	0	0	0	0	1	1	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	1	0	1	0	1	1	0	0	0	1	0	1	1	0	1	1		
<i>Sematophyllum reitzii</i>	?	?	?	1	0	0	0	1	1.0	0	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?		
<i>Sematophyllum subfulvum</i> 1	2	1	1	1	0	0	0	1	0.1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	1	
<i>Sematophyllum subfulvum</i> 2	2	1	1	1	0	0	0	1	1.0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	1
<i>Sematophyllum subpinnatum</i> 1	2	1	1	1	1	0	0	0	1.0	0	1	1	0.1	0	0	0	0	1	0	0	1	0	0	1																		