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ORIGINAL ARTICLE

Phylogenetic relationships in the '*Pinnatella*' clade of the moss family Neckeraceae (Bryophyta)

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Abstract The family Neckeraceae is composed of three distinct clades, of which two, i.e. the *Neckera* and *Thamnobryum* clades, are well defined. The third clade, consisting of species belonging to *Caduciella*, *Curvicladium*, *Handeliobryum*, *Himantocladium*, *Homaliodendron*, *Hydrocryphaea*, *Neckera*, *Neckeropsis*, *Pinnatella*, *Shevockia* and *Taiwanobryum*, is the focus of this study. Based on sequence data from the *trnS-rps4-trnT-trnL-trnF* plastid cluster and the *rpl16* intron as well as from nuclear ITS1&2, the phylogenetic relationships of these genera are reconstructed. The nearest relatives of this clade are resolved shedding more light on the evolution of the family. The generic composition of the clade and its individual genera are discussed; polyphyly requires redefinition of *Pinnatella*, *Neckeropsis* and *Homaliodendron*. The positions of *Touwia* and *Homalia* within the family are addressed in an additional analysis based on more extensive sequence data, and the corresponding new combinations are made. Several further taxonomic changes are proposed, including *Circulifolium* gen. nov., comprising the former *Homaliodendron exiguum* and *H. microdendron*.

Keywords Pleurocarpous mosses · *Circulifolium* gen. nov. · Molecular systematics · *Pinnatella* section *Tenuinervia*

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Introduction

With around 5,000 species the pleurocarpous mosses represent one of the major groups of first branching land-plants. The plant habit typically is creeping, branching; in contrast to most other mosses sporophyte development is restricted to the apices of short, lateral branches. According to the latest studies, the pleurocarpous mosses as defined by Bell et al. (2007) form a monophylum ("core pleurocarps") that can be divided in four orders: Hypnodendrales, Ptychomniales, Hookeriales and Hypnales, the latter including the Neckeraceae. This family contains mainly temperate and tropical species; the species number is estimated at around 200 (Enroth 1994a; Olsson et al. 2009a). The species are mostly epiphytic or epilithic, but there are also some aquatic (rheophytic) ones. A morphological characterization of the Neckeraceae is provided by Olsson et al. (2009a).

Olsson et al. (2009b) resolved the backbone relationships of the Neckeraceae, its sister-group relation to the Lembophyllaceae, and revealed that the Neckeraceae can be divided in three distinct clades. The three resolved

clades were named: *Neckera* clade, *Thamnobryum* clade and '*Pinnatella*' clade, the first two after the respective most species-rich genus included. In addition, morphological definitions of, and evolutionary trends in, the clades were discussed (Olsson et al. 2009a).

The '*Pinnatella*' clade is mainly tropical (except for *Handeliobryum*) and Asiatic, only *Pinnatella minuta* occurs in Africa and South America. The clade is not clearly characterized by only a single dominant genus; instead, three major genera, *Pinnatella*, *Homaliodendron* and *Neckeropsis*, are located in this group. The remaining genera belonging here are *Caduciella*, *Curvicladium*, *Handeliobryum*, *Himantocladium*, *Hydrocryphaea*, *Shevockia*, and *Taiwanobryum*; in addition, several Asian species currently placed in *Neckera* belong here as well, thus rendering polyphyletic the genus as defined so far. The estimated total number of species in this clade is 70–80, but the exact number cannot be known before analyses with a more thorough sampling of *Neckera* and also *Neckeropsis* are carried out. The members of this clade usually have a strong costa and a long seta; a weak costa and immersed capsules are found only in some species of *Neckeropsis*, *Hydrocryphaea* and one species of *Homaliodendron*. The seta is often mammillose in its upper part, a character state shared by all *Pinnatella* species for which the sporophytes are known, by *Taiwanobryum*, *Neckeropsis calcutensis*, *Neckera crenulata*, and *Neckera himalayana*. In *Homaliodendron flabellatum* the seta is occasionally mammillose above, and in *Himantocladium* it is consistently smooth.

The position of the *Homalia* clade (*H. trichomanoides*, *H. lusitanica* and *Anomodon giraldii*) remained controversial in our earlier phylogenetic analyses of the Neckeraceae. It was resolved as sister either to the '*Pinnatella*' clade (Olsson et al. 2009a) or to the *Thamnobryum* clade, but with low support (Olsson et al. 2010). Morphologically the *Homalia* clade is heterogenic, and does not clearly belong to any of the bigger clades. Therefore, the purpose of the present study is to analyse in more detail the composition of the '*Pinnatella*' clade. In addition, we address the relationships of the *Homalia* clade within the Neckeraceae with additional analyses including five marker sequences.

Material and methods

Taxon sampling and molecular markers

The material used was taken from herbarium specimens; the taxon names (with citation of authorities), specimen voucher numbers and herbaria are listed in Tables 1 and 2. The analyses included 71 taxa from 29 genera.

For the initial analysis (see Table 1), the ingroup species were selected based on previous classifications (e.g. Buck

and Goffinet 2000; Goffinet and Buck 2004), our earlier molecular analyses of a wider taxon sampling (Olsson et al. 2009a, 2009b), as well as on the distribution of morphological characters, to cover the morphological variation within the study group as completely as possible. The outgroup species were selected from the other Neckeraceae clades that were resolved as sister-groups in our previous analyses (Olsson et al. 2009a), and from Lembophyllaceae, the sister group to Neckeraceae (Olsson et al. 2009a; Quandt et al. 2009). *Homalia webbiana*, *Heterocladium dimorphum* and *Heterocladium procurrens* are the most distant outgroups in this analysis. Since the sequence variation within the family turned out to be low, we chose for the phylogenetic reconstructions markers that are known to evolve fast: internally transcribed spacers 1 & 2 of nuclear ribosomal DNA, the plastid *rpl16* intron, as well as the plastid *trnT-trnL* and *trnL-trnF* intergenic spacers (IGS) and the *trnL* intron.

To resolve the broader relationships of the '*Pinnatella*' clade and to pinpoint the positions of *Homalia* (*H. trichomanoides*, *H. lusitanica* and *Anomodon giraldii*) and *Touwia*, an additional analysis with a reduced taxon sampling was conducted (see Table 2). This second data set was based on data from our previous study resolving the backbone phylogeny of the Neckeraceae (Olsson et al. 2009a; Quandt et al. 2009), but modified by adding taxa relevant to the present study. Compared to the first data set, the second includes two additional markers (*rps4* and *nad5*). Since some of the material was used in both analyses, Tables 1 and 2 are partly redundant.

DNA isolation, PCR amplification and sequencing

DNA was extracted using the DNeasy® Plant Mini Kit from Qiagen (Qiagen GmbH, Germany) following the manufacturer's protocol. For details of the DNA extraction, PCR amplification of the ITS1-5.8S-ITS2 and the *rps4-trnT-trnL-trnF* cluster, purification protocols and sequencing strategies employed, see Olsson et al. (2009b). The amplification protocols for *rpl16* are described in Olsson et al. (2009a, 2009b), whereas sequencing and amplification of *nad5* followed Buchbender and Quandt (in press). The cleaned PCR products were sequenced by Macrogen Inc., South Korea (www.macrogen.com). Primer sequences were deleted before the final sequences were deposited in EMBL; the corresponding accession numbers are listed in Tables 1 and 2.

Alignment and phylogenetic analyses

Nucleotide sequences were edited manually and aligned to existing data sets of Olsson et al. (2009a, 2009b) using PhyDE® v0.995 (Müller et al. 2005), based on the criteria

Table 1 Taxa and specimens in the initial data set, voucher information, and EMBL or GenBank accession numbers for the generated or downloaded sequences

Taxon	Herbarium	Voucher ID	GenBank accession		
			rps4-trnT-trnL-trnF [b]	*rpl16*	ITS1&2
Anomodon giraldii Müll. Hal[a]	H	H3194078	AM990342	FM210763	FM161075
Caduciella guangdongensis Enroth[a]	H	Koponen et al. 57241	FM210281	FM160952	FM161083
Caduciella mariei (Besch.) Enroth	H	Koponen 28035	FM210282	FM160953	FM161084
Camptochaete arbuscula var. tumida (Sm.) Reichardt	H	Streimann 51408	AM990353	FM160955	FM161087
Chileobryon callicostelloides (Broth. ex Thér.) Enroth	H	H3107865	FM210283	FM200841	FM161088
Curvicladium kurzii (Kindb.) Enroth	NYBG	Akiyama Th-85	FM210285	FM160959	FM161093
Dolichomitriopsis diversiformis (Mitt.) Nog.	H, MHA	Nedoluzhko s.n.	AM990362; AF397777[b]	FM160963	FM161098
Echinodium hispidum (Hook. f. & Wilson) Reichardt	Buchbender	Downing s.n., 29.10.2000	FM210286	FM160964	FM161099
Forsstroemia producta (Hornsch.) Paris	H	Koponen 46545	FM201504	FM160967	FM161102
Handeliobryum sikkimense (Paris) Ochyra	H	Redfearn et al. 33981	FM210287	FM160969	FM161110
Heterocladium dimorphum (Brid.) Schimp.	H	H3212307	AM990376	FM160970	FM161115
Heterocladium procurrens (Mitt.) A. Jaeger	H	H3212289	AM990379	FM160973	FM161118
Himantocladium cyclophyllum (Müll. Hal.) M. Fleisch.[a]	NYBG	Redfearn Jr. 36081	FM210288	FM160974	FM161120
Himantocladium implanum (Mitt.) M. Fleisch.	NYBG	De Sloover 21124	FM210289	FM160975	FM161121
Himantocladium plumula (Nees) M. Fleisch.	H	Tan et al. 92–232	AM990381	FM160976	FM161122
Homalia lusitanica Schimp.	B	B275202	AM990383	FM160978	FM161124
Homalia trichomanoides (Hedw.) Schimp.	Quandt	Olsson 105	AM990385	FM160980	FM161126
Homalia webbiana (Mont.) Schimp.	H	Müller K68	AM990387	FM160982	FM161127
Homaliodendron exiguum (Bosch & Sande Lac.) M. Fleisch[a]	B	B263509	AM990389	FM160984	FM161130
Homaliodendron flabellatum (Sm.) M. Fleisch.	H	H3071675	FM210290	FM160985	FM161132
Homaliodendron flabellatum (Sm.) M. Fleisch.	Enroth	Schwarz 3801	FM210291	FM160986	FM161131
Homaliodendron microdendron (Mont.) M. Fleisch.[a]	H	Redfearn, Jr. 35901	AM990390	FM160987	FM161133
Homaliodendron neckeroides Broth.	H	H3071953	FM210306	FM161015	FM161168
Homaliodendron scalpellifolium (Mitt.) M. Fleisch.	H	H3071976	FM210292	FM160989	FM161135
Hydrocryphaea wardii Dix.	H	Shevock 23460	FM210293	FM160992	FM161139
Lembophyllum clandestinum (Hook. f. & Wilson) Lindb. in Par.	H	Vitt 29644	AM990401; AF397823[b]	FM160996	FM161145
Neckera complanata (Hedw.) Huebener	Buchbender	Buchbender 204	AM990413	FM161005	FM161158
Neckera crenulata Harv.[a]	H	Long 33980	FM210297	FM161006	FM161159
Neckera crispa Hedw.	Buchbender	Buchbender 385	FM210298	FM161007	FM161160
Neckera himalayana Mitt.	B	B253876	FM210301	FM161010	FM161163
Neckera pennata Hedw.	H	H3203794	AM990414	FM161016	FM161169
Neckera polyclada Müll. Hal.	H	Koponen 45441	FM210307	FM161017	FM161170
Neckera warburgii Broth.	B	Bryo 253855	FM210311	FM161023	FM161176
Neckeropsis calcicola Nog.	H	Enroth 64632	AM990417	FM161025	FM161178
Neckeropsis calcutensis (M. Fleisch.) Enroth	H	H3212832	AM990418	FM161026	FM161179
Neckeropsis disticha (Hedw.) Kindb.	NYBG	Heras 901/93	FM210313	FM161027	FM161180
Neckeropsis fimbriata (Harv.) M. Fleisch.	Enroth	Schäfer-Verwimp 16212	FM210314	FM161028	FM161181
Neckeropsis gracilenta (Bosch & Sande Lac.) M. Fleisch.	S	B105716	FM210315	FM161029	FM161182
Neckeropsis nitidula (Mitt.) M. Fleisch.	S	B105713	AM990419	FM161030	FM161183

Table 1 (continued)

Taxon	Herbarium	Voucher ID	GenBank accession		
			rps4-trnT-trnL-trnF[b]	*rpl16*	ITS1&2
Neckeropsis undulata (Hedw.) Reichardt	B	B238406	FM210316	FM161031	FM161184
Pendulothecium punctatum (Hook. f. & Wilson) Enroth & S. He	S	Streimann 53845	AM990421	FM161033	FM161187
Pinnatella alopecuroides (Mitt.) M. Fleisch.	Enroth	Schäfer-Verwimp 16824	AM990423	FM161034	FM161188
Pinnatella ambigua (Bosch & Sande Lac.) M. Fleisch.	Enroth	Schäfer-Verwimp 16252	FM210317	FM161035	FM161189
Pinnatella anacamptolepis (Müll. Hal.) Broth.[a]	S	B104516	FM210318	FM161036	FM161190
Pinnatella foreauana Thér. & P. de la Varde	H	Linis 757–03	FM210319	FM161037	FM161191
Pinnatella kuehliana (Bosch & Sande Lac.) M. Fleisch.	Enroth	Müller S116	FM20150	FM161038	FM161192
Pinnatella makinoi (Broth.) Broth.	HIRO	Deguchi 36762	FM210320	FM161039	FM161193
Pinnatella minuta (Mitt.) Broth.	H	Rikkinen et al. 32	AM990424	FM161040	FM161194
Pinnatella mucronata (Bosch & Sande Lac.) M. Fleisch.[a]	S	Hedenäs MY92-22	AM990425	FM161041	FM161195
Pinnatella taiwanensis Nog.	H	Koponen et al. 54169	FM210321	FM161042	FM161196
Porotrichodendron superbum (Taylor) Broth.	H	H3121100	AM990427	FM161043	FM161198
Porotrichum fruticosum (Mitt.) A. Jaeger[a]	H	Shevock 28269	AM990430	FM161047	FM161202
Rigodium pseudothuidium Dusén	H	H3134254	AM990438; AF543547[b]	FM161051	–
Shevockia inunctocarpa Enroth & M.C.Ji	H	Shevock 25325	FM210323	FM161052	FM161212
Taiwanobryum robustum Veloira	H	Taiwan 1544	AM990441	FM864218	FM161215
Taiwanobryum speciosum Nog.	H	Enroth 64877	AM990442	FM161055	FM161216
Thamnobryum alopecurum (Hedw.) Nieuwl. ex Gangulee	Buchbender	Buchbender s.n. 11.7.2003	AM990444	FM161056	FM161218
Thamnobryum ellipticum (Bosch & Sande Lac.) Nieuwl.[a]	Enroth	Müller S114	FM210325	FM161058	FM161220
Thamnobryum maderense (Kindb.) Hedenäs	S	B44108	AM990445	FM161061	FM161223
Thamnobryum negrosense (E.B. Bartram) Z. Iwats. & B.C. Tan[a]	H	Schäfer-Verwimp & Verwimp 16852	FM210327	FM161063	FM161225
Thamnobryum pumilum (Hook. & Wilson) B.C. Tan	B	B268163	FM210329	FM200843	FM161227
Touwia laticostata Ochyra	Quandt	Cairns 27.8. 2005	FM210330	FM161070	FM161233
Weymouthia mollis (Hedw.) Broth.	CHR, Quandt	99-Mo2	AM990452	FM161072	FM161237

[a] Denotes taxa for which nomenclatural changes are suggested

[b] In three cases, sequences had been submitted to GenBank in a previous study, thus there are two accession numbers in the "*rps4-trnT*; *trnL-trnF*" column

laid out in Kelchner (2000) and Quandt and Stech (2005). The alignment process was straightforward due to low sequence length variation. The reported hairpin-associated inversion in the *trnL-F* intergenic spacer (IGS) (Quandt and Stech 2005; Quandt et al. 2004) was positionally isolated in the alignment and included in the analysis as reverse complement in order to gain information from substitutions within the detected inversion, as discussed in Quandt et al. (2003). Indels were incorporated as binary data using a simple indel coding (SIC) strategy (Simmons and Ochoterena 2000) as implemented in SeqState (Müller 2005). Command files for using the parsimony ratchet (Nixon 1999) were generated using PRAP2 (Müller 2007) and executed in PAUP 4.0b10 (Swofford 2002). Ratchet settings were as follows: 10 random addition cycles of 200 iterations each, with 25% upweighting of the characters in the iterations. Heuristic

bootstrap searches under parsimony were performed with 1,000 replicates and 10 random addition cycles per bootstrap replicate.

Bayesian analyses were performed with MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001), applying the GTR+Γ+I model for the sequence data and the restriction site model for the binary indel partition. To allow for possible deviating substitution models for the different regions, the first data set was divided in four partitions (partition 1: rps4-trnF; partition 2: nuclear DNA; partition 3: rpl16; partition 4: indels) whereas the five-region data set with reduced taxon sampling was divided in five partitions (partition 1: trnS-trnF; partition 2: nuclear DNA; partition 3: rpl16; partition 4: mitochondrial DNA; partition 5: indels).

The a priori probabilities supplied were those specified in the default settings of the program. Posterior probability (PP) distributions of trees were calculated using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method and the search strategies suggested by Huelsenbeck et al. (2001, 2002). In each analysis ten runs with four chains (2.5×10^6 generations each) were run simultaneously, with the temperature of the heated chains set to 0.1. Chains were sampled every 10 generations and the respective trees written to a tree file. Calculations of the consensus tree and of the posterior probabilities of clades were performed based upon the trees sampled after the chains converged (<generation 500,000). Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph (Müller and Müller 2004). The alignments and trees are available on request from the authors.

Results

Alignment and sequence analyses

Before analysing the matrix, 14 hotspots with poly-homonucleotide repeats were recognized and excluded from the analyses following Olsson et al. (2009b). Hotspots (regions of ambiguous alignment (see Borsch and Quandt 2009; Borsch et al. 2003), were regularly distributed among the partitions: six hotspots were located in the plastid rps4-trnF region (H1–H6), the remainder in the nrDNA and the rpl16 intron, with four in each region. The resulting alignment contained 3,891 positions of which 1,429 belonged to the (rps4)-trnT-trnL-trnF partition, 1,554 positions to the nuclear ribosomal partition, and 908 positions to the rpl16 partition. There were 3,142 constant characters; 434 characters were parsimony-informative. In the data matrix where the information based on indel coding was included, a total of 4,416 positions were

available. This raised the number of parsimony-informative characters to 677, but the constant characters remained the same.

The second data set, after exclusion of 11 hotspots, contained 5,222 positions of which 1,916 belonged to the rps4-trnT-trnL-trnF partition, 865 positions to the rpl16 partition, 1,281 to the nad5 region, and 1,160 to the ITS. Of the characters 4,477 were constant and 407 parsimony-informative. When the information based on indel coding was included, the data matrix included 5,568 positions (4,485 constant and 549 parsimony informative).

Phylogenetic analyses

The parsimony analysis with indel coding resulted in 566 most parsimonious trees (length 2,548, CI=0.558, RI=0.701), whereas analysis without indel coding returned 1,440 most parsimonious trees (length 1,595, CI=0.562, RI=0.720). The strict consensus trees of these analyses showed no conflict with the results from Bayesian inference (BI), but less resolution. Therefore, only the BI tree is illustrated in Fig. 1, with posterior probabilities (PP) and, where applicable, bootstrap values (BS) from the parsimony analysis. Values resulting from analyses with an indel-coding approach precede the values from analyses with the SIC matrix excluded. Thus, in the text below support values from the various analyses will be referred to in the following format: (PPsic / PP / BSsic / BS).

The outgroup species belonging to the Neckeraceae form the following clades (Fig. 1): a fully supported Neckera clade (PP 100, BS 100), a clade containing Thamnobryum among other genera (PP 100 / 100, BS 98 / 90), and the genus Touwia, the latter well supported (PP 100 / 100, BS 100 / 100) but in an unresolved position. The ingroup is well supported in the Bayesian analyses (PP 100), including species from Caduciella, Curvicladium, Handeliobryum, Himantocladium, Homaliodendron, Hydrocryphaea, Neckera, Neckeropsis, Pinnatella, the recently described genus Shevockia, and Taiwanobryum. The ingroup is divided in three clades (A–C), but Curvicladium kurzii and three Neckera species (N. himalayana, N. polyclada and N. warburgii) are located outside of these clades. The first clade (A in Fig. 1) is well supported (PP 100 / 100, BS 88 / 91) and includes Homaliodendron species (H. neckeroides, H. scalpellifolium and H. flabellatum) together with Porotrichum fruticosum. This grouping shows Homaliodendron to be polyphyletic, since some 'Homaliodendron' species are found in the next clade. The second clade (B) gets high support in both the Bayesian and parsimony analyses (PP 100 / 100, BS 98 / 99) and includes the unispecific genera Hydrocryphaea and Handeliobryum, as well as Neckeropsis, the two remaining Homaliodendron species, Caduciella and Himantocladium. Even though all

Table 2 Taxa and specimens in the reduced data set, voucher information, and EMBL or GenBank accession numbers for the generated or downloaded sequences

DNA no.	Taxon	Herbarium	Voucher ID	GenBank accession				
				rps4-trnT-trnL-trnF[a]	rps4	rpl16	nad5	ITS
B141	*Anomodon giraldii* Müll. Hal.[b]	H	H3194078	AM990342		FM210763	FM161240	FM161075
SH10	*Camptochaete arbuscula* var. *tumida* (Sm.) Reichardt	H	Streimann 51408	AM990353	AY908330[b]	FM160955	FM161249	FM161087
B617	*Chileobryon callicostelloides* (Broth. ex Thér.) Enroth	H	H 3107865	FM210283	FM882222	FM200841	FM882226	FM161088
B423	*Cryptoleptodon longisetus* (Mont.) Enroth	H	H3038483	AM990356	AY908260[b]	FM160957	FM161252	FM161091
B223	*Curvicladium kurzii* (Kindb.) Enroth	NYBG	Akiyama Th-85	FM210285	AY908266[b]	FM160959	AY908670[b]	FM161093
SH146	*Dolichomitriopsis diversiformis* (Mitt.) Nog.	H, MHA	Nedoluzhko s.n.	AM990362; AF397777[a]	AY908329[b]	FM160963	FM161257	FM161098
B258	*Echinodium umbrosum* var. *glaucoviride*	Schäfer-Verwimp	Streimann 49634	EU434010	AY908269[b]	FM160965	AY908680[b]	EU477602
B196	*Forsstroemia trichomitria* (Hedw.) Lindb.	Buchbender	Streimann & Pocs 65120A	AM990365		FM160968	FM161260	FM161103
B349	*Heterocladium dimorphum* (Brid.) Schimp.	H	H3212307	AM990376		FM160970	FM161271	FM161115
B352	*Heterocladium procurrens* (Mitt.) A. Jaeger	H	H3212289	AM990379		FM160973	FM161274	FM161118
B310	*Himantocladium plumula* (Nees) M. Fleisch.	H	Tan et al. 92–232	AM990381		FM160976	FM161276	FM161122
B422	*Homalia glabella* (Hedw.) Schimp.	H	Townsend 93/291	AM990382		FM160977	FM161277	FM161123
B111	*Homalia lusitanica* Schimp.	B	B275202	AM990383		FM160978	FM161278	FM161124
B218	*Homalia trichomanoides* (Hedw.) Schimp.	Quandt	Olsson 105	AM990385	AY908276[b]	FM160980	FM161280	FM161126
B474	*Homalia webbiana* (Mont.) Schimp.	H	Müller K68	AM990387		FM160982	FM161282	FM161127
B110	*Homaliodendron exiguum* (Bosch & Sande Lac.) M. Fleisch	B	B263509	AM990389		FM160984	FM161284	FM161130
B230	*Homaliodendron flabellatum* (Sm.) M. Fleisch.	H	H3071675	FM210290	AY908271[b]	FM160985	AY908671[b]	FM161132
SH249	*Homaliodendron microdendron* (Mont.) M. Fleisch.	H	Redfearn, Jr. 35901	AM990390		FM160987	FM161285	FM161133
SH103	*Lembophyllum clandestinum* (Hook. f. & Wilson) Lindb. in Par.	H	Vitt 29644	AM990401; AF397823[a]		FM160996	FM161295	FM161145
B131	*Leptodon smithii* (Hedw.) F. Weber & D. Mohr	B	B268385	AM990403	AY908261[b]	FM160997	FM161297	FM161147
B193	*Neckera complanata* (Hedw.) Huebener	Buchbender	Buchbender 204	AM990413		FM161005	FM161305	FM161158
B128	*Neckera himalayana* Mitt.	B	B253876	FM210301	FM882219	FM161010	FM882223	FM161163
B347	*Neckera pennata* Hedw.	H	H3203794	AM990414	AY908265[b]	FM161016	–	FM161169
B250	*Neckera polyclada* Müll. Hal.	H	Koponen 45441	FM210307	FM882220	FM161017	FM882224	FM161170
B307	*Neckera remota* Bruch & Schimp. ex Müll. Hal.	S	B29895	AM990415		FM161018	FM161307	FM161171
SH301	*Neckera urnigera* Müll. Hal.	S	B15194	AM990416		FM161021	FM161308	FM161174
B247	*Neckeropsis calcicola* Nog.	H	Enroth 64632	AM990417		FM161025	FM161309	FM161178
B138	*Neckeropsis calcutensis* (M. Fleisch.) Enroth	H	H3212832	AM990418		FM161026	FM161310	FM161179
B313	*Neckeropsis nitidula* (Mitt.) M. Fleisch.	S	B105713	AM990419		FM161030	FM161311	FM161183

Code	Taxon	Herb.	Voucher					
B476	Pendulothecium punctatum (Hook. f. & Wilson) Enroth & S. He	S	Streimann 53845	AM990421		FM161033	FM161314	FM161187
B242	Pinnatella alopecuroides (Mitt.) M. Fleisch.	Enroth	Schäfer-Verwimp 16824	AM990423		FM161034	FM161315	FM161188
B150	Pinnatella minuta (Mitt.) Broth.	H	Rikkinen et al. 32	AM990424		FM161040	FM161316	FM161194
B309	Pinnatella mucronata (Bosch & Sande Lac.) M. Fleisch.	S	Hedenäs MY92-22	AM990425		FM161041	FM161317	FM161195
B294	Porotrichodendron superbum (Taylor) Broth.	H	H3121100	AM990427		FM161043	FM161319	FM161198
B098	Porotrichum bigelovii (Sull.) Kindb.	B	B230549	–		–	FM161320	–
B244	Porotrichum bigelovii (Sull.) Kindb.	H	Shevock & Kellman 27467	AM990428		FM161045	–	FM161200
B369	Porotrichum fruticosum (Mitt.) A. Jaeger	H	Shevock 28269	AM990430		FM161047	FM161322	FM161202
B559	Rigodium pseudothuidium Dusén	NYBG	NYBG 00892248		AM990437	FM161051	FM161328	FM161210
Rp47	Rigodium pseudothuidium Dusén	H	H3134254		AM990438; AF543547	–	–	–
B149	Taiwanobryum speciosum Nog.	H	Enroth 64877	AM990442	AY908272[b]	FM161055	FM161332	FM161216
B238	Thamnobryum alopecurum (Hedw.) Nieuwl. ex Gangulee	Buchbender	Buchbender s.n. 11.7.2003	AM990444	AF023834[b]	FM161056	FM161334	FM161218
B546	Thamnobryum ellipticum (Bosch & Sande Lac.) Nieuwl	Enroth	Müller S114	FM210325	AY908270[b]	FM161058	AY908674[b]	FM161220
SH300	Thamnobryum maderense (Kindb.) Hedenäs	S	B44108	AM990445		FM161061	FM161335	FM161223
B148	Thamnobryum subserratum (Hook. ex Harv.) Nog. & Z. Iwats.	H	Enroth 64595	AM990446		FM161067	FM161336	FM161230
B429	Thamnobryum tumidicaule (K.A. Wagner) F.D. Bowers	H	H3141850	AM990447		FM161068	FM161337	FM161231
B261	Touwia laticostata Ochyra	Quandt	Cairns 27.8. 2005	FM210330	FM882221	FM161070	FM882225	FM161233
SH15	Weymouthia mollis (Hedw.) Broth.	H	Streimann 58249	–		–	FM161341	–
DQ	Weymouthia mollis (Hedw.) Broth.	CHR, Quandt	99-Mo2	AM990452	AY307014[b]	FM161072	–	FM161237

[a] In two cases, sequences had been submitted to GenBank in a previous study, thus there are two accession numbers in the "*rps4–trnT*; *trnL–trnF*" column

[b] Denotes sequences obtained from GenBank, i.e. from specimens other than those listed in unmarked cells of the respective line
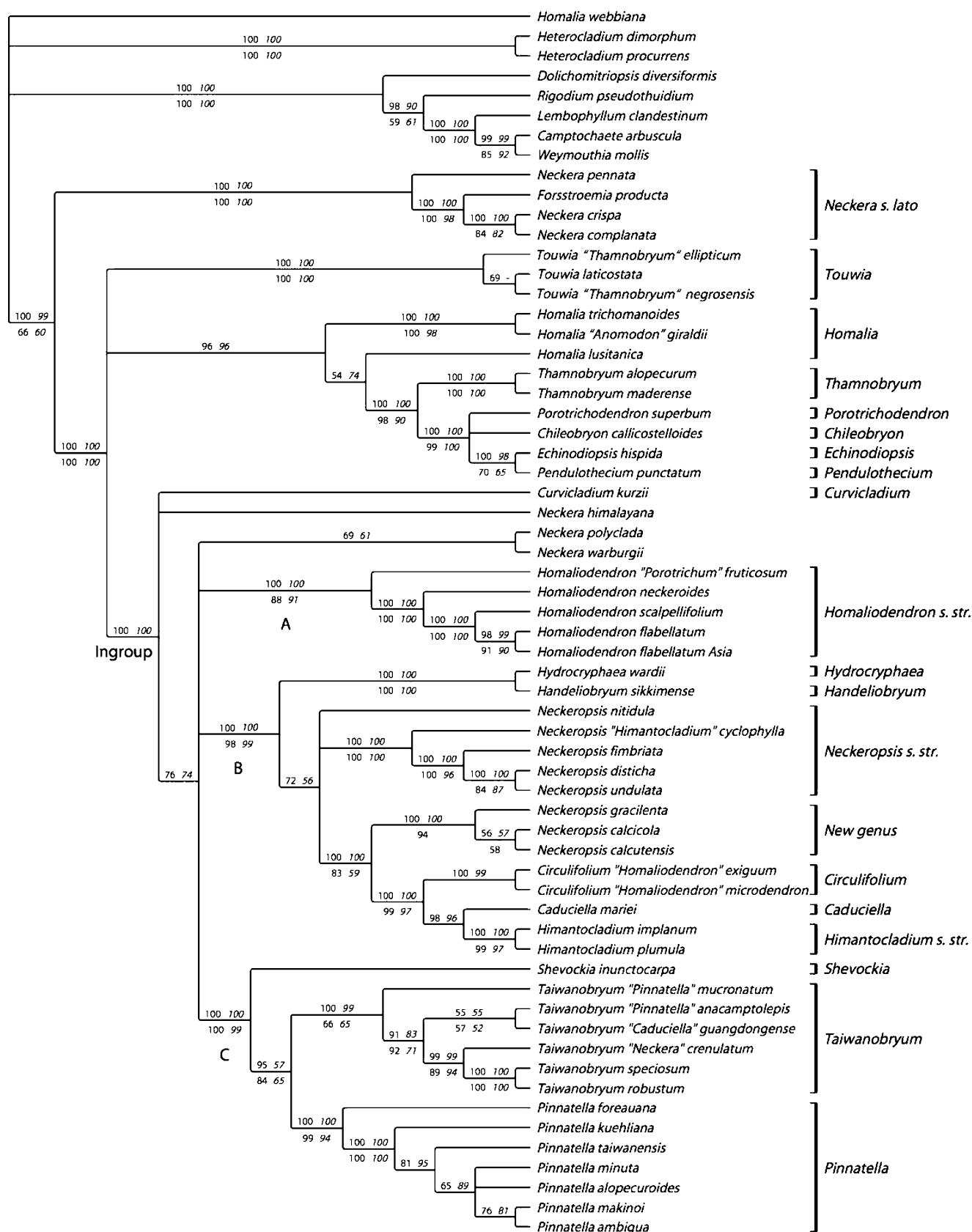
Fig. 1 Phylogenetic relationships among selected Neckeraceae taxa based on *rps4-trnT-trnL-trnF*, *rpl16*, and ITS1&2 sequences. Posterior probability values from Bayesian inference indicated above branches; bootstrap values from parsimony analysis below branches, where applicable (respective *left* value, with indel coding; *right* value, without indel coding)

Himantocladium and *Neckeropsis* species are situated within this clade, the relationships within the clade render these genera non-monophyletic. *Caduciella*, with just two species, also turns out to be polyphyletic, because one of the species referred to this genus is found in the next clade. The third clade (C) is highly supported in the analyses (PP 100 / 100, BS 100 / 99). It includes all *Pinnatella* species as well as *Caduciella guangdongensis*, *Neckera crenulata*, *Shevockia inunctocarpa*, *Taiwanobryum speciosum* and *T. robustum*. *Shevockia inunctocarpa* is resolved as the sister-group to the remaining species in the clade. *Pinnatella* is paraphyletic, since the *Pinnatella* species are divided among two clades. The bigger clade (*Pinnatella* sensu stricto) receives good statistical support (PP 100 / 100, BS 99 / 94). Two species (*P. mucronata*, *P. anacamptolepis*) as well as *Neckera crenulata* and *Caduciella guangdongensis* group with *Taiwanobryum*, with lower support.

The results from the second set of analyses, which were performed to resolve the relationships within the Neckeraceae in a wider framework and focused on the problematic placements of *Homalia* and *Touwia*, are illustrated in Fig. 2. In the Bayesian analyses without indel coding *Homalia lusitanica* forms a clade together with *Homalia trichomanoides* and *Anomodon giraldii*, but the support remains low (PP 74). Furthermore, this analysis suggests that both *Touwia* and the *Homalia-Anomodon* clade belong to the 'Pinnatella' clade (i.e. the ingroup species treated in the current study), even if the position does not receive statistical support. The exact position of these taxa is a particularly difficult problem to solve, since even the five markers used do not provide enough information to resolve their position reliably. The Bayesian analysis without an indel-coding approach had the highest resolution, thus is shown in Fig. 2, the latter also including support values from the other analyses.

Discussion

Phylogenetic analyses and taxonomic relationships

The analyses by Olsson et al. (2009a, 2009b) resulted in a robust backbone structure for the Neckeraceae. This was used to guide the taxon sampling for further analyses and showed that more detailed analyses with additional molecular data were needed to resolve the circumscriptions of the genera belonging to the 'Pinnatella' clade, since some genera (e.g. *Pinnatella* and *Neckeropsis*) appeared to be polyphyletic. In the present study the outgroup species form groups that are congruent with earlier studies (Olsson et al. 2009a, 2009b). The inclusion of *Anomodon giraldii* and the genus *Touwia* in the backbone data set clarified the

branching order and the relationships of the sister-groups of the 'Pinnatella' clade. In the more detailed study, taxon sampling for the 'Pinnatella' clade was increased and the phylogenetic relationships turned out to be more complicated than they had appeared at first glance, resulting in the loss of resolution in some branches. This is a natural consequence of adding more taxa and using fewer markers. However, no true conflicts exist between the results of our different analyses, since the apparently conflicting branches are not statistically supported, except for the position of the *Homalia* clade. Our present results contradict previous results by Olsson et al. (2009a) regarding the placement of *Homalia lusitanica*, since in the previous study this species formed a clade with *H. trichomanoides* with maximum support. The analysis based on more extensive sequence data resolves this incongruence and supports, at least weakly, a clade including the two *Homalia* species together with *Anomodon giraldii*. This demonstrates that even when a laborious sequencing effort was undertaken, resulting in an alignment including almost 4,000 positions, additional sequence data were needed to resolve a few remaining questions regarding the phylogenetic relationships within the family. Based on these results we suggest that *Anomodon giraldii* be included in the genus *Homalia*.

Ingroup relationships and previous major treatments of the genera in the *Pinnatella* group

According to the results of the present study, *Homaliodendron exiguum* and *H. microdendron* are close to each other but not to the other *Homaliodendron* species, thus should be placed in a separate genus (see the chapter on "Taxonomic and nomenclatural changes" below). Due to the polyphyly of *Caduciella*, *Himantocladium*, *Homaliodendron*, *Neckeropsis*, *Pinnatella*, *Shevockia* and *Taiwanobryum*, we also suggest some changes to the respective generic delimitations. As *Thamnobryum ellipticum* and *T. negrosense* are clearly resolved inside the genus *Touwia*, new combinations for both taxa will be provided in the section on "Taxonomic and nomenclatural changes" below.

Clade A

Homaliodendron Homaliodendron is a tropical genus, with the centre of diversity in Asia. The type of the genus is *H. flabellatum*. Ninh (1984) revised the Indochinese taxa and recognized ten species, but Enroth (1989b) found that some of them could not be distinguished from the highly variable and wide-ranging *H. flabellatum*. The genus was divided in the sections *Homaliodendron* and *Circulifolia* by Fleischer (1905–1906), and Ninh (1984) followed that arrangement. Given the apparent high variability of *H. flabellatum*

(Enroth 1989b), the species number in *Homaliodendron* was estimated at about 12 by Enroth (1994a), with two species in section *Circulifolia* and the remainder in section *Homaliodendron*. All species of *Homaliodendron* are stipitate-frondose (*H. exiguum* not distinctly so) and have appressed, usually overlapping stipe leaves. In the stems a central strand is not differentiated. The leaf dentation is very coarse in section *Homaliodendron*, in which there are large, multicellular teeth in the apical parts of the leaves, whereas in section *Circulifolia* the marginal teeth are small and unicellular. All species are dioicous. The seta is 1.5–4.5 mm long (Ninh 1984), smooth or in the upper part mammillose, and yellow. The capsules are exserted, orthotropous and symmetric and have 5–12 stomata in the apophysis (Ninh 1984). The peristome is of the reduced, i.e. neckeroid type. The lower dorsal plates of the exostome teeth are often somewhat cross-striolate, and their upper parts, as well as the endostome segments, are variably papillose. *Homaliodendron piniforme* (see Enroth 1990b), which occurs in Africa and South America, has been shown not to belong within the Neckeraceae (Olsson et al. 2009a).

Due to its demonstrated polyphyly, *Homaliodendron* has to be divided in two genera. In *Homaliodendron* sensu stricto the type, *H. flabellatum*, is joined by *Homaliodendron scalpellifolium*, *H. neckeroides* and *Porotrichum fruticosum*. Our analyses included one exemplar of *H. flabellatum* from the Philippines and one from Honduras. Earlier, the Central and South American specimens had been called *H. decompositum* and the Asian ones *H. flabellatum*, but the two names were synonymised by Enroth (1989b), which has been followed by others (e.g. Buck 1998). The American plants display much more homogeneous morphology than the Asian ones (J. Enroth, pers. obs.). They resemble specimens from the Pacific island groups (such as Hawaii); the species may have dispersed via those islands to tropical America. It is noteworthy that, as reported by Buck (1998), sporophytes are unknown from the American plants, although they are not rare in Asia. Thus *H. flabellatum* probably reproduces only by asexual propagulae in tropical America.

Homaliodendron neckeroides was so named by Brotherus (1929), but treated as *Neckera neckeroides* by Enroth and Tan (1994) based mainly on the sporophyte and perichaetial leaf characters, especially the immersed capsule typical in *Neckera* but not encountered in any other species of *Homaliodendron*. Our results indicate that the original placement and name, *Homaliodendron neckeroides* Broth., are correct and should be reinstated.

Porotrichum fruticosum is resolved as the sister group to the four *Homaliodendron* species in this clade, but differs from them mainly in the spreading rather than appressed stipe leaves and a much longer seta (>1.5 cm, whereas in

the other species it does not exceed c. 4.5 mm). In addition, it has a higher (c. 130 μm) endostome basal membrane with reduced cilia between the segments. Cilia are lacking in the other *Homaliodendron* species. However, *P. fruticosum* differs much more from the rest of the *Porotrichum* species. It occurs only in the Himalayan general region, while no other species of *Porotrichum* is known from Asia. Furthermore, the lack of a central strand in the stem (also lacking in *Homaliodendron*), the very thick-walled and porose laminal cells (also found in *Homaliodendron* sensu stricto), and the large composite marginal teeth in the leaves (present in some species of *Porotrichum* but much more pronounced in and typical of *Homaliodendron* sensu stricto) all suggest a close relationship with *Homaliodendron* sensu stricto. Since it is clearly not justified to keep this species in *Porotrichum* or to establish a new genus for it, we transfer it to *Homaliodendron*.

Clade B

The members of the second group in *Homaliodendron* sensu lato, *H. microdendron* and *H. exiguum*, belong to clade B; thus, a new genus is warranted to accommodate them. Fleischer (1905–1906) placed them in his *Homaliodendron* sect. *Circulifolia*, therefore we propose to elevate the section to generic rank (see chapter on "Taxonomic and nomenclatural changes"). They differ from *H. flabellatum* and its allies (cf. Enroth 1989b; Ninh 1984) in typically being smaller, having more strongly complanate leaves, in the minute, crenulate leaf dentation, in the filiform rather than leaf-like pseudoprapaphyllia, and in the relatively thin-walled, non-porose laminal cells. The sporophytes do not markedly differ.

Handeliobryum and Hydrocryphaea In a detailed taxonomic analysis of *Handeliobryum*, Ochyra (1986) recognized only one species and placed it in the Thamnobryaceae. *Handeliobryum sikkimense* is a rheophytic moss growing in fast-flowing streams in the Himalayan region, including Yunnan in China. It is a very stout, rigid plant, with a dendroid habit, well-differentiated stipe leaves, a very strong costa, and a bistratose leaf lamina with multistratose margins.

Hydrocryphaea was originally (Dixon 1931) placed in the Cryphaeaceae, as the generic name reflects. Manuel (1975) thought it was related to the 'thamnobryoid'
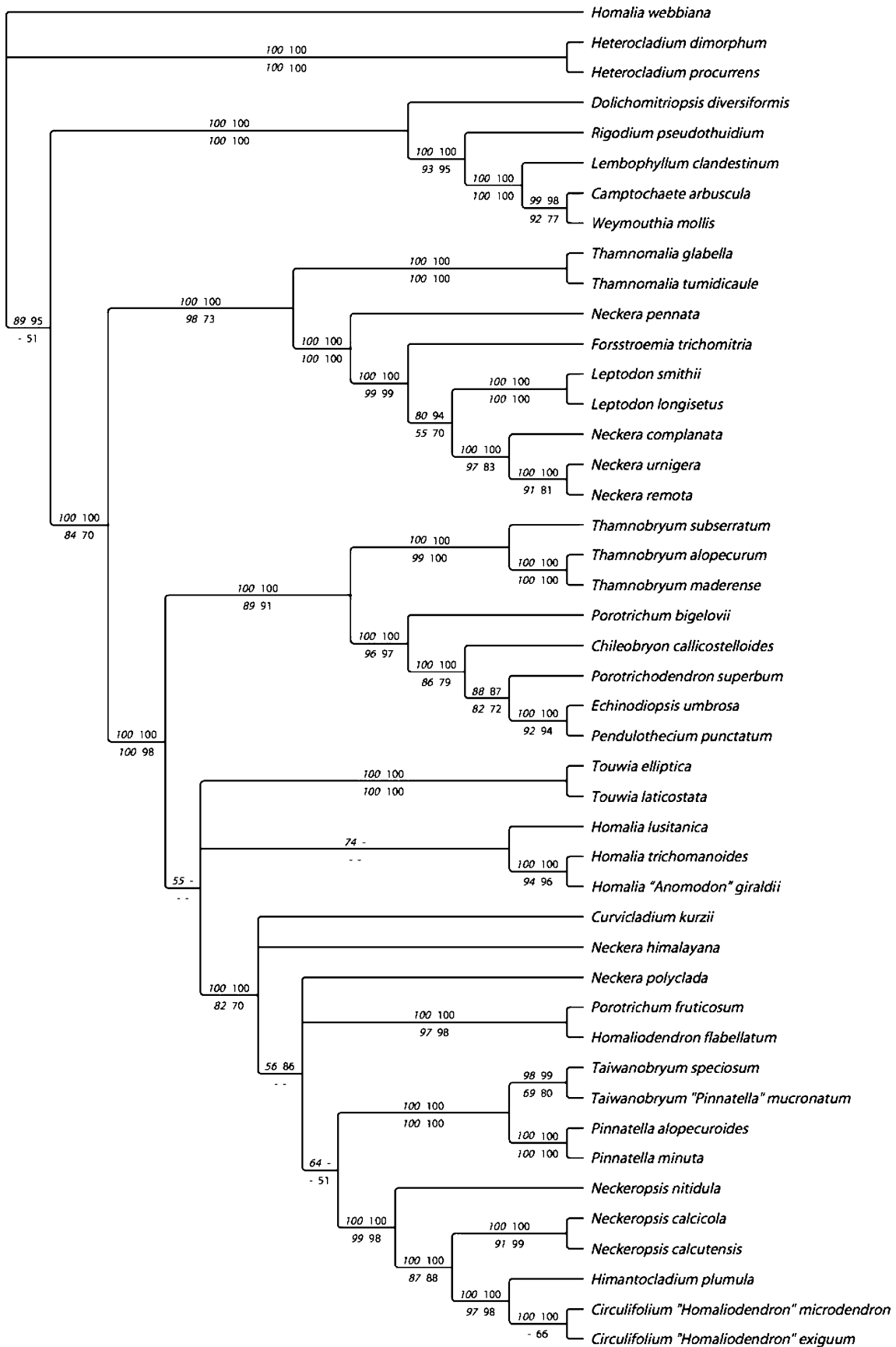
Neckeraceae, a view agreed with by Enroth (1999). The single species, *H. wardii*, is known from North India, China (Yunnan), North Vietnam and North Laos, and recently several new locations have been spotted especially in Yunnan (Shevock et al. 2006). It grows at least periodically submerged in flowing water. It is a rigid plant with a strong, subpercurrent costa in the weakly limbate leaves. The seta is just up to 0.2 mm long, rendering the erect capsule deeply immersed among the perichaetial leaves. The peristome is reduced, basically of the 'neckeroid' type, but there is no basal membrane in the endostome (Shevock et al. 2006).

Handeliobryum and *Hydrocryphaea* are both Asian taxa growing in flowing water and in the same general area. Even if some of the characters that the species share may have evolved independently due to the similar habitats, the molecular data support them being closely related. Yet their gametophytes differ (cf. Ochyra 1986; Shevock et al. 2006); thus, there is no justification for uniting the species in one genus, particularly since the sporophytes of *Handeliobryum* remain undescribed.

Neckeropsis As currently defined, *Neckeropsis* is a pan-tropical genus with 27 species. The majority of the taxa are Asian (Ochyra and Enroth 1989; Touw 1962, 1972; Touw and Ochyra 1987), but there are four species in South America (Enroth 1995; Sastre-De Jesús 1987) and eight in Africa (Enroth 1993b; Enroth and Magill 1994). The section *Pseudo-Paraphysanthus* of *Neckeropsis* consists of rheophytic taxa with several morphological adaptations to the harsh environment (Enroth 1999; Higuchi et al. 1989; Ochyra and Enroth 1989). In the papers cited above, the genus has been revised separately for South America, Africa and Asia-Oceania, but it has not been subjected to rigorous phylogenetic analysis. *Neckeropsis* consists of non-stipitate (except *Himantocladium cyclophyllum*), typically remotely and irregularly branched plants with a complanate, "pseudotetrastichous" (Touw 1962) foliation and lacking a central strand in the stem. The leaves can be undulate or not, and the leaf apex is mostly obtuse, rounded or truncate. The sexual condition varies with the species. Post-fertilization growth of the perichaetial leaves is common and often considerable. In some species the perichaetial paraphyses become leaf-like and multiseriate; they have been called "ramenta" (e.g. Buck 1998; Sastre-De Jesús 1987). The seta is short, rendering the sporophytes immersed in most species. The capsules are orthotropous and symmetrical, and the peristome is of the reduced neckeroid type with spiculose-papillose exostome teeth and endostome segments, and lacking cilia. The type is *Neckeropsis undulata*.

According to our results, *Neckeropsis* sensu lato is polyphyletic and divided in two genera. To *Neckeropsis*

sensu stricto belong *N. undulata, N. disticha, N. fimbriata*, and *Himantocladium cyclophyllum*. While *N. disticha* and *N. undulata* are synoicous, *H. cyclophyllum* and *N. fimbriata* are dioicous. All species in this group have a fairly strong costa, but the leaves can be either distinctly undulate (*N. fimbriata, N. undulata*) or not. A synapomorphy shared by *N. disticha, N. undulata* and *N. fimbriata* is the presence of ramenta, or modified, leaf-like paraphyses. Such paraphyses are absent in *H. cyclophyllum* and in all species in the other '*Neckeropsis*' clade. There are, however, three more species in Asia (not included in the current study) that also have ramenta: *N. andamana, N. crinita* and *N. nano-disticha* (Touw 1962). It remains to be determined if those three also belong in *Neckeropsis* sensu stricto. One feature that seems to be common to all species of *Neckeropsis* sensu lato is the absence of apophysal stomata (Touw 1962), but this needs to be confirmed.

The basal *Himantocladium cyclophyllum* is somewhat anomalous in this genus, since it is stipitate, has non-auriculate leaves and an exserted capsule with apophysal stomata, and lacks ramenta. However, the support for the clade is maximal.

In the other, still undefined genus, which includes *N. calcicola, N. gracilenta* and *N. calcutensis*, all species are dioicous. The last of these species was treated in *Neckeropsis* by Enroth (1990a), but due to some morphological characters (especially the leaf areolation strongly reminiscent of *Pinnatella alopecuroides*) it was later placed in *Pinnatella* (Enroth 1994c). Although *Neckeropsis* as currently circumscribed is clearly polyphyletic, we do not feel it justified to make any taxonomic rearrangements yet, mainly because our analysis contains only seven of the 27 species. Also, the genus containing *N. calcicola, N. gracilenta* and *N. calcutensis* appears as very heterogeneous morphologically; therefore, more taxa must be sampled in it. Furthermore, *Neckeropsis nitidula* is closely related to the other *Neckeropsis* species but remains in an unresolved position.

Himantocladium The tropical genus *Himantocladium* was established by Fleischer (1906–1908) and revised by Enroth (1992), who recognized eight species. The latter author subdivided the genus in the two sections *Himantocladium* with five synoicous species, and *Cyclophyllum* with three dioicous species. Enroth (1994b) transferred one of the dioicous species (*H. warburgii*) back to its original genus *Neckera*, leaving *Himantocladium* with seven species. In our analysis *Neckera warburgii* forms a clade with *N. polyclada*, but the clade is in an unresolved position and weakly supported; consequently no taxonomic changes are made here.

Himantocladium is an Asian-Oceanian genus, with just one species present in the Seychelles. A close relationship

between *Himantocladium* and *Neckeropis* was emphasized by Touw (1962) as well as by Enroth (1989a); these authors also discussed the generic distinctions. *Himantocladium* is characterized by the following combination of character states: stipitate-frondose plants, with the fronds usually branching sub-pinnately or pinnately; absence of a central strand in the stem; appressed, overlapping stipe leaves; fairly strong, single costa; absence of post-fertilization growth of the perichaetial leaves; a straw-yellow seta usually up to 2.0 (rarely 2.5) mm long; orthotropous, symmetrical capsules that have 2–3 apophysal stomata; and a reduced, spiculose-papillose 'neckeroid' peristome. The type is *Himantocladium implanum*.

In the present paper we transfer *H. cyclophyllum* to *Neckeropis*. This leaves *Himantocladium* with six species, only one of which (*H. formosicum*, endemic to Taiwan) is dioicous. The relationships of *H. formosicum* require further study.

Caduciella Caduciella was described and placed in the Leptodontaceae by Enroth (1991) to accommodate a single species, *Caduciella mariei*, previously known as *Pinnatella mariei*. A second species (*C. guangdongensis*) from SE China was described as new 2 years later (Enroth 1993a). The total distribution area (of *C. mariei*) ranges from Tanzania to India and SE China, Thailand and Vietnam through Indonesia and New Guinea to Queensland in Australia; the species is also known from Micronesia. The two species of *Caduciella* are small, stipitate-frondose plants, with overlapping and appressed stipe leaves. There is no central strand in the stem. The costa is single and reaches to midleaf or above; the leaf margins are entire or serrulate near the leaf apex. The leaf cells are in distinct rows and the pseudoparaphyllia are numerous and leaf-like. The species are also connected by the presence of caducous distal branch leaves, often leaving the branch tips naked. This type of vegetative propagation is uncommon in the Neckeraceae as a whole. Sporophytes are unknown from both species.

According to the current analyses, *Caduciella mariei* is closely related to *Himantocladium implanum* and *H. plumula*. Due to the much smaller size, entire leaf margins, leaf areolation, numerous leaf-like pseudoparaphyllia, and caducous leaves we recognize *Caduciella* as a genus distinct from *Himantocladium* and encompassing only *C. mariei*; *Caduciella guangdongensis* is now excluded.

Clade C

Pinnatella and Shevockia The pantropical genus *Pinnatella* was established by Fleischer (1905–1906) and monographed by Enroth (1994c). The latter author recognized 15 species, of which only *P. minuta* is pantropical, the other species being mainly Asian-Oceanic. Enroth subdivided the genus in the subgenera *Urocladium* with three species, and *Pinnatella* with 12 species. The subdivision resulted from a cladistic analysis based on 44 morphological characters (see also Hyvönen and Enroth 1994). That analysis did not support an earlier subdivision by Enroth (1989a), in which he had proposed a section *Tenuinervia* for two species (*P. anacamptolepis* and *P. mucronata*) which, in contrast to the remainder of *Pinnatella*, share a relatively weak costa and median laminal cells distinctly longer than the apical ones. The current number of species in *Pinnatella* is 13, since *P. calcutensis* actually belongs to *Neckeropis*, a placement advocated by Enroth (1990a) before the monographic study. *Pinnatella anacamptolepis* was transferred to the recently described genus *Shevockia* by Enroth and Ji (2006), but our current analysis does not support that placement. In general terms *Pinnatella* consists of stipitate-frondose plants with usually pinnately to bi-pinnately branched fronds. The stipe leaves are distinctly differentiated, not overlapping and spreading. The laminal cells are short and the marginal cells quadrate to short-elongate in a few to several rows; the cell corners often have small papillae. The costa is single and strong, often reaching near the leaf apex. All species for which gametangia are known are dioicous and there is no post-fertilization growth of the perichaetial leaves. The seta is straw-yellow, 2.0–4.5 mm long, straight and mammillose in the upper part. The capsule is orthotropous and symmetric, with up to five phaneroporous stomata in the apophysis. The peristome is double, reduced ('neckeroid-type'), with densely spiculose papillose exostome teeth and endostome segments. There are no cilia in the endostome. Vegetative propagation takes place through flagelliform, microphyllous branches produced in the leaf axils.

The genus *Pinnatella* sensu lato results as polyphyletic from the current study, requiring restriction of the name (*Pinnatella* sensu stricto) to the species grouping with the type, *P. kuehliana*. *Shevockia inunctocarpa* remains as the only representative of its genus, since *S. anacamptolepis* (= *Pinnatella anacamptolepis*) groups with *Taiwanobryum*. This well-supported *Taiwanobryum* clade also includes *Pinnatella mucronata*, *Neckera crenulata*, *Taiwanobryum speciosum*, *T. robustum* and *Caduciella guangdongensis*. Since the genus name *Caduciella* must be applied to the clade including the type, *C. mariei*, *Caduciella guangdongensis* needs to be renamed. We suggest to include it in the genus *Taiwanobryum* (see the chapter on "Taxonomic and nomenclatural changes"), along with all species in its clade.

Taiwanobryum Taiwanobryum in its previous circumscription, with two species (*T. speciosum* being the type), occurs in East Asia, from Japan through Taiwan and SE China to the Philippines and Borneo. It has usually been placed in the Prionodontaceae (e.g. Lai and Koponen 1981), but more

recently in the Leptodontaceae by Buck and Goffinet (2000), who included only *Prionodon* in the Prionodontaceae. In the phylogenetic analysis by Tsubota et al. (2002), *Taiwanobryum speciosum* appeared in the Neckeraceae, close to *Pinnatella ambigua*. Lai and Koponen (1981) suggested a close relationship between *Taiwanobryum robustum* and *Neolindbergia* (*brassii*), based mainly on the peculiar gemmate-tipped, axillary rhizoids. However, *Neolindbergia* is currently placed in the heterogeneous Pterobryaceae (Buck and Goffinet 2000) and was not included in the current study.

The gametophytic characters of the two species thus far constituting *Taiwanobryum* are very similar; the sporophyte of *T. robustum* remains unknown. The plants are relatively robust, sparsely branched, with a poorly defined stipe, have crowded, ovate-lanceolate leaves with coarsely toothed margins in the upper parts, a strong, single costa, strongly incrassate and, especially in *T. robustum*, porose walls of the laminal cells, an elongate seta that is mammillose in its upper part, an orthotropous, symmetrical capsule, and a reduced peristome with papillose exostome teeth and no endostome.

Adding the four species *T. crenulatum*, *T. mucronatum*, *T. anacamptolepis* and *T. guangdongense* renders *Taiwanobryum* far more heterogeneous and difficult to define morphologically, especially relative to *Pinnatella*. The robust *T. crenulatum* fits relatively well with *T. speciosum* and *T. robustum*, but the three other taxa pose problems in this grouping. Among themselves, they form a morphologically 'acceptable' group, being relatively small, often densely branched, with a relatively weak costa mostly ending near midleaf, and slightly asymmetric leaves with mucronate apices. However, at the same time they differ markedly from each other. For example, the stipe leaves of *T. mucronatum* are spreading and not overlapping, while in the two other species they are overlapping, squarrose in *T. anacamptolepis* and appressed in *T. guangdongense*. *Taiwanobryum mucronatum* has a stem central strand, while the two other species do not. The leaf cell walls are incrassate and porose in *T. anacamptolepis*, but thinner and non-porose in the other two species. The pseudoparaphyllia of *T. anacamptolepis* and *T. guangdongense* are numerous, but *T. mucronatum* has much fewer of them. The sporophyte is known only for *T. mucronatum*, and closely resembles that in *Pinnatella*, but has a clearly more strongly mammillose seta (Enroth 1994c).

Taxonomic and nomenclatural changes

Circulifolium S. Olsson, Enroth & D. Quandt, gen. nov.

Type Circulifolium microdendron (Mont.) S. Olsson, Enroth & D. Quandt.

Diagnosis Genus hoc ab *Homaliodendron* praecipue statura plantae minore, foliis valde complanatis, cellulis foliorum non porosis, dentibus unicellularis foliorum, apicibus foliorum rotundatis vel truncatis, apicibus obtusis foliorum perichaetialium et pseudoparaphylliis filiformibus differt.

Circulifolium exiguum (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Homalia exigua Bosch & Sande Lac. in Dozy & Molk., Bryol. Jav. 2: 55. 1862; *Thamnium exiguum* (Bosch & Sande Lac.) Kindb., Hedwigia 41: 240. 1902; *Homaliodendron exiguum* (Bosch & Sande Lac.) M. Fleisch., Musci Fl. Buitenzorg 3: 897. 1908.

Circulifolium microdendron (Mont.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Hookeria microdendron Mont., Ann. Sci. Nat. Bot. sér. 2(19): 240. 1843; *Hypnum microdendron* (Mont.) Müll. Hal., Syn. Musc. Frond. 2: 231. 1851; *Homaliodendron microdendron* (Mont.) M. Fleisch., Hedwigia 45: 78. 1906.

Homalia giraldii (Müll. Hal.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Anomodon giraldii Müll. Hal., Nuov. Giorn. Bot. Ital. n. ser. 3: 117. 1896.

Homaliodendron fruticosum (Mitt.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Porotrichum fruticosum (Mitt.) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1875–76: 306, Sp. Musc. 2. 1877.

Neckeropsis cyclophylla (Müll. Hal.) S. Olsson, Enroth & Quandt, comb. nov.

Basionym Neckera cyclophylla Müll. Hal., Syn. Musc. Frond. 2: 664. 1851; *Thamnium cyclophyllum* (Müll. Hal.) Kindb., Hedwigia 41: 224. 1902; *Himantocladium cyclophyllum* (Müll. Hal.) M. Fleisch., Musci Fl. Buitenzorg 3: 887. 1908.

Taiwanobryum anacamptolepis (Müll. Hal.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Neckera anacamptolepis Müll. Hal., Syn. Musc. Frond. 2: 663. 1851; *Thamnium anacamptolepis* (Müll. Hal.) Kindb., Hedwigia 41: 251. 1902; *Pinnatella anacamptolepis* (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3):

857. 1906; *Shevockia anacamptolepis* (Müll. Hal.) Enroth, J. Hattori Bot. Lab. 100: 74. 2006.

Taiwanobryum crenulatum (Harv.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Neckera crenulata Harv. in Hook., Icon. Pl. Rar. 1: 21. f. 6. 1836.

Taiwanobryum guangdongense (Enroth) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Caduciella guangdongensis Enroth, Bryologist 96: 471. 1994.

Taiwanobryum mucronatum (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Neckera mucronata Bosch & Sande Lac. in Dozy & Molk., Bryol. Jav. 2: 68. 1863; *Porotrichum mucronatum* (Bosch & Sande Lac.) Broth., Monsunia 1: 49. 1899; *Thamnium mucronatum* (Bosch & Sande Lac.) Kindb., Hedwigia 41: 249. 1902; *Pinnatella mucronata* (Bosch & Sande Lac.) M. Fleisch., Hedwigia 45: 80. 1906.

Touwia elliptica (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Porotrichum ellipticum Bosch & Sande Lac., Bryol. Jav. 2: 70. 1863; *Thamnium ellipticum* (Bosch & Sande Lac.) Kindb., Hedwigia 41: 247. 1902; *Thamnobryum ellipticum* (Bosch & Sande Lac.) Nog. & Z. Iwats., J. Hattori Bot. Lab. 36: 470. 1972; *Parathamnium ellipticum* (Bosch & Sande Lac.) Ochyra, Fragm. Flor. Geobot. 36(1): 77. 1991.

Touwia negrosensis (E.B. Bartr.) S. Olsson, Enroth & D. Quandt, comb. nov.

Basionym Thamnium negrosense E.B. Bartr., Philipp. J. Sci. 68: 251. 1939; *Thamnobryum negrosense* (E.B. Bartr.) Z. Iwats. & B.C. Tan, Miscell. Bryol. Lichenol. 7(7): 152. 1977; *Parathamnium negrosense* (E.B. Bartr.) Ochyra, Fragm. Flor. Geobot. 36(1): 77. 1991.

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