Neckera and *Thamnobryum* (Neckeraceae, Bryopsida): Paraphyletic assemblages

Sanna Olsson,[1,2,6] Johannes Enroth,[3] Volker Buchbender,[1,6] Lars Hedenäs,[4] Sanna Huttunen[4,5] & Dietmar Quandt[1,6]

1 *Institute of Botany, Plant Phylogenetics and Phylogenomics Group, Dresden University of Technology, 01062 Dresden, Germany*
2 *Department of Agricultural Sciences, P.O. Box 27, 00014 University of Helsinki, Finland*
3 *Department of Biosciences and Botanical Museum, P.O. Box 7, 00014 University of Helsinki, Finland*
4 *Department of Cryptogamic Botany, Swedish Museum of Natural History, Box 50007, 104 05 Stockholm, Sweden*
5 *Laboratory of Genetics, Department of Biology, 20014 University of Turku, Finland*
6 *Nees Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany*
Authors for correspondence: *Sanna Olsson, sanna.olsson@helsinki.fi* and *Dietmar Quandt, quandt@uni-bonn.de*

Abstract Recent phylogenetic analyses indicated that the backbone phylogeny of the pleurocarpous moss family Neckeraceae falls into three distinct clades. Here the detailed composition and phylogenetic relationships of the two major clades (the *Neckera* clade and the *Thamnobryum* clade) are analysed. The phylogenetic analyses, based on sequence data from the plastid *rpl16* intron and the *rps4-trnT-trnL-trnF* cluster as well as the nuclear ITS1 and 2, retained this tripartition and revealed a strong biogeographic pattern, especially inside the *Neckera* clade. In addition, several morphological characters that have been held as unique and characteristic to a certain group of mosses and therefore valuable in taxonomic classification, were shown to be highly homoplastic and subjected to convergent evolution. Consequently, the circumscriptions of *Leptodon* and *Thamnobryum* are amended, the new genera *Exsertotheca*, *Echinodiopsis* and *Thamnomalia* (each with two species), and *Alleniella* (with ten species) are formally described and several implied nomenclatural changes are proposed, including synonymisation of *Alsia* with *Neckera* and *Cryptoleptodon* with *Leptodon*.

Keywords convergent evolution; molecular phylogeny; nomenclature; pleurocarpous mosses; taxonomy

■ INTRODUCTION

With around 5000 species, pleurocarpous mosses represent the largest radiation of early land-plants that occur in nearly all terrestrial ecosystems. Typically they have a creeping, profusely branching habit, and the sporophyte development takes place in the apices of short, lateral branches. This contrasts to the so-called acrocarpous condition, in which the sporophytes develop at the apices of the main shoots. As defined by Bell & al. (2007) the pleurocarpous mosses form a monophylum ("core pleurocarps") with four orders: Hypnodendrales, Ptychomniales, Hookeriales and Hypnales.

The moss family Neckeraceae belongs to the order Hypnales. The family consists of temperate and tropical taxa, with the total species number estimated to be ca. 200 (Enroth, 1994a; Olsson & al., 2009a). Most of the species are epiphytic or epilithic, but there are also a few aquatic (rheophytic) species. Most typically Neckeraceae are large, glossy plants that have a creeping stolon bearing very small leaves and tufts of rhizoids located just below the leaf insertions, and more or less frondose (rarely dendroid) stems with or without distinct stipes. The leaf cells are almost always smooth, relatively short, and the marginal cells are typically quadrate to short-rectangular in few to several rows. The sporophyte features are variable but usually fairly consistent within genera. A more detailed morphological characterisation of the Neckeraceae was provided by Olsson & al. (2009b). According to the current classification by Goffinet & Buck (2004) the family comprises 28 genera, although detailed phylogenetic analyses based on a wider taxon sampling suggest that several of these genera, such as *Homaliadelphus* and *Bissetia* (both Miyabeaceae) or *Dixonia* (OPP-clade) belong elsewhere (Olsson & al., 2009a,b) and more changes in generic composition are expected. However, the most recent attempt to resolve the backbone phylogeny and broad relationships of Neckeraceae by Olsson & al. (2009b) identified three distinct clades. As one of the three, the well defined *Pinnatella* clade was already the focus of a detailed study that clarified most of the taxonomic and nomenclatural aspects in this group (Olsson & al., 2010). This paper focuses on the composition, phylogenetic relationships and nomenclature of the two remaining clades, containing the largest neckeraceous genera (*Neckera*, *Thamnobryum*) that were used to denominate each clade (Olsson & al., 2009b).

Members of both the *Neckera* and *Thamnobryum* clades as defined by Olsson & al. (2009b) are mainly non-Asiatic and non-tropical, although the *Neckera* clade includes some species which have a wide, often disjunct (possibly relict) distribution, e.g., *Leptodon smithii*, *Forsstroemia trichomitria* and *F. producta*. Most species of the *Neckera* clade sensu Olsson & al. (2009b) have a weak costa and immersed capsules with reduced peristomes and the teeth at the leaf margins are usually unicellular. In the *Thamnobryum* clade sensu Olsson & al. (2009b) the few truly tropical taxa are almost exclusively limited to South America. The members of this clade are typically fairly robust, distinctly stipitate, and have a single, at least relatively strong costa. In addition, the setae are long (capsules exserted) and the peristomes are well developed, perfect or only somewhat reduced (in *Porotrichodendron*) but not as strong as in the *Neckera* clade.

Due to different concepts of character evolution, i.e., different weighting of morphological characters, the taxonomic placement of several species and genera that have been discussed in relation to Neckeraceae was subjected to various changes in the past. In order to avoid a lengthy discussion we provide a historical overview presenting the relevant treatments dealing with genera inside the *Neckera* and *Thamnobryum* clades sensu Olsson & al. (2009b). The historical overview (Table 1) that summarises the distribution, morphology and systematic placement of these genera, reflects fluctuations in the systematic treatments according to changes in homology assumptions or simply different weighting schemes of morphological characters. In general, homology assessment is problematic in these rather inconspicuous organisms and convergent evolution almost exclusively assessable via molecular phylogenetics (e.g., Hedenäs, 2007; Olsson & al., 2009c; Sotiaux & al., 2009; Huttunen & Ignatov, 2010).

In contrast to vascular plants, classifications dealing with bryophytes are traditionally based on gametophytic as well as sporophytic characters, with the shorter-lived sporophyte generation being regarded as the evolutionarily more conservative one (e.g., Crum, 2001). The latter view, however, is currently changing, as molecular approaches in mosses reveal that gametophytic characters provide a better phylogenetic signal on family-level relationships than sporophytic ones, which seem to be prone to convergent evolution (e.g., Buck & al., 2000; Goffinet & al., 2004; Huttunen & al., 2004; Hedenäs, 2007; Hernández-Maqueda & al., 2008; Olsson & al., 2009b, Quandt & al., 2009).

Although reports of convergent evolution in bryophytes are scarce, recent studies indicate that this phenonemon is more common in mosses than previously thought (e.g., Olsson & al., 2009c; Sotiaux & al., 2009; Huttunen & Ignatov, 2010). The aquatic mosses that until recently were often placed in *Platyhypnidium* are a good example of a case where morphologically very similar species belong to several distinct evolutionary lineages (Huttunen & Ignatov, 2010). In contrast, the rheophilic *Thamnobryum alopecurum* populations differ considerably from the terrestrial ones to the point that they have been described as independent species, while molecular analyses revealed their independent origin from neighbouring terrestrial populations (Olsson & al., 2009c).

This study aims to evaluate whether the relationships suggested by the traditionally-used morphological characters in two major clades of the moss family Neckeraceae are congruent with the phylogenetic analyses based on molecular data.

■ MATERIALS AND METHODS

Taxon sampling and molecular markers. — The taxon sampling was intended to be representative and to completely cover the morphological variation within Neckeraceae. The results from earlier studies together with previous taxonomic classifications (e.g., Buck & Goffinet, 2000; Goffinet & Buck, 2004; Olsson & al., 2009a,b) were used as guidelines when choosing the species to be included. *Homalia webbiana*, *Heterocladium dimorphum* and *Heterocladium procurrens* together with representatives of Lembophyllaceae were used as outgroup since they seem to be the closest relatives of Neckeraceae (Olsson & al., 2009a,b; Quandt & al., 2009). For this selection of taxa we sequenced three genomic regions: the internal transcribed spacers of nuclear ribosomal DNA (ITS1 & 2), the plastid *rps4-trnT-trnL-trnF* cluster (including the 3′ of the *rps4* gene), and the group II intron in *rpl16* (plastid).

Two genera could not be included in the analyses due to lack of material. *Neomacounia nitida* is a monospecific genus based on the basionym *Forsstroemia nitida*. It is known only from two specimens from Ontario (Canada), collected in 1862 and 1864 (Ireland, 1974). The type locality and its surroundings were searched in the early 1970s to rediscover the taxon, but it was not found. It seems that *Neomacounia* is extinct. Based on the description by Ireland (1974) there is nothing in the morphology of *Neomacounia* that belies a placement in Neckeraceae; it is probably closely related to some *Neckera* species. *Noguchiodendron sphaerocarpum*, the single species of the genus, is distributed in the Himalayan region and Thailand. As discussed by Ninh & Pócs (1981), it is probably closely related to *Homaliodendron*, where it was originally placed, but it differs in certain morphological characters in the gametophyte (e.g., presence of a central strand in the stem) as well as in the sporophyte (e.g., capsule shape, presence of an annulus), justifying the maintenance of it as a separate genus. There was no adequately fresh material available to be included in the present molecular analyses.

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. Methods of cleaning and grinding of plants prior to extraction and amplification of the ITS1-5.8S-ITS2 as well as the *rps4-trnT-trnL-trnF* region followed Olsson & al. (2009a), whereas the protocols for *rpl16* were obtained from Olsson & al. (2009b). Gel-cleaned PCR products were sequenced by Macrogen Inc., South Korea (www.macrogen.com). Sequences were edited manually with PhyDE® v0.995 (Müller & al., 2005) and primer sequences were eliminated. All sequences are deposited in EMBL; accession numbers are listed together with voucher information in the Appendix.

Sequence analyses and phylogenetic analyses. — Alignment of the sequence data was performed manually in PhyDE® v.0.995 (Müller & al., 2005), based on the criteria laid out in Kelchner (2000), and Quandt & Stech (2005) using the alignment of Olsson & al. (2009a) as scaffold. As length variation of the sequence data was very low, alignment was straightforward. The reported hairpin-associated inversion in the *trnL-F* intergenic spacer (IGS) (Quandt & al., 2004; Quandt & Stech, 2005) 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 & al. (2003). Alignments are available on request from the authors. Indels were incorporated as binary data using a simple indel coding (SIC) strategy (Simmons & Ochoterena,

Table 1. Historical overview of the genera in the *Neckera* and *Thamnobryum* clades (plus *Touwia*), including remarks on species number, distribution, …

	Alsia	*Chileobryon*
Established	Sullivant (1855)	Enroth (1992b)
Further reference(s)	Lawton (1971)	–
Other placements	Cryphaeaceae, Leucodontaceae, Leptodontaceae	Anomodontaceae
No. of species	1	1
Distribution	NW North America	Chile
Leaf shape	ovate	ovate(-oblong)
Costa	short and double or single and to 3/4 of leaf length	single, to below leaf apex
Leaf cells	smooth	papillose
Cell walls	thick, porose	firm, not porose
Alar cells	distinct, transverse	indistinct
Paraphyllia	present	absent
Vegetative propagulae	absent	absent
Sexual condition	dioicous	dioicous
Seta	3–5 mm	?
Capsule	exserted, orthotropous	?
Peristome	reduced	?
	Homalia	*Leptodon*
Established	Schimper (1850)	Mohr (1803)
Further reference(s)	He (1997)	Pócs (1960); Nelson (1973); Enroth (1992a)
Other placements	–	Leptodontaceae
No. of species	5	4
Distribution	wide, tropical-temperate	wide, temperate, highly disjunct
Leaf shape	oblong-ovate to spatulate or nearly rounded, asymmetric	ovate(-oblong)
Costa	short and double or single and to c. 4/5 leaf length	single, to over midleaf
Leaf cells	smooth	smooth
Cell walls	firm, mostly not porose	firm, not porose
Alar cells	indistinct	fairly distinct, small
Paraphyllia	absent	present
Vegetative propagulae	flagelliform branches (uncommon)	absent
Sexual condition	dioicous (one sp. autoicous)	dioicous
Seta	8–20 mm	1.5–2.5 mm
Capsule	exserted, orthotropous or orthogonal	exserted, orthotropous
Peristome	perfect	reduced
	Porotrichopsis	*Porotrichum (incl. Porothamnium)*
Established	Herzog (1916)	Hampe (1863)
Further reference(s)	Enroth (1995)	Sloover (1983); Sastre-De Jesús (1987); Allen (1994)
Other placements	Thamnobryaceae	Thamnobryaceae
No. of species	1	ca. 15
Distribution	South America	Africa, South & Central America
Leaf shape	narrowly elliptic to nearly lingulate	ovate(-oblong)
Costa	single, to midleaf	single, to near leaf apex (rarely short)
Leaf cells	smooth	smooth or prorulose
Cell walls	firm, not porose	firm, not porose
Alar cells	small, thick-walled	indistinct
Paraphyllia	absent	absent
Vegetative propagulae	caducous leaves	flagelliform branches
Sexual condition	dioicous	dioicous
Seta	15–28 mm	ca. 5–30 mm
Capsule	exserted, orthogonal to homotropous	exserted, orthotropous
Peristome	slightly reduced	slightly reduced

… and prevalent morphological characters. ? = character unknown. Terminology for the capsule orientation follows Hedenäs (2007).

Cryptoleptodon	*Echinodium*	*Forsstroemia*
Renauld & Cardot (1900)	Juratzka (1866)	Lindberg (1863)
Buck (1980); Enroth (1992a); Hedenäs (1992)	Churchill (1986); Stech & al. (2008)	Stark (1987)
Leptodontaceae, Pterobryaceae	Echinodiaceae	Leucodontaceae, Leptodontaceae
4	6	10
India, East Africa, Macaronesia	Macaronesia, Australasia	wide, temperate-subtropical
ovate(-oblong)	ovate-subulate	ovate(-lanceolate)
single, to above mid-leaf	single, excurrent	single, variable in length
smooth/mammillose	smooth	smooth
firm, not porose	firm, not porose	firm, porose or not
fairly distinct, small	indistinct	distinct, quadrate to transverse
present	absent	absent
absent	absent	absent
dioicous	dioicous	dioicous or autoicous
1.5–6.0 mm	11–35 mm	to 4.6 mm
exserted, orthotropous	exserted, orthogonal to homotropous	immersed to exserted
reduced	perfect	reduced

Neckera	*Pendulothecium*	*Porotrichodendron*
Hedwig (1801)	Enroth & He (1991)	Fleischer (1906–08)
Sloover (1977); Sastre-De Jesús (1987)	–	Buck (1998)
–	–	Lembophyllaceae, Thamnobryaceae
ca. 50	3	2–3 (Churchill & Linares, 1995)
wide, mainly temperate	Australasia	Central & South America
variable, mostly ovate(-oblong), asymmetric	ligulate to spatulate or obovate	ovate(-oblong)
variable, often short and weak	single, to half or 5/6 of leaf length	single, to above midleaf
smooth	smooth	smooth
firm, porose or not	firm, not porose	firm, slightly porose
fairly indistinct, small	indistinct	small, thick-walled
mostly absent, sometimes present	absent	absent
flagelliform branches sometimes present	flagelliform branches sometimes present	flagelliform branches
dioicous or autoicous	dioicous	dioicous
0.5 to ca. 20 mm	13–14 mm	to ca. 40 mm
immersed or exserted, orthotropous	exserted, reclinate to antitropous	exserted, orthotropous
reduced	perfect	slightly reduced

Thamnobryum	*Touwia*	
Schimper (1852, as *Thamnium* hom. illeg.); Nieuwland (1917)	Ochyra (1986)	
Kindberg (1902); Ochyra (1990, 1991); Mastracci (2003)	Olsson & al. (2010)	
Thamnobryaceae	–	
ca. 35	3	
temperate, mainly Northern Hemisphere	Southeast Asia, Australasia	
ovate(-oblong), sometimes lanceolate or ligulate	lanceolate or elliptic	
single, to near leaf apex	single, to near leaf apex	
smooth, rarely mammillose	smooth	
firm, not porose	firm, not porose	
indistinct	indistinct	
absent	absent	
absent	absent	
dioicous, rarely polyoicous	dioicous	
ca. 10–25 mm	15–18 mm	
exserted, orthogonal to homotropous	orthogonal	
perfect	perfect	

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* v.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 1000 replicates and 10 random addition cycles per bootstrap replicate.

Bayesian analyses were performed with MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001), applying the $GTR+\Gamma+I$ model for the sequences data and the restriction site model for the binary indel partition. To allow for possible deviating substitution models for the different regions, the dataset was further divided into three sequence partitions (partition 1: *rps4-trnF*; partition 2: *rpl16*; partition 3: nuclear DNA). 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 & al. (2002) and Huelsenbeck & al. (2001). 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 1000 generations and the respective trees written to a tree file. Calculations of the consensus tree and of the posterior probability of clades were performed based upon the trees sampled after the chains converged (less than generation 50,000). Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph2 (Stöver & Müller, 2010).

In order to evaluate the monophyly versus para- or polyphyly of *Neckera* inside clade A, a topology test was conducted. Therefore a constrained analysis forcing *Neckera* to be monophyletic (not including the remote *Neckera* taxa of clade C: *N. himalayana*, *N. polyclada*, *N. warburgii*, and *N. crenulata*) using the program MrBayes v.3.1.2. was performed, and harmonic means of the likelihoods for both topologies were compared and evaluated using the Bayes Factor (BF; Kass & Raftery, 2007).

■ RESULTS

Alignment and sequence analyses. — In total 21 hotspots with poly-homonucleotid repeats were recognized following Olsson & al. (2009a) and excluded from the analyses (compare Table 2). The observed inversion was treated as reverse complement for the phylogenetic analyses (compare Table 2). Hotspots were more frequent in the plastid region (H1–17), while only four were found in the nrDNA (H18–21). The resulting combined and aligned sequence matrix contained 3464 positions of which 1476 positions belong to the *rps4-trnT-trnL-trnF* partition, 880 positions to the *rpl16* partition and 1106 positions to the nuclear ribosomal partition. Of the characters 2760 were constant and 405 characters were parsimony-informative. Including the data matrix based on indel coding raised the number of parsimony-informative characters to 547 (a total of 3808 characters with 1041 being variable).

Phylogenetic analyses. — The parsimony analysis without indel coding retained 56 most parsimonious trees (MPT, length 1489, consistency index CI = 0.556, retention index RI = 0.783). After inclusion of the indel matrix 25 MPTs were retained (length 2039, CI = 0.571, RI = 0.778). The strict consensus tree of both analyses showed no conflict with the results from the Bayesian inference (BI), but had less resolution compared to the BI tree. Therefore, only the BI tree is illustrated in Fig. 1, with posterior probabilities (PP) indicated and complemented with bootstrap values (BS) of the parsimony analysis when applicable. When the indel matrix was included in the analyses, the only topological difference observed was the poorly resolved position of the clade consisting of *Neckera crispa* and *N. intermedia*. However, differences in the magnitude of support values at some of the nodes were observed. Therefore, both the values without and with the indel matrix included are illustrated and discussed. Values resulting from analyses without indel coding precede the values from analyses with the SIC-matrix included. Thus support values from the different analyses will be referred to in the text following this scheme (PP/PPsic/BS/BSsic).

The ingroup species belong to Neckeraceae as defined by Olsson & al. (2009b). Three clades can be distinguished:

Table 2. Location, i.e., absolute position in the combined dataset and corresponding region of mutational hotspots (H) and the observed inversion (I). Location of the inversion is given with respect to the corrected and analysed matrix (i.e., the inversion is included as reverse complement).

No.	Position	Region
H1	265–266	*rps4-trnT* IGS
H2	326–330	*rps4-trnT* IGS
H3	379–394	*rps4-trnT* IGS
H4	483–484	*rps4-trnT* IGS
H5	850–852	*trnT-trnL* IGS
H6	879–881	*trnT-trnL* IGS
H7	989–991	*trnT-trnL* IGS
H8	1035–1038	*trnT-trnL* IGS
H9	1638–1639	*rpl16*
H10	1682–1687	*rpl16*
H11	1740–1742	*rpl16*
H12	1766–1767	*rpl16*
H13	1977–1978	*rpl16*
H14	1997–2000	*rpl16*
H15	2322–2326	*rpl16*
H16	2336–2338	*rpl16*
H17	2392–2394	*rpl16*
H18	2491–2495	ITS1
H19	2737–2740	ITS1
H20	2875–2878	ITS1
H21	3256–3293	ITS2
I1	1451–1457	*trnL-trnF* IGS

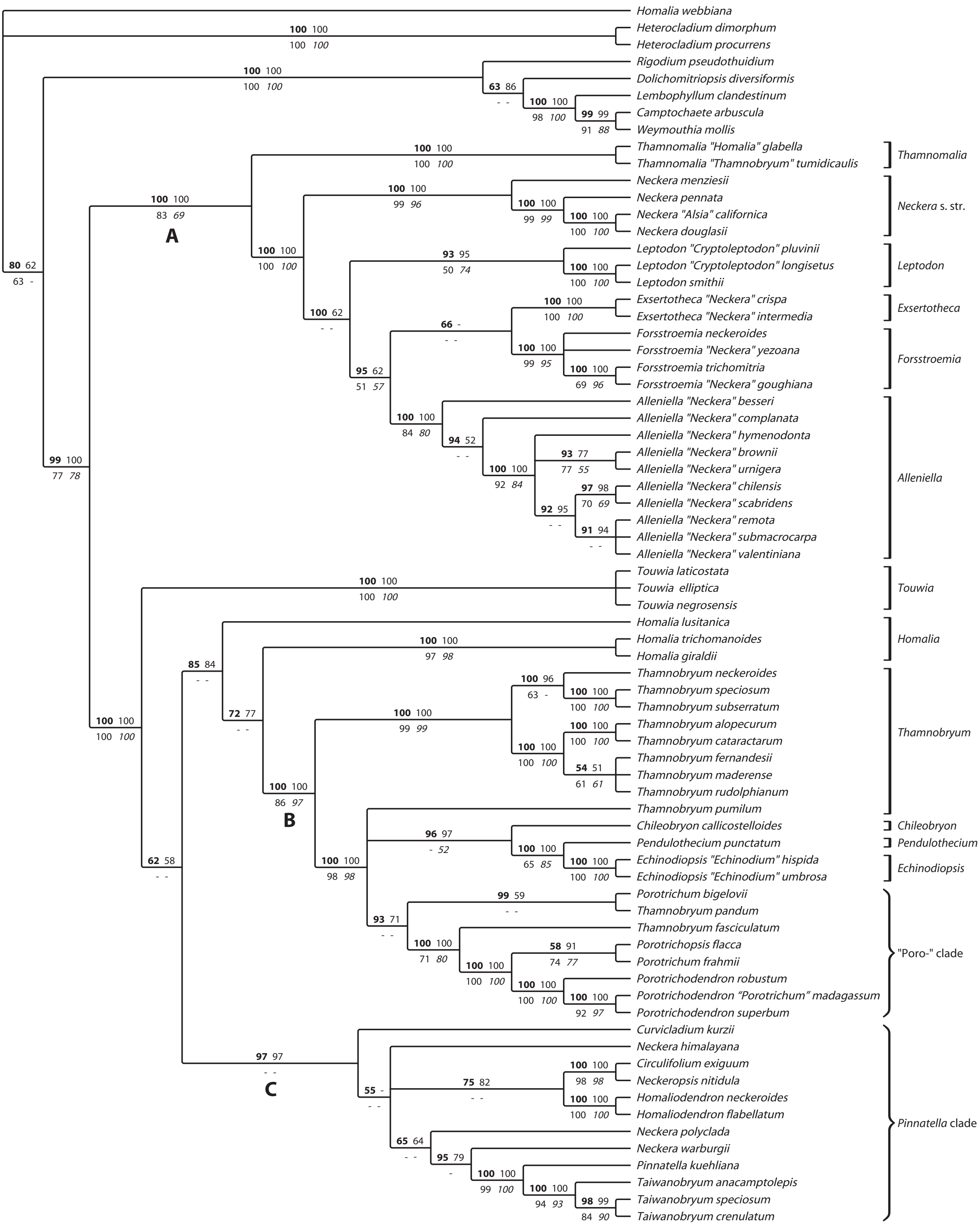

Fig. 1. Phylogenetic relationships of selected Neckeraceae taxa based on *rps4-trnT-trnL-trnF*, *rpl16* and ITS1 & 2 sequences. The PP values from the MrBayes analyses (without indel coding first, then with indel coding) are indicated above, the bootstrap values of the parsimony analysis below when applicable (without indel coding first, then with indel coding).

clade A formed by *Neckera* and related taxa, clade B having *Thamnobryum* as the most prominent genus, and clade C including *Pinnatella* and *Neckeropsis* among others. The positions of the genera *Touwia* and *Homalia* s.str. (*H. lusitanica*, *H. trichomanoides*, *H. giraldii*) remained in a poorly supported position within a maximally supported clade uniting the *Thamnobryum* and the *Pinnatella* clades.

In addition to most of the *Neckera* species, *Forsstroemia*, *Cryptoleptodon*, *Leptodon*, *Alsia californica*, *Homalia glabella* and *Thamnobryum tumidicaule* belong to clade A, which receives maximum support in the BI. The two last-mentioned species render *Homalia* and *Thamnobryum* polyphyletic and formed a maximally supported clade that is resolved as a sistergroup to all the remaining taxa in this clade. The second branching lineage included *Neckera menziesii*, *N. pennata*, *Alsia californica* and *Neckera douglasii* (100/100/99/96) followed by *Leptodon* (including *Cryptoleptodon*). Inside clade A, *Leptodon* and *Cryptoleptodon* are resolved as a third branching lineage in all analyses and with maximal support in the BI analyses without indels coded. However support for this clade drops drastically once the indel matrix is included, while no support was generated using bootstrapping (100/62/–/–). *Neckera crispa* groups together with *N. intermedia*, receiving full support in all analyses. The clade including *Forsstroemia neckeroides*, *Neckera yezoana*, *Forsstroemia trichomitria* and *Neckera goughiana* is very well supported (100/100/99/95), but the relationships within this clade are not totally resolved. Similarly, the placement of the *Neckera crispa*/*N. intermedia* clade was not resolved with confidence. The last major clade receives maximum support in the BI as well as high bootstrap support and includes ten species of *Neckera*. However, *Neckera* in its current circumscription is resolved with multiple polyphyletic branches. Harmonic mean likelihood for the topology (–ln L = 14,034.94) where *Neckera* was constrained to monophyly was significantly lower (BF = 11.32, compare Kass & Raftery, 2007 for details on the interpretation of the BF) than that of the unconstrained topology with a polyphyletic *Neckera* (–ln L = 14029.28), and thus strongly supports the polyphyly of *Neckera*.

Clade B was divided into two well-defined clades: one included only *Thamnobryum* species and the other has species of *Thamnobryum*, *Chileobryon*, *Pendulothecium*, *Echinodium*, *Porotrichum*, *Porotrichopsis* and *Porotrichodendron*, rendering the genera *Porotrichum* and *Porotrichodendron* polyphyletic. Both clades received maximal or high support values, but the relationships within the clades are not totally resolved.

Clade C was composed of diverse taxa: *Circulifolium*, *Curvicladium*, *Homaliodendron*, *Neckeropsis*, *Pinnatella*, *Taiwanobryum*, and some Asian *Neckera* species. Even if the clade received high support in the Bayesian analyses (97/97), the internal nodes in this clade are largely unresolved or lacking support, except for the clade containing *Pinnatella kuehliana*, *Taiwanobryum anacamptolepis*, *T. speciosum* and *T. crenulata* (100/100/99/100) and two small clades with *Circulifolium exiguum* together with *Neckeropsis nitidula* (100/100/98/98) and *Homaliodendron neckeroides* together with *H. flabellatum* (100/100/100/100), respectively.

■ DISCUSSION

Additional data is most often expected to increase resolution and group support, especially the addition of microstructural characters has been reported to significantly increase resolution and support at all levels (e.g., Graham & al., 2000; Simmons & al., 2001; Hamilton & al., 2003; Müller & Borsch, 2005; Löhne & Borsch 2005; Borsch & al., 2007). In addition, microstructural characters are often considered less homoplasious compared to substitutions, with secondary losses of acquired simple sequence repeats being less likely, especially with regard to sequence data from plastid regions (compare Borsch & Quandt, 2009). The inclusion of the SIC matrix in the presented phylogenetic analyses, however, seems to have slightly opposite effects in some cases. Similar results were obtained by, e.g., Sotiaux & al. (2009), where especially indels in the *rpl16* region were shown to be homoplasious on deeper levels such as the Neckeraceae backbone, but adding information at shallow nodes, and, e.g., supported a geographic pattern among *Leptodon smithii* populations. In the present analyses posterior probability values for some groups, such as the clade consisting of *Neckera* species from *N. complanata* to *N. valentiana*, were clearly higher without indel data. We assume this to be due to likely convergent evolution of some of the coded indels that can give slightly misleading evolutionary information. For some groups, however, inclusion of the indel matrix leads to better support (for example clade B plus *Homalia trichomanoides* and *H. giraldii*, and the *Cryptoleptodon-Leptodon* clade). The support seems to be due to a combination of indels rather than to significant single indel events, since only few indels supporting these groups were found. Clade B is supported by three indels in the ITS region (positions 2685–2687, 2723–2725 and 3211–3213 in the original matrix) and the *Cryptoleptodon-Leptodon* clade is supported by only one short indel in the ITS region (positions 2693–2694). Overall, it seems that the contribution of indels towards the phylogenetic signal is more complex than previously thought and dependent on the study group, the hierarchical level and the evolutionary constraints of the chosen marker that vice versa most likely depends on the study group.

Convergent evolution or incongruence between morphology and molecular data? — Incongruence among molecular partitions is common and can have many different causes, such as insufficient data, rapid diversification, horizontal gene transfer, hybridization, incomplete lineage sorting, convergence caused by natural selection, and variations in evolutionary rate (cf., Wendel & Doyle, 2005). Several of these causes could potentially also explain incongruence between molecular and morphological data. Phylogenetic analyses can often not decide which of these causes is behind a particular case unless additional evidence is at hand (Wendel & Doyle, 2000).

Incongruence between morphology and molecular data that have other reasons than convergent morphological evolution are known for other pleurocarps, for example in *Isothecium* (Draper & al., 2007), *Leptodon* (Sotiaux & al., 2009) and *Sciuro-hypnum* (Draper & Hedenäs, 2009), suggesting that especially non-coding markers may not always trace the evolution of the morphologically and biologically meaningful species correctly. We therefore believe it is risky to assume a priori that molecular information is always superior to morphology, and suggest that taxonomic novelties should only be proposed when molecular information or other data leave no doubt regarding the relationships among the taxa.

Earlier results on the morphological evolution in Neckeraceae (Olsson & al., 2009b) showed that certain morphological states, especially sporophytic ones, such as reduced peristome structures or short setae, evolved several times independently. In addition, conflict between gametophytic and sporophytic characters has been reported from several other bryophyte groups such as Grimmiaceae (Hernández-Maqueda & al., 2008), Splachnaceae (Goffinet & Shaw, 2002), Brachytheciaceae (Huttunen & Ignatov, 2004), Lembophyllaceae (Quandt & al., 2009), Vittiaceae (Vanderpoorten & al., 2003) and Hypnales in general (Buck & al., 2000). In the present study the phylogenetic inferences imply that several morphological character states, especially gametophytic ones that were held as unique and characteristic for *Neckera*, actually evolved independently. For example, the typical "*Neckera* characters" (deeply undulate, glossy, complanate and asymmetric leaves and a weak costa) seem to represent the ancestral state and were later lost independently in *Leptodon* and *Forsstroemia*, which is in accordance with the ancestral state reconstructions performed by Olsson & al. (2009b) on a smaller taxon sampling. Compared with angiosperms, the lack of a sufficient amount of morphological characters in bryophytes makes it more difficult to reveal convergent evolution in this group based on morphology alone, but with well-resolved and highly supported phylogenies this can be addressed.

Phylogenetic analyses and taxonomic relationships. — Generally the phylogenetic analyses rendered nearly all genera of the family polyphyletic, including the largest genus in the family, *Neckera*. Even taxa that were recognized as families such as Leptodontaceae are deeply nested inside Neckeraceae and should therefore be merged with the latter (compare Olsson & al., 2009b). Within Leptodontaceae, the paraphyletic genus *Cryptoleptodon* should be included in *Leptodon* (see also Sotiaux & al., 2009).

Clade A. — In this clade, *Thamnobryum tumidicaule* and *Homalia glabella* form the first diverging branch with high support. We recognise this clade at the genus level and thus describe the new genus *Thamnomalia* below.

***Neckera*. —** In earlier studies evidence accumulated that this genus, as currently understood, is not monophyletic (Tsubota & al., 2004; Ignatov & al., 2007; Olsson & al., 2009b), which is also found in this study based on a more comprehensive taxon sampling. In the current analyses we included taxa that cover the morphological variation and geographical distribution of the genus. Since *Neckera pennata* is the type of the generic name, the clade including that species, *N. menziesii*, *N. douglasii* and *N. californica* (syn. *Alsia californica*), forms *Neckera* s.str. Yet, the majority of the sampled species currently placed in the genus *Neckera* belong to another clade containing only "*Neckera*" species. Additionally, two *Neckera* species, *N. goughiana* and *N. yezoana*, are resolved in the clade including *Forsstroemia neckeroides* and *F. trichomitria* (type of the generic name), thus both *Neckera* species will be transferred to *Forsstroemia*. A close relationship of some *Neckera* species with *Forsstroemia* was also suggested by the results of Tsubota & al. (2002), but due to the sparse taxon sampling (*Forsstroemia trichomitria*, *F. japonica*, *F. neckeroides*, *Neckera urnigera*) the supporting evidence remained weak. The taxon sampling in our analyses is more comprehensive, and the individual clades are distinct, receiving good support on a statistically significant level. Therefore, we establish two new genera to accommodate the "*Neckera*" species that fall outside of *Neckera* s.str. and *Forsstroemia* in clade A. It might be mentioned that the Australasian *N. hymenodonta* has previously been treated as a taxonomic synonym of *N. pennata* (e.g., Fife, 1995). However, Ji & Enroth (2008) showed that *N. hymenodonta* is morphologically distinct from *N. pennata* (e.g., the former has paraphyllia), which is supported by the present analysis that resolved *N. hymenodonta* outside of *Neckera* s.str. in one of the new genera described below.

The three "*Neckera*" species belonging to clade C (*N. himalayana*, *N. polyclada*, *N. warburgii*) are morphologically different from the other *Neckera* species and belong in a peculiar group of robust Asian species (Enroth, 1996; Enroth & Ji, 2007). According to our results they are neither closely related to the "true" *Neckera*s nor to the other sampled "*Neckera*" species, and they do not form an own clade. As the phylogenetic estimates regarding these three species are inconclusive, taxonomic changes are not yet warranted. Further analyses are needed to uncover their phylogenetic relationships and to provide a taxonomic and evolutionary concept regarding these morphologically peculiar taxa.

Leptodon smithii and the two paraphyletic *Cryptoleptodon* species form a clade, implying that *Cryptoleptodon* should be included in *Leptodon*, as it traditionally has been (e.g., Jaeger & Sauerbeck, 1876–1879: 105). It has been suggested in previous studies (Maeda & al., 2000; Goffinet & al., 2001; Tsubota & al., 2004; Olsson & al., 2009a,b) that *Forsstroemia*, *Echinodium*, *Leptodon*, and *Anomodon giraldii* have close affinities with *Neckera* species, although based on limited datasets. The morphological similarity between *Forsstroemia* and *Leptodon* was pointed out by Stark (1987), and the affinities of *Forsstroemia* to Neckeraceae (when Leptodontaceae become included in it) has morphological support as discussed by Buck (1980) and Enroth (1992a).

Inside clade A several phytogeographically distinct groups can be recognized with an interesting evolutionary and phytogeographic pattern. For example, the first branching group consisting of *Homalia glabella* and *Thamnobryum tumidicaule* is South American and tropical. The following group, with four species of *Neckera* s.str. is essentially temperate and North American, with the exception of *N. pennata* which has a much wider distribution especially in the Northern Hemisphere, and which may in fact contain more than one species (cf. Appelgren & Cronberg, 1999). It thus seems that this group originated and diversified in the "New World", since apart from *N. pennata*, none of the European (*N. complanata* [which also occurs in North America], *N. crispa*, *N. intermedia*, *N. besseri*), Asian (*N. yezoana*, *N. goughiana*, *Forsstroemia neckeroides*) or African (*N. remota*, *N. submacrocarpa*, *N. valentiniana*) species belong in *Neckera* s.str. In addition, it should be noted that the South American species *N. urnigera*, *N. chilensis* and *N. scabridens* as well as the New Zealandian *N. brownii* and *N. hymenodonta*, and the three African species just mentioned form a clade with maximum support under BI (Fig. 1), with the African species grouping together.

The topography of the clade from *N. besseri* to *N. valentiniana*, which is recognized in the present paper as a new genus, has some intriguing evolutionary implications. For example, the first branching species *N. besseri* and *N. complanata* are dioicous (sporophytes rare) and produce flagelliform branchlets that serve as vegetative propagula; the rest of the species are autoicous (sporophytes frequent) and lack vegetative propagula. This suggests that vegetative reproduction compensates for the infrequent sexual reproduction in the dioicous taxa. Also, the two basal taxa have long-exserted capsules, while the other taxa have either immersed or short-exserted (*N. chilensis*) capsules. These differences may indicate evolutionary trends within the clade that need to be confirmed by a more comprehensive evolutionary study based on a more complete taxon sampling. However, with the present sampling a strong phytogeographic structure can be observed in this clade. Both species forming the early branching grade are species from temperate regions of the Northern Hemisphere. *Neckera besseri* is a western Eurasiatic taxon, and *N. complanata* occurs in North America and western Eurasia (with some reports from Africa). Whereas *Neckera hymenodonta* and *N. brownii* are Australasian species (Australia, New Zealand) that can be described as Southern Hemisphere temperate taxa, the remaining taxa occur at high elevations in the tropics. *Neckera urnigera*, *N. chilensis* and *N. scabridens* are exclusively South American, and *N. remota*, *N. submacrocarpa* and *N. valentiniana* that form a monophylum occur exclusively in Africa. Since these taxa occur at relatively high elevations, mostly above 2000 m (Sloover, 1977; Churchill & Linares, 1995), their habitats are in some respects similar to those found in the temperate regions (cf. Hedenäs, 1999).

Clade B. — Enroth & Tan (1994) pointed out that Thamnobryaceae, comprising "the dendroid Neckeraceae sensu Brotherus (1929) with cross-striolate exostomes" (Buck & Vitt, 1986), cannot be kept separate from Neckeraceae. This view is supported by recently published molecular phylogenies (see also Olsson & al., 2009a,b), as well as by the present study that reveals all "Thamnobryaceae" species to be deeply nested inside the Neckeraceae, with the largest genus *Thamnobryum* itself being highly polyphyletic. For example, *Thamnobryum tumidicaule* is placed in the first branching lineage of clade A (*Neckera* group) forming a new genus together with *Homalia glabella*, as described below. Similarly, *Touwia elliptica* and *T. negrosensis* were until recently included in *Thamnobryum*. The transfer to *Touwia* (Olsson, 2010) is not only confirmed in the present study by the molecular analyses but is also morphologically sound since the two *Thamnobryum* species share morphological similarities with the type of the generic name *Touwia laticostata*, and are morphologically distinct from *Thamnobryum*, as noted earlier by Ochyra (1990). In the new concept, the three species of *Touwia* that are all rheophytic (growing in flowing water) have a restricted distribution area in Australasia and SE Asia (Ochyra, 1986, 1990; Enroth, 1989). However, all the rheophytic taxa in Neckeraceae (cf. Enroth, 1999) do not form a monophyletic group despite some similar morphological adaptations. It has been pointed out earlier that, e.g., the rheophytic *Thamnobryum* species (*T. fernandesii*, *T. cataractarum*, *T. angustifolium*) are radiations from the surrounding *T. alopecurum* populations showing the same morphological response to the extreme habitat (Olsson & al., 2009c).

The majority of the *Thamnobryum* species, including the type of the generic name *T. alopecurum*, however, form an almost maximally supported clade sister to the remaining species of clade B. Although this sister clade also hosts three additional *Thamnobryum* species (*T. pandum*, *T. pumilum*, *T. fasciculatum*), the phylogenetic relationships are uncertain. The exclusion of *T. tumidicaule* and *T. fasciculatum* (see Fig. 1) from *Thamnobryum* renders the peculiar *T. liesneri* from Venezuela as the single representative of the genus in the South American continent (Allen & Churchill, 2002).

We expect that a more thorough sampling inside clade B, as indicated by an upcoming study (Buchbender & al. unpub.), will resolve the remaining questions related to the phylogenetic relationships of *Thamnobryum pandum*, *T. pumilum* and *T. fasciculatum* as well as the other polyphyletic taxa inside the "*Poro*-"clade. We therefore refrain from any further nomenclatural changes in this group at this stage. The only exception is *Porotrichum madagassum* that is resolved among *Porotrichodendron* species. Since this grouping also receives morphological support a transfer of *Porotrichum madagassum* is justified.

The placement of *Chileobryon callicostelloides* (previously *Pinnatella callicostelloides*), a unispecific genus from Chile (including the Juan Fernández Islands), has been uncertain. Our analyses support the view of Brotherus (1925), who placed it in Neckeraceae. It is in fact not close to *Pinnatella* but forms a group together with the Australasian *Pendulothecium punctatum*, *Echinodium hispidum* and *E. umbrosum*. The latter two species were only recently excluded from *Echinodium* s.str., and transferred to *Thamnobryum* by Stech & al. (2008) in an attempt to clarify the phylogeography of Echinodiaceae. Therefore, the sampling inside Neckeraceae was limited, and with a more extensive taxon sampling it becomes evident that these species do not belong in *Thamnobryum* but form an independent clade sister to *Pendulothecium punctatum*. The sporophytes of the two *Echinodium* species and the three *Pendulothecium* species (Enroth & He, 1991) are almost identical, but the apophysal stomata in the former are immersed (vs. superficial in *Pendulothecium*) and the spores are smaller (12–14 µm in the *Echinodium* species and 16–20 µm in *Pendulothecium*; cf. Churchill, 1986; Enroth & He, 1991). However, there are clearer differences in the gametophytes, justifying erecting a new genus that we name *Echinodiopsis* for *Echinodium hispidum* and *E. umbrosum*. Those two species have a stem central strand (lacking in *Pendulothecium*), foliose pseudoparaphyllia (lacking in *Pendulothecium*), long, very strong and excurrent costae with internal differentiation (in *Pendulothecium* ending in mid-leaf or reaching to 5/6 leaf length at most, and of homogeneous cells), and a completely different leaf shape with bistratose parts. The clade formed of *Chileobryon*, *Pendulothecium* and *Echinodiopsis* is phytogeographically coherent and southern amphi-Pacific. *Chileobryon* is known from the Juan Fernández Islands and mainland Chile, while the two other genera are distributed in Australasia, especially in New Zealand and some of the adjacent islands. All species also grow in very similar, moist and shady habitats, with soil and rocks being the preferred substrates, but also on tree bases and logs (Churchill, 1986; Enroth & He, 1991; Enroth, 1992b).

The polyphyly of the genus *Homalia* is intriguing, since it is a morphologically fairly coherent group (cf. He, 1997). *Homalia webbiana* and *H. pennatula* were excluded from Neckeraceae in a previous study (Olsson & al., 2009b), and *H. glabella* belongs to clade A in the present study. With the transfer of *Homalia glabella* to a new genus, *Homalia* s.str. is left with three species: *H. lusitanica*, *H. trichomanoides* and *H. giraldii*. However, in the current analyses *H. lusitanica* and the remaining *Homalia* species are resolved in a grade to clade B, which contradicts our previous results based on more extensive sequence data (Olsson & al., 2009b). However, there is no significant support backing up this scenario. It is probably an artefact due to the lesser amount of available sequence-level information, which was discussed in more detail by Olsson & al. (2010); therefore there is no need to make any nomenclatural changes considering *H. lusitanica*. The systematic position of *Homalia* seems to differ according to taxon sampling and the markers used for inferring phylogenies, indicating the importance of taxon sampling and the quality of the sequence markers.

■ TAXONOMIC AND NOMENCLATURAL CHANGES

Forsstroemia goughiana (Mitt.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera goughiana* Mitt. in J. Proc. Linn. Soc., Bot. 1 (Suppl.): 120. 1859.

Forsstroemia yezoana (Besch.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera yezoana* Besch. in Ann. Sci. Nat., Bot., sér. 7, 17: 358. 1893.

See Enroth (1994b) for a discussion of the species and its distribution.

Neckera Hedw., Sp. Musc. Frond.: 200. 1801, nom. cons. – Type: *Neckera pennata* Hedw. (typ. cons.).
= *Alsia* Sull., Proc. Amer. Acad. Arts 3: 184. 1855, **syn. nov.** – Type: *Alsia californica* (Hook. f. & Arn.) Sull. (*Neckera californica* Hook. f. & Arn.).

Leptodon D. Mohr, Observ. Bot.: 27. 1803, nom. cons. – Type: *Leptodon smithii* (Hedw.) F. Weber & D. Mohr (*Hypnum smithii* Hedw.).
= *Cryptoleptodon* Renauld & Cardot in Bull. Soc. Roy. Bot. Belgique 38: 30. 1899, **syn. nov.** – Type (see Enroth, 1992a): *Cryptoleptodon pluvinii* (Brid.) Broth.

Leptodon acuminatus (M. Fleisch.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Cryptoleptodon acuminatus* M. Fleisch. in Hedwigia 59: 212. 1917.

Exsertotheca S. Olsson, Enroth & D. Quandt, **gen. nov.**

Genus *Exsertotheca* plantis dioicis relative robustis foliis nitidis undulatis, parietibus cellularum foliorum crassis et porosis et costis vulgo brevissimis, capsulis longe exsertis, typice operculis oblique et longissime rostratis, in Europa, Macaronesia et Asia austro-occidentali distributum.

Type: *Exsertotheca crispa* (Hedw.) S. Olsson, Enroth & D. Quandt.

Plants medium-sized to large, with the fronds irregularly to pinnately branched. Central strand absent in the stem. Leaves usually strongly undulate and glossy (although expressions with smooth and falcate leaves frequent in *E. intermedia*, rare in *E. crispa*), not very complanate, asymmetric, oblong to elongate-oblong or ovate-oblong, distinctly decurrent, with a blunt to shortly acuminate apex. Leaf margins plane, entire or nearly so below and denticulate towards the apex; costa very short and double, occasionally (in *E. crispa*) reaching to 2/5 of leaf length. Leaf cells smooth, with strongly to moderately incrassate and distinctly porose walls; alar cells quadrate or rectangular, often forming triangular groups. Paraphyllia lacking. Pseudoparaphyllia (cf. Cubero & al., 2006) leaf-like (sometimes with few filamentous ones intermixed), usually 3–4 (but number varying from 1 to 7) per branch primordium, to ca. 0.9 mm long. Plants dioicous, sporophytes relatively infrequently produced. Perichaetial leaves erect and closely sheathing, oblong to ovate, narrowed to an acuminate apex (in *N. intermedia* more abruptly than in *N. crispa*), with a short, often double costa; post-fertilization growth considerable, the inner leaves eventually reaching over 5 mm long. Seta smooth, in *N. crispa* 8–12 mm (Brotherus, 1923; Smith, 2004), in *N. intermedia* 10–17 mm long (Hedenäs, 1992). Capsule orthotropous, ovoid, ca. 2.5 mm long; a columella reaching to over half of the capsule length present in mature capsules. Apophysal stomata phaneroporous. Peristome double; exostome teeth yellowish, when dry curved inwards, lacking borders and with reduced dorsal ridges, striolate and with papillose upper parts in *N. crispa*, but rather papillose throughout in *N. intermedia*; endostome reduced, consisting of a relatively high (ca. 100–150 µm), faintly papillose basal membrane and vestiges of segments. Calyptra cucullate, smooth or with few hairs in the basal parts. Operculum obliquely long-rostrate. Spores 15–25(–30) µm in diameter, fairly coarsely papillose. *Exsertotheca* is a European—SW Asian genus, both species also occurring in Macaronesia (Hedenäs, 1992).

Exsertotheca crispa (Hedw.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera crispa* Hedw., Sp. Musc. Frond.: 206. 1801.

Exsertotheca intermedia (Brid.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera intermedia* Brid., Muscol. Recent. Suppl. 2: 24. 1812.

Alleniella S. Olsson, Enroth & D. Quandt, **gen. nov.**

Genus hoc *Neckerae* similis. Species duae dioicae, foliis levibus, setis longis, capsulis exsertis et propagula vegetativa producentes. Species ceterae huius generis autoicae, foliis praecipue undulatis, setis brevibus, capsulis immersis vel emergentibus et propagula vegetativa non producentes.

Type: *Alleniella complanata* (Hedw.) S. Olsson, Enroth & D. Quandt.

Etymology. – The genus is named after Dr. Bruce Allen of the Missouri Botanical Garden, one of the foremost moss taxonomists of our time.

Plants from small (*A. besseri*) to robust; branching more or less pinnate. Central strand absent in the stem. Leaves complanate, smooth (*A. besseri*, *A. complanata*, *A. brownii*) or distinctly undulate and glossy; the smooth-leaved species with rounded or obtuse-mucronate leaf apices, the others with more acute leaf apices. Costa short and often double, or virtually absent. Leaf cells smooth, relatively thin-walled and non-porose except often near the leaf base; alar cells shorter, often quadrate or nearly so, but not in sharply delimited groups. Pseudoparaphyllia leaf-like, lanceolate to nearly filamentous. Four species (*A. besseri*, *A. complanata*, *A. brownii*, *A. chilensis*) lack paraphyllia, six species have them. Dioicous and often with flagelliform branchlets as vegetative propagula (*A. besseri*, *A. complanata*) or autoicous and without vegetative propagula. Perichaetial leaves with strong post-fertilization growth. Seta 7–10 mm long, capsule long-exserted (*A. besseri*, *A. complanata*), or seta short and capsule immersed (in *A. chilensis* capsule short-exserted). Capsule orthotropous, ovoid to cylindric. Apophysal stomata phaneroporous, in *A. besseri*, *A. complanata*, *A. brownii* and *A. hymenodonta* very few (less than five per capsule) and highly vestigial. Peristome double; exostome teeth papillose throughout or striolate at base and papillose elsewhere, or rather papillose throughout, unbordered; median line slightly zig-zag, weakly developed trabeculae at back; endostome with a well-developed, up to ca. 100 µm high basal membrane, segments mostly subulate, papillose throughout and often with narrow median perforations. Calyptra cucullate, glabrous or with some hairs in the basal part. Operculum obliquely rostrate. Spores mostly fairly coarsely papillose, (15–)20–35 µm in diameter.

Alleniella besseri (Lob.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Homalia besseri* Lobarz. in Naturwiss. Abh. (Vienna) 1: 48. 1847 (*Neckera besseri* (Lobarz.) Jur. in Verh. Zool.-Bot. Ges. Wien 10: 368. 1860).

Alleniella brownii (Dixon) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera brownii* Dixon in New Zealand Inst. Bull. 3(5): 266. 1927.

Alleniella chilensis (Schimp. ex Mont.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera chilensis* Schimp. ex Mont. in Ann. Sci. Nat., Bot., ser. 2, 6: 147. 1836.

Alleniella complanata (Hedw.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Leskea complanata* Hedw., Sp. Musc. Frond.: 231. 1801 (*Neckera complanata* (Hedw.) Huebener, Muscol. Germ.: 576. 1833).

Alleniella hymenodonta (Müll. Hal.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera hymenodonta* Müll. Hal. in Bot. Zeitung (Berlin) 9: 564. 1851.

Alleniella remota (Bruch & Schimp. ex Müll. Hal.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera remota* Bruch & Schimp. ex Müll. Hal., Syn. Musc. Frond. 2: 51. 1850.

Alleniella scabridens (Müll. Hal.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera scabridens* Müll. Hal. in Bot. Zeitung (Berlin) 5: 828. 1847.

Alleniella submacrocarpa (Dixon) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera submacrocarpa* Dixon in Smithsonian Misc. Collect. 72(3): 12. 1920.

Alleniella urnigera (Müll. Hal.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera urnigera* Müll. Hal., Syn. Musc. Frond. 2: 57. 1850.

Alleniella valentiniana (Besch.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Neckera valentiniana* Besch. in Ann. Sci. Nat., Bot., sér. 6, 10: 273. 1880.

Thamnomalia S. Olsson, Enroth & D. Quandt, **gen. nov.**

Genus hoc cognoscitur caulibus frondosis, irregulatim ramosis, areolatione foliorum cellulis apicalibus parietibus satis crassis et cellulis medianis parietibus clare tenuioribus et cellulis alaribus infirme vel haud differentiatis. Species duo praecipue in America centrali et in archipelago Indiae occidentalis distributae sunt et plerumque ad rupes in silvis humidis habitant.

Type: *Thamnomalia glabella* (Hedw.) S. Olsson, Enroth & D. Quandt.

Plants frondose, branching rather irregular. Central strand present in the stem (sometimes quite indistinct). Leaves strongly complanate, symmetric in *T. tumidicaulis*, asymmetric in *T. glabella*. Apical teeth in the leaves of *T. glabella* unicellular, in *T. tumidicaulis* often composed of 2–3 cells. Costa single and strong, ending shortly below the leaf apex in *T. tumidicaulis*, in *T. glabella* weak and short, often double. Leaf cells smooth; apical cells relatively strongly incrassate and sometimes porose, median laminal and their subjacent cells with clearly thinner walls; alar cells scarcely if at all differentiated. Pseudoparahyllia, foliose, in *T. glabella* intermingled with filamentous ones. Dioicous. Sporophytes known only for *T. glabella*, as described by He (1997).

Thamnomalia glabella (Hedw.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Leskea glabella* Hedw., Sp. Musc. Frond.: 235. 1801. (*Neckera glabella* (Hedw.) F. Weber & D. Mohr, Index Mus. Pl. Crypt.: 3. 1803. *Hypnum glabellum* (Hedw.) Sw. ex P. Beauv., Prodr. Aethéogam.: 64. 1805. *Homalia glabella* (Hedw.) Schimp., Bryol. Eur. 5, fasc. 44–45, Monogr. 2: 54. 1850).

Thamnomalia tumidicaulis (K.A. Wagner) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Thamnium tumidicaule* K.A. Wagner in Bryologist 55: 145. 1952 (*Thamnobryum* *tumidicaule* (K.A. Wagner) F.D. Bowers in Bryologist 77: 162. 1974).

The two species of *Thamnomalia* have very similar geographic ranges. Both species occur in Central America and the West Indies; *T. glabella* is also known from SE Brazil (cf. He, 1997; Buck, 1998). Both species grow mainly on rocks and rarely on tree trunks; *T. glabella* thrives at 400–2500 m and *T. tumidicaulis* at 600–1200 m (Buck, 1998).

Echinodiopsis S. Olsson, Enroth & D. Quandt, **gen. nov.**

Genus hoc simile generis *Echinodii* in Macaronesia, se praecipue cellulis alaribus non differentiatis, cellulis foliorum plerumque leviter mamillosis et seta gradatim verus capsulam inspissata differt. In Australasia distributum est.

Type: *Echinodiopsis hispida* (Hook. f. & Wilson) S. Olsson, Enroth & D. Quandt.

Plants dark-green to blackish, dull, variably branched, thriving in shady, moist places, and most often growing on rocks or soil, sometimes also on tree bases. Leaves narrow, lanceolate or subulate from a triangular or an ovate base. Costa very strong, long-excurrent in *E. hispida* and percurrent to short-excurrent in *E. umbrosa*. Leaf margins and apical parts of the lamina at least partly bistratose. Alar cells not differentiated. Pseudoparaphyllia leaf-like. Dioicous. Seta red or reddish-orange, distinctly flaring below the apophysis. Stomata immersed. Capsule orientation varying from reclinate to antitropous, sometimes homotropous. Annulus well-differentiated with 1–3 cell rows. Peristome unreduced “hypnoid”.

Echinodiopsis hispida (Hook. f. & Wilson) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Hypnum hispidum* Hook. f. & Wilson in London J. Bot. 3: 552. 1844 (*Leskea hispida* (Hook. f. & Wilson) Mitt. in J. Proc. Linn. Soc., Bot. 4: 91. 1859. *Echinodium hispidum* (Hook. f. & Wilson) Reichardt, Reise Novara 1(3): 127. 1870. *Thamnobryum hispidum* (Hook. f. & Wilson) M. Stech & al. in Organisms Divers. Evol. 8: 290. 2008).

Echinodiopsis umbrosa (Mitt.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Leskea umbrosa* Mitt. in J. Linn. Soc., Bot. 4: 92. 1859 (*Echinodium umbrosum* (Mitt.) A. Jaeger in Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 314. 1878. *Thamnobryum umbrosum* (Mitt.) M. Stech & al. in Organisms Divers. Evol. 8: 290. 2008).

Echinodiopsis umbrosa var. ***glaucoviride*** (Mitt.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Hypnum glaucoviride* Mitt. in Hooker, Handb. New Zeal. Fl.: 473. 1867 (*Sciaromium glaucoviride* (Mitt.) Mitt. in Seemann, Fl. Vit.: 400. 1873. *Echinodium glaucoviride* (Mitt.) A. Jaeger in Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1876–77: 314. 1878. *Echinodium hispidum* var. *glaucoviride* (Mitt.) Dixon in New Zealand Inst. Bull. 3(5): 249. 1927. *Echinodium umbrosum* var. *glaucoviride* (Mitt.) S.P. Churchill in J. Bryol. 14: 129. 1986. *Thamnobryum umbrosum* var. *glauco-viride* (Mitt.) M. Stech & al. in Organisms Divers. Evol. 8: 290. 2008).

Note. – Stech & al. (2008) tabulated the morphological distinctions in the gametophytes of *Echinodium* s.str. and in the two species placed here in *Echinodiopsis*. Most of the differences are rather relative, and the single clear-cut one is the well-differentiated alar cells in *Echinodium* vs. the non-differentiated alar cells in *Echinodiopsis*. There are also some differences in the sporophytes. In *Echinodiopsis* the capsules are mostly reclinate to antitropous, while in *Echinodium* they vary from nearly orthotropous to orthogonal (Hedenäs, 1992). The seta in *Echinodiopsis* distinctly flares below the apophysis. The stomata in *Echinodium* (at least in *E. setigerum* and *E. renauldii*, cf. Hedenäs, 1992) are superficial, but in *Echinodiopsis* they are immersed (Churchill, 1986; also our own observation).

Porotrichodendron madagassum (Kiaer ex Besch.) S. Olsson, Enroth & D. Quandt, **comb. nov.** ≡ *Porotrichum madagassum* Kiaer ex Besch. in Ann. Sci. Nat., Bot., sér. 6, 10: 332. 1880 (*Thamnium madagassum* (Kiaer ex Besch.) Kindb. in Hedwigia 41: 236. 1902).

Note. – Crosby & al. (1983) regarded *Porotrichum madagassum*, *Porothamnium hildebrandtii* (Müll. Hal.) M. Fleisch. and *Porotrichum pennaefrondeum* Müll. Hal. as taxonomic synonyms of *Porothamnium comorense* (Müll. Hal.) Sim. According to Sloover (1983) however, *Porothamnium comorense* is a synonym of *Porotrichum elongatum* (Welw. & Duby) Gepp, *Porothamnium hildebrandtii* is a synonym of *Porothamnium stipitatum* (Mitt.) Touw ex De Sloover (= *Porotrichum stipitatum* (Mitt.) W.R. Buck), and *Porotrichum pennaefrondeum* is a synonym of *P. madagassum* (cf. also Een, 1976). We agree with De Sloover’s concepts.

■ ACKNOWLEDGEMENTS

SO acknowledges financial support by the Helsingin Sanomat Centennial Foundation and the Research Foundation of the University of Helsinki. Furthermore, the authors received support from two researcher exchange grants Finnish Academy/DAAD (JE, DQ) and DAAD/STINT (VB, LH, SH, SO, DQ), which is highly acknowledged. Research was funded by the Deutsche Forschungsgemeinschaft (DFG QU 153/3-1 153/3-2) and SYNTHESYS (VB, JE, SO), which was financed by the European Community Research Infrastructure Action under the FP6 “Structuring the European Research Area” Program (http://www.sysnthesys.info). Mr. Heino Vänskä, Lic. Phil., is cordially thanked for the Latin diagnoses. In addition, we thank Frank Müller (Dresden), Andy Cairns (James Cook University), Terry Hedderson (University of Cape Town) and Ron Porley (English Nature) for providing us with additional research material.

■ LITERATURE CITED

Allen, B. 1994. *Porotrichum tenuinerve* (Musci: Neckeraceae), a new species from Honduras, with a provisional key to *Porotrichum* in Central America. *Novon* 4: 315–318.

Allen, B. & Churchill, S.P. 2002. A new species of *Thamnobryum* (Musci: Neckeraceae) from Venezuela, with a key to the neotropical species of *Thamnobryum*. *Novon* 12: 155–158.

Appelgren, L. & Cronberg, N. 1999. Genetic and morphological variation in the rare epiphytic moss *Neckera pennata* Hedw. *J. Bryol.* 21: 97–107.

Bell, N.E., Quandt, D., Brien, T.J., & Newton, A.E. 2007. Taxonomy and phylogeny in the earliest diverging pleurocarps: Square holes and bifurcating pegs. *Bryologist* 110: 533–560.

Borsch, T., Hilu, K.W., Wiersema, J.H., Löhne, C., Barthlott, W. & Wilde, V. 2007. Phylogeny of *Nymphaea* (Nymphaeaceae): evidence from substitutions and microstructural changes of the chloroplast *trnT-trnF* region. *Int. J. Pl. Sci.* 168: 639–671.

Borsch, T. & Quandt, D. 2009. Mutational dynamics and phylogenetic utility of non-coding plastid DNA. *Pl. Syst. Evol.* 282: 169–199.

Brotherus, V.F. 1923. *Die Laubmoose Fennoskandias*. Helsingfors: Societas pro Fauna et Flora Fennica.

Brotherus, V.F. 1925. Neckeraceae. Pp. 178–202 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, ed. 2, vol. 11, part 2, *Musci (Laubmoose)*. Leipzig: Engelmann.

Brotherus, V.F. 1929. Musci. Pp. 1–147 in: Handel-Mazzetti, H. (ed.), *Symbolae sinicae*: *Botanische Ergebnisse der Expedition der Akademie der Wissenschaften in Wien nach Südwest-China 1914/1918*. Wien: Springer.

Buck, W.R. 1980. Animadversions on *Pterigynandrum* with special commentary on *Forsstroemia* and *Leptopterigynandrum*. *Bryologist* 83: 451–465.

Buck, W.R. 1998. Pleurocarpous mosses of the West Indies. *Mem. New York Bot. Gard.* 82: 1–400.

Buck, W.R. & Goffinet, B. 2000. Morphology and classification of mosses. Pp. 71–123 in: Shaw, A.J. & Goffinet, B. (eds.), *Bryophyte biology*. Cambridge: Cambridge Univ. Press.

Buck, W.R., Goffinet, B. & Shaw, A.J. 2000. Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on *trnL-trnF* and *rps4* sequences. *Molec. Phylog. Evol.* 16: 180–198.

Buck, W.R. & Vitt, D.H. 1986. Suggestions for a new familial classification of pleurocarpous mosses. *Taxon* 35: 21–60.

Churchill, S.P. 1986. A revision of *Echinodium* Jur. (Echinodiaceae: Hypnobryales). *J. Bryol.* 14: 117–133.

Churchill, S.P. & Linares, E.C. 1995. Prodromus Bryologiae Novo-Granatensis. Introduccion a la Flora de Musgos de Colombia. *Bibliot. Jose Jeronimo Triana* 12: 1–924.

Crosby, M.R., Schultze-Motel, U. & Schultze-Motel, W. 1983. Katalog der Laubmoose von Madagaskar und den umliegenden Inseln. *Willdenowia* 13: 187–255.

Crum, H. 2001. *Structural diversity of bryophytes*. Ann Arbor: The University of Michigan Herbarium.

Cubero, J.I., Marcos-Samaniego, N. & Enroth, J. 2006. Pseudoparaphyllia in the European and Macaronesian species of *Neckera* Hedw. (Neckeraceae, Musci). *Cryptog. Bryol.* 27: 333–342.

Draper, I. & Hedenäs, L. 2009. Circumscription of European taxa within the *Sciuro-hypnum reflexum* complex (Brachytheciaceae, Bryophyta), based on molecular and morphological data. *Taxon* 58: 572–584.

Draper, I., Hedenäs, L. & Grimm G.W. 2007. Molecular and morphological incongruence in European species of *Isothecium* (Bryophyta). *Molec. Phylog. Evol.* 42: 700–716.

Een, G. 1976. Mosses from the Mascarenes. *Lindbergia* 3: 213–217.

Enroth, J. 1989. Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXVII. Neckeraceae (Musci). *Acta Bot. Fenn.* 137: 41–80.

Enroth, J. 1992a. Corrections to *Cryptoleptodon*, *Forsstroemia* and *Leptodon* (Leptodontaceae, Musci). *J. Hattori Bot. Lab.* 71: 75–82.

Enroth, J. 1992b. Notes on the Neckeraceae (Musci) 11–12: The taxonomic position of *Pinnatella callicostelloides* and *Bissetia lingulata*, with the description of *Chileobryon* (Anomodontaceae). *Nova Hedwigia* 54: 137–146.

Enroth, J. 1994a. On the evolution and circumscription of the Neckeraceae (Musci). *J. Hattori Bot. Lab.* 76: 13–20.

Enroth, J. 1994b. Notes on the Neckeraceae (Musci). 20. *Neckera goughiana* and its geographic distribution. *Hikobia* 11: 539–542.

Enroth, J. 1995. Notes on the Neckeraceae (Musci). 21–22. *Porotrichopsis flacca* and *Neckeropsis inundata*. *Fragm. Florist. Geobot.* 40: 181–188.

Enroth, J. 1996. *Porothamnium frahmii* (Neckeraceae, Musci), a new species from Colombia and Peru, and *P. stipitatum* new for the neotropics. *J. Bryol.* 19: 33–38.

Enroth, J. 1999. A review of the rheophytic Neckeraceae (Musci). *Haussknechtia Beih.* 9: 121–127.

Enroth, J. & He, S. 1991. Notes on the Neckeraceae (Musci) 8. *Pendulothecium*, a new genus from New Zealand and Norfolk Island. *New Zealand J. Bot.* 29: 7–16.

Enroth, J. & Ji, M. 2007. A new species of *Neckera* (Neckeraceae, Bryopsida) from Xizang, China. *Edinburgh J. Bot.* 64: 295–301.

Enroth, J. & Tan, B.C. 1994. Contributions to the bryoflora of China 10. The identity of *Homaliodendron neckeroides* (Neckeraceae, Musci). *Ann. Bot. Fenn.* 31: 53–57.

Fife, A.J. 1995. Checklist of the mosses of New Zealand. *Bryologist* 98: 313–337.

Fleischer, M. 1906–1908. *Die Musci der Flora von Buitenzorg*, vol. 3. Leiden: Brill.

Goffinet, B. & Buck, W.R. 2004. Systematics of the Bryophyta (mosses): From molecules to a revised classification. *Monogr. Syst. Bot. Missouri Bot. Gard.* 98: 205–239.

Goffinet, B., Cox, C.J., Shaw, A.J. & Hedderson, T.A.J. 2001. The Bryophyta (mosses): Systematic and evolutionary inferences from an *rps4* Gene (cpDNA) phylogeny. *Ann. Bot.* 87: 191–208.

Goffinet, B. & Shaw, A.J. 2002. Independent origins of cleistocarpy in the Splachnaceae: Analyses of cpDNA sequences and polyphyly of the Voitioideae (Bryophyta). *Syst. Bot.* 27: 203–208.

Goffinet, B., Shaw, A.J. & Cox, C.J. 2004. Phylogenetic inferences in the dung-moss family Splachnaceae from analyses of cpDNA sequence data and implications for the evolution of entomophily. *Amer. J. Bot.* 91: 748–759.

Graham, S.W., Reeves, P.A., Burns, A.C.E. & Olmstead, R.G. 2000. Microstructural changes in noncoding chloroplast DNA: Interpretation, evolution, and utility of indels and inversions in basal angiosperm phylogenetic inference. *Int. J. Pl. Sci.* 161: S83–S96.

Hamilton, M.B., Braverman, J.M. & Soria-Hernanz, D.F. 2003. Patterns and relative rates of nucleotide and insertion/deletion evolution at six chloroplast intergenic regions in new world species of the Lecythidaceae. *Molec. Biol. Evol.* 20: 1710–1721.

Hampe, E. 1863. Species novas muscorum ab Alexandro Lindigio in Nova-Granada collectas. *Linnaea* 32: 127–164.

He, S. 1997. A revision of *Homalia* (Musci: Neckeraceae). *J. Hattori Bot. Lab.* 81: 1–52.

Hedenäs, L. 1992. Flora of Madeiran pleurocarpous mosses (Isobryales, Hypnobryales, Hookeriales). *Bryophyt. Biblioth.* 44: 1–165.

Hedenäs, L. 1999. Altitudinal distribution in relation to latitude; with examples among wetland mosses in the Amblystegiaceae. *Bryobrothera* 5: 99–115.

Hedenäs, L. 2007. Morphological characters and their use in pleurocarpous moss systematics. Pp. 227–245 in: Newton, A.E. & Tangney, R. (eds.), *Pleurocarpous mosses: Systematics and evolution*. Boca Raton: Taylor & Francis; CRC Press.

Hedwig, J. 1801. *Species muscrorum frondosorum*. Leipzig: sumtu Ioannis Ambrosii Barthii; Paris: apud Amand Koenig.

Hernández-Maqueda, R., Quandt, D., Werner, O. & Muñoz, J. 2008. Phylogeny and classification of the Grimmiaceae/Ptychomitriaceae complex (Bryophyta) inferred from cpDNA. *Molec. Phylog. Evol.* 46: 863–877.

Herzog, T. 1916. Die Bryophyten meiner zweiten Reise durch Bolivia. *Biblioth. Bot.* 87: 1–347.

Huelsenbeck, J.P., Larget, B., Miller, R.E. & Ronquist, F. 2002. Potential applications and pitfalls of bayesian inference of phylogeny. *Syst. Biol.* 51: 673–688.

Huelsenbeck, J.P. & Ronquist, F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Huelsenbeck, J.P., Ronquist, F., Nielsen, R. & Bollback, J.P. 2001. Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310–2314.

Huttunen, S. & Ignatov, M. 2010. Evolution and taxonomy of aquatic species in the genus *Rhynchostegium* (Brachytheciaceae, Bryophyta). *Taxon* 59: 791–808.

Huttunen, S., Ignatov, M.S., Müller, K. & Quandt, D. 2004. The phylogeny and evolution of epiphytism in three moss families Meteoriaceae, Brachytheciaceae, and Lembophyllaceae. Pp 328–364 in: Goffinet, B., Hollowell, V. & Magill, R. (eds.), *Molecular systematics of bryophytes*. St. Louis: Missouri Botanical Garden Press.

Ignatov, M.S., Gardiner, A.A., Bobrova, V.K., Milyutina, I.A., Huttunen, S. & Troitsky, A.V. 2007. On the relationships of mosses of the order Hypnales, with special reference to taxa traditionally classified in the Leskeaceae. Pp. 177–213 in: Newton, A.E. & Tangney, R. (eds.), *Pleurocarpous mosses: Systematics and evolution*. Boca Raton: Taylor & Francis; CRC Press.

Ireland, R.R. 1974. *Neomacounia*, a new genus in the Neckeraceae (Musci) from Canada. *Bryologist* 77: 453–459.

Jaeger, A. & Sauerbeck, F. 1876–1879. *Genera et species muscorum systematice disposita seu adumbration florae muscorum totius orbis terrarum*. St. Gallen: ex officina Zollikoferi.

Ji, M.C. & Enroth, J. 2008. *Neckera hymenodonta* (Neckeraceae, Bryopsida) reinstated, with an emended description. *Ann. Bot. Fenn.* 45: 277–280.

Juratzka, J. 1866. Muscorum frondosorum species novae. *Bot. Zeit. (Berlin)* 24: 20–21.

Kass, R.E. & Raftery, A.E. 2007. Bayes Factors. *J. Amer. Statist. Assoc.* 90: 773–795.

Kelchner, S.A. 2000. The evolution of non-coding chloroplast DNA and its application in plant systematics. *Ann. Missouri Bot. Gard.* 87: 482–498.

Kindberg, N.C. 1902. Grundzüge einer Monographie der Laubmoosgattung *Thamnium*. *Hedwigia* 41: 203–268.

Lawton, E. 1971. *Moss flora of the Pacific Northwest*. Nichinan: The Hattori Botanical Laboratory.

Lindberg, S.O. 1863. Om ett nytt slägte, *Epipterygium*, bland bladmossorna. *Öfvers. Kongl. Vetensk.-Akad. Förh.* 19: 599–609.

Löhne, C. & Borsch, T. 2005. Molecular evolution and phylogenetic utility of the *petD* group II intron: A case study in basal angiosperms. *Molec. Biol. Evol.* 22: 317–332.

Maeda, S., Kosuge, K., Gonzalez, D., Luna, E. de & Akiyama, H. 2000. Molecular phylogeny of the suborder Leucodontineae (Musci; Leucodontales) inferred from *rbcL* sequence data. *J. Pl. Res.* 113: 29–38.

Mastracci, M. 2003. *Thamnobryum neckeroides* (Bryopsida: Neckeraceae): Lectotypification, synonymies, diagnostic characters, habitat and distribution. *J. Bryol.* 25: 115–120.

Mohr, D.M.H. 1803. *Observationes botanicae*. Kiel: typis C.F. Mohr.

Müller, K. 2005. SeqState: Primer design and sequence statistics for phylogenetic DNA data sets. *Appl. Bioinformatics* 4: 65–69.

Müller, K. 2007. PRAP2: Likelihood and parsimony ratchet analysis, v.0.9. http://systevol.nees.uni-bonn.de/software/PRAP2.

Müller, K. & Borsch, T. 2005. Phylogenetics of *Utricularia* (Lentibulariaceae) and molecular evolution of the *trnK* intron in a lineage with high mutational rates. *Pl. Syst. Evol.* 250: 39–67.

Müller, K., Quandt, D., Müller, J. & Neinhuis, C. 2005. PhyDE® 0.983: Phylogenetic Data Editor. http://www.phyde.de.

Nelson, P.P. 1973. *Leptodon smithii* (Musci, Neckeraceae), a genus new to North America. *Bryologist* 76: 434–437.

Nieuwland, J.A. 1917. Critical notes on new and old genera of plants. *Amer. Midland Naturalist* 5: 50–52.

Ninh, T. & Pócs, T. 1981. *Noguchiodendron*, a new genus of the moss family Neckeraceae. *Acta Bot. Acad. Sci. Hung.* 27: 161–168.

Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.

Ochyra, R. 1986. *Touwia laticostata*, a remarkable new genus and species of moss from Queensland, Australia. *J. Bryol.* 14: 103–108.

Ochyra, R. 1990. On the relationships of *Thamnobryum negrosense* (Bartr.) Iwats. & Tan (Musci: Thamnobryaceae). *J. Hattori Bot. Lab.* 68: 293–302.

Ochyra, R. 1991. *Crassiphyllum* (Thamnobryaceae), a new moss genus from Madeira. *Fragm. Florist. Geobot.* 36: 71–79.

Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L., Huttunen, S. & Quandt, D. 2009a. Phylogenetic analyses reveal high levels of polyphyly among pleurocarpous lineages as well as novel clades. *Bryologist* 112: 447–466.

Olsson, S., Buchbender, V., Enroth, J., Hedenäs, L., Huttunen, S. & Quandt, D. 2010. Phylogenetic relationships in the "*Pinnatella*" clade. *Organisms Divers. Evol.* 10: 107–122.

Olsson, S., Buchbender, V., Enroth, J., Huttunen, S., Hedenäs, L. & Quandt, D. 2009b. Evolution of the Neckeraceae: Resolving the backbone phylogeny. *Syst. Biodivers.* 7: 419–432.

Olsson, S., Rumsey, F., Grundmann, M., Russell, S., Enroth, J. & Quandt, D. 2009c. The origin of the British and Macaronesian endemic *Thamnobryum* species (Neckeraceae). *J. Bryol.* 31: 1–10.

Pócs, T. 1960. Die Verbreitung von *Leptodon smithii* (Dicks.) Mohr und die Verhältnisse seines Vorkommens. *Ann. Hist.-Nat. Mus. Natl. Hung.* 52: 169–176.

Quandt, D., Huttunen, S., Streimann, H., Frahm, J.P. & Frey, W. 2004. Molecular phylogenetics of the Meteoriaceae s. str.: Focusing on the genera *Meteorium* and *Papillaria*. *Molec. Phylog. Evol.* 32: 435–461.

Quandt, D., Huttunen, S., Tangney, R. & Stech, M. 2009. Back to the future? Molecules take us back to the 1925 classification of the Lembophyllaceae (Bryophyta). *Syst. Bot.* 34: 443–454.

Quandt, D., Müller, K. & Huttunen, S. 2003. Characterisation of the chloroplast DNA *psbT-H* region and the influence of dyad symmetrical elements on phylogenetic reconstructions. *Pl. Biol.* 5: 400–410.

Quandt, D. & Stech, M. 2005. Molecular evolution and secondary structure of the chloroplast *trnL* intron in bryophytes. *Molec. Phylog. Evol.* 36: 429–443.

Renauld, F. & Cardot, J. 1900. Musci novi vel minus cogniti, IX. *Bull. Soc. Roy. Bot. Belgique* 38: 1–48.

Sastre-De Jesús, I. 1987. *A revision of the Neckeraceae Schimp. and the Thamnobryaceae Marg. & Dur. in the Neotropics*. Dissertation, City University of New York.

Schimper, W.P. 1850. *Omalia*. Pp. 53–55 in: Bruch, W.P., Schimper, P. & Gümbel, T., *Bryologia europaea seu genera muscorum europaeorum monographice illustrata*, vol. 5, fasc. 44–45. Stuttgart: Schweizerbart.

Schimper, W.P. 1852. *Thamnium*. Pp. 211–215 in: Bruch, W.P., Schimper, P. & Gümbel, T., *Bryologia europaea seu genera muscorum europaeorum monographice illustrata*, vol. 5, fasc. 49–51. Stuttgart: Schweizerbart.

Simmons, M.P. & Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49: 369–381.

Simmons, M.P., Ochoterena, H. & Carr, T.G. 2001. Incorporation, relative homoplasy, and effect of gap characters in sequence-based phylogenetic analyses. *Syst. Biol.* 50: 454–462.

Sloover, J.L. de. 1977. Note de bryologie africaine VII. *Neckera*, *Neckeropsis*. *Bull. Jard. Bot. Natl. Belg.* 47: 31–48.

Sloover, J.L. de. 1983. Note de bryologie africaine XII. *Porotrichum* et *Porothamnium*. *Bull. Jard. Bot. Natl. Belg.* 53: 97–152

Smith, A.J.E. 2004. *The moss flora of Britain and Ireland*, ed. 2. Cambridge: Cambridge Univ. Press.

Sotiaux, A., Enroth, J., Olsson, S., Quandt, D. & Vanderpoorten, A. 2009. When morphology and molecules tell us different stories: A case-in-point with *Leptodon corsicus*, a new and unique endemic moss species from Corsica. *J. Bryol.* 31: 186–196.

Stark, L.R. 1987. A taxonomic monograph of *Forsstroemia* Lindb. (Bryopsida: Leptodontaceae). *J. Hattori Bot. Lab.* 63: 133–218.

Stech, M., Sim-Sim, M., Glória Esquível, M., Fontinha, S., Tangney, R., Lobo, C., Gabriel, R. & Quandt, D. 2008. Explaining the 'anomalous' distribution of *Echinodium* (Bryopsida: Echinodiaceae): Independent evolution in Macaronesia and Australasia. *Organisms Divers. Evol.* 8: 282–292.

Stöver, B.C. & Müller, K.F. 2010. TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* 11: 7. DOI: 10.1186/1471-2105-11-7.

Sullivant, W.S. 1855. Notices on some new mosses in the collection of the United States Exploring Expedition, continued Jan. 1855. *Proc. Amer. Acad. Arts* 3: 13–16.

Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4b10. Sunderland, Massachusetts: Sinauer.

Tsubota, H., Arikawa, T., Akiyama, H., Luna, E. de, Gonzales, D., Higuchi, M. & Deguchi, H. 2002. Molecular phylogeny of hypnobryalean mosses as inferred from a large-scale dataset of chloroplast *rbc*L, with special reference to the Hypnaceae and possibly related families. *Hikobia* 13: 645–665.

Tsubota, H., Luna, E. de, Gonzales, D., Ignatov, M. & Deguchi, H. 2004. Molecular phylogenetics and ordinal relationships based on analyses of a large-scale data set of 600 *rbcL* sequences of mosses. *Hikobia* 14: 149–170.

Vanderpoorten, A., Goffinet, B., Hedenäs, L., Cox, C.J. & Shaw, A.J. 2003. A taxonomic reassessment of the Vittiaceae (Hypnales, Bryopsida): Evidence from phylogenetic analyses of combined chloroplast and nuclear sequence data. *Pl. Syst. Evol.* 241: 1–12.

Wendel, J.F. & Doyle, J.J. 2005. Polyploidy and evolution in plants. Pp. 97–117 in: Henry, R. (ed.), *Diversity and evolution in plants.* Oxon: CABI Publishing.

Appendix. List of specimens used in the study including EMBL or GenBank accession numbers for the sequenced or downloaded regions and voucher details. In three cases sequence data have been already submitted to GenBank from previous studies and thus the accession numbers for *rps4-trnT-trnL-trnF* are composed of two different accession numbers. * denotes taxa for which nomenclatural changes are suggested in this article.

DNA no, species, herbarium, voucher ID, EMBL or GenBank acc. no *rps4- trnF, rpl16*, ITS.

B116, ***Alsia californica*** (Hook. & Arn.) Sull.*, B, *Bryo 234031*, FM210280, FM160946, FM161073; B141, ***Anomodon giraldii*** Müll. Hal*, H, H3194078, AM990342, FM210763, FM161075; SH10, ***Camptochaete arbuscula*** var. ***tumida*** (Sm.) Reichardt, H, *Streimann 51408*, AM990353, FM160955, FM161087; B617, ***Chileobryon callicostelloides*** (Broth. ex Thér.) Enroth, H, H 3107865, FM210283, FM200841, FM161088; B423, ***Cryptoleptodon longisetus*** (Mont.) Enroth*, H, H3038483, AM990356, FM160957, FM161091; B421, ***Cryptoleptodon pluvinii*** (Brid.) Broth.*, Huttunen, *Huttunen s.n.*, China, Hunan, FM210284, FM160958, FM161092; B223, ***Curvicladium kurzii*** (Kindb.) Enroth, NYBG, *Akiyama Th-85*, FM210285, FM160959, FM161093; SH146, ***Dolichomitriopsis diversiformis*** (Mitt.) Nog., H, MHA, *Nedoluzhko s.n.*, AM990362; (*trnLF* = AF397777), FM160963, FM161098; B195, ***Echinodium hispidum*** (Hook. f. & Wilson) Reichardt*, Buchbender, *Downing s.n.*, 29.10.2000, FM210286, FM160964, FM161099; B258, ***Echinodium umbrosum*** (Mitt.) A. Jaeger var. ***glaucoviride*** (Mitt.) S.P. Churchill*, Schäfer-Verwimp, *Streimann 49634*, EU434010, FM160965, EU477602; B768, ***Forsstroemia neckeroides*** Broth., H, *Akiyama & al. 381*, FN868963, FN868978, FN868972; B226, ***Forsstroemia producta*** (Hornsch.) Paris, H, *Koponen 46545*, FM201504, FM160967, FM161102; B196, ***Forsstroemia trichomitria*** (Hedw.) Lindb., Buchbender, *Streimann & Pocs 65120A*, AM990365, FM160968, FM161103; B349, ***Heterocladium dimorphum*** (Brid.) Schimp., H, H3212307, AM990376, FM160970, FM161115; B352, ***Heterocladium procurrens*** (Mitt.) A. Jaeger, H, H3212289, AM990379, FM160973, FM161118; B422, ***Homalia glabella*** (Hedw.) Schimp.*, H, *Townsend 93/291*, AM990382, FM160977, FM161123; B111, ***Homalia lusitanica*** Schimp., B, B275202, AM990383, FM160978, FM161124; B218, ***Homalia trichomanoides*** (Hedw.) Schimp., Quandt, *Olsson 105*, AM990385, FM160980, FM161126; B474, ***Homalia webbiana*** (Mont.) Schimp., H, *Müller K68*, AM990387, FM160982, FM161127; B110, ***Homaliodendron exiguum*** (Bosch & Sande Lac.) M. Fleisch, B, B263509, AM990389, FM160984, FM161130; B230, ***Homaliodendron flabellatum*** (Sm.) M. Fleisch., H, H3071675, FM210290, FM160985, FM161132; B424, ***Homaliodendron neckeroides*** Broth., H, H3071953, FM210306, FM161015, FM161168; SH103, ***Lembophyllum clandestinum*** (Hook. f & Wilson) Lindb., H, *Vitt 29644*, AM990401; (*trnLF* = AF397823), FM160996, FM161145; B131, ***Leptodon smithii*** (Hedw.) F. Weber & D. Mohr, B, B268385, AM990403, FM160997, FM161147; B253, ***Neckera besseri*** (Lobarz.) Jur.*, Quandt, *Olsson 107*, FM210294, FM161003, FM161156; B367, ***Neckera brownii*** Dixon*, H, *Tangney 2330*, FM210295, FM161004, FM161157; B106, ***Neckera chilensis*** Taylor*, B, B264587, FM210304, FM161013, FM161166; B193, ***Neckera complanata*** (Hedw.) Huebener*, Buchbender, *Buchbender 204*, AM990413, FM161005, FM161158; B248, ***Neckera crenulata*** Harv., H, *Long 33980*, FM210297, FM161006, FM161159; B192, ***Neckera crispa*** Hedw.*, Buchbender, *Buchbender 385*, FM210298, FM161007, FM161160; B127, ***Neckera douglasii*** Hook., B, B253879, FM210299, FM161008, FM161161; B249, ***Neckera goughiana*** Mitt.*, H, *Koponen 46476*, FM210300, FM161009, FM161162; B128, ***Neckera himalayana*** Mitt., B, B253876, FM210301, FM161010, FM161163; B427, ***Neckera hymenodonta*** Müll. Hal.*, H, H3206871, FM210302, FM161011, FM161164; B471, ***Neckera intermedia*** Brid.*, H, *Samaniego & Manso s.n.* 12.10.1999, FM210303, FM161012, FM161165; B161, ***Neckera menziesii*** Drumm., NYBG, *Halse 4878*, FM210305, FM161014, FM161167; B347, ***Neckera pennata*** Hedw., H, H3203794, AM990414, FM161016, FM161169; B250, ***Neckera polyclada*** Müll. Hal., H, *Koponen 45441*, FM210307, FM161017, FM161170; B307, ***Neckera remota*** Bruch & Schimp. ex Müll. Hal.*, S, B29895, AM990415, FM161018, FM161171; B105, ***Neckera scabridens*** Müll. Hal.*, H, *Kürschner & al. 95-498*, FM210308, FM161019, FM161172; B470, ***Neckera submacrocarpa*** Dixon*, Enroth, *Pocs 90021/AL*, FM210309, FM161020, FM161173; SH301, ***Neckera urnigera*** Müll. Hal.*, S, B15194, AM990416, FM161021, FM161174; B544, ***Neckera valentiniana*** Besch.*, Bolus Herb., Univ. Cape Town, *Hedderson 16404*, FM210310, FM161022, FM161175; B298, ***Neckera warburgii*** Broth., B, *Bryo 253855*, FM210311, FM161023, FM161176; B251, ***Neckera yezoana*** Besch.*, H, *Enroth 70675*, FM210312, FM161024, FM161177; B313, ***Neckeropsis nitidula*** (Mitt.) M. Fleisch., S, B105713, AM990419, FM161030, FM161183; B476, ***Pendulothecium punctatum*** (Hook. f. & Wilson) Enroth & S. He, S, *Streimann 53845*, AM990421, FM161033, FM161187; B260, ***Pinnatella anacamptolepis*** (Müll. Hal.) Broth., S, B104516, FM210318, FM161036, FM161190; B472, ***Pinnatella kuehliana*** (Bosch & Sande Lac.) M. Fleisch., Enroth, *Müller S116*, FM20150, FM161038, FM161192; B099, ***Porotrichodendron robustum*** Broth., B, B264620, AM990426, FM200845, FM161197; B294, ***Porotrichodendron superbum*** (Taylor) Broth., H, H3121100, AM990427, FM161043, FM161198; SH372, ***Porotrichopsis flacca*** Herzog, S, *Churchill & al. 17201*, FM201506, FM161044, FM161199; B244, ***Porotrichum bigelovii*** (Sull.) Kindb., H, *Shevock & Kellman 27467*, AM990428, FM161045, FM161200; B117, ***Porotrichum frahmii*** (Enroth) Enroth, B, B255332, AM990429, FM161046, FM161201; SH252, ***Porotrichum madagassum*** Kiaer ex Besch.*, Vanderpoorten, Quandt, *Vanderpoorten FSA 244*, FM210322, FM210764, FM161203; B559, ***Rigodium pseudothuidium*** Dusén, NYBG, NYBG 00892248, –, –, FM161210; Rp47, ***Rigodium pseudothuidium*** Dusén, H, H3134254, AM990438 (*trnLF* = AF543547), FM161051, –; B149, ***Taiwanobryum speciosum*** Nog., H, *Enroth 64877*, AM990442, FM161055, FM161216; B238, ***Thamnobryum alopecurum*** (Hedw.) Nieuwl. ex Gangulee, Buchbender, *Buchbender s.n.* 11.7.2003, AM990444, FM161056, FM161218; B539, ***Thamnobryum cataractarum*** N. Hodgetts & Blockeel, S, B3725, FM201507, FM161057, FM161219; B546, ***Thamnobryum ellipticum*** (Bosch & Sande Lac.) Nieuwl.*, *Enroth, Müller S114*, FM210325, FM161058, FM161220; B190, ***Thamnobryum fasciculatum*** (Sw. ex Hedw.) I. Sastre, NYBG, *Buck 26902*, FM210326, FM161059, FM161221; B549, ***Thamnobryum fernandesii*** Sérgio, S, B9965, FM201508, FM161060, FM161222; SH300, ***Thamnobryum maderense*** (Kindb.) Hedenäs, S, B44108, AM990445, FM161061, FM161223; B165, ***Thamnobryum neckeroides*** (Hook.) E. Lawton, NYBG, *Buck 37648*, FM201509, FM161062, FM161224; B420, ***Thamnobryum negrosense*** (E.B. Bartram) Z. Iwats. & B.C. Tan*, H, *Schäfer-Verwimp & Verwimp 16852*, FM210327, FM161063, FM161225; B311, ***Thamnobryum pandum*** (Hook. f. & Wilson) I.G. Stone & G.A.M. Scott, H, H3208440, FM210328, FM161064, FM161226; B120, ***Thamnobryum pumilum*** (Hook. & Wilson) B.C. Tan, B, B268163, FM210329, FM200843, FM161227; B574, ***Thamnobryum rudolphianum*** Mastracci, BM, BM000919859, FM201510, FM161065, FM161228; B233, ***Thamnobryum speciosum*** (Broth.) Hoe, H, H3141827, FM201511, FM161066, FM161229; B148, ***Thamnobryum subserratum*** (Hook. ex Harv.) Nog. & Z. Iwats., H, *Enroth 64595*, AM990446, FM161067, FM161230; B429, ***Thamnobryum tumidicaule*** (K.A. Wagner) F.D. Bowers*, H, H3141850, AM990447, FM161068, FM161231; B261, ***Touwia laticostata*** Ochyra, JCT, *Cairns B349*, FM210330, FM161070, FM161233; DQ, ***Weymouthia mollis*** (Hedw.) Broth., CHR, *Quandt, 99-Mo2*, AM990452, FM161072, FM161237.