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Phylogeny of *Neckeropsis* and *Himantocladium* (Neckeraceae, Bryophytina)

SANNA OLSSON^{1,2*}, JOHANNES ENROTH^{3*}, SANNA HUTTUNEN⁴ & DIETMAR QUANDT⁵

¹Department of Agricultural Sciences, University of Helsinki, P.O. Box 27, FI-00014 Helsinki, Finland

²INIA Forest Research Centre (INIA-CIFOR), Dept. Forest Ecology and Genetics, Carretera de A Coruña km 7.5, E-28040 Madrid, Spain

³Department of Biological and Environmental Sciences and Botanical Museum, University of Helsinki, P.O. Box 7, FI-00014 Helsinki, Finland

⁴Department of Biology, FI-20014 University of Turku, Finland

⁵Nees-Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany

*Corresponding author: Sanna Olsson, e-mail: sanna.olsson@helsinki.fi, tel.: +34634509635 or Johannes Enroth, e-mail: Johannes.enroth@helsinki.fi, tel.: +3580294157792

Abstract

Two closely related tropical genera from the pleurocarpous moss family Neckeraceae are revised: the second largest genus in the family, *Neckeropsis*, currently with 29 species, and *Himantocladium*, comprising six species. Twenty-one species of *Neckeropsis* and five of *Himantocladium* were included in this study, which is based on phylogenetic analyses using sequence level data from the plastid (*rps4*)-*trnT-trnL-trnF* cluster and *rpl16* as well as nuclear ITS1 & 2. *Neckeropsis* appeared as polyphyletic. *Neckeropsis s. str.* comprises 12 species and a further four species, not included in the analysis, are tentatively retained in the genus based on morphology. Four new genera are segregated from *Neckeropsis*: *Pengchengwua* (with one species), *Planicladium* (two species), *Pseudoparaphysanthus* (five species), and *Neckeromnion* (five species). *Neckeropsis gracilis* is synonymized with *Neckeromnion urocladum* and reported for the first time from Laos. Four molecularly analyzed species are resolved in the *Himantocladium s. str.* clade, with a fifth species being retained solely on morphological basis. *Himantocladium formosicum* is transferred to *Neckeropsis*. Leaf-like paraphyses (ramenta), unique in *Neckeropsis s. str.*, have evolved twice. In addition, the rare *Noguchiodendron sphaerocarpum* from the Himalayan region, the single species in its genus, was included in a phylogenetic analysis for the first time and was found to be closely related to the Asian genus *Taiwanobryum*.

Key words: convergent evolution; molecular systematics; *Noguchiodendron*; nomenclature; pleurocarpous mosses; taxonomy

Introduction

The Neckeraceae, a moss family with c. 200 species (Olsson *et al.* 2009b), belongs to the order Hypnales of the pleurocarpous mosses. In contrast to acrocarpous mosses, pleurocarps produce archegonia and thus sporophytes on reduced lateral branches rather than on the tips of main shoots. With ca. 5000 species pleurocarpous mosses, as defined by Bell *et al.* (2007), represent the major moss radiation comprising ~50% of moss diversity. Within the Neckeraceae, three well-supported clades have been recognized in previous studies: the *Neckera* clade, the *Thamnobryum* clade and the *Pinnatella* clade (Olsson *et al.* 2009a), each of which was analysed subsequently with a more comprehensive taxon sampling by Olsson *et al.* (2010, 2011). *Neckeropsis* Reichardt and *Himantocladium* (Mitt.) M. Fleisch, on which the present paper focuses, are part of the *Pinnatella* clade that comprises mainly tropical Asiatic genera (Olsson *et al.* 2009a, 2010). A combination of morphological characters that distinguish this clade from other Neckeraceae include a strong costa, leaves with an inframarginal (rarely marginal) limbidium consisting of elongate cells, and a seta that is mammillose in its upper part. However, those characters are not ubiquitous in the clade and, in the neckeraceous context, only the mammillose seta is exclusive in it.

Neckeropsis was established by Reichardt (1868) based on the Neotropical *Neckera undulata* Hedw. Fleischer (1906–1908) considerably amended and expanded the generic concept, placing in *Neckeropsis* all species in the sections *Paraphysanthus* Spruce, *Pseudoparaphysanthus* Broth. and *Taeniocladium* Mitt. of *Neckera* Hedw. In the new

circumscription, *Neckeropsis* had 21 species and was a pantropical genus most diverse in SE Asia. When Reichardt (1868) established *Neckeropsis*, he emphasized characters such as the roundish leaf cells, cap-like (“mützenförmig”) calyptra with a lobed base, and perichaetial paraphyses that develop into linear, leaf-like structures. In Fleischer’s concept, *Neckeropsis* consisted of plants with complanate, tetrastichous leaves, immersed capsules and cap-like calyptrae. Brotherus (1925) adopted Fleischer’s subdivision and recognized a total of 36 species in *Neckeropsis*. Over the last 55 years, *Neckeropsis* has been taxonomically revised for the various parts of its geographic distribution: Asia and Pacific (Touw 1962, 1972, Touw & Ochyra 1987, Ochyra & Enroth 1989, Higuchi *et al.* 1989), neotropics (Sastre de Jesús 1987, Enroth 1995), and Africa (Enroth 1993, Enroth & Magill 1994). The species currently recognized in *Neckeropsis* are listed in alphabetical order in Table 1.

TABLE 1. Species placed in *Neckeropsis* and *Himantocladium* before the present study. An asterisk (*) denotes that the species was included in the present analysis.

<i>Neckeropsis</i>	<i>Himantocladium</i>
<i>Neckeropsis andamana</i> (Müll. Hal.) M. Fleisch.*	<i>H.</i> sect. <i>Himantocladium</i>
<i>N. beccariana</i> (Hampe) Touw*	<i>H. plumula</i> (Nees) M. Fleisch.*
<i>N. boiviniana</i> (Besch.) Card.	<i>H. giulianettii</i> (Broth.) M. Fleisch.*
<i>N. boniana</i> (Besch.) Touw & Ochyra	<i>H. pacificum</i> (Broth. & Paris) Broth.
<i>N. calcicola</i> Nog.*	<i>H. submontanum</i> Enroth*
<i>N. calcutensis</i> (M. Fleisch.) Enroth*	<i>H. implanum</i> (Mitt.) M. Fleisch.*
<i>N. crinita</i> (Griff.) M. Fleisch.*	<i>H.</i> sect. <i>Cyclophyllum</i>
<i>N. cyclophylla</i> (Müll. Hal.) S. Olsson, Enroth & D. Quandt*	<i>H. formosicum</i> Broth. & Yas.*
<i>N. disticha</i> (Hedw.) Kindb.*	<i>H. warburgii</i> (Broth.) M. Fleisch.
<i>N. exserta</i> (Hook.) Broth.*	
-- var. <i>scrobiculata</i> (Nees) Touw*	
<i>N. fimbriata</i> (Harv.) M. Fleisch.*	
<i>N. foveolata</i> (Mitt.) Broth.*	
<i>N. gracilentata</i> (Bosch & Sande Lac.) M. Fleisch.*	
<i>N. gracilis</i> Nog.*	
<i>N. inundata</i> (Broth.) Broth.	
<i>N. lepineana</i> (Mont.) M. Fleisch.*	
<i>N. liliana</i> (Ren.) Broth.	
<i>N. madecassa</i> (Besch.) M. Fleisch.*	
<i>N. moutieri</i> (Broth. & Paris) M. Fleisch.*	
<i>N. nanodisticha</i> (Geh.) M. Fleisch.	
<i>N. nitidula</i> (Mitt.) M. Fleisch.*	
<i>N. obtusata</i> (Mont.) Broth.*	
<i>N. pocsii</i> Enroth & Magill*	
<i>N. semperiana</i> (Müll. Hal.) Touw*	
<i>N. spuriotruncata</i> (Dus.) M. Fleisch.	
<i>N. submarginata</i> Card. ex Touw	
<i>N. takahashii</i> Hig. & al.*	
<i>N. touwii</i> Ochyra & Enroth	
<i>N. undulata</i> (Hedw.) Reichardt*	

Himantocladium was first recognized by Mitten (1868) as *Neckera* section *Himantocladium* Mitt. He included three species, *Neckera implana* Mitt., *N. loriformis* Bosch & Sande Lac. and *N. mucronata* Bosch & Sande Lac. *Himantocladium* was raised to generic status by Fleischer (1906–1908), who also added several species in it. Wijk *et al.* (1964) cited *H. implanum* (Mitt.) M. Fleisch. as the lectotype. In the original generic concept, Fleischer (1906–1908) recognized *Himantocladium* as an essentially Asian-Polynesian genus morphologically intermediate between the “*Neckera*-like” and the “*Thamnobryum*-like” taxa (“*Neckereen*” and “*Thamnieen*”). Fleischer emphasized in *Himantocladium* the combination of a dendroid habit, 8-ranked leaves, small [post-fertilization] perichaetial leaves and an exerted capsule with a small, cucullate calyptra.

The generic affinity and distinctions between *Himantocladium* and *Neckeropsis* were discussed by Touw (1962) and summarized in a taxonomic revision of *Himantocladium* by Enroth (1992a). The latter author considered *Himantocladium* as a genus morphologically intermediate between *Neckeropsis* and *Pinnatella*, and discussed the clearest generic distinctions. Enroth (1992a) further subdivided the eight accepted species in *Himantocladium* into two sections (Table 1). The section *Himantocladium* contained species with a synoicous sexual condition and essentially solid leaf cell walls, and the section *Cyclophyllum* Enroth had dioicous species with distinctly porose leaf cell walls at least in the basal lamina.

Subsequent analyses based on molecular data confirmed that the two genera are indeed closely interrelated, but also showed that neither of them is monophyletic (Olsson *et al.* 2010). *Neckeropsis* is characterized by the following combination of morphological features: plants non-stipitate [except *N. cyclophylla* (Müll. Hal.) S. Olsson, Enroth & D. Quandt, *N. formosica* (Broth. & Yasuda) S. Olsson, Enroth, Huttunen & D. Quandt, and *N. madecassa* (Besch.) M. Fleisch.]; branching remote and irregular; stem central strand lacking; foliation complanate, pseudotetrastichous (cf. Touw 1962); post-fertilization growth of perichaetial leaves common; seta mostly short, thus capsules immersed. To these can be added a nearly consistent absence of apophysal stomata (except in *N. cyclophylla* and *N. formosica*), which are consistently present in *Himantocladium s. str.*

As in the generic concept of Fleischer (1906–1908), there is no single character that would separate *Himantocladium*, as currently understood, from the allied genera. Rather, it has the following combination of characters, unique among the Neckeraceae: plants stipitate, mostly frondose; stipe leaves appressed; stem central strand absent; leaves not deeply and regularly undulate; costa strong, single; no post-fertilization growth of perichaetial leaves; capsules exerted; and apophysal stomata few, usually just two or three per capsule. The generic placement of *H. warburgii* (Broth.) M. Fleisch. remains unclear, but it is not in *Himantocladium s. str.* (Olsson *et al.* 2011). Enroth (1994a) treated it in its original genus, as *Neckera warburgii* Broth., but it belongs in the *Pinnatella* clade and is not closely related to *Neckera s. str.* (Olsson *et al.* 2011).

As our earlier studies focused on resolving the backbone structure and genus-level relationships within the Neckeraceae, the taxon sampling was in most cases incomplete to reveal within-genus relationships. For example, only eight species out of the 28 that then were placed in *Neckeropsis* were included in Olsson *et al.* (2010). In this study, we aimed at gathering an almost complete taxon sampling for *Neckeropsis* and *Himantocladium* in order to better resolve the generic taxonomy and species relationships, and to elaborate the morphological evolution in *Neckeropsis s. str.*

Material and methods

Taxon sampling and molecular markers:—Phylogenetic analyses were performed on a slightly altered data set of Olsson *et al.* (2010) that was complemented by more taxa focusing on *Neckeropsis* and *Himantocladium*. In the current study, 21 species out of total of 29 species in *Neckeropsis* and five out of six *Himantocladium* species are included. The missing eight *Neckeropsis* species and *Himantocladium pacificum* could not be included due to lack of adequately fresh material. In addition, we included *Noguchiodendron sphaerocarpum* (Nog.) T.N. Ninh & Pócs, the single species in its genus (Ninh & Pócs 1981) and not included in phylogenetic analyses previously. For this selection of taxa, we sequenced three genomic regions: the internal transcribed spacer 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).

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 PCR amplification of genetic regions followed Olsson *et al.* (2009a, 2009b). Gel cleaned PCR products were sequenced by Macrogen Inc., South Korea (www.macrogen.com). Sequences were edited manually with PhyDE® v0.997 (Müller *et al.* 2005) and primer sequences were eliminated. All sequences are deposited

in EMBL (European Molecular Biology Laboratory); accession numbers are listed together with voucher information (Appendix 1).

Sequence analyses and phylogenetic analyses:—Alignment of the sequence data was performed manually in PhyDE® v0.997 (Müller *et al.* 2005), based on the criteria laid out in Kelchner (2000) and Olsson *et al.* (2009b), using the alignment of Olsson *et al.* (2010) as scaffold. The reported hairpin associated inversion in the *trnL-F* intergenic spacer (IGS) (Quandt & Stech 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) and Borsch & Quandt (2009). Alignments are available on request from the authors. Indels were incorporated as binary data using a simple indel coding (SIC) strategy (Simmons & Ochoterena 2000) as implemented in SeqState (Müller 2005).

Maximum likelihood (ML) analyses were performed with RAxML (Stamatakis 2006; Stamatakis *et al.* 2008) on CIPRES Science Gateway (Miller *et al.* 2010). The models GTR+ Γ and GTR+CAT were tried out, and since GTR+CAT resulted in slightly better support values, it was used for the final analyses. Bootstrap analysis was performed with 1000 ML bootstrap replicates on the concatenated data matrix. The data matrix set was divided in a partition of subsets according to the boundaries of the genetic regions.

Bayesian analyses were performed with MrBayes v3.2.6 (Huelsenbeck & 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 data set 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 *et al.* (2001, 2002). Ten runs with four chains (1×10^6 generations each) were run simultaneously. Chains were sampled every 1000 generations and the respective trees written to a tree file. Tracer v1.6 (Rambaut *et al.* 2014) was used for the output of the model parameters to examine the sampling and convergence results. Calculations of the consensus tree and of the posterior probability of clades were performed based upon the trees sampled after the chains converged (< generation 50 000). Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph2 (Stöver & Müller 2010). Phylogenetic analyses were conducted on each partition separately. No incongruence was detected, therefore the analyses were performed on the combined data matrix.

Results

Alignment and sequence analyses:—Before analysing the matrix, 21 hotspots with poly-homonucleotide repeats were recognized and excluded from the analyses following Olsson *et al.* (2009b). The resulting alignment contained 4038 positions of which 1444 positions belonged to the (*rps4*)-*trnT*-*trnL*-*trnF* partition, 1680 positions to the nuclear ribosomal partition and 914 positions to the *rpl16* partition. Of all characters 800 (19.8%) were variable and 482 (11.9%) parsimony informative. When the information based on indel coding was included, the data matrix included 4548 positions, of which 1307 (28.7%) were variable and 721 (15.9%) parsimony informative.

Phylogenetic analyses:—The best scoring ML tree with bootstrap support values showed no topological conflict with the results from the Bayesian inference. Therefore, only the BI tree is illustrated (Fig. 1), with posterior probabilities (PP) indicated and complemented with bootstrap values (BS) of the ML analysis when applicable. Values resulting from analyses without indel coding approach 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 the scheme: (PP / PPsic / BS / BSsic).

The monophyly of the Neckeraceae is fully supported in the Bayesian analyses (PP 1 / 1, BS 82 / 86). The Neckeraceae species that belong to the outgroups in the present analyses confirm the within-family structure found in earlier analyses: a maximally supported *Neckera*-clade (PP 1 / 1, BS 100 / 100,) (including *Neckera*, *Forsstroemia* Lindb., *Leptodon* D. Mohr. and *Alleniella* S. Olsson, Enroth & D. Quandt) and a *Thamnobryum*-clade (PP 0.97 / 0.99, BS 67 / 78) that also includes *Homalia* Brid., *Pendulothecium* Enroth & S. He and *Porotrichodendron* M. Fleisch.

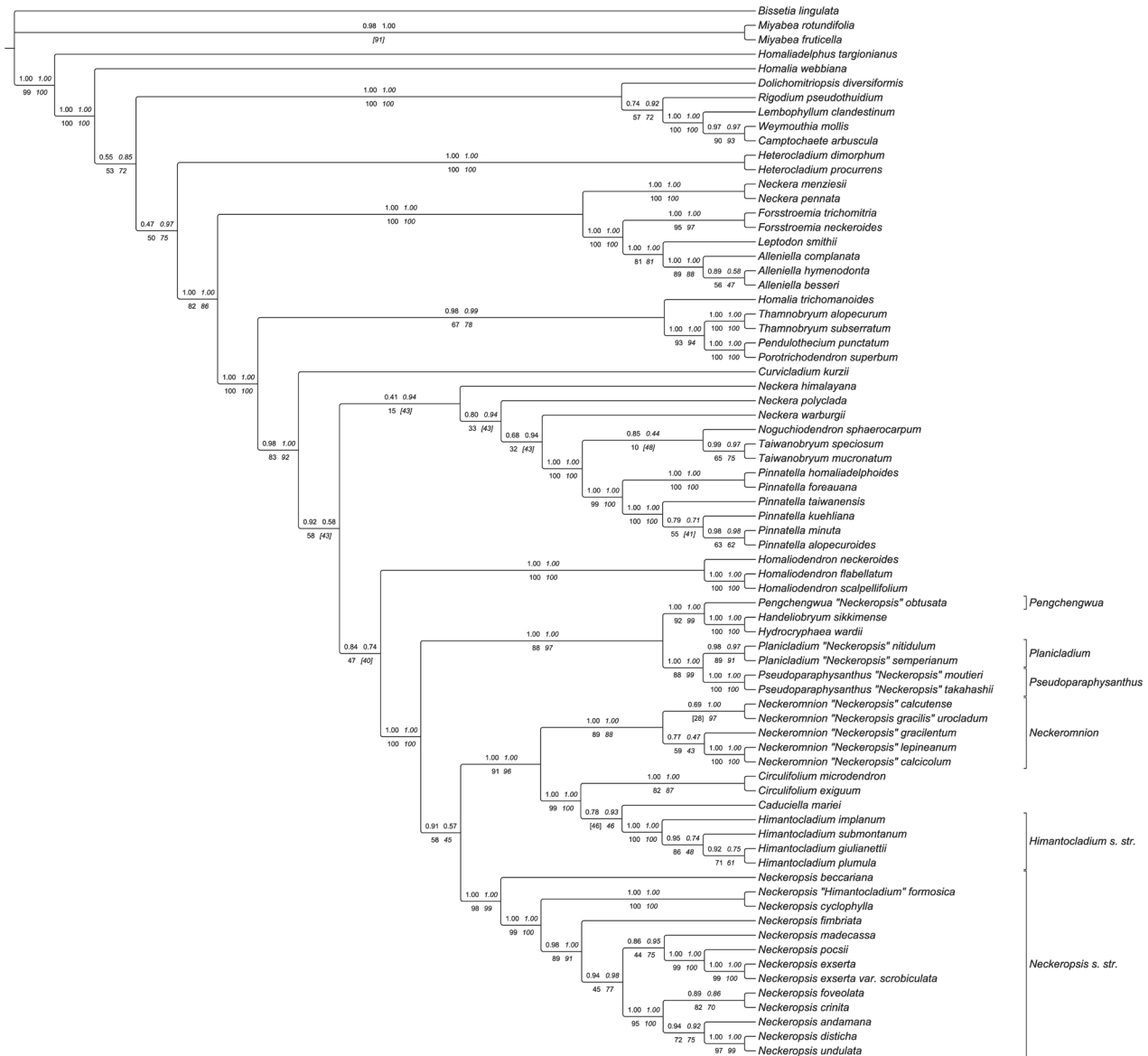


FIGURE 1. Phylogenetic relationships of selected Neckeraceae taxa based on *rps4-trnT-trnL-trnF*, *rpl16* and ITS1 & 2 sequences. The tree represents the majority consensus of trees sampled after stationarity in the Bayesian analysis. PP values from the Bayesian inference are indicated above (first without indels, then with indel data), the corresponding bootstrap values of the parsimony analysis below (first without indels, then with indel data), when applicable.

Curviciadium kurzii, the single species in its genus, is sister (PP 0.98 / 1, BS 83 / 92) to the ingroup, the so-called *Pinnatella*-clade. The three “*Neckeras*” in this clade, i.e. *N. himalayana* Mitt., *N. warburgii* and *N. polyclada* Müll. Hal. will be included in a forthcoming analysis by us, focusing on *Neckera s.l.* Within the ingroup, several well supported clades are identified. *Noguchiodendron* is resolved as sister to *Taiwanobryum* although without support (PP 0.85 / 0.44, BS - / -). *Pinnatella* forms a clade with very high support (PP 1 / 1, BS 99 / 100). *Homaliocladium* receives full support in all analyses. The rest of the species form the clade (PP 1 / 1, BS 100 / 100) that is the focal point of this paper. It includes members of *Neckeropsis*, *Circulifolium* S. Olsson, Enroth & D. Quandt, and *Himantocladium* as well as *Handeliobryum sikkimense* (Paris) Ochyra, *Hydrocryphaea wardii* Dixon and *Caduciella mariei* (Besch.) Enroth.

Neckeropsis and *Himantocladium* are both polyphyletic. Four *Himantocladium* species, *H. implanum*, *H. submontanum* Enroth, *H. giulianettii* (Broth.) M. Fleisch. and *H. plumula* (Nees) M. Fleisch. form a fully supported *Himantocladium s. str.* clade. *Neckeropsis* species are resolved in five well supported clades (Fig. 1): 1) a *Neckeropsis s. str.* clade (PP 1 / 1, BS 98 / 99), which also includes *Himantocladium formosicum* Broth.; 2) a *Neckeromnion* clade with *Neckeropsis calcutensis* (M. Fleisch.) Enroth, *N. gracilis* Nog., *N. gracilentata* (Bosch & Sande Lac.) M. Fleisch., *N. lepianeana* (Mont.) M. Fleisch. and *N. calcicola* Nog. 3) a fully supported *Pseudoparaphysanthus* clade with *N.*

moutieri (Broth. & Paris) M. Fleisch. and *N. takahashii* Higuchi, Iwatsuki, Ochyra & Li, and 4) a *Planicladium* clade comprising *N. semperiana* (Hampe ex Müll. Hal.) Touw and *N. nitidula* (Mitt.) M. Fleisch. (PP 0.98 / 0.97, BS 89 / 91). The two last mentioned clades are together forming a clade that is sister to a well-supported 5) *Pengchengwua* “*Neckeropsis*” *obtusata* – *Handeliobryum* – *Hydrocryphaea* clade (PP 1 / 1, BS 92 / 99). The *Neckeromnion* clade is sister to a fully supported *Circulifolium-Caduciella-Himantocladium* clade, and together these two form a clade with the *Neckeropsis s. str.* clade, though only with moderate (PP 0.91 / 0.57, BS 58 / 45) support.

Discussion

The phylogenetic results support the division of *Neckeropsis s. l.* into five monophyletic lineages. The largest one, with 21 species, comprises *Neckeropsis s. str.*, while the four remaining clades are recognized as new genera, which are discussed and described below. A clade including *Neckeropsis gracilentata*, *N. calcicola* and *N. calcutensis* was already identified by Olsson *et al.* (2010), but taxonomic changes were pending for the more comprehensive analyses provided here.

Neckeropsis s. str.:—Of the taxa included in our study, *Neckeropsis andamana* (Müll. Hal.) M. Fleisch., *N. beccariana* (Hampe) Touw, *N. crinita* (Griff.) M. Fleisch., *N. cyclophylla*, *N. disticha* (Hedw.) Kindb., *N. exserta* (Hook.) Broth., *N. exserta* var. *scrobiculata* (Nees) Touw, *N. fimbriata* (Harv.) M. Fleisch., *N. formosica* (*Himantocladium formosicum* Broth. & Yasuda), *N. foveolata* (Mitt.) Broth., *N. madecassa*, *N. pocsii* Enroth & Magill and *N. undulata* are placed in *Neckeropsis s. str.* Because of the polyphyly of *Neckeropsis s. l.* the morphological delimitation used in early treatments by Reichardt (1868) and Fleischer (1906–1908) requires some adjusting (see below).

Biogeography:—Even in its new circumscription, *Neckeropsis s. str.* remains a pantropical genus that has its highest species diversity in Asia. The topology of the *Neckeropsis s. str.* clade does not convey a clear biogeographic pattern. Six of the sequenced species (*N. beccariana*, *N. fimbriata*, *N. formosica*, *N. exserta*, *N. crinita*, *N. andamana*) are exclusively Asian and are scattered across the clade without a single exclusively Asian species pair. *Neckeropsis beccariana* is endemic to Borneo and *N. formosica* has been recorded from Taiwan, Laos and the Philippines (Enroth 1996); the record of the latter from a completely different climate and environment in Xizang (Wu 2011) requires verification. The remaining three species have wider distributions in the continental SE Asia, *N. andamana* being known also from the Andamans and Philippines, but none of them are known from the Indonesian archipelago.

We did not have adequately fresh material available of *Neckeropsis boiviniana* (Besch.) Cardot, *N. boniana* (Besch.) Touw & Ochyra, *N. inundata* (Broth.) Broth., *N. liliana* (Renauld) Paris, *N. nanodisticha* (Geh.) M. Fleisch., *N. submarginata* Card. ex Touw, *N. touwii* Ochyra & Enroth and *N. spuriotruncata* (Dusén) M. Fleisch. Of those, *N. boniana*, *N. submarginata* and *N. touwii* are here transferred to *Pseudoparaphysanthus* based on morphology (see below), while the other five are retained in *Neckeropsis s. str. incertae sedis*.

Neckeropsis boiviniana is a narrow endemic, known only from three specimens collected in northern Madagascar and the small island of Nosy Bé NW of Madagascar. The type collection dates back to 1851 and the most recent one to 1972 (Enroth 1993). The name *Neckeropsis inundata* was reduced into synonymy under *N. disticha* by Sastre-De Jesús (1987), but Enroth (1995) thought there were adequate morphological differences to justify recognizing *N. inundata* as a distinct species. It is known only from the original material collected in 1900 along Río Juruá in the W Amazonas region (cf. Enroth 1995). *Neckeropsis nanodisticha* was described in detail by Touw (1962). It is known from Indonesia, Papua New Guinea and Queensland in Australia. Its specialized paraphyses (ramenta) represent the same subtype as those of *N. crinita* (Merced-Alejandro & Sastre-De Jesús, 2009); thus *N. nanodisticha* probably belongs in *Neckeropsis s. str.* *Neckeropsis liliana* and *N. spuriotruncata* are rare African species. *Neckeropsis liliana* is known from W and Central Africa: Ivory Coast, Ghana, Cameroon, Central African Republic and the Democratic Republic of the Congo (= Zaire; Enroth 1993). All of the known material of the species is quite old, collected between 1895 and 1936. *Neckeropsis spuriotruncata* is reported from Ivory Coast, Cameroon, Gabon, Republic of Congo (Enroth 1993), and from Guinea and the Democratic Republic of the Congo (Ellis *et al.* 2016); all the known material is old. Based on morphology, Enroth (1993) concluded that *N. spuriotruncata*, *N. liliana* and *N. madecassa* form a coherent group, for example by having identical sporophytes. If the two former indeed are close to *N. madecassa*, they belong in *Neckeropsis s. str.*

Neckeropsis madecassa is known from Africa (Cameroon, Gabon, Zaire, Madagascar, Réunion; Enroth 1993), while the morphologically variable *N. cyclophylla* ranges from the Seychelles in the Indian Ocean through tropical and subtropical Asia to northern Australia and Samoa in the east (Enroth 1992a).

Neckeropsis pocsii, the sister species of the SE Asian *N. exserta*, is known only from the Comoro Islands in the

Indian Ocean (Enroth & Magill 1994). Its gametophyte most closely resembles that of *N. disticha*, but the two species are not closely related.

The remaining clade of six species is also a biogeographical mélange. *Neckeropsis foveolata* and *N. disticha*, not closely related to each other, are distributed in Central and South America and Africa; *N. crinita* is the closest relative of *N. foveolata* but is exclusively distributed in SE Asia. *Neckeropsis undulata* is the sister of *N. disticha* and the single species in the genus restricted to Central and South America (plus the Caribbean Islands and Florida; Buck 1998).

Morphology and evolutionary trends:—In contrast to genera such as *Himantocladium*, *Taiwanobryum* and *Pinnatella*, species of *Neckeropsis s. str.* lack clearly differentiated stipes and fronds. *Neckeropsis cyclophylla*, *N. formosica* and *N. madecassa* are sometimes indistinctly stipitate, but the stipe bears only slightly differentiated leaves (as compared to the upper leaves). The leaf base is distinctly widened in *N. formosica*, *N. foveolata*, *N. fimbriata*, *N. exserta*, *N. crinita*, *N. andamana* and *N. undulata*, and with a distinct basispicopic auricle in *N. fimbriata*, *N. madecassa*, *N. crinita*, *N. exserta*, *N. foveolata*, *N. andamana* and *N. undulata*. Elsewhere in the Neckeraceae, such auricles are encountered only in *Pinnatella homaliadelphoides* Enroth, S. Olsson, S. He, Shevock & D. Quandt (Enroth *et al.* 2010), which in an intriguing way “mimics” the genus *Homaliadelphus* of the Miyabeaceae (Olsson *et al.* 2009b).

The leaves are deeply and regularly undulate in *Neckeropsis foveolata*, *N. fimbriata*, *N. crinita*, *N. exserta*, *N. andamana* and *N. undulata*. It is noteworthy that in the first diverging lineages in *Neckeropsis s. str.* comprising of *N. beccariana*, *N. cyclophylla*, *N. fimbriata*, and *N. formosica*, only *N. fimbriata* has such undulate leaves. Evolution of undulate leaves appears to be a recurring trend in various neckeraceous lineages, particularly in *Neckera s. str.*, *Exsertotheca* S. Olsson, Enroth & D. Quandt and *Alleniella* (cf. Olsson *et al.* 2011) in addition to *Pengchengwua*, *Neckeromnion* (both established in the present paper) and *Neckeropsis s. str.* In these taxa, the undulations are typically lunate, or semi-circular, and it can be assumed that they are able to retain water on the often pendent gametophytes. It is also clear however that without a single exception in the Neckeraceae, when the leaves are deeply and regularly undulate they are also glossy, often strongly so. In our opinion, this clearly suggests that such undulate, glossy leaf surfaces have some kind of a photobiological function, as the leaf surfaces reflect light (and heat) to various directions and may enhance photosynthesis in conditions of reduced light availability.

Within the genus there is a shift from dioicous sexual condition in first diverging species to autoicy and/or synoicy in the crown clade. The four species that branch off first (*N. beccariana*, *N. cyclophylla*, *N. formosica*, *N. fimbriata*) are dioicous. Crown clade taxa from *Neckeropsis madecassa* onwards are autoicous; *N. pocsii* and *N. undulata* are at least partly synoicous, and *N. disticha* is exclusively so. The same trend from dioicy to autoicy was observed by Olsson *et al.* (2011) in the genus *Alleniella*. It is well established that autoicous mosses reproduce sexually and produce sporophytes and thus spores much more frequently than dioicous ones. Recently Laenen *et al.* (2016) showed that shifts to bisexuality may increase diversification rates in liverworts. They suggested that this could be related to higher dispersal capacity and higher potential for long distance dispersal and allopatric speciation. Sexual reproduction enhances dispersal and genetic variability, which may have been the driving evolutionary force behind the trend.

Development and structure of perichaetial paraphyses in *Neckeropsis s. str.* have some unique features. Most mosses have sterile filaments called paraphyses intermixed with antheridia in perigonia and with archegonia in perichaetia. Paraphyses are almost always uniseriate and thread-like. Six species of *Neckeropsis s. str.* have in their post-fertilization perichaetia wider, bi- to multiseriate and “leaf-like” structures that have been called *ramenta* (in Latin *ramentum* = a thin membranous or chaffy flattened scale; Stearn 1993). Their origin has been uncertain, as they have been interpreted as ligulate perichaetial leaves (cf. Touw 1962) or modified, multiseriate paraphyses.

Merced-Alejandro & Sastre-De Jesús (2009) studied the ontogeny and structure of these alleged perichaetial paraphyses in several species of *Neckeropsis*. They showed that the *ramenta* found in the perichaetia of *N. andamana*, *N. crinita*, *N. disticha*, *N. fimbriata*, *N. nanodisticha* and *N. undulata* are indeed derived from uniseriate paraphyses and are thus not homologous with perichaetial leaves. Those authors recognized three types of fully developed *ramenta* based on their development and structure. In *N. nanodisticha* and *N. crinita* the *ramenta* are relatively thin and fully developed at early mature stage in the developmental sequence. In *N. undulata* and *N. disticha* they develop further, being narrowly ligulate when mature and representing middle mature stage. The widest, ligulate to lanceolate *ramenta* are present in *N. andamana* and *N. fimbriata* and they were interpreted as representing late mature stage.

Of the six species with *ramenta*, we were able to include five in this analysis: *N. crinita*, *N. fimbriata*, *N. andamana*, *N. disticha* and *N. undulata*. With the exception of *N. fimbriata*, they all are placed in the crown clade (Fig. 1), which also contains *N. foveolata*, which has plesiomorphic, uniseriate paraphyses. *Neckeropsis disticha* and *N. undulata* are resolved as sister taxa and their *ramenta* are similar (middle mature stage). *Neckeropsis crinita* is resolved as sister to *N. foveolata* and it has thin, early mature stage *ramenta*, so it is plausible to hypothesize that in this clade such *ramenta* represent the first evolutionary stage and that the other two types of *ramenta* (in *N. andamana*, *N. disticha* and *N.*

undulata) are more advanced. *Neckeropsis fimbriata*, however, has mature stage rameta (as does *N. andamana*) and it does not belong in this clade, so such rameta must have evolved twice.

Within the *Neckeropsis s. str.* clade there is an evolutionary trend leading from species with relatively long setae and exserted capsules to ones with immersed capsules and very short setae. All species in the crown clade, *N. foveolata*, *N. crinita*, *N. andamana*, *N. disticha* and *N. undulata*, have a derived condition, very short setae and thus capsules immersed among perichaetial leaves. Of the rest of the species, excluding *N. beccariana*, for which sporophytes are unknown, *N. madecassa* and *N. fimbriata* have immersed capsules (De Sloover 1977, as *N. hookeriacea* (Müll. Hal. ex Dusén) M. Fleisch.), while *N. cyclophylla* (Wu 2011, as *Himantocladium cyclophyllum*), *N. formosica* (Noguchi 1950 as *Himantocladium formosicum*), *N. pocsii* (Enroth & Magill 1994), and *N. exserta* (Touw 1962) have longer setae and exserted capsules. Notably, all species with rameta have immersed capsules, so it appears clear that rameta have evolved to shelter the maturing capsules.

Otherwise, there is little variation in the sporophyte structure. In all species the capsules are erect and symmetric, ovoid to ellipsoid or cylindrical, their length varying from 1.0 to c. 1.5 (–1.8) mm without clear differences among the species. The operculum is conical and shortly rostrate. The peristome varies little among the species, having narrowly lanceolate, densely papillose and often partly perforated exostome teeth and linear, papillose and perforated endostome segments on a low basal membrane. The peristome of *N. disticha* was illustrated by Florschütz-De Waard (1986), that of *N. undulata* by Buck (1998), that of *N. madecassa* by De Sloover (1977 as *N. hookeriacea*), and that of *N. crinita* by Touw (1962).

The absence of apophysal stomata in *Neckeropsis*, considered an unequivocal distinction from *Himantocladium* by Enroth (1992a) no longer holds, because the early diverging *N. cyclophylla* and *N. formosica* have 2 or 3 phaneroporously stomata per capsule. All other species of *Neckeropsis s. str.* lack stomata.

Himantocladium s. str.—In the current analysis *Himantocladium s. str.* becomes a morphologically coherent group, corresponding to Enroth's (1992a) *Himantocladium* sect. *Himantocladium* (Table 1). *Himantocladium cyclophyllum* (Olsson *et al.* 2010) and *H. formosicum* (Fig. 1) form a monophyletic clade in *Neckeropsis s. str.* Both of them are dioicous and have leaves with distinctly porose walls in the basal laminal cells, and with rather irregularly crenate apices. All of the five species in *Himantocladium s. str.* are synoicous (and thus frequently with sporophytes), have solid-walled leaf cells, and crenulate leaf apices. The sporophytes are remarkably uniform, the erect, symmetric capsules being exserted on a seta 1.0–2.0(–2.5) mm long and slightly mammillose in the upper part. There are no consistent interspecific differences in the peristome, which closely resembles that of several other neckeraceous genera, such as *Neckeropsis s. str.* and *Pinnatella*.

Whether the species of *Himantocladium* are indeed functionally synoicous is unclear. Akiyama (1993) observed that in the gametoecea of *H. plumula* there were mature archegonia intermixed with “totally immature” antheridia. One of us (J. Enroth) has made similar observations. This suggests some kind of “protogyny”; Akiyama (1993) used the term “sequential synoicy”. It is not known if it is consistent and if it indeed serves to hamper self-fertilization.

Enroth (1992a) considered *Himantocladium* to be morphologically intermediate between *Neckeropsis* and *Pinnatella*. The analysis by Olsson *et al.* (2010) included *H. implanum* and *H. plumula* and they formed a clade with the unispecific genus *Caduciella* Enroth and *Circulifolium*, which was segregated from *Homaliodendron* in the same paper. That result is supported by the present analysis; *Pinnatella* in its current circumscription and *Neckeropsis s. str.* are in fact more distant relatives of *Himantocladium*.

Himantocladium is essentially a SE Asian – Oceanian genus. Two of the species have wide distributions, while three of them are more narrowly distributed. *Himantocladium implanum* has been recorded from the Ascension Island in the mid-Atlantic (Enroth 1992a), but its main range extends from Papua New Guinea (New Britain) to the Society Islands. *Himantocladium plumula* has a wider distribution in Asia, being known from Japan and China through Indonesia to Australia (Queensland), and eastwards to the Society Islands. It is however much less frequent than *H. implanum* in Oceania.

Himantocladium giulianettii is known from Indonesia, New Guinea and the Society Islands, but without any interjacent records between the two latter areas. *Himantocladium submontanum* is restricted to Indonesia and New Guinea (Akiyama 1993), while *H. pacificum* (Broth. & Paris) Broth., the single species not sampled for this study, is endemic to New Caledonia.

Pengchengwua obtusata—*Pengchengwua obtusata* is nested in a small but heterogeneous SE Asian clade with two other unispecific genera: the rheophytic *Handeliobryum* and *Hydrocryphaea*. Broadly speaking, this clade of just three taxa covers the range of gametophytic as well as sporophytic variation present in the whole Neckeraceae. The gametophytes of *Handeliobryum sikkimense* are robust, dendroid, distinctly stipitate and very rigid, and the leaves have a strong, single costa (Ochyra 1986). These characters were taken to suggest a close relationship with *Pinnatella* (Ochyra 1986). However, sporophytes were found only later and they resemble those of *Thamnobryum* Nieuwl. and

members of the “Poro-clade” of the Neckeraceae (Olsson *et al.* 2011), having, e.g., long setae and nearly unreduced, hypnoid peristomes (Ochyra & Shevock 2012).

The gametophytes of *Hydrocryphaea wardii* Dixon are not drastically different from those of *Handeliobryum*, but the sporophytes are (Shevock *et al.* 2006). The seta is very short, rendering the capsule immersed among the perichaetial leaves. The peristome is reduced, of the “neckeroid” type, which is also encountered in e.g. *Pinnatella*, *Himantocladium* and *Neckeropsis s. l.* (e.g. Enroth, 1994b). Also *Pengchengwua obtusata* has immersed capsules and a “neckeroid” peristome. Its gametophytes, however, differ strongly from those of *Handeliobryum* and *Hydrocryphaea*, being non-stipitate and having undulate, mostly complanate leaves with a fairly weak costa reaching only to midleaf. *Handeliobryum* and *Hydrocryphaea* have some gametophytic morphological adaptations to rheophytic habitats (Ochyra 1986, Enroth 1999, Shevock *et al.* 2006). *Pengchengwua* however grows on tree trunks, branches and rocks (Touw 1962, Wu 2011) and lacks all such adaptations.

Although a distinct species, *P. obtusata* has no striking generic distinctions from the undulate-leaved species in *Neckeropsis s. str.*, or from *Neckeromnion*, which it resembles also in being dioicous. The costa reaching to about midleaf and the mostly rounded leaf tips are characteristic, as are the deeply immersed capsules. A further character worth noting is the presence of short, few-celled, filiform pseudoparaphyllia which we have not observed in *Neckeropsis s. str.* or *Neckeromnion*. The pseudoparaphyllia of *Hydrocryphaea* are also very small, less than 100 µm long, but they are not filiform (Shevock *et al.* 2006). Those of *Handeliobryum* are leaf-like and up to c. 200 µm long (Ochyra 1986), so small pseudoparaphyllia does not qualify as a synapomorphy in this clade.

Pengchengwua is a SE Asian taxon, known from Japan through southeastern China (including Taiwan) to northern Vietnam. The rheophytic *Handeliobryum* and *Hydrocryphaea* have narrower distributions. *Handeliobryum* was considered a “typical Sino-Himalayan endemic genus” by Ochyra & Shevock (2012), being known from Nepal, NE India, and Xizang, Yunnan and Sichuan in China. *Hydrocryphaea* has a similar but slightly wider general distribution, ranging from NE India through Yunnan to Laos and Vietnam (Shevock *et al.* 2006).

Planicladium clade:—The two SE Asian species *Planicladium semperianum* and *P. nitidulum* (cf. Wu 2011, as *Neckeropsis semperiana* and *N. nitidula*) have a similar appearance, both being strongly glossy plants with complanate, non-undulate, non-auriculate and often apiculate leaves. *Neckeropsis beccariana*, which is endemic to Borneo (Touw & Ochyra 1987, Akiyama 1992, as *Neckeropsis fleischeri* (Dix.) Touw) has a somewhat similar habit and leaf shape, but it has the laminal cells in the basiscopic side of the leaves much longer than in the acroscopic side, a feature not present in *N. semperiana* or *N. nitidula*. The latter two species form a morphologically and biogeographically coherent group that we recognize at the generic level.

Planicladium semperianum is a tropical species known from S China, Vietnam and the Philippines (Wu 2011). The distribution of *P. nitidulum* partly overlaps that of *P. semperianum* in China, but its range extends further northwards, as it is known also from Korea and Japan (Wu 2011).

Pseudoparaphysanthus clade:—*Neckeropsis boniana*, *N. submarginata*, *N. touwii*, *N. takahashii*, and *N. moutieri* were placed in *Neckeropsis* sect. *Pseudoparaphysanthus* by Touw & Ochyra (1987) and Ochyra & Enroth (1989). The section comprised SE Asian, mostly rheophytic species (cf. Enroth 1999). *Neckeropsis takahashii* and *N. moutieri* are included in the genus *Pseudoparaphysanthus* based on the molecular data used in this analysis. These two species share many morphological similarities, such as inframaginal, bi- to multistratose limbidia in the leaves, and they have in fact sometimes been confused with each other (cf. He & Zhang 2007).

In the lack of fresh material for sequencing, *N. boniana*, *N. submarginata* and *N. touwii* are transferred to *Pseudoparaphysanthus* on morphological grounds. All of these five species have very distinct and sharply demarcated limbidia reaching to leaf apex or nearly so along both leaf margins, and consisting of elongate, thick-walled cells. Further distinctions from *Neckeropsis s. str.* are the generally obtuse or broadly acute leaf apices, the very strong costa reaching to leaf apex or ending just a few cells below it, and the lack of basal auricles in the leaves. Limbidia are present in several species of *Neckeropsis s. str.*, but they are always more distinct only along the basiscopic leaf margin and can be quite indistinct or absent in the acroscopic one; also, the leaf costae in *Neckeropsis s. str.*, although fairly strong, end well below the leaf apex in almost all species, the leaf apices are typically rounded to truncate, and most of the species have distinctly widened to auricled leaf bases.

The five species of *Pseudoparaphysanthus* are all Asiatic. *Pseudoparaphysanthus takahashii* is endemic to southern China and *P. moutieri* is known from southern China and northern Vietnam (Wu 2011). *Pseudoparaphysanthus bonianus* is known from Myanmar, northern Vietnam, China, Philippines and probably the Nicobar Islands (Touw & Ochyra 1987, Wu 2011), *P. submarginatus* from the Andaman Islands, Malay Peninsula, Thailand and N India (Touw 1972, Touw & Ochyra 1987), and *P. touwii* is endemic to Papua New Guinea (Enroth 1992b).

Neckeromnion clade:—This clade is divided into two subclades that are morphologically fairly consistent among themselves but differ from each other.

Neckeromnion calcutense and *N. urocladum* form a clade. They were treated and described in detail in *Pinnatella* by Enroth (1994b), although the first-mentioned was earlier placed in *Neckeropsis* by the same author (Enroth 1991). The clade is characterized by often arcuate, sparsely branched stems, especially in *P. calcutensis*. The leaves are generally ovate-lingulate and symmetric to somewhat asymmetric and have a single costa, which in *P. calcutensis* vanishes just below leaf apex and in *P. uroclada* reaches c. 2/3–4/5 of leaf length. The erect, symmetric capsules are well exserted on setae 2.3–4.3 mm long and distally mammillose. *Neckeromnion calcutense* has very distinct inframarginal limbidia in the leaves, not unlike those in *Pinnatella alopecuroides* (Mitt.) M. Fleisch. (cf. Enroth 1994b) or in the *Pseudoparaphysanthus* clade treated in the present paper.

All three species in the other clade, *Neckeromnion gracilentum*, *N. lepineanum*, and *N. calcicolum*, are dioicous, lax, sparsely branched, and have deeply and regularly undulate, glossy leaves. There are several species in *Neckeropsis* s. str. with deeply undulate leaves (*N. exserta*, *N. fimbriata*, *N. foveolata*, *N. crinita*, *N. andamana*, *N. undulata*), but they are all autoicous, having the perigonia and perichaetia in the same plants but on different branches, or synoicous (Touw 1962, Buck 1998).

Neckeromnion lepineanum and *N. calcicolum* form a clade with full support. They are in fact difficult to distinguish from each other if mature sporophytes or post-fertilization perichaetial leaves are lacking (e.g., Touw 1962, 1972). In *N. lepineanum* the capsule is immersed among perichaetial leaves that are to 4.5 mm long, while *N. calcicolum* has a shortly exserted capsule and the perichaetial leaves are to 1.5 mm long (Touw 1962). Both species have a short, weak costa in the leaves.

Neckeromnion gracilentum is slightly more discordant in this clade. It differs from the two other species in being smaller and more slender, and in having a strong and long, simple costa in the leaves, which are distinctly auricled at the base. The sporophytes are unknown.

Four of the five species of *Neckeromnion* are exclusively Asian, or nearly so. *Neckeromnion calcutense* is known from Sri Lanka, India, Bhutan, Burma and Thailand (Enroth 1994). *Neckeromnion urocladum* was first described (Mitten 1859, as *Neckera uroclada* Mitt.) and long known only from Myanmar (= Burma; Enroth 1994b); however, *Neckeropsis gracilis*, described from Thailand (Noguchi 1972) and soon afterwards reported from Myanmar (Touw 1972, Tan & Iwatsuki 1993), is a taxonomic synonym of *P. uroclada* (see Taxonomic and nomenclatural changes below). This specimen examined by us represents the first record of *N. urocladum* from Laos: “Prov. Vientiane, Vang Vieng, 102°26’01” N 18°55’35” E, cave entrance”, 12 Dec. 2010, *A. Vanderpoorten LAO154* (H).

Neckeromnion lepineanum is distributed from E Africa through tropical Asia to the Pacific, the easternmost localities being in Hawaii, Society Islands and Marquesas Islands (Enroth 1989). Its sister *N. calcicolum* has a much narrower distribution, as it is known only from Japan and China (Wu 2011). *Neckeromnion gracilentum* has been recorded from the Nicobar Islands and S Thailand through the SE Asian archipelago to New Guinea and Samoa in the east (Enroth 1989).

Noguchiodendron:—The only species in *Noguchiodendron*, *N. sphaerocarpum*, was sequenced for this study and the phylogenetic results confirm its generic position among the Neckeraceae and sister to *Taiwanobryum* (Fig. 1). The latter genus in its current circumscription (Olsson *et al.* 2010) is fairly morphologically heterogeneous. All of the six species are stipitate-frondose, but for example the plant size, leaf shape and costa length vary considerably. Originally (Ninh & Pócs 1981) *Noguchiodendron* was thought to be close to *Homaliodendron* sect. *Homaliodendron* as defined by Fleischer (1906–1908) and Ninh (1984), which is the same as *Homaliodendron* s. str. of Olsson *et al.* (2010). The main differences between *Noguchiodendron* and *Homaliodendron*, used to justify establishing the former genus in the first place, were tabulated by Ninh & Pócs (1981). The most significant of the generic differences are: stem central strand present in *Noguchiodendron*, lacking in *Homaliodendron*; branches of frond curved in *Noguchiodendron*, straight in *Homaliodendron*; capsule subglobose in *Noguchiodendron*, ovoid to cylindrical in *Homaliodendron*; and annulus well differentiated in *Noguchiodendron*, not or weakly differentiated in *Homaliodendron*. There are some additional differences in the shape of the exothecial cells, papillosity of the exostome teeth, shape of the endostome segments, and spore size; however, such differences are generally considered specific rather than generic.

Noguchiodendron sphaerocarpum remains a morphologically distinct taxon also in its new placement near *Taiwanobryum*. The plants are about as large as those of *Taiwanobryum crenulatum* (Harv.) S. Olsson, Enroth & D. Quandt and *T. speciosum* Nog. (the generitype); the other species currently placed in *Taiwanobryum* are much smaller. However, *N. sphaerocarpum* differs from the above-mentioned large species by several characters: the presence of a stem central strand, the asymmetric leaves, the essentially non-porose upper laminal cells, the subglobose capsule, and the well differentiated annulus. There are also some notable similarities among the three large taxa: the numerous,

appressed stipe leaves, the coarsely serrate upper leaf margins, the long single costa, the distinct, small and mostly rectangular alar cells, and the long-exserted capsules, the setae being c. 1 cm long in *T. crenulatum*, 1.5 cm in *T. speciosum*, and 2–2.7 cm in *Noguchiodendron* (Ninh & Pócs 1981; we have not seen the sporophytes of the latter taxon). It might be mentioned that in those taxa of *Taiwanobryum* for which the sporophytes are known (*T. speciosum*, *T. crenulatum* and *T. mucronatum* (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt) the seta is distinctly mammillose in the upper part, but according to Ninh & Pócs (1981) the seta of *Noguchiodendron* is smooth.

Based on our results, placing *Noguchiodendron* in a monophyletic *Taiwanobryum* would seem possible, but that solution would render the already morphologically heterogeneous *Taiwanobryum* even more so. We consider *Noguchiodendron* worthy of recognition at the generic level, based especially on the very long and apparently smooth vs. mammillose seta, subglobose vs. ovoid or cylindrical capsules, and the well differentiated vs. not or poorly differentiated annulus.

Taxonomic and nomenclatural changes

Neckeropsis formosica (Broth. & Yasuda) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Himantocladium formosicum* Broth. & Yas., Rev. Bryol. 53: 2. 1926.

Illustrations: Wu (2011: plate 369, figs. 1–8, as *Himantocladium formosicum*).

Pengchengwua S. Olsson, Enroth, Huttunen & D. Quandt, **gen. nov.**

Type: *Pengchengwua obtusata* (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt

Etymology: We are pleased to name this genus after our colleague Prof. Peng-Cheng (Pang-cheng) Wu (Beijing), who has contributed so much to Chinese bryology.

Description: Plants medium-sized to fairly robust, green to yellowish green, slightly glossy, often forming flat mats. Stems not stipitate, arising from creeping stolons, simple or sparsely and complanately branched. Stem and branch leaves imbricate, more or less complanate, distinctly undulate, asymmetrically lingulate, adscopical side of leaf base distinctly decurrent, apices mostly rounded, margins crenulate at apex, entire elsewhere. Costa single, reaching to midleaf, sometimes shorter and/or bifurcate. Leaf cells smooth, relatively incrassate, pellucid, apical ones nearly isodiametric, quadrate to rhomboid or penta- to hexagonal, becoming more elongate towards leaf base, basal ones with porose walls. Branch primordia covered with broad embryonic leaves; pseudoparaphyllia few, short and few-celled, filiform, sometimes mixed with leaf-like, lanceolate ones. Dioicous (possibly polyoicous), sporophytes uncommon. Inner post-fertilization perichaetial leaves to c. 2.5 mm long. Seta 0.5 mm long, capsules oblong to narrowly ovoid, erect, symmetric, immersed; apophysal stomata absent. Peristome double, neckeroid, exostome teeth smooth or finely papillose, endostome segments as long as teeth, with elongate perforations. Calyptra hairy. Spores 15–25 µm, faintly papillose.

Pengchengwua obtusata (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckera obtusata* Mont. Ann. Sci. Nat. Bot. Sér. 2, 19: 240. 1843 (*Neckeropsis obtusata* (Mont.) M. Fleisch. in Broth, Nat. Pfl. ed. 2, 11: 187).

Illustrations (as *Neckeropsis obtusata*): Noguchi (1989: fig. 313); Wu (2011: plate 386, figs. 1–6).

Planicladium S. Olsson, Enroth, Huttunen & D. Quandt, **gen. nov.**

Type: *Planicladium nitidulum* (Mitt.) S. Olsson, Enroth, Huttunen & D. Quandt

Etymology: In reference to the gametophytes with strongly complanate leaves and appearance.

Description: Plants medium-sized to fairly robust, yellowish green to brownish, mostly strongly glossy, forming flat mats. Stems not or only indistinctly stipitate, arising from creeping stolons, simple or sparsely and complanately branched. Stipe leaves smaller than stem leaves. Stem and branch leaves imbricate, strongly complanate, plane or somewhat homomalous, asymmetric, lingulate to spatulate, apices rounded or truncate to broadly obtuse, often apiculate, margins crenulate or serrulate at apex, mostly entire elsewhere. Costa single, reaching to midleaf or ending just below leaf apex, sometimes shorter and/or bifurcate. Leaf cells relatively incrassate, pellucid, apical ones rhomboid to elliptic or hexagonal, becoming more elongate towards leaf base, basal ones with more or less distinctly porose

walls; inframarginal limbidium absent or short and weakly differentiated at basiscopic side of leaf. Branch primordia covered with broad embryonic leaves; pseudoparaphyllia absent. Dioicous, sporophytes uncommon (not seen by us in *P. semperianum*). Inner post-fertilization perichaetial leaves to c. 3 mm long. Seta 0.5–1 mm long, capsules oblong to narrowly ovoid, erect, symmetric, immersed or shortly exerted; apophysal stomata absent. Peristome double, neckeroid; exostome teeth papillose above, striolate below, endostome segments about as long as teeth, perforate. Calyptra hairy. Spores 12–20 µm, faintly papillose.

Planicladium semperianum (Hampe ex Müll. Hal.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckera semperiana* Hampe ex Müll. Hal., Bot. Zeit. 20: 381. 1862 (*Homalia semperiana* (Hampe ex Müll. Hal.) Paris, Ind. Bryol. ed. 2, 2: 321. 1904. *Himantocladium semperianum* (Hampe ex Müll. Hal.) Broth. ex Paris, Coll. Nom. Broth. 13. 1909. *Homaliodendron semperianum* (Hampe ex Müll. Hal.) Broth., Nat. Pfl. ed. 2, 11: 192. 1925. *Neckeropsis semperiana* (Hampe ex Müll. Hal.). Touw, Blumea 11: 414. 1962).

Illustrations (as *Neckeropsis semperiana*): Touw (1962: plate 18: B, figs. 1–4); Wu (2011: plate 386, figs. 7–14).

Planicladium nitidulum (Mitt.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Homalia* [“*Omalia*”] *nitidula* Mitt., J. Linn. Soc. Bot. 8: 155. 1864 (*Neckera nitidula* (Mitt.) Broth., Hedwigia 38: 228. 1899. *Neckeropsis nitidula* (Mitt.) M. Fleisch., Musci Fl. Buitenzorg 3: 882. 1908).

Illustrations (as *Neckeropsis nitidula*): Noguchi (1989: fig. 312); Wu (2011: plate 385, figs. 6–14).

Pseudoparaphysanthus (Broth.) S. Olsson, Enroth, Huttunen & D. Quandt, **stat. & comb. nov.**

Basionym: *Neckera* sect. *Pseudoparaphysanthus* Broth., Nat. Pflanzenfam. 1(3): 842. 1906 (*Neckeropsis* sect. *Pseudoparaphysanthus* (Broth.) M. Fleisch., Musci Fl. Buitenzorg 3: 876. 1907).

Lectotype (cf. Ochyra & Enroth, 1989): *Pseudoparaphysanthus moutieri* (Broth. & Paris) S. Olsson, Enroth, Huttunen & D. Quandt

Plants medium-sized, dull or slightly glossy. Stems indistinctly stipitate, relatively rigid, sparsely and irregularly to subpinnately branched, to 5(–12) cm long, erect or ascending, arising from creeping stolons. Stem and branch leaves weakly to distinctly complanate, variously twisted when dry, flat and erect-patent when wet, ovate-oblong to oblong-lingulate or obovate-lingulate, symmetric to slightly asymmetric, base decurrent or not, apex obtuse to broadly acute; leaf margins coarsely dentate to nearly entire at apex, serrulate or entire at midleaf and base. Costa single, very strong, subpercurrent or percurrent. Leaf cells relatively incrassate, often opaque; inframarginal limbidia consisting of elongate, linear cells distinct from leaf base to apex or ending slightly below apex, 3 to 6 cells wide, 1- to 8-layered. Branch primordia covered by embryonic leaves; pseudoparaphyllia few, leaf-like, lanceolate, to c. 150 µm long. Presumably dioicous, sporophytes rare (known only from *P. moutieri* and *P. boniana*; description based on Touw & Ochyra 1987). Post-fertilization inner perichaetial leaves to 2.7 mm long. Capsule symmetric, ovoid, erect. Seta c. 0.3 long and capsule immersed, c. 0.8 × 0.8 mm (*P. moutieri*), or seta 1.6 mm long, capsule exerted, c. 1.3–1.5 mm long (*P. boniana*); apophysal stomata absent. Peristome double, neckeroid; exostome teeth lanceolate-subulate, finely papillose below, smooth to faintly papillose above, median perforations indistinct to absent; endostome segments linear to lanceolate, papillose, indistinctly to strongly perforated. Operculum conical, with a straight to oblique beak. Calyptra (known for *P. moutieri*) cucullate, bearing paraphyses at base. Spores 18–30 µm, finely papillose.

Pseudoparaphysanthus moutieri (Broth. & Paris) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Sciaromium moutieri* Broth. & Paris, Rev. Bryol. 27: 78. 1900 (*Neckera moutieri* (Broth. & Paris) Broth., Nat. Pfl. 1(3): 842. 1906. *Neckeropsis moutieri* (Broth. & Paris) M. Fleisch., Musci Fl. Buitenzorg 3: 882. 1908).

Illustrations (as *Neckeropsis moutieri*): Touw & Ochyra (1987: fig. 1); He & Zhang (2007: fig. 1); Wu (2011: plate 385, figs. 1–5).

Pseudoparaphysanthus takahashii (Higuchi, Iwatsuki, Ochyra & Li) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckeropsis takahashii* Higuchi, Iwatsuki, Ochyra & Li, Nova Hedwigia 48: 432. 1989.

Illustrations: Higuchi *et al.* (1989: figs. 1–29, as *Neckeropsis takahashii*).

Pseudoparaphysanthus bonianus (Besch.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Porotrichum bonianum* Besch., Bull. Soc. Bot. France 34: 97. 1887 (*Pinnatella boniana* (Besch.) Pócs, Egri Tanárképző Főisk. Tud. Közlem. 3: 471. 1965. *Neckeropsis boniana* (Besch.) Touw & Ochyra, Lindbergia 13: 101. 1987).

Illustrations (as *Neckeropsis boniana*): Touw & Ochyra (1987: fig. 2); Wu (2011: plate 383, figs. 1–7).

Pseudoparaphysanthus submarginatus (Cardot ex Touw) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckeropsis submarginata* Cardot ex Touw, Blumea 11: 417. 1962.

Illustrations: Touw (1962: plate 21, A as *Neckeropsis submarginata*).

Pseudoparaphysanthus touwii (Ochyra & Enroth) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckeropsis touwii* Ochyra & Enroth, Ann. Bot. Fennici 26: 128. 1989.

Illustrations: Ochyra & Enroth (1989: fig. 1 & 2)

Neckeromnion S. Olsson, Enroth, Huttunen & D. Quandt, **gen. nov.**

Type: *Neckeromnion lepineanum* (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt

Description: Plants medium-sized to very robust (sometimes several dozens of cm long). Stems not or indistinctly stipitate, more or less flexuose and arcuate, sparsely and irregularly branched, arising from creeping stolons. Flagelliform, microphyllous branches (vegetative propagulae) sometimes present. Stem and branch leaves complanate to erect-patent, slightly to distinctly asymmetric, lingulate to ovate-lingulate, oblong or subelliptic, mostly not auricled, from shallowly and irregularly to deeply and regularly undulate with lunate undulations, or smooth to plicate, leaf apices obtuse to rounded or truncate or slightly emarginate, sometimes indistinctly apiculate; leaf margins nearly entire throughout or crenulate to serrulate near apex. Costa nearly absent to short and faint, sometimes bifurcate, to simple, strong and reaching to near leaf apex. Leaf cells smooth, relatively thick-walled, pellucid, apical ones nearly isodiametric, median and basal cells elongate, basal cells often longer in basiscopic (proximal) side of leaf than in acroscopic, marginal cells usually shorter in 1–2 row(s), inframarginal limb of elongate cells sometimes present and sharply demarcated, alar cells indistinct but much shorter than adjacent laminal cells, short-rhomboid or rectangular to irregular. Branch primordia covered by embryonic leaves; pseudoparaphyllia absent or few, small, subulate to lanceolate. Dioicous. Post-fertilization inner perichaetial leaves from 0.9 mm (with no post-fertilization growth) to 4.5 mm long (with strong post-fertilization growth). Seta from 0.5 to 4.3. mm long, yellowish, smooth or slightly mammillose in upper part, capsule erect, symmetric, ovoid to nearly elliptic or cylindric, 1.4–2.0 mm long; apophysal stomata absent or few, phaneropore. Peristome double; exostome teeth lanceolate-subulate, lanceolate, dorsal side spiculose-papillose nearly throughout, often with median perforations; endostome segments as long as teeth or nearly so, on a low basal membrane, subulate, with elongate median perforations, faintly papillose throughout. Operculum conical, obliquely rostrate. Calyptra cucullate, with long paraphyses attached to its lower part. Spores c. 12–30 µm, faintly papillose.

Neckeromnion calcutense (M. Fleisch.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Pinnatella calcutensis* M. Fleisch., Hedwigia 45: 84. 1906 (*Pinnatella alopecuroides* var. *calcutensis* (M. Fleisch.) Gangulee, Mosses Eastern India 5: 1440. 1976. *Neckeropsis calcutensis* (M. Fleisch.) Enroth, Acta Bryolichenol. Asiatica 2: 9. 1991).

Illustrations: Gangulee (1976: fig. 714, as *Pinnatella alopecuroides* var. *calcutensis*); Enroth (1994b: fig. 21, as *Pinnatella calcutensis*).

Neckeromnion urocladum (Mitt.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckera uroclada* Mitt., J. Proc. Linn. Soc., Suppl. Bot. 1: 122 (*Himantocladium urocladum* (Mitt.) M. Fleisch., Musci Fl. Buitenzorg 3: 888. 1908. *Pinnatella uroclada* (Mitt.) Enroth, Acta Bot. Fennica 151: 57. 1994).

Neckeropsis gracilis Nog., Lindbergia 1: 177. 1972, *syn. nov.* Holotype: Thailand. Chantaburi, Kao Sabab, 1–300 m, 18. Jan. 1958 leg. *Th. Sørensen et al.* 7254a (C!). Paratype: Same locality and date, leg. *Th. Sørensen et al.* 7254b (C!).

Illustrations: Noguchi (1972: fig. 2, as *Neckeropsis gracilis*); Enroth (1994b: fig. 22, as *Pinnatella uroclada*).

Neckeromnion calcicolum (Nog.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckeropsis calcicola* Nog. J. Hattori Bot. Lab. 16: 124. 1956.

Illustrations (as *Neckeropsis calcicola*): Noguchi (1989: fig. 314); Wu (2011: plate 383, figs. 8–14).

Neckeromnion gracilentum (Bosch & Sande Lac.) S. Olsson, Enroth, Huttunen & D. Quandt, **comb. nov.**

Basionym: *Neckera gracilenta* Bosch & Sande Lac., Bryol. Jav. 2: 62. 1863 (*Neckeropsis gracilenta* (Bosch & Sande Lac.) M. Fleisch., Musci Fl. Buitenzorg 3: 876. 1908).

Illustrations (as *Neckeropsis gracilenta*): Touw (1962: plate 5, figs. 3–6); Enroth (1989: fig. 2a–h).

Neckeromnion lepineanum (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt, *comb. nov.*

Basionym: *Neckera lepineana* Mont., Ann. Sci. Nat. Bot. Sér. 10: 107. 1848 (*Neckeropsis lepineana* (Mont.) M. Fleisch., Musci Fl. Buitenzorg 3: 879. 1908).

Illustrations (as *Neckeropsis lepineana*): Touw (1962: plate 3; plate 5, figs. 1 & 2); Enroth (1989: fig. 1); Wu (2011: plate 384, figs. 9–15).

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Appendix 1. Species names, voucher information, and EMBL or GenBank accession numbers for the sequences used in the molecular analyses (*rps4 - trnT & trnL - trnF*; *rpl16*; ITS1 & 2, respectively). A dash (–) indicates a missing sequence. In two cases sequences were submitted to GenBank in previous studies and thus the accession numbers for *rps4-trnT-trnL-trnF* are composed of two different accession numbers. Sequences newly generated for this study are marked with an asterisk (*).

Alleniella besseri (Lob.) S. Olsson, Enroth & D. Quandt; *Olsson 107* (herb. Quandt); FM210294, FM161003, FM161156. *Alleniella complanata* (Hedw.) S. Olsson, Enroth & D. Quandt; *Buchbender 204* (herb. Buchbender); AM990413, FM161005, FM161158. *Alleniella hymenodonta* (Müll. Hal.) S. Olsson, Enroth & D. Quandt; H3206871 (H); FM210302, FM161011, FM161164. *Bissetia lingulata* (Mitt.) Broth.; H3194160 (H); AM990346, FM160949, FM161079. *Caduciella mariei* (Besch.) Enroth; *Koponen 28035* (H); FM210282, FM160953, FM161084. *Camptochaete arbuscula* var. *tumida* (Sm.) Reichardt; *Streimann 51408* (H); AM990353, FM160955, FM161087. *Circulifolium exiguum* (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt; B263509 (B); AM990389, FM160984, FM161130. *Circulifolium microdendron* (Mont.) S. Olsson, Enroth & D. Quandt; *Redfearn, Jr. 35901* (H); AM990390, FM160987, FM161133. *Curviciadium kurzii* (Kindb.) Enroth; Akiyama Th-85 (NYBG); FM210285, AM990362 *trnL*, FM160959, FM161093. *Dolichomitriopsis diversiformis* (Mitt.) Nog.; *Nedoluzhko s.n.* (H, MHA); AM990362, *trnL* AF397777, FM160963, FM161098. *Forsstroemia neckeroides* (Hornsch.) Paris; H3064115 (H); FN868963, FN868978, FN868972. *Forsstroemia trichomitria* (Hedw.) Lindb.; *Streimann & Pócs 65120A* (herb. Buchbender); AM990365, FM160968, FM161103. *Handeliobryum sikkimense* (Paris) Ochyra; *Redfearn et al. 33981* (H); FM210287, FM160969, FM161110. *Heterocladium dimorphum* (Brid.) Schimp.; H3212307 (H); AM990376, FM160970, FM161115. *Heterocladium procurrens* (Mitt.) A. Jaeger; H3212289 (H); AM990379, FM160973, FM161118. *Himantocladium giulianettii* (Broth) M. Fleisch.; L0837454 (L); FN869002*, FN869019*, FN868982*. *Himantocladium implanum* (Mitt.) M. Fleisch.; *De Sloover 21124* (NYBG); FM210289, FM160975, FM161121. *Himantocladium plumula* (Nees) M. Fleisch.; *Tan et al. 92-232* (H); AM990381, FM160976, FM161122. *Himantocladium submontanum* Enroth; H3071191 (H); FN869003*, FN869020*, FN868983*. *Homalia trichomanoides* (Hedw.) Schimp.; *Olsson 105* (herb. Quandt); AM990385, FM160980, FM161126. *Homalia webbiana* (Mont.) Schimp.; *Müller K68* (H); AM990387, FM160982, FM161127. *Homaliadelphus targionianus* (Mitt.) Dixon & P. de la Varde; *Koponen et al. 55009* (H); AM990388, FM160983, FM161129. *Homaliodendron flabellatum* (Sm.) M. Fleisch.; H3071675 (H); FM210290, FM160985, FM161132. *Homaliodendron neckeroides* Broth.; H3071953 (H); FM210306, FM161015, FM161168. *Homaliodendron scalpellifolium* (Mitt.) M. Fleisch.; H3071976 (H); FM210292, FM160989, FM161135. *Hydrocryphaea wardii* Dix.; *Shevock 23460* (H); FM210293, FM160992, FM161139. *Lembophyllum clandestinum* (H. f & W.) Lindb.; *Vitt 29644* (H); AM990401, *trnL* AF397823, FM160996, FM161145. *Leptodon smithii* (Hedw.) F. Weber & D. Mohr; B268385 (B); AM990403, FM160997, FM161147. *Miyabea fruticella* (Mitt.) Broth.; *Koponen 45838* (H); AM990411, FM161001, FM161154. *Miyabea rotundifolia* Cardot; *Tan 93-771* (H); AM990412, FM161002, FM161155. *Neckera himalayana* Mitt.; B253876 (B); FM210301, FM161010, FM161163. *Neckera menziesii* Drumm.; *Halse 4878* (NYBG); FM210305, FM161014, FM161167. *Neckera pennata* Hedw.; H3203794 (H); AM990414, FM161016, FM161169. *Neckera polyclada* Müll. Hal.; *Koponen 45441* (H); FM210307, FM161017, FM161170. *Neckera warburgii* Broth.; *Bryo253855* (B); FM210311, FM161023, FM161176. *Neckeromnion calcicolum* (Nog.) S. Olsson, Enroth, Huttunen & D. Quandt; *Enroth 64632* (H); AM990417, FM161025, FM161178. *Neckeromnion calcutense* (M. Fleisch.) S. Olsson, Enroth, Huttunen & D. Quandt; H3212832 (H); AM990418, FM161026, FM161179. *Neckeromnion gracilentum* (Bosch & Sande Lac.) S. Olsson, Enroth, Huttunen & D. Quandt; B105716 (S); FM210315*, FM161029*, FM161182*. *Neckeromnion lepineanum* (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt; *Shevock 32240* (H); FN869006*, FN869024*, FN868987*. *Neckeromnion urocladum* (Mitt.) S. Olsson, Enroth, Huttunen & D. Quandt; *Schäfer-Verwimp & Verwimp s.n.* (herb. Enroth); FN869005, FN869023, FN868986. *Neckeropsis andamana* (Müll. Hal.) M. Fleisch.; *Tan 91-267* (FH); FN869015, FN869031, FN868994. *Neckeropsis beccariana* (Hampe) Touw; *Suleiman 3334* (BORH); FN869014*, FN869035*, FN868998*. *Neckeropsis crinita* (Griff.) M. Fleisch.; H3236231 (H); missing, missing, missing. *Neckeropsis cyclophylla* (Müll. Hal.) S. Olsson, Enroth & Quandt; *Redfearn Jr. 36081* (NYBG); FM210288, FM160974, FM161120. *Neckeropsis disticha* (Hedw.) Kindb.; *Heras 901/93* (NYBG); FM210313, FM161027, FM161180. *Neckeropsis exserta* (Hook. ex Schwägr.) Broth.; PE01098512 (PE); FN869011*, FN869034*, FN868997*. *Neckeropsis exserta* var. *scrobiculata* (Nees) Touw; NYBG 01127000 (NYBG); FN869012*, FN869033*, FN868996*. *Neckeropsis fimbriata* (Harv.) M. Fleisch.; H3220430 (H); missing, missing, missing. *Neckeropsis formosica* (Broth. & Yasuda) S. Olsson, Enroth, Huttunen & D. Quandt; TAI B16113 (TAD); FN869001*, FN869021*, FN868984*. *Neckeropsis foveolata* (Mitt.) Broth.; *Allen 17467A* (MO); FN869004*, FN869022*, FN868985*. *Neckeropsis madecassa* (Besch.) M. Fleisch.; H3098198 (H); FN869007*, FN869025*, FN868988*. *Neckeropsis pocsii* Enroth & Magill; H3098218 (H); FN869009*, FN869027*, FN868990*.

Neckeropsis undulata (Hedw.) Reichardt; B238406 (B); FM210316, FM161031, FM161184. *Noguchiodendron sphaerocarpum* (Nog.) Ninh & Pócs; H3214425 (H); FN869016, FN869029, FN868992. *Pendulothecium punctatum* (Hook. f. & Wilson) Enroth & S. He; *Streimann 53845* (S); AM990421, FM161033, FM161187. *Pengchengwua obtusata* (Mont.) S. Olsson, Enroth, Huttunen & D. Quandt; *Shevock 28881* (H); FN869008*, FN869026*, FN868989*. *Pinnatella alopecuroides* (Mitt.) M. Fleisch.; *Schäfer-Verwimp 16824* (herb. Enroth); AM990423, FM161034, FM161188. *Pinnatella foreauana* Thér. & P. de la Varde; *Linis 757-03* (H); FM210319, FM161037, FM161191. *Pinnatella homaliadelphoides* Enroth, S. Olsson, S. He, Shevock & D. Quandt; *Shevock 31181* (H); FN557038, FN557037, FN557036. *Pinnatella kuehliana* (Bosch & Sande Lac.) M. Fleisch.; *Müller S116* (herb. Enroth); FM20150, FM161038, FM161192. *Pinnatella minuta* (Mitt.) Broth.; *Rikkinen et al. 32* (herb. Enroth); AM990424, FM161040, FM161194. *Pinnatella taiwanensis* Nog.; *Koponen et al. 54169* (H); FM210321, FM161042, FM161196. *Planicladium nitidulum* (Mitt.) S. Olsson, Enroth, Huttunen & D. Quandt; B105713 (S); AM990419, FM161030, FM161183. *Planicladium semperianum* (Hampe) S. Olsson, Enroth, Huttunen & D. Quandt; *He 40426* (MO); FN869010*, FN869028*, FN868991*. *Porotrichodendron superbum* (Taylor) Broth.; H3121100 (H); AM990427, FM161043, FM161198. *Pseudoparaphysanthus moutieri* (Broth. & Paris) S. Olsson, Enroth, Huttunen & D. Quandt; *Liu et al. 448* (HSNU); –, FN869032*, FN868995*. *Pseudoparaphysanthus takahashii* Higuchi, Z. Iwats., Ochyra & X.J. Li; *He 40411* (MO); FN869013*, FN869030*, FN868993*. *Rigodium pseudothuidium* Dusén; H3134254 (H); AM990438, *trnLF AF543547*, FM161051, –. *Rigodium pseudothuidium* Dusén; NYBG 00892248 (NYBG); –, –, FM161210. *Taiwanobryum mucronatum* (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt; *Hedenäs MY92-22* (S); AM990425, FM161041, FM161195. *Taiwanobryum speciosum* Nog.; *Enroth 64877* (H); AM990442, FM161055, FM161216. *Thamnobryum alopecurum* (Hedw.) Nieuwl. ex Gangulee; *Buchbender s.n.* 11. July 2003 (herb. Buchbender); AM990444, FM161056, FM161218. *Thamnobryum subserratum* (Hook.) Nog. & Z. Iwats.; *Enroth 64595* (H); AM990446, FM161067, FM161230. *Weymouthia mollis* (Hedw.) Broth.; *99-Mo2* (CHR); AM990452, FM161072, FM161237.