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***Neckera*, *Forsstroemia* and *Alleniella* (Neckeraceae, Bryophyta) redefined based on phylogenetic analyses**

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ABSTRACT. Phylogenetic relationships of species within the pleurocarpous moss genus *Neckera* s.l. (Neckeraceae) are reconstructed based on three genomic regions: the plastid *rps4-trnT-trnL-trnF* cluster and the *rpl16* group II intron, as well as the internal transcribed spacer region of the nuclear ribosomal DNA (ITS1-5.8S-ITS2). The phylogenetic reconstruction suggests numerous taxonomic changes within the Neckeraceae. Two unispecific Asian genera are described as new: *Taiwanobryopsis* to accommodate *Neckera warburgii*, and *Indoneckera* to accommodate *Neckera himalayana*. Seven of the other “*Neckera*” species, all distributed in Asia, are transferred to *Forsstroemia*, and a further four Asian species to *Taiwanobryum*. Six Southern Hemisphere or tropical species (one from New Zealand, one from Africa, four from South America) are transferred to *Alleniella*. After these adjustments, *Neckera* becomes a northern hemisphere, mainly temperate, genus of c. 10 species that are absent from the tropics. It is in this context morphologically characterized by lack of paraphyllia (except *N. californica*) and an absent or weak costa. *Alleniella* has two species—the first diverging lineages—in the northern hemisphere, but the rest of the currently 15 species are distributed in the southern hemisphere and most of the species occur in mountain habitats in the tropics; it is however absent from tropical Asia and very scarce in Asia in general. Twelve of the 54 species have paraphyllia, which is the clearest morphological distinction from *Neckera*. *Forsstroemia* with 19 species, heavily concentrated in Asia, is the largest genus in the Neckeraceae. Clearly longer and more distinct costa distinguishes the genus from *Neckera* and *Alleniella*. *Taiwanobryum* is a morphologically heterogeneous Asian genus of nine species. *Neckera decurrens* Broth. is synonymized with *Forsstroemia fauriei* and *Neckera valentiniana* Besch. with *Alleniella ehrenbergii*.

KEYWORDS. Bryophyte evolution, molecular phylogenetics, taxonomy, new taxa, morphological evolution.

The phylogenetic structure and systematics of the pleurocarpous moss family Neckeraceae, sister to the Lembophyllaceae (Quandt et al. 2009), have been analysed by us based on molecular data for over a decade (Enroth et al. 2019; Olsson et al. 2009a,b, 2010, 2011, 2012, 2016). The generic content of the family as well as the circumscriptions of many of the genera have undergone major changes compared to the “classical” concept by Brotherus (1925) or even to much more recent mainly morphology-based classifications, such as those by Enroth (1994a) or Goffinet et al. (2008). The small family Miyabeaceae, established by Olsson et al. (2009a), contains two genera

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(*Homaliadelphus* Dixon & P.de la Varde, *Bissetia* Broth. ex M.Fleisch.) previously placed in the Neckeraceae, and the Orthostichellaceae with six genera and 19 species was segregated from the Neckeraceae by Enroth et al. (2019).

The analysis by Olsson et al. (2009b) resolved the backbone phylogeny of the Neckeraceae s.str. (containing also the previously recognized Leptodontaceae; e.g., Enroth 1991; Goffinet et al. 2008; Stark 1987). Three main clades were found and after their most prominent genera named the *Neckera*-clade, the *Thamnobryum*-clade and the *Pinnatella*-clade. The *Neckera*-clade is generally characterized by a weak costa, immersed capsules with reduced peristomes, and mostly unicellular teeth at leaf margins. The *Thamnobryum*-clade contains mostly robust plants, distinctly stipitate-frondose, with a single, mostly fairly strong costa, long setae and the peristomes are perfect hypnoid or only slightly reduced. The *Pinnatella*-clade is essentially Asian and clearly most diverse in the tropics. The plants mostly have a strong costa and the elongate setae are mammillose in the upper part. Both hypnoid and reduced peristomes occur in this clade. The ancestral state reconstructions by Olsson et al. (2009b) showed that some “reduced” sporophyte features evolved independently in the three main clades of the Neckeraceae, most probably in concert with a shift of the more advanced taxa to epiphytic habitats (see also Huttunen et al. 2012), which was evident in all three clades.

In the previously cited analyses several “*Neckera*” species were scattered among different clades—even among the three main clades recognized by Olsson et al. (2009b)—and *Neckera* Hedw. s.str. contained only four species. It was clear that since *Neckera* s.l. accommodated many more accepted species not included in our analyses, further scrutiny with a more comprehensive taxon sampling was necessary to clarify the phylogenetic position, biogeography and morphological circumscription. The current paper is an attempt to fulfill this need with a sampling of 29 species placed in *Neckera* s.l. prior to this analysis. Taxonomic databases, such as Tropicos (<https://www.tropicos.org/name/Search?name=Neckera>) contain several dozens of “accepted” names in *Neckera*, but most of those are obsolete or “alternative accepted” names and many species have in phylogenetic analyses already been transferred to other genera, such as *Alleniella* S.Olsson, Enroth & D.Quandt, *Exsertothea* S.Olsson, Enroth & D.Quandt, *Forsstroemia* Lindb. and *Taiwanobryum* Nog. For example, *Flora of North America* (http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=121748) treats five species under *Neckera*, but of those three belong in other genera (*Alleniella*, *Metaneckera* Steere). Enroth (2017) included 26 species of *Neckera* s.l. in a key to the Chinese species, of which only six belong in *Neckera* s.str. We sampled all species in *Neckera* s.l. of which we were able to get adequately fresh material for molecular analyses in order to provide a comprehensive phylogenetic overview.

MATERIAL AND METHODS

Taxon sampling and molecular markers. Phylogenetic analyses were performed on a data set which included 81 taxa and three genomic regions: the plastid *rps4-trnT-trnL-trnF* cluster (including the 3' of the *rps4* gene) and the *rpl16* group II intron, as well as the internal transcribed spacer region of the nuclear ribosomal DNA (ITS1-5.8S-ITS2).

DNA isolation, PCR-amplification and sequencing. DNA was extracted using the DNeasy® Plant Mini Kit (Qiagen GmbH, Germany) or the Nucleospin Plant II DNA Extraction Kit (Machery-Nagel) following the respective manufacturer’s protocol. Methods of cleaning and grinding of plants prior to extraction as well as PCR amplification protocols, cleaning of the PCR products and primers for the target regions followed Olsson et al. (2009a,b). Gel cleaned PCR products were sequenced by Macrogen Inc., South Korea (www.macrogen.com). Sequences were edited manually with PhyDE® v1.0 (Müller et al. 2005) and primer sequences were eliminated. All sequences are deposited in EMBL (European Molecular Biology Laboratory) or NCBI (The National Center for Biotechnology Information) GenBank. Accession numbers of the sequences and voucher information of the specimens are listed in **Supplementary Table S1**.

Sequence analyses and alignments. Seventeen hypervariable regions with uncertain homology assessment or poly-homonucleotide repeats were excluded from the analyses following Olsson et al. (2009b). Alignment of the sequence data was performed manually in PhyDE, based on the criteria laid out in Kelchner (2000) and Olsson et al. (2009a). 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). Similarly, a 31 bp long inverted sequence was identified and reverse complemented in the *Neckera denigrans rpl16* sequence (positions 720–750 in the submitted sequence). Indels were incorporated as binary data using a simple indel coding (SIC) strategy (Simmons & Ochoterena 2000) as implemented in SeqState (Müller 2005). Concatenated data matrixes were used for phylogenetic analyses.

Phylogenetic analyses. Maximum likelihood (ML) analyses were performed with RAxML v8.1.12 (Stamatakis et al. 2014) on the CIPRES Science Gateway (Miller et al. 2010) applying the GTRCAT model. Bootstrap analysis was performed with 1000 ML bootstrap replicates on the concatenated data matrix. Bayesian analyses were performed with MrBayes v3.2.6 (Ronquist et al. 2012). Best-fit substitution models were inferred from jModeltest v.2.1.10 (Darriba et al. 2012) for three sequence partitions (partition 1: *rps4-trnF*; partition 2: *rpl16*; partition 3: nuclear DNA). Based on the AIC values the GTR+ Γ +I model was applied for the sequence data and the restriction site model for the binary indel partition in MrBayes. 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 & Ronquist (2001) and Huelsenbeck et al. (2002). Ten runs with four chains (1×10^6 iterations each) were run simultaneously and chains were sampled every 1000 generations. 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 posterior probability of clades were performed based upon the trees sampled after the chains converged after removing 25% burn-in. Phylogenetic analyses were conducted on each partition separately. No significant incongruence was detected, and therefore the analyses were performed on the concatenated data matrix. Phylogenetic trees were displayed and edited using TreeGraph2 v2.14 (Stöver & Müller 2010). Data matrices and trees are deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S29361>).

RESULTS AND DISCUSSION

Alignment and sequence analyses. The alignment contained 4312 positions, of which 2035 belonged to the *rps4-trnT-trnL-trnF* partition (353 variable/183 parsimony informative), 981 to the *rpl16* partition (188/100) and 1296 to the nuclear ribosomal partition (284/155). Of all characters, 825 were variable and 438 parsimony informative. In addition, the data matrix contained 402 characters based on indel coding.

Phylogenetic analyses. The best scoring ML tree and the consensus tree from Bayesian inference did not show topological conflict with respect to statistically supported clades. Therefore, only the BI tree is illustrated (**Fig. 1**), with Bayesian posterior probabilities (PP) and bootstrap support values (BS) of the respective ML analysis indicated at the branches, both from analyses without and with indels included (order: PP / PPsic / BS / BSSic).

The monophyly of the Neckeraceae is confirmed with maximal support (**Fig. 1**). The three main clades (*Neckera*, *Thamnobryum* and *Pinnatella* clades) recognized by Olsson et al. (2009b) are retained with very high support (PP 0.99 or 1 and BS ranging from 81 to 97). *Touwia* Ochyra is an independent lineage. Neither the *Thamnobryum*-clade nor *Touwia* are further considered in the current study. The genera now recognized in the Neckeraceae s.str. and their species numbers are listed in **Table 1**.

PINNATELLA-CLADE

The phylogeny of the *Pinnatella*-clade was analysed by Olsson et al. (2010). The main results included splitting of *Homaliodendron* M.Fleisch. into two morphologically very distinct and monophyletic genera and transferring two species of *Pinnatella* M.Fleisch. and one of both *Neckera* and *Caduciella* Enroth to a monophyletic but morphologically heterogeneous *Taiwanobryum* Nog. A further consequential result was that *Neckeropsis* Reichardt in its erstwhile circumscription was not monophyletic and not as closely related to *Himantocladium* (Mitt.) M.Fleisch. as was thought on morphological grounds (e.g., Enroth 1992b; Touw 1962). For that reason, Olsson et al. (2016) analyzed those two genera in more detail, segregating four new genera from *Neckeropsis* and establishing a monophyletic *Himantocladium* s.str.

The present treatment adds two unispecific genera, *Indoneckera* Enroth and *Taiwanobryopsis* Enroth, to the clade and three species to the Asian genus *Taiwanobryum*. The clade has good support, but the two main subclades are poorly supported (**Fig. 1**).

Indoneckera Enroth, gen. nov.

Differs from Neckera s.str. and Alleniella by the long costa, and from those genera and Forsstroemia by the 1.8–2.2 cm long seta with mammillose-papillose upper parts.

GENERITYPE AND ONLY SPECIES: *Indoneckera himalayana* (Mitt.) Enroth, *comb. nov.*

Description. Plants gregarious, complanate, medium-sized to robust, glossy, various shades of green but older parts often brownish or blackish, stipitate-frondose, rather rigid and subpinnately branched to flexuose, indistinctly stipitate-frondose and irregularly branched, to c. 13 cm long. Stolons creeping, bearing small leaves and tufts of rhizoids emerging from just below leaf insertions; leaves triangular to ovate-ligulate, apex acute, costa single, reaching to above midleaf, margins entire throughout or weakly crenulate-denticulate near apex; rhizoids orange-brown, sparsely branched, smooth. Stipe in cross-section elliptic, cortex consisting of 5–8 layers of stereids that grade to larger, thinner-walled medullary cells, central strand none. Stipe leaves hardly differentiated from stem/branch leaves. Stem leaves complanate-spreading, to c. 3.5 × 1.3 mm, glossy, mostly regularly or irregularly undulate, basal parts also somewhat plicate, asymmetrically ovate-lanceolate, apex acute, acroscopic margin more strongly curved than basiscopic, decurrencies narrow, c. 0.2 mm long in stem leaves; costa single, tapering upwards and reaching to 2/3 or 3/4 of leaf length; leaf margins plane, irregularly denticulate near apex, entire elsewhere; leaf cells smooth, walls fairly thick and porose throughout, apical cells mostly rhombic or oblong, 20–30 × 5–10 μm, median cells linear and slightly vermicular, 25–50 × 5–7 μm, basal cells linear, 30–80 × 5–8 μm, cells at leaf insertion shorter, wider and thicker-walled; marginal cells in a few rows shorter than corresponding laminal cells; alar cells not differentiated. Branch leaves similar but somewhat smaller. Axillary hairs 3–5-celled, 1 or 2 apical cells long, hyaline, basal cells shorter and with brownish tinge. Paraphyllia none. Branch primordia covered by embryonic leaves; pseudoparaphyllia triangular to narrow-lanceolate, to c. 130 μm long. Dioicous. Perigonia and perichaetia on upper parts of stems and sometimes on upper branches. Perigonia gemmiform, c. 1.5 mm, largest perigonial leaves ovate-lanceolate, ecostate. Post-fertilization inner perichaetial leaves to c. 2.5 mm long, bases ovate and sheathing, upper parts somewhat cucullate, lanceolate and spreading, apex acuminate, costa ill-defined, ending below midleaf, margins entire throughout. Vaginula c. 2 mm long, bearing filiform paraphyses and few decrepit archegonia. Seta 1.8–2.2 cm long, reddish-brown, flexuous, slightly sinistrorse, smooth below, distinctly mammillose-papillose above (walls of bulging cells strongly thickened). Capsule ovoid, orthogonal, pale brown to chestnut brown when mature, c. 1.8 × 1.0 mm; apophysal stomata few, phaneropore, round-pored; exothecial cells slightly collenchymatous, irregular, mostly 25–50 × 20–25 μm; annulus not observed. Peristome double, hygrocastigae; exostome teeth c. 0.5 mm long, yellowish-grey, narrow-lanceolate, outer face densely spiculose-papillose throughout, with a slightly zig-zag median line; endostome basal membrane c. 100 μm high, faintly spiculose-papillose but not as densely as

exostome teeth, cilia none, segments c. 0.4 mm long, yellowish-grey, subulate, with narrow median perforations, densely spiculose-papillose throughout. Spores finely papillose, c. 13–18 µm diameter. Operculum not observed, described as “conic long rostrate” by Gangulee (1976). Calyptra cucullate, glabrous.

Etymology. Combined from the general distribution area (India, Himalayan region) and *Neckera*.

Indoneckera himalayana (Mitt.) Enroth, *comb. nov.*

≡ *Neckera himalayana* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1(2): 121. 1859. TYPE: INDIA.

SIKKIM: Tonglo, 10,000 ft., *J.D. Hooker s.n.* (lectotype [designated here], NY947398!; isolectotype, BM000844600 [image!]).

Illustrations. Gangulee 1976 (p. 1388: fig. 683, as *Neckera himalayana*).

Distribution. (Enroth 2017): India (Himalayan region, Kerala, Tamil Nadu), Sri Lanka, Nepal, Bhutan, Myanmar, NW Thailand, China (Yunnan).

Selected specimens examined (see also Enroth 2017). INDIA. KERALA: *S. Kumar 87139* (H3220432); TAMIL NADU: Nilghiri, *C.C. Townsend 73/697* (herb. J. Enroth); UTTARAKHAND: *D.G. Long 30930* (H3214374); KARNATAKA: *J. Pfeleiderer 54* (H-BR2892015); WEST BENGAL: *P. Decoly s.n.* (H-BR2892012). SRI LANKA: *T. Herzog s.n.* (H-BR2892017). MYANMAR: *J. Kurz 2823* (H-BR2892006). THAILAND. CHIANGMAI: *L. Zhang 4352* (H3225221). NEPAL. RASUWA DISTRICT: *D.G. Long 30543* (H3214371). BHUTAN. *H. Hara et al. s.n.* (H3097217). CHINA. YUNNAN: Tengchong Co., *J.R. Shevock 45547* (H3231665); Jingdong Co., *J.R. Shevock 45646* (H3231670, CAS); Yangbi Co., *P.L. Redfearn et al. 256* (H3227626).

Although not closely related, morphologically *Indoneckera* combines some characters of *Neckera* s.str., *Alleniella*, and *Forsstroemia* Lindb. The leaves are asymmetric, glossy and strongly undulate as in most species of *Neckera* and *Alleniella*, however the costa is single and relatively long, as in most species of *Forsstroemia*. As in most species of *Neckera* but unlike *Alleniella*, paraphyllia are lacking. The 1.8–2.2. cm long seta is much longer than in any species of the three genera, and its upper parts are distinctly mammillose-papillose, a character in the Neckeraceae present (and almost ubiquitous) only in the *Pimmatella* clade.

Taiwanobryopsis Enroth, *gen. nov.*

Differs from Taiwanobryum by the long, ligulate upper parts of the leaves and by the truncate leaf apices.

GENERITYPE AND ONLY SPECIES: *Taiwanobryopsis warburgii* (Broth.) Enroth, *comb. nov.*

Description. Plants gregarious, medium-sized to robust, shaggy, slightly glossy, sordid-green to brownish-green, stipitate-frondose, rigid, subpinnately to irregularly branched or sometimes not branched at all, to c. 12 cm tall. Stolons creeping, bearing small leaves and tufts of rhizoids emerging just below leaf insertions; leaves appressed, triangular to ovate-lanceolate, apex acute to obtuse, ecostate to distinctly single-costate; rhizoids orange-brown, sparsely branched, smooth. Stipe distinct, in cross-section elliptic, cortex consisting of 3–5 layers of stereids that grade to larger, thinner-walled medullary cells, central strand none. Well-differentiated stipe leaves few, closely appressed, c. 2 mm long, triangular to ovate, often brown to blackish, apex acute to obtuse, costa strong and reaching near leaf apex, margins crenulate below, irregularly denticulate above, walls of leaf cells strongly incrassate and porose; leaves on upper part of stipe grading to stem leaves. Stem leaves spreading to patent when dry, hardly altered when wet, from an ovate base gradually narrowed to a ligulate lamina c. 2/3 of whole leaf length, ligulate parts mostly distinctly undulate; stem leaves to c. 4.5 mm long, base to 1.1 mm wide and with c. 0.2 mm long decurrencies, ligulate part c. 0.5 mm wide; apex mostly truncate, often retuse or notched, sometimes slightly spatulate; costa single, wide below but tapering upwards, reaching to c. 5/6 of leaf length; margins denticulate elsewhere but at apex additionally rather strongly and irregularly dentate. Leaf

cells smooth, with strongly incrassate and porose walls throughout; apical cells irregularly rhombic to oblong, c. 10–20 × 7–10 µm, median cells oblong to linear, c. 20–30 × 5–7 µm, basal cells c. 30–80 × 5 µm, cells at leaf insertion shorter; alar cells not differentiated; marginal cells in 1(–2) row(s) shorter than corresponding laminal cells, their walls nearly aporose. Branch leaves similar but somewhat smaller. Axillary hairs very fragile and apparently deciduous, to 7 cells long, 1 or 2 basal cells short and brownish-tinged. Branch primordia covered by embryonic leaves; pseudoparaphyllia uniseriate and subulate to multiseriate and lanceolate, to c. 0.25 mm long. Dioicous. Perigonia and perichaetia on upper parts of stems and sometimes on upper branches. Perigonia gemmiform, c. 1.5 mm, largest perigonial leaves ovate-lanceolate, ecostate, upper part somewhat spreading, apex obtuse. Pre-fertilization inner perichaetial leaves to 1.8 mm long, from a sheathing, ovate base narrowed at midleaf to a spreading, ligulate acumen, apex acute or obtuse, costa ill-defined, ending c. at midleaf, margins irregularly denticulate at apex, entire elsewhere, laminal cells with strongly incrassate and porose walls throughout. Sporophytes unknown.

Etymology. The name refers to a habitual resemblance with *Taiwanobryum*, especially *T. undulatifolium* (Tixier) W.Z.Ma, Enroth & Shevock (cf. Ma et al. 2018).

Taiwanobryopsis warburgii (Broth.) Enroth, *comb. nov.*

≡ *Neckera warburgii* Broth., *Monsunia* 1: 49. 1899; ≡ *Himantocladium warburgii* (Broth.)

M.Fleisch., *Musci Buitenzorg* 3: 892. 1908. TYPE: PHILIPPINES. MINDANAO: “Süd Mindanao, Mt. Dagatpan, 2000 ft.“, *O. Warburg s.n.* (quote from specimen label) (lectotype [designated by Enroth 1992b: 86, as „holotype“], H-BR1973007!).

Distribution (Enroth 1994b). Philippines, Malaysia (Sabah).

Selected specimens examined. PHILIPPINES. MINDANAO: *F. Schumm & U. Schwartz 4407* (H), *J.R. Shevock 44851* (H3231640), see also holotype cited above. MALAYSIA. SABAH: *J. Sinclair et al. 9184* (L).

The shaggy habit, leaf size and leaf areolation of *Taiwanobryopsis warburgii* resemble *Taiwanobryum undulatifolium*, which is known from Vietnam and China (Guangxi, Guizhou, Yunnan). However, the leaf shape and apex are different in the two species. In *T. warburgii* the ligulate upper part is relatively much longer and the apex is truncate, whereas in *T. undulatifolium* the apex is acute (Enroth 1992a; Ma et al. 2018; Tixier 1966; Wu 2011). The sporophyte of *T. warburgii* remains unknown, but the peculiar gametophytes could not be confused with any other species than *T. undulatifolium*.

Taiwanobryum Nog.

Trans. Nat. Hist. Soc. Formosa 26(150): 141. 1936.

Taiwanobryum was originally (Noguchi 1936) established to accommodate only *T. speciosum* Nog. and placed in the Prionodontaceae, which also comprised the tropical genera *Prionodon* Müll.Hal. and *Neolindbergia* M.Fleisch.; the latter was taxonomically revised by Akiyama et al. (1991). Currently *Prionodon* is placed in its own family probably closely related to the Cryphaeaceae, and *Neolindbergia* in the Pterobryaceae (Cox et al. 2010; Goffinet et al. 2008). Lai & Koponen (1981) revised *Taiwanobryum* and recognized two species, *T. speciosum* and *T. robustum* Velloira, the latter later (Akiyama et al. 1991) synonymized with *Neolindbergia velloirae* H.Akiyama. Those authors still placed *Taiwanobryum* in the Prionodontaceae, but since then it has by various authors been placed in the now redundant Leptodontaceae, until Olsson et al. (2009b; see also Cox et al. 2010) showed that it, along with all other “Leptodontaceae”, belongs in the Neckeraceae.

Our phylogenetic results support transferring two species, *Neckera praetermissa* Enroth & Touw, and *N. serrulatifolia* Enroth & M.C.Ji to *Taiwanobryum*. The genus then contains nine species, which constitute a morphologically heterogeneous tropical genus most diverse in Asia. The present analysis covers eight of the species (**Fig. 1**), the ninth being *T. guangdongense* (Enroth)

S.Olsson, Enroth & D.Quandt (Enroth 1993; Olsson et al. 2010), closely related to *T. anacamptolepis* (Müll. Hal.) S.Olsson, Enroth & D.Quandt. The first diverging species *T. mucronatum* (Bosch & Sande Lac.) S.Olsson, Enroth & D.Quandt has the widest distribution, ranging from the Seychelles in the west through tropical Asia to American Samoa in the east (Enroth 1994c, as *Pinnatella mucronata* (Bosch & Sande Lac.) M.Fleisch.). It is also morphologically the most aberrant species in the genus. It is the single species with a central strand in the stem; small, spreading to squarrose and non-overlapping stipe leaves; a relatively weak costa (a character present also in *T. anacamptolepis*); and leaf cells with relatively thin and non-porose walls.

All species of *Taiwanobryum* are dioicous and sporophytes are therefore infrequent. Vegetative propagation is common and takes place through caducous branch leaves (*T. guangdongense*, *T. serrulatifolium* (Enroth & M.C.Ji) Enroth, *T. praetermissum* (Enroth & Touw) Enroth, *T. undulatifolium*) or flagelliform, microphyllous branchlets (*T. mucronatum*, *T. anacamptolepis*), but apparently not by both means in any species. *Taiwanobryum crenulatum* (Harv.) S.Olsson, Enroth & D.Quandt, *T. speciosum* and *T. yunnanense* (Enroth) Enroth (see Enroth & Shevock 2021) seem to lack specialized means of vegetative propagation.

Sporophytes are known for *Taiwanobryum guangdongense*, *T. mucronatum*, *T. crenulatum*, *T. speciosum*, and *T. undulatifolium*. As in the *Pinnatella* clade in general, the upper parts of setae are distinctly mammillose in all of those species, and the seta length varies from 2.5–3.5(–4.5 mm) in *T. guangdongense* (Akiyama & Enroth 2016) and *T. mucronatum* (Enroth 1994c, as *Pinnatella mucronata*) to c. 12 mm in *T. crenulatum* (Gangulee 1976 as *Neckera crenulata* Harv.; JE pers. obs.) and c. 15 mm in *T. speciosum* (Noguchi 1989; Wu 2011) and *T. undulatifolium* (Ma et al. 2018). The capsules are symmetric, orthotropous to slightly orthogonal, and ovoid to short-cylindric in the other species except *T. undulatifolium*, which has globose capsules (Ma et al. 2018). There are few (up to 11, Ma et al. 2018) phaneroporous, round-pored stomata in the apophysis except in *T. speciosum*, which lacks stomata (cf. Akiyama & Enroth 2016). An annulus is apparently not differentiated. The peristome is double except in *T. speciosum* which has no endostome (Noguchi 1989; Wu 2011) and possibly in *T. guangdongense*; for the latter, Akiyama & Enroth (2016) did not find an endostome in the unoperculated capsules they studied. The peristome teeth are c. 100 µm long in *T. guangdongense*, 350 µm in *T. mucronatum*, 450 µm in *T. speciosum*, and 550–600 µm in *T. undulatifolium* (not observed for *T. crenulatum*). The peristome teeth and, in species with double peristome, the endostome segments are spiculose-papillose throughout. The operculum is obliquely conic-rostrate.

TAXONOMIC CHANGES IN *TAIWANOBRYUM*

Taiwanobryum praetermissum (Enroth & Touw) Enroth, *comb. nov.*

≡ *Neckera praetermissa* Enroth & Touw, *Phytotaxa* 195(2): 179. 2015. TYPE: VIETNAM. NINH-BINH PROV.: in reservato silv. Cuc-Phuong pr. pag. Bong, 600 m., ad corticem arborum cacuminis altissimis, 14 Dec. 1965, *T. Pócs et al. s.n.* [Expediitio tertia Hungaro-Vietnamica No. 3031/G"] (holotype, H3235164!).

Illustrations. Enroth & Touw 2015 (p. 179: fig. 1; p. 180: figs. 2 & 3).

Distribution (Enroth & Touw 2015; Ellis et al. 2018): Vietnam, China (Guangxi).

Specimens examined. VIETNAM (see holotype cited above). CHINA. GUANGXI: *Y.-M. Wei 10-85* (H3239048), *Y.-M. Wei 10-158A* (H3239049), *Y.-M. Wei 10-621B* (H3239089).

Taiwanobryum serrulatifolium (Enroth & M.C.Ji) Enroth, *comb. nov.*

≡ *Neckera serrulatifolia* Enroth & M.C. Ji, *Edinburgh J. Bot.* 64: 295. 2007. TYPE: CHINA.

XIZANG: Lang Chu, 2300 m., *Quercus? tungmaiensis* forest on left bank of lower Lang Chu, 23 Aug. 1994, *G. Miehe & U. Wündisch 10112:14* (holotype, H3235442!).

Illustrations. Enroth & Ji 2007 (p. 296: fig. 1; p. 297: fig. 2)

Commented [JL1]: There are 3 of these "taxonomic changes" sections (in green here and below). I'm assuming these are all equivalent sections, correct? Should everything below each heading be considered part of the section? I've indicated this with small caps for these headings.

Commented [EJ2R1]: Yes you are correct.

Distribution (Enroth & Ji 2007): China (Xizang).

Specimen examined. CHINA (see holotype cited above).

NECKERA-CLADE

In the analysis by Olsson et al. (2011) *Neckera* turned out to be “seriously” paraphyletic, resulting in the description of two monophyletic generic segregates *Exsertotheca* (then with two species, but Draper et al. 2011 added a third one) and its sister clade *Alleniella* (with ten species). Among *Alleniella*, the two first diverging species *A. besseri* (Lobarz.) S.Olsson, Enroth & D.Quandt and *A. complanata* (Hedw.) S.Olsson, Enroth & D.Quandt are temperate and occur mainly in the Northern Hemisphere, whereas the remaining eight are mainly Southern Hemisphere temperate species or occur on mountains at tropical latitudes. The present analysis elaborates the species diversity, morphology and biogeography of *Alleniella* and *Forsstroemia* farther. It also supports the morphological distinctness and generic status of the unispecific *Metaneckera* (relative to *Neckera* s.str.) in its novel phylogenetic context.

The basal dichotomy separates the *Neckera*-clade (1/0.90/93/74) from the sister clade comprising the *Touwia*, *Thamnobryum* and *Pinnatella*-clades (**Fig. 1**). The first diverging, maximally supported lineage within the *Neckera*-clade consists of two tropical species of *Thammomalina*, both distributed in S and Central America (Olsson et al. 2011). Also the next diverging clade, consisting of *Metaneckera* and *Neckera* s.str., is maximally supported. It is temperate and exclusively distributed in the Northern Hemisphere (N America and Eurasia). The next large clade, again with maximal support, contains the genera *Forsstroemia*, *Leptodon* D.Mohr, *Exsertotheca* and *Alleniella*. Of those, the first diverging *Forsstroemia* lacks significant support (0.67/0.49). The *Leptodon-Exsertotheca-Alleniella* subclade has no significant support based on the nucleotide characters (PP 0.57) but adding characters from indel coding it raises to PP 1. Within this clade, *Leptodon* and *Alleniella* have very good support (1/1/92/93 and 1/1/89/89, respectively) and *Exsertotheca* is fully supported.

Neckera is distributed in the temperate Northern Hemisphere but has only few species in eastern Asia, which is the area where *Forsstroemia* is most diverse. Both genera have only few or no species at all in the tropical areas and temperate Southern Hemisphere (Australasia), where *Alleniella* is mainly distributed. *Exsertotheca* with three species is a Eurasian genus (Draper et al. 2011), and the distribution of *Leptodon* (including *Cryptoleptodon* Renaud & Cardot) with seven species is highly disjunctive. Only *Leptodon smithii* (Dicks. ex Hedw.) F.Weber & D.Mohr has a wide distribution (Enroth 2012; Nelson 1973; Pócs 1960), the rest not and some of them are narrow endemics (Enroth 1992c; Olsson et al. 2011, 2012; Sotiaux et al. 2009).

A general note on paraphyllia in the neckeraceous context is pertinent here, as in the Neckeraceae they occur only in the *Neckera*-clade (*Metaneckera*, *Neckera californica* Hook. & Arn., *Leptodon*, *Alleniella*, some species of *Forsstroemia*). Spirina et al. (2020) studied the development and location of paraphyllia in various genera of pleurocarpous mosses. Based on where the paraphyllia are located, those authors divided them into two groups they called *Leskea*-type and *Climacium*-type. In the latter type the paraphyllia are distributed all over the stems and branches, but in the former paraphyllia occur only near branch primordia. Spirina et al. (2020) made close observations on the paraphyllia development in *Leptodon smithii*, and visually observed their distribution in *Metaneckera menziesii* and *Neckera californica*, and in all of those the paraphyllia represented the *Leskea*-type. While we have not made comprehensive studies on the paraphyllia in the Neckeraceae, observations on numerous species by the author Enroth suggests that in this family they are exclusively of the *Leskea*-type.

Metaneckera Steere

Metaneckera is sister to *Neckera* s.str., and the genus was erected, originally as *Neckeradelphus* Steere *hom. illeg.* (cf. Steere 1967), for *Neckera menziesii* Drumm. by Steere

(1941). Steere (1941) emphasized the presence of paraphyllia, distinct costa, strongly incrassate and porose walls of the laminal cells, and dioicous sexual condition as generic distinctions from *Neckera*. *Metaneckera* was previously not recognized by the first author of the present paper (e.g., Enroth 1994a), based on the fact that there were several Asian species of *Neckera* s.l. with that same character combination (e.g., *N. polyclada* Müll.Hal., *N. setschwanica* Broth.). Our present analyses, however, show that none of those species are closely related to *Neckera* s.str. but they belong in *Forsstroemia* in the *Neckera*-clade, or in *Taiwanobryum* or form their own unispecific genera in the Asian *Pinnatella*-clade. *Neckera polyclada* was recently placed in its own genus *Enrothia* Ignatov & Fedosov (Ignatov & Fedosov 2019). *Neckera* s.str. lacks several of the mentioned characters (paraphyllia, strongly incrassate and porose leaf cell walls, a long and distinct costa; save *Neckera californica* (syn. *Alsia californica* (Hook. & Arn.) Sull.), which has paraphyllia and a variable costa), so in addition to the molecular evidence also morphology supports recognizing *Metaneckera* at generic level. It is distributed along the western parts of North America from California to Alaska and eastwards to Idaho, Montana, Colorado, South Dakota and New Mexico (Flora of North America, http://www.efloras.org/object_page.aspx?object_id=125636&flora_id=1) and the Mediterranean region and sporadically in Central Europe to the Black Sea region (Abkhazia; specimen examined H3091821) and Middle East (Ros et al. 2013). The distribution area in North America is sympatric with *Neckera douglasii* Hook. and *N. californica*, the two species forming the first diverging clade in *Neckera* s.str.

Neckera Hedwig s.str.

Neckera has long been a "catch-all" for species with a more or less frondose, complanate habit, wide and asymmetric, mostly glossy and undulate leaves, and mostly short-exserted or immersed capsules, regardless of their geographic provenance. *Neckera* s.str., however consists of about ten temperate, strictly Northern Hemisphere species. With the exception of *N. californica*, they do have the habit and leaf characters mentioned above, and additional defining characters are lack of costa or presence of a fairly weak and short one (main difference from *Forsstroemia*), firm-but not very thick-walled leaf cells, lack of paraphyllia (main difference from *Alleniella* and most species of *Forsstroemia*), and immersed capsules. *Neckera californica*, however, belonging in the first diverging lineage in the genus (**Fig. 1**), has a distinct costa reaching to $\frac{3}{4}$ of leaf length and also paraphyllia (Malcolm et al. 2009, as *Alsia californica*). These characters, as also the rather thick-walled cells, resemble those of *Metaneckera*, the sister of *Neckera*, and may thus be plesiomorphic in *Neckera*.

A notable evolutionary shift among *Neckera* is a change in the sexual condition. Of the eight species included in the analysis, the two first diverging lineages (*N. californica* – *N. douglasii* and *N. cephalonica* Jur. & Unger – *N. pumila* Hedw.) are dioicous and the crown clade with four species, *N. bhutanensis* Nog., *N. borealis* Nog., *N. oligocarpa* Bruch, and *N. pennata* Hedw. are autoicous. The same shift has occurred in *Neckeropsis* s.str. (*Pinnatella* clade), where the first diverging taxa are dioicous and the "crown clade" taxa are autoicous (Olsson et al. 2016), as well as in *Alleniella* (Olsson et al. 2011; see also below). According to Laenen et al. (2016), in liverworts shifts to autoicy may increase diversification rates due to better dispersal capacity (by spores) and the ensuing allopatric speciation. It is very likely that this holds true also for mosses.

Three endemic *Neckera* species in the Himalayan region resemble the wide-spread *N. pennata*, which in fact can be a complex of two or several, morphologically quite similar cryptic species (cf. Appelgren & Cronquist 1999). Of the Himalayan species *N. bhutanensis* (see Noguchi 1971) was included in the present analysis but it is not resolved as closely related to *N. pennata*. We were however unable to have *N. noguchiana* M.C.Ji & Enroth (Ji et al. 2005) and *N. xizangensis* Enroth & M.C.Ji (Enroth & Ji 2010) in the analysis. The former morphologically agrees well with *Neckera* s.str., but the latter deviates e.g. by having paraphyllia and leaf cells with fairly thick and

porose walls. This suggests the genus *Alleniella*, but in the absence of molecular evidence we prefer to keep it in *Neckera* for now.

Forsstroemia Lindb.

In the present analysis 16 species form a monophyletic *Forsstroemia*-clade. Molecular phylogeny supports transferring seven Asian species, *Neckera setschwanica*, *N. fauriei* Cardot, *N. denigricans* Enroth, *N. flexiramea* Cardot, *N. pusilla* Mitt., *N. humilis* Mitt., and *N. inopinata* Enroth & M.Ji to *Forsstroemia*. The specific diversity of *Forsstroemia* is heavily focused in Asia: of the 19 species 16 are strictly Asian. Only *F. producta* (Hornsch.) Paris and *F. trichomitria* (Hedw.) Lindb. are widely distributed and *F. coronata* (Mont.) Paris is endemic to South America (Stark 1987). We were unable to include *F. thomsonii* (Mitt.) Buck and *F. indica* (Mont.) Paris in the analysis and their phylogenetic position thus still remains untested.

In his revision of *Forsstroemia*, Stark (1987) recognized 10 species. Of those, *F. tripinnata* (Dix.) Nog. was synonymized with *Pseudopterobryum tenuicuspis* Broth. by Noguchi & Li (1988). We point out that the placement of *P. tenuicuspis* in *Forsstroemia* by Olsson et al. (2012) was an error caused by a mix-up of specimens of *P. tenuicuspis* and *Forsstroemia japonica* (Besch.) Paris in the laboratory (cf. Akiyama 2016). In the present analysis the phylogenetic positions of those two species are corrected (**Fig. 1**).

Morphologically *Forsstroemia* is very heterogenous, and even the four infrageneric clades have little morphological consistency. Some species assume a *Neckera*-like habit, having more or less distinctly undulate and glossy leaves (*F. setschwanica* (Broth.) Enroth, *F. yezoana* (Besch.) S.Olsson, Enroth & D.Quandt, *F. fauriei* (Cardot) Enroth, *F. denigricans* (Enroth) Enroth, *F. flexiramea* (Cardot) Enroth), which in the latter three species are also complanate and asymmetric, as in *Neckera*. However, even these species have a distinct costa, which is the most consistent difference from *Neckera*. Species such as *F. japonica*, *F. cryphaeoides* Cardot and *F. producta* rather resemble taxa in the family Cryphaeaceae, being much smaller and having dull, symmetric and ovate-acuminate leaves. Most species lack paraphyllia, but *F. setschwanica*, *F. fauriei*, *F. denigricans* and *F. humilis* (Mitt.) Enroth have them.

The sexual condition also varies among the species. All species in the first diverging (**Fig. 1**) *Forsstroemia setschwanica* – *F. noguchii* L.R.Stark – *F. fauriei* – *F. denigricans* clade are dioicous. In the next diverging *F. producta* – *F. flexiramea* – *F. cryphaeoides* – *F. japonica* clade only *F. producta* is autoicous (sometimes synoicous, cf. Stark 1987), the rest being dioicous. In the *F. pusilla* – *F. yezoana* – *F. humilis* clade, the latter two are autoicous and the sexual condition of *F. pusilla* is not known. Finally, in the *F. neckeroides* Broth. – *F. konoii* (Broth.) Enroth, Fedosov & Ignatov – *F. goughiana* (Mitt.) S.Olsson, Enroth & D.Quandt – *F. coronata* – *F. trichomitria* clade the three first-mentioned species are dioicous, and according to Stark (1987) *F. coronata* is (gonio)autoicous and *F. trichomitria* is autoicous or sometimes polyoicous.

Sporophytes are unknown for *Forsstroemia setschwanica* and *F. noguchii*, both being dioicous. Most of the other species have short setae and immersed to slightly emergent capsules, but *F. flexiramea* consistently has 3–4 mm long and *F. konoii* 5–6 mm long setae and thus the capsules in both are fully exserted. According to Stark (1987) there is some infraspecific variation in the seta length. *Forsstroemia producta* has 0.6–4.5 mm long setae and the capsules are immersed to fully exserted, and in the same clade *F. japonica* has 0.8–2.3 mm long setae and emergent to exserted capsules. In *F. coronata* the capsules are emergent to exserted on setae 1.0–2.7 mm long, and *F. trichomitria* has 0.4–3.9 mm long setae and immersed to exserted capsules.

The variation in the seta length is widest in *Forsstroemia trichomitria* and *F. producta*, which are also the two species with the widest yet quite disjunctive geographical distributions. *Forsstroemia producta* is known from all continents, and *F. trichomitria* is lacking only from Africa. Stark (1987) observed some geographical patterns in the seta length (and several other characters) in both species, but he recognized only one infraspecific taxon, *F. trichomitria* subsp.

australis (Müll.Hal.) Stark, distributed in eastern Australia and consistently having exerted capsules.

TAXONOMIC CHANGES IN *FORSSTROEMIA*

Forsstroemia setschwanica (Broth.) Enroth, *comb. nov.*

≡ *Neckera setschwanica* Broth., Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 131: 215. 1923. TYPE: CHINA. SICHUAN: in montium Daliang-schan, (territorii Lolo) ad orientem urbis Ningyüen regione temperata, ca. 2600–2800 m, in silva elata mixta tergi Soso-liangde ad rupes 25 Apr. 1914, *H. Handel-Mazzetti 1695* [“*Diar. nr. 394b*”] (lectotype [designated here], H-BR2892001!; isotypes, BM000987873 [image!], JE04008126 [image!], PC01379322 [image!]).

Illustrations (as *Neckera setschwanica*): Gangulee 1976 (p. 1391, fig. 685); Wu 2011 (p. 355: plate 381, figs. 1–13).

Distribution (Enroth 2017; Wu 2011, both as *Neckera setschwanica*). China (Guangxi, Hunan, Sichuan, Yunnan, Xizang), Bhutan.

Selected specimens examined. BHUTAN. *G. Miehe & S. Miehe 98-378-22* (H3236551). CHINA. GUANGXI: Napo Co., *Y.-M. Wei 10378A* (H3239071). HUNAN: Shimen Co., *T. Koponen et al. 53639* (H3222572). SICHUAN: Yajiang Co., *J.R. Shevock 35980* (H3223107), Wen-chuan Co., *J. Lou s.n.* (H3097773). YUNNAN: Yangbi Co., *P.L. Redfearn et al. 947* (H32227580); Anning Co., *P.L. Redfearn et al. 34322* (H3227677); Gongshan Co., *D.G. Long 35988* (3214383); Weixi Co., *J.R. Shevock 32254* (H4226156).

Forsstroemia fauriei (Cardot) Enroth, *comb. nov.*

≡ *Neckera fauriei* Cardot, Bull. Soc. Bot. Genève ser. 2, 3: 277. 1911. TYPE: SOUTH KOREA. Jeju Island (“île Quelpaert”), 1906, *J. Faurie 206* (lectotype [designated here], PC0052679 [image!]; isotype, H-BR2893008!).

= *Neckera decurrens* Broth., Sitzungsber. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Abt. 1, 131: 215. 1923, syn. nov. TYPE: CHINA. HUNAN: “prope urbem Tschangscha in monte Yolu-schan ad corticem viv. Liquidambaris”, ca. 150 m., 16 Feb. 1918, *H. Handel-Mazzetti 11449* [*Diar. Nr. 2287a*] (lectotype [designated by Enroth 1996: 5, as “holotype”], H-BR2892020!; isotypes, BM000987869 [image!], JE04008127 [image!], PC0147551 [image!]).

Illustrations. Noguchi 1989 (p. 701: fig. 309B, as *Neckera fauriei*); Wu 2011 (p. 344: plate 377, figs. 1–11, as *Neckera decurrens*).

Distribution (Noguchi 1989; Wu 2011 as *Neckera decurrens*; this report). Japan (Honshu, Shikoku, Kyushu), Korea, China (Guangxi, Guizhou, Hubei, Hunan, Yunnan).

Selected specimens examined. CHINA. GUANGXI (first report): Napo Co., *Y.-M. Wei 10-502D* (H3239073). HUNAN: Sangzhi Co., *V. Virtanen 61157* (H3222562); Shimen Co., *T. Koponen et al. 54072* (H3222567); Liyuang Co., *V. Virtanen 61877* (H3222564). TAIWAN: *J.R. Shevock 43726* (H3232658). YUNNAN: Fugong Co., *J.R. Shevock 24969* (H3219182); Gongshan Co., *J.R. Shevock 43050* (H3232679); Jingdong Co., *J.R. Shevock 45647* (H3231671); Tengchong Co., *J.R. Shevock 28280B* (H3225110).

Forsstroemia denigricans (Enroth) Enroth, *comb. nov.*

≡ *Neckera denigricans* Enroth, *Hikobia* 12: 1. f. 1. 1996. TYPE: VIETNAM. Montes Hoang_Lien-Son, in rupibus marmoreis umbrosis supra opp. Sapa, 1800 m., 27 Sept. 1963, *T. Pócs 2573/3* (holotype, EGR!).

Illustrations. Enroth 1996 (p. 2: fig. 1, as *Neckera denigricans*).

Distribution (Ji & Enroth 2010). Vietnam, China (Yunnan).

Selected specimens examined. VIETNAM (see holotype cited above). CHINA. YUNNAN: Fugong Co., *J.R. Shevock 31088* (H3235014); Gongshan Co., *J.R. Shevock 30854* (H3215509).

Forsstroemia flexiramea (Cardot) Enroth, *comb. nov.*

≡ *Neckera flexiramea* Cardot, Bull. Soc. Bot. Genève 3: 277. 1911. TYPES: SOUTH KOREA. Jeju Island ("île Quelpaert"), 700 m, *J. Faurie 200* (lectotype [designated here], PC0052682 [image!]; isotype, H-BR2901005!). SYNTYPES: JAPAN. Sendai Tojogu, 24 Nov. 1907, *Y. Iishiba 436* (H-BR2901002!), 15 Sep. 1907, *Y. Iishiba 386* (H-BR2901004!); Sendai, Koeji, 1 Dec. 1906, *Y. Uyematsu 396* (H-BR2901008!), 9 Dec. 1906, *Y. Uyematsu 66* (H-BR2901015!).

Illustrations (as *Neckera flexiramea*). Noguchi 1989 (p. 701: fig. 309A); Wu 2011 (p. 344: plate 377, figs. 12–23).

Distribution (Wu 2011, as *Neckera flexiramea*). Japan, Korea, China (Anhui, Chongqing, Guangxi, Hunan, Taiwan).

Selected specimens examined. JAPAN. HONSHU: *Z. Iwatsuki s.n.* (H3097212). CHINA. HUNAN: *T. Koponen et al. 55093* (H3222573). ZHEJIANG: *W.R. Buck 23845* (H3097213). TAIWAN: *J.R. Shevock 41313* (H3235339).

Forsstroemia pusilla (Mitt.) Enroth, *comb. nov.*

≡ *Neckera pusilla* Mitt., Trans. Linn. Soc. London, Bot. 3: 174. 1891. TYPE: JAPAN. "Challenger Exp.", without collector (lectotype [designated here], NY00943794!).

Illustrations (as *Neckera pusilla*). Noguchi 1989 (p. 690: fig. 305B); Ji & Enroth (p. 64: fig. 2).

Distribution (Ji & Enroth 2010b): Japan, Korea, China (Shanxi).

Selected specimens examined. CHINA. SHANXI: *E. Licent 151, 204b, 205* (BM). JAPAN. HONSHU: *M. Mizutani s.n.* (H3097745). KYUSHU: *H. Deguchi s.n.* (H3194572).

Forsstroemia humilis (Mitt.) Enroth, *comb. nov.*

≡ *Neckera humilis* Mitt., Trans. Linn. Soc. London, Bot. 3: 174. 1891. TYPE: JAPAN. "Challenger Exp.", 1 Jan. 1875, *H.N. Moseley s.n.* (lectotype [designated here], NY00710473 [image!]); isotypes, BM000844629!, PC0137201 [image!]).

Illustrations (as *Neckera humilis*). Noguchi 1989 (p. 703: fig. 310A); Wu 2011 (p. 346: plate 378, figs. 16–24).

Distribution (Wu 2011, as *Neckera humilis*). Japan, Korea, China (Anhui, Jiangsu, Shanghai, Zhejiang).

Selected specimens examined. JAPAN. HONSHU: *H. Deguchi 38346* (H3223831). KYUSHU: *T. Osada s.n.* (H3097225).

Forsstroemia inopinata (Enroth & M.Ji) Enroth, *comb. nov.*

≡ *Neckera inopinata* Enroth & M.Ji, Polish Bot. J. 57: 64. 2012. TYPE: CHINA. HUNAN: Wulingyuan World Heritage Area, Zhangjiajie, Pipajie, 29°19N, 110°24E, subtropical (warm temperate) zone, on roadside, in bushes, alt. 687 m., on *Liquidambar formosana*, 15 Sept. 1999, *P. Rao 58379* (holotype, H3235454!).

Illustrations (as *Neckera inopinata*). Enroth & Ji 2012 (p. 65: fig. 1; p. 66: fig. 2).

Distribution. China (Hunan, Zhejiang).

Specimens examined. CHINA. HUNAN (see holotype cited above); ZHEJIANG: *T. Simon 39* (EGR, paratype).

Forsstroemia inopinata was not included in the molecular analysis, but it is placed in this genus due to the distinct costa and its distribution in eastern China. Sporophytes are not known (Enroth & Ji 2012).

Alleniella Enroth, S.Olsson, Huttunen & D.Quandt

In the phylogenetic tree five additional species are resolved in the *Alleniella*-clade: *Neckera laevigata* Hook. f. & Wilson, *N. ehrenbergii* Müll.Hal., *N. platyantha* (Müll.Hal.) Paris, *N. andina* Mitt., and *N. obtusifolia* Taylor (**Fig. 1**). Species of *Alleniella* have a striking resemblance to those of *Neckera* s.str. The main morphological difference at the generic level is in the presence of paraphyllia. In *Neckera* s.str. only the first diverging species *N. californica* has paraphyllia, and they are lacking in all other species. In *Alleniella* the two first diverging species *A. besseri* and *A. complanata* lack paraphyllia, and the other species have them, although in variable abundance. Paraphyllia are always numerous in the clades *A. brownii* – *A. laevigata*, *A. andina* – *A. obtusifolia* and *A. submacrocarpa* – *A. ehrenbergii*. The other species have intraspecific variation, as paraphyllia are either sparse or sometimes lacking altogether. *Alleniella remota* (Bruch & Schimp. ex Müll.Hal.) S.Olsson, Enroth & D.Quandt however apparently always has paraphyllia but they can be very few (De Sloover 1977).

The geographic distributions of *Alleniella* and *Neckera* s.str. overlap only slightly. The latter is a Northern Hemisphere, temperate genus while most species of *Alleniella* are distributed in the tropics (mainly in montane rain forests) or in the temperate regions of the Southern Hemisphere, viz. in Australasia (*A. hymenodonta* (Müll.Hal.) S.Olsson, Enroth & D.Quandt, *A. brownii* (Dixon) S.Olsson, Enroth & D.Quandt, *A. laevigata* (Hook. f. & Wilson) Enroth). The exceptions in *Alleniella* are, again, the two first diverging species *A. besseri* and *A. complanata*, which are distributed in the temperate regions of the Northern Hemisphere, although *A. complanata* is known from few localities in central and South Africa (Hedderson & Enroth 2006). The genus is not represented in tropical Asia at all and is most speciose in South America. The crown clade (**Fig. 1**) contains the African species *A. remota*, *A. platyantha* (Müll.Hal.) Enroth and *A. submacrocarpa* (Dixon) S.Olsson, Enroth & D.Quandt plus *A. ehrenbergii* (Müll.Hal.) Enroth, which is the only species distributed in addition to South America also in Africa, where it was known as *Neckera valentiniana* Besch. (e.g., Magill & van Rooy 1998).

TAXONOMIC CHANGES IN ALLENIELLA

Alleniella laevigata (Hook. f. & Wilson) Enroth, *comb. nov.*

≡ *Neckera laevigata* Hook. f. & Wilson, Fl. Nov. Zel. 2: 103. 88 f. 3. 1854. TYPE: NEW ZEALAND. “Middle Island: Banks’ Peninsula and Port Cooper: Banks, Peninsula and Port Cooper, *Lyal*”. Probable syntype: “Banks Peninsula, New Zealand, 1854”, without collector (BM000987914 [image!]). – Note: We were not able to examine specimens collected by Lyall, but the author Enroth has seen ample material (H, H-BR) of this species from New Zealand.

Illustrations (as *Neckera laevigata*). Hooker 1855 (pl. LXXXVIII, fig. 3); Dixon 1929 (pl. X, fig. 9a & 9b).

Distribution (Fife 1995, as *Neckera laevigata*). Endemic to New Zealand.

Selected specimens examined. NEW ZEALAND. NORTH ISLAND, Hawke’s Bay, *J.R. Shevock* 39153A (H3235349). SOUTH ISLAND, DUNEDIN: Mar. 1874 *S. Bergren s.n.* (H3097607).

Alleniella ehrenbergii (Müll.Hal.) Enroth, *comb. nov.*

≡ *Neckera ehrenbergii* Müll.Hal., Syn. Musc. Frond. 2: 51. 1850. TYPE: MEXICO. Without location, *C. Ehrenberg s.n.* (lectotype [designated by Sastre-De Jesús 1987, cf. Allen 2010: 284], BM000961325 [image!]; isotype NY1140804 [image!]).

= *Neckera valentiniana* Besch., Ann. Sci. Nat., Bot., sér. 6, 10: 273. 1880, syn. nov. TYPE: LA RÉUNION. Pavés Saint-Leu, 1876, *Valentin s.n.* (lectotype [designated by De Sloover 1977: 44, as “holotype”], BM000919801!). – Note: The author Enroth has in 2007 erroneously annotated this specimen as *Neckera remota*. *Alleniella remota* and *A. ehrenbergii* are distinct taxa (cf. **Fig. 1**).

Illustrations. Sastre-De Jesús 1987 (p. 28, fig. 6B, as *Neckera spruceana*; p. 37, fig. 8B, as *N. ehrenbergii*); Smith 1994 (p. 748, fig. 556, as *N. ehrenbergii*; p. 751, fig. 558, as *N. chlorocaulis*); Magill & van Rooy 1998 (p. 591, fig. 164, as *N. valentiniana*); Allen 2010 (p. 285, fig. 92, as *N. ehrenbergii*).

Distribution (Sastre-De Jesús 1987, as *Neckera ehrenbergii*; O'Shea 2006, as *N. valentiniana*; Allen 2010, as *N. ehrenbergii*). Central America, Ecuador, Peru; southern Africa, Madagascar, Réunion.

Selected specimens examined. MEXICO. TLAXCALA: 23 Sep. 1997, A. Cárdenas s.n. (H3194579); CHIAPAS: Sep. 1907, G. Münch s.n. (H-BR2878001). PANAMA. CHIRIQUI: B. Goffinet 862 (H3096624). SOUTH AFRICA. CAPE TOWN: 25 Feb. 1824, C. F. Ecklon s.n. (H-BR2882101). MADAGASCAR. 1877, M. Borgen s.n. (H-BR2876006).

Alleniella platyantha (Müll.Hal.) Enroth, *comb. nov.*

≡ *Distichia platyantha* Müll.Hal., Flora 73: 489. 1890; ≡ *Neckera platyantha* (Müll.Hal.) Paris, Index Bryol.: 856. 1897. TYPE: TANZANIA. Kilimanjaro, 1887, L. Höhnelt s.n. (lectotype [designated here], PC0137118 [image!], isotype, H-BR2876012!). – Note: The PC specimen is larger than the one at H-BR and its label is hand-written by Carl Müller (“*Distichia platyantha mihi*”).

Illustrations (as *Neckera platyantha*): De Sloover 1977 (p. 33, fig. 1–21).

Distribution (De Sloover 1977; O'Shea 2006, both as *Neckera platyantha*). Central and eastern Africa.

Selected specimens examined. DEMOCRATIC REPUBLIC OF THE CONGO. KIVU: T. Pócs 7607 (H3097638). TANZANIA (see also type specimen cited above); MOROGORO: T. Pócs et al. 881114/AN (H3097932). UGANDA. VIRUNGAS: R.D. Porley U683a (H3240265).

Alleniella andina (Mitt.) Enroth, *comb. nov.*

≡ *Neckera andina* Mitt., J. Linn. Soc., Bot. 12: 457. 1869. TYPE: ECUADOR. Andes Quitenses [...] in monte Pichincha, 10,000 ped., R. Spruce 1344 (lectotype [designated here, see also Sastre De-Jesús 1987] NY 02160561 [image!]; isotypes, BM000722057 [image!], BM000722059 [image!], BM000722060 [image!], E00165408 [image!], MO-2085727 [image!], NY 02169234, 02169235 [image!], NY 02160559 [image!], PC0137277 [image!]).

Illustrations (as *Neckera andina*). Sastre-De Jesús 1987: p. 51, fig. 10A).

Distribution (Sastre-De Jesús 1987). Ecuador, Peru, Bolivia, Argentina.

Selected specimens examined. BOLIVIA. COCHABAMBA: S. Churchill et al. 20580 (H3230193). COLOMBIA. CUNDINAMARCA: S. Churchill et al. 19428 (H3194574). ECUADOR. COTOPAXI: Frahm & Gradstein 16 (H3097858). PERU. CONTUMAZÁ: A. Sagástegui 9705 (H3096524).

Alleniella obtusifolia (Taylor) Enroth, *comb. nov.*

≡ *Neckera obtusifolia* Taylor, London J. Bot. 7: 193. 1848. TYPE: ECUADOR. PICHINCHA: 1827, Jameson s.n. (lectotype [designated here], E00414683 [image!], “holotype”); isotypes FH [Sastre De-Jesús 1987, as “lectotype”, n.v.], NY01307553 [image!]. – Note: The specimen described by Taylor as *N. obtusifolia* came from Greville's herbarium at E, so it is logical to have the lectotype there.

Illustrations (as *Neckera obtusifolia*). Sastre-De Jesús 1987 (p. 28, fig. 6A); Churchill & Linares 1995 (p. 585, fig. 131 a–f).

Distribution (Sastre-De Jesús 1987). Venezuela, Colombia, Peru.

Specimen examined. COLOMBIA. CAUCA: S. Churchill & Wilson Renfijo M. s.n. (H3097279).

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Supplementary documents online:

Supplementary Table S1. 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). In six cases sequences were submitted to GenBank in previous studies and thus the accession numbers for *rps4-trnT-trnL-trnF* are composed of more than one different accession number. Sequences newly generated for this study are marked with an asterisk (*). The three *rps4* accessions marked with an upper-case a (^a) were published by Shaw et al. (2005) and obtained by us from the GenBank.

Figure 1. Phylogenetic relationships of mosses in the family Neckeraceae based on *rps4-trnT-trnL-trnF*, *rpl16* and ITS1 & 2 sequences. Focus is on *Neckera* s.l. and the positions of *Indoneckera* and *Taiwanobryopsis* in the *Pinnatella* clade. 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 maximum likelihood analysis below (first without indels, then with indel data), when applicable. Only bootstrap values ≥ 50 are indicated.