Bry. Div. Evo. 045 (1): 188–198
https://www.mapress.com/bde
Copyright © 2022 Magnolia Press

ISSN 2381-9677 (print edition)
BRYOPHYTE DIVERSITY & EVOLUTION
ISSN 2381-9685 (online edition)

Article

https://doi.org/10.11646/bde.45.1.12

Rediscovery of the Chinese endemic *Florschuetziella scaberrima* (Bryophyta: Orthotrichaceae) a century after its description leads to its transfer to *Leratia*

SI HE[1], JAMES R. SHEVOCK[2], NIKISHA PATEL[3], OLIVIA LEMIEUX[3] & BERNARD GOFFINET[3*]
[1]*Missouri Botanical Garden, 4344 Shaw Blvd., St. Louis, MO 63110, U.S.A. si.he@mobot.org; https://orcid.org/0000-0001-6560-6933*
[2]*Department of Botany, California Academy of Sciences, 55 Music Concourse Dr., Golden Gate Park, San Francisco, CA 94118-4503, U.S.A. jshevock@calacademy.org; https://orcid.org/0000-0003-1283-0709*
[3]*75 North Eagleville Road, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, 06269-3043, U.S.A. nikisha.patel@uconn.edu; https://orcid.org/0000-0002-3504-7314; olivia.lemieux@uconn.edu*
**Corresponding author: bernard.goffinet@uconn.edu; https://orcid.org/0000-0002-2754-3895*

Abstract

Florschuetziella scaberrima (Broth.) Vitt, previously known only from the type material collected in 1915 from Yunnan, China, was rediscovered nearly a century later in 2005. The species is morphologically indistinguishable from the Mexican endemic *F. steerei* Vitt, but given the paucity of material the two are provisionally retained as distinct, allopatric species. Both species exhibit traits reminiscent of *Leratia neocaledonica* Broth. & Paris, a species endemic to New Caledonia. A shared ancestry with the other species currently accommodated in *Leratia* Broth. & Paris, i.e., *L. exigua* (Sull.) Goffinet and *L. obtusifolia* (Hook.) Goffinet, and the phylogenetically nested position of *Florschuetziella* Vitt within *Leratia* supports the merger of the two generic names, and hence the transfer of species of *Florschuetziella*, prompting the proposed new combinations *Leratia steerei* (Vitt) Goffinet, S.He & Shevock and *Leratia scaberrima* (Broth.) Goffinet, S.He & Shevock.

Keywords: China, *Florschuetziella*, Mexico, *Orthotrichum scaberrimum*, Orthotrichaceae

Introduction

Systematic concepts of the class Bryophyta sensu Goffinet *et al.* (2009), and of genera, in particular, have historically reflected a patristic interpretation of phenotypic diversity, which may have led to the recognition of numerous, small and even monospecific genera based on their perceived distance from established taxa. Among the Hypnales, for example, the checklist of mosses (Crosby *et al.* 1999) listed 484 genera, of which 198 (ca. 40%) held a single species, whereas about 5% comprised 50% of total species diversity. A similar pattern long characterized the Funariales, with three genera holding nearly 95% of species and 15 genera exhibiting "unique" combinations of morphological traits harboring a single, or perhaps four, species (Fife 1982, 1985; Ochyra 1990; Werner *et al.* 2007; Goffinet & Buck 2011; Ignatov *et al*. 2015). Within the Funariaceae, such systematic concepts, based primarily on the degree of modification of the sporophyte only, were recently rejected (Liu *et al*. 2012; Medina *et al*. 2018, 2019), highlighting that the perceived morphological distance may be a poor indicator of phylogenetic relatedness. Testing the phylogenetic isolation of monospecific genera from their speciose relatives, especially based on inferences from molecular characters, may often be delayed by the lack of recent and well-preserved collections to extract and sequence specific loci. Indeed, many small or monospecific genera may be narrow endemics, erected following the exploration of then exotic regions by European and North American collectors, and never collected again since. Such is the case of the genus *Florschuetziella* in the Orthotrichaceae.

Florschuetziella Vitt (1979: 16) was established to accommodate a single species, *F. steerei* Vitt (1979: 16), known from a single specimen collected by Düll in 1966, and not relocated in the wild since (Delgadillo, pers. com. 2021). Vitt (1981) later added another species transferring the Chinese endemic *Orthotrichum scaberrimum* Brotherus (1929: 70), which he anticipated to be likely conspecific with the Mexican material. Since both species were previously only known from their types, and initial extraction of DNA from the type of *F. steerei* failed, the genus could not be represented in the original phylogenetic studies by Goffinet *et al.* (1998, 2004a). Vitt (1979) erected the genus on the basis of its unique combination of gametophytic and sporophytic traits. The affinities of the genus were considered enigmatic

Submitted: 23 Jul. 2022; Accepted by Jessica Budke: 2 Dec. 2022; published: 30 Dec. 2022

given the similarities to *Macrocoma* (Hornsch ex Müller Hal. 1845: 522) Grout (1944: 4) in the Macromitrioideae or *Orthotrichum* Hedwig (1801: 162) in the Orthotrichoideae. Noteworthy is the observation by Vitt (1979) that "the most distinctive feature of the gametophyte is the bulging, pluri-papillose (c-shaped to conical forked) upper leaf cells" which he noted resembled those of *Orthotrichum exiguum* Sullivant (1856: 633). Goffinet (1997) drew attention to these cell features also being shared with *Zygodon obtusifolius* Hooker (1819: 159) and *Leratia neocaledonica* Brotherus & Paris (Brotherus 1909: 14). In the absence of molecular data, Goffinet and Vitt (1998) retained these species in distinct genera, including *Bryomaltaea* Goffinet (1998: 151) [formerly *Zygodon* sect. *Obtusifolii* Malta (1923: 282)], while including *Leratia* Brotherus & Paris (Brotherus 1909: 14) in the Zygodonteae rather than the Macromitrioideae as earlier suggested by Crum (1987). Subsequent phylogenetic inferences resolved *Leratia, Bryomaltaea* and *O. exiguum* as the sole members of a clade sister to the Macromitrioideae, prompting Goffinet *et al*. (2004a) to accommodate all species within a single genus, with *Leratia* taking priority. The members of this genus all share strongly bulging upper laminal cells with conical or forked papillae as well as prorate cells of the calyptra that are unique within the Orthotrichaceae (Goffinet 1997).

Continuous exploration of the bryophyte flora of Yunnan by the second author, David G. Long and Chinese collaborators has resulted in the discovery of numerous new species (e.g., Enroth & Ji 2006; Enroth *et al*. 2018; Yi *et al*. 2015; Ma *et al*. 2018; Shevock *et al*. 2011) or rediscovery of rare species (e.g., Shevock *et al*. 2006; Ma *et al*. 2014; Ochyra & Shevock 2012; Yi *et al*. 2021). Among collections made in 2005 is a sample of plants (*Shevock 27391*) that resembled *Leratia obtusifolia* (Hooker 1819: 159) Goffinet (2004a: 286), known from China (Wilbraham & Long 2005), but differed by its larger size (20 mm vs 5–10 mm), features that immediately pointed to *Florschuetziella scaberrima* (Brotherus 1929: 70) Vitt (1981: 108), a species only known from the original type specimens (Plášek *et al*. 2021). Since *Orthotrichum scaberrimum* was transferred to *Florschuetziella* by Vitt (1981), the genus name has been unnoticed in nearly all literature dealing with Chinese Orthotrichaceae (Redfearn *et al*. 1996; Jia 2005; Jia *et al*. 2011a, 2011b; Jia & He 2013; Wang & Jia 2020). The basionym, *O. scaberrimum*, was only briefly mentioned in *Genera Muscorum Sinicorum* (Chen 1978), in the checklist of Chinese mosses (Redfearn *et al*. 1996), and in the recent synopsis of Chinese species of *Orthotrichum* (Plášek *et al*. 2021).

The generic circumscription of the Orthotrichaceae has been extensively revised since Vitt (1982), with the merger of genera (i.e., *Muelleriella* Dusén [1905: 304] and *Orthomitrium* Lewinsky & Crosby [1996: 2] in *Orthotrichum* [Goffinet *et al*. 2004a] and Allen [2002], respectively; *Leptodontiopsis* Brotherus [1910: 146] in *Zygodon* Hooker & Taylor [1818: 70] [Goffinet *et al*. 2004a], *Pleurorthotrichum* Brotherus [1905: 1] in *Pentastichella* Müller Hal. [1897: 421] [Draper *et al*. 2021]), the resurrection of former genera (i.e., *Codonoblepharon* Schwägrichen [1824: 142] [Goffinet & Vitt 1998], *Nyholmiella* Holmen & E. Warncke [Damsholt *et al*. 1969: 179] [Sawicki *et al*. 2010]), or the segregation of new genera (i.e., *Ceuthotheca* Lewinsky [1994: 18] [Lewinsky-Haapasaari 1994] from *Pleurorthotrichum*, *Matteria* Goffinet [1998: 154] [Goffinet & Vitt 1998] from *Macrocoma*, *Stoneobryum* D.H. Norris & H. Rob. [1981: 86], *Sehnemobryum* Lewinsky & Hedenäs [1998: 549] and *Pulvigera* Plášek, Sawicki & Ochyra [2015: 171] from *Orthotrichum*, *Atlantichella* F. Lara, Garilleti & Draper [Draper *et al*. 2021: 12], *Plenogemma* Plášek, Sawicki & Ochyra [2015: 172], and *Rehubryum* F. Lara, Garilleti & Draper [Draper *et al*. 2022: 10] from *Ulota* D. Mohr [1806: 540]), and *Australoria* F. Lara, Garilleti & Draper [Draper *et al*. 2021: 10] from *Zygodon*. The status of several of the older genera holding a single or few species, such as *Desmotheca* Lindberg (1872: 184) (see Vitt 1990), *Florschuetziella* or *Leiomitrium* Mitten (1879: 390) have not hitherto been assessed within a comprehensive phylogenetic framework.

Here, we report the rediscovery of *Orthotrichum scaberrimum* (≡*Florschuetziella scaberrima*) nearly a century after its discovery, confirm its morphological indistinguishability from *F. steerei*, and provide phylogenetic evidence for its uniquely shared ancestry with species of, and in fact nested position in, *Leratia* sensu Goffinet *et al*. (2004a).

Material and Methods

Taxa targeted

For the morphological study we examined the collection by *Shevock 27391* (CAS, CONN, MO), and the isotype material of *Florschuetziella steerei* (MO, NY). To complement the phylogenetic study by Goffinet *et al*. (2004a) we extracted DNA from *Shevock 27391* (CONN) and made new attempts at PCR amplification based on formerly extracted DNA from the isotype of *F. steerei* (ALTA, NY). To test the affinities of these species to *Leratia* based on two plastid loci (i.e., trnL-trnF and *rps*4) and given that neither locus could be sequenced by Goffinet *et al*. (2004a) we obtained recently collected material (*Thouvenot NC2937*, CONN) of the type of the genus *Leratia* (*L. neocaledonica*), and extracted and amplified DNA for it. Finally, we also resampled *L. obtusifolia* (*Hax 14*, CONN) to confirm the previously acquired molecular data.

Extraction-amplification and sequencing

DNA was extracted from several pooled individual sporophytes using a modified CTAB protocol (Porebskit *et al*. 1997). The two organellar loci, *rps*4-trnS and trnL-trnF were amplified and sequenced following the methodology presented in Goffinet *et al*. (2004b). Amplicons were sequenced by Eurofins Genomics (Louisville, KY, USA), manually edited and added to the *rps*4-trnS and trnL-trnF matrices assembled by Goffinet *et al*. (2004a).

Phylogenetic analyses

Consensus sequences were aligned using MUSCLE (Edgar 2004) as implemented in Geneious Prime version 5.0.3 (http:www.geneious.com). One dataset was used for phylogenetic inference. The concatenated matrix, comprising plastid markers trnL-trnF and *rps*4 (Supplementary Table X), was 1081 base pairs in length. Sites with ambiguous homology were excluded from Bayesian Inference (BI) and Maximum Likelihood analysis (ML) (Supplementary file/table X). For Bayesian Inference (BI) the concatenated cpDNA sequences were analyzed using MrBayes version 3.2.6 (Ronquist *et al*. 2012). BI using MrBayes was run for 10 million generations with trees sampled every 1000 generations. The first 500,000 trees were discarded as the burn-in phase, and a 50% majority rule consensus tree was calculated for the remaining trees. Posterior probabilities were obtained using MrBayes. ML analysis was performed with RAxML (vers. 7.0.4; Stamatakis 2006). A majority consensus tree was inferred. The program FigTree version 1.4.4 (Rambaut 2018) was used to view a 50% majority rule consensus tree with posterior probabilities.

Results and Discussion

Florschuetziella scaberrima was known only from two type specimens collected in 1915 by Handel-Mazzetti, in Yunnan Province, China. In 2005, an exploration of the Hengduan Shan Range in Shangri-la County (formerly known as Zhong-dian County) of Yunnan, led to the discovery, in an area within approximately 100 km of Shangri-la, of a moss (*Shevock 27391*) reminiscent of the genus *Florschuetziella* (Vitt 1979) and its Chinese species*, F. scaberrima* (Vitt 1981) originally described within *Orthotrichum* (Brotherus 1929), in all its morphological features: orthotropic plants, stiff leaves, strongly bulging upper laminal cells with forked or C-shaped stellate papillae, long exerted and 8-ribbed capsules with superficial stomata, double peristomes (with well-developed non-ciliate endostome composed of broad segments and a reflexed exostome), and smooth spores (Fig. 1).

Based on the study of an isotype (MO) of *F. steerei*, the above Chinese specimen appears morphologically identical with the Mexican specimen. Vitt (1981, p. 108) considered the two species to "differ somewhat in capsule shape and other [unspecified] characters" but predicted that studies of more specimens may lead to treating plants from both continents as conspecific. In the protologue of *F. steerei*, Vitt (1979) considered the species as dioicous, although he described the perigonia as terminal on short branches of the erect, somewhat procumbent stems, rather than terminal on the actual stems. This original interpretation was maintained by Vitt (1994) and Goffinet (1997). The isotype (*R. Düll 13*, MO) is, however, clearly autoicous, with perigonia located terminally on short branches of the same stem or located just below perichaetia on the same branch with mature sporophytes. The collection of *F. scaberrima* from China also bears perigonia and perichaetia on the same stem or the same branches, and plants are thus clearly autoicous, a condition that is congruent with the abundance of sporophytes.

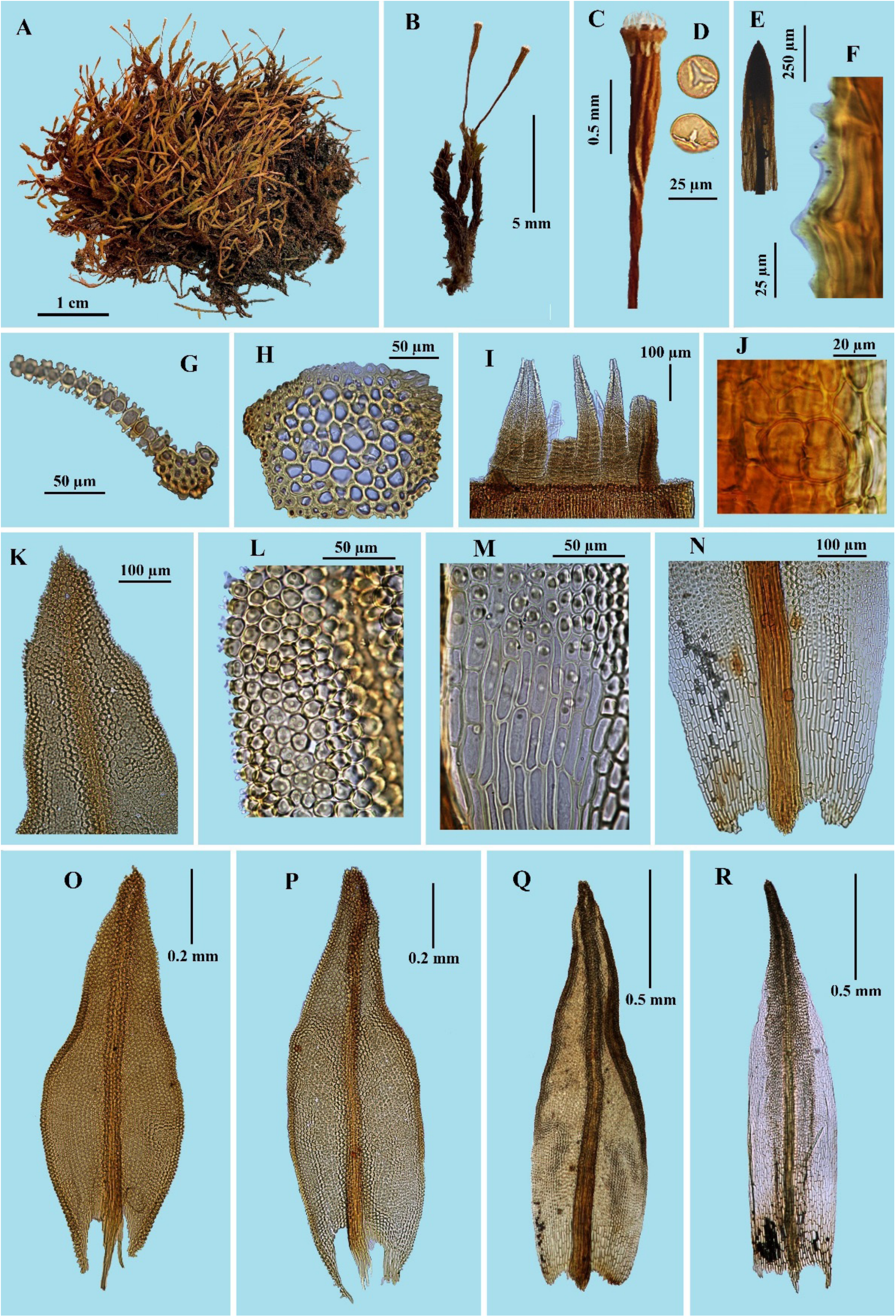

FIGURE 1. *Florschuetziella scaberrima*. **A–B,** habit. **C,** dry capsule. **D,** spores. **E,** calyptra. **F,** surface cells of the upper portion of calyptra. **G,** cross section of leaf. **H,** cross section of stem. **I,** peristome. **J,** stoma. **K,** leaf apex. **L,** median laminal cells near margin. **M,** basal laminal cells. **N,** leaf base. **O–P,** leaves. **Q,** upper leaf. **R,** perichaetial leaf. (All images prepared from *Shevock 27391*, MO).

We obtained sequences of trnL-trnF and *rps*4 for *Florschuetziella scaberrima* from Yunnan (*Shevock 27391*, CONN; respective GenBank accession numbers: ON960149 and ON677526), for *Leratia neocaledonica* (*Thouvenot NC2937*, CONN; respectively ON677524 and ON677527) and *Leratia obtusifolia* (*Hax 14*, CONN; respectively ON950397 and ON677525). Attempts to obtain sequences for the type material of *F. steerei* in ALTA and NY were unsuccessful. Phylogenetic inferences from these concatenated loci yield maximum likelihood and Bayesian topologies consistent with those presented in Goffinet *et al*. (2004a) and most recently by Wang *et al*. (2022) based on a more extensive locus sampling, whereby *Leratia neocaledonica* shares a unique common ancestor with *L. exigua* (formerly *Orthotrichum exiguum*), *L. obtusifolia* (formerly *Zygodon obtusifolius* or *Bryomaltaea obtusifolia* [Hooker 1819: 159] Goffinet [1998: 151]), composing a robust lineage sister to the Macromitrioideae (Fig. 2). Although these two plastid loci do not provide sufficient and robust signal to fully resolve the relationships within the Orthotrichaceae as evidenced by Goffinet *et al*. (2004a), they do strongly support the resolution of *Florschuetziella scaberrima* within *Leratia*, and its uniquely shared ancestry with *L. exigua* (Fig. 2).

Florschuetziella shares with *Leratia* the ornamentation of the upper laminal cells as well as prorate cells of the calyptra, traits that cannot unambiguously be considered plesiomorphic in the family Orthotrichaceae (Goffinet 1997) and should instead be viewed as diagnostic of *Leratia* (Goffinet *et al*. 2004a). We therefore propose transferring *Florschuetziella scaberrima* to *Leratia*. We provide a full description based on the new collection marking its rediscovery after nearly a century.

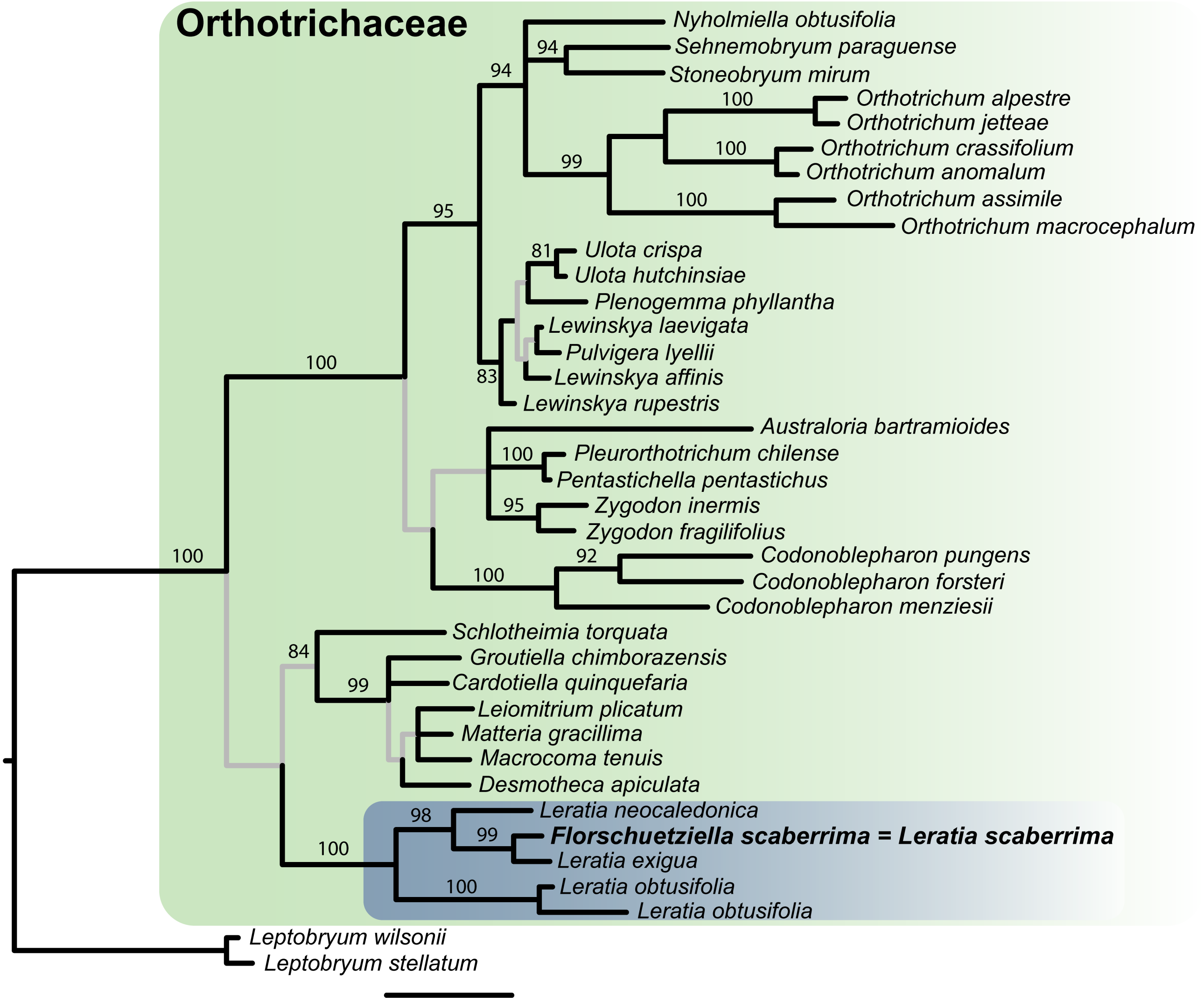

FIGURE 2. Phylogenetic relationships within the Orthotrichaceae based on Bayesian analysis of variation in two plastid loci, i.e., trnL-trnF and *rps*4, highlighting the affinities of *Florschuetziella scaberrima* to species currently accommodated within *Leratia*. Black branches lead to maximally supported nodes (i.e., 100% Bayesian posterior probability) whereas grey branches mark those characterized by BPP <0.96%. Values above branches correspond to ML bootstrap values, with only those >0.80% included.

Leratia scaberrima **(Broth.) Goffinet, S.He & Shevock, comb. nov. (Fig. 1)**

Basionym: *Orthotrichum scaberrimum* Broth., Symb. Sin. 4: 70. 1929. *Florschuetziella scaberrima* (Broth.) Vitt, J. Hattori Bot. Lab. 49: 108. 1981, **syn. nov**. **Type:** China. NW-Yunnan: "Zwischen Djinscha-djiang ('Yangtse') und Landsang-djiang (Mekong) am

> Wege von Djitsung nach Kakatang, an Eichenstämmen, c. sp., in der wtp. St. zwischen Yato und Lienfu, 27°35’, 2350 m, 28. VIII. 1915 (7853) und in der tp. St. ober Golo, 27°19’, 2900—3000 m. 30. VIII. 1915 (7927)”, *Handel-Mazzetti 7927* (lectotype, H-BR, designated by Vitt 1981, not seen; isolectotypes (PC0135018, WU0046025, images seen!); syntypes *Handel-Mazzetti 7853* (WU46024, images seen! MO1146230!, MO3365773!).

Plants medium-sized, rigid, to ca. 2 cm tall, dull, dark green to brownish, in tufted mats. Stems irregularly branched, with more or less erect to ascending branches, with dense brownish rhizoids throughout basal stems; in cross section stems somewhat pentagon-angled, epidermal and outer cortical cells smaller, in 2–3 layers of thick-walled cells; central strand absent. Leaves erect-appressed when dry, rather stiff and fragile, tips broken off easily wide-spreading when moist, slightly to moderately keeled or concave above; stem and branch leaves similar, lower leaves smaller than the upper leaves, shortly ovate-lanceolate to narrowly ovate-lanceolate, 0.9–1.5 × 0.35–0.45 mm, narrowly obtuse to apiculate due to papillose tips, margins slightly recurved above leaf base, entire below, papillose denticulate above; costa strong, percurrent or just ending below the apex; upper and median laminal cells rounded quadrate, 12–16 µm as long as wide, strongly bulging, often with forked or C-shaped stellate papillae; basal laminal cells transitioning from rounded quadrate to shortly rectangular to elongate cells, from papillose to smooth cells. Autoicous (with perigonia located terminally on short branches or just below perichaetia on the same branch). Perichaetial leaves similar to upper branch leaves in shape, but larger, with less papillose laminal cells, median and basal cells hyaline, elongate-rectangular. Setae up to 4 mm long, smooth, somewhat twisted; capsules cylindrical, ca. 1.1 mm long, 8-ribbed, gradually tapered with a neck; annuli differentiated by 2–3 rows of smaller, thick-walled cells; stomata numerous at capsule neck, superficial; peristome double; exostome teeth fused into eight, completely reflexed downward when dry, erect when moist, densely papillose, cross-striate below, coarsely papillose above; endostome segments 8, broad lanceolate, whitish, moderately papillose, longitudinally striate. Spores smooth, 15–20 µm in diameter. Calyptrae mitrate, plicate, smooth below 2/3 the length and prorate papillose in the upper 1/3 of the calyptra length.

Distribution and habitat: Only known from the Province of Yunnan, China, in *Pinus*-*Quercus* and *Populus* dominant forests near river bank on open sunny slope or in filtered light, on bases of *Populus* trunks.

Specimens examined: Recent collected specimen: **China**. Yunnan: Shangri-la Co., Hengduan Shan, Tributary of Ganqu River, above Birong Village along Birong Gorge Trail. 28°24’22.5” N, 99°46’54.8” E, 3070 m, *Pinus-Quercus* forests with marble rock outcrops. At base on *Populus* trunks along trail and river in filtered light. 9 June 2005, *Shevock 27391* with C. Tam, D. Melich & W. Yucheng (CAS, CONN, E, KUN, MAUAM, MO, NY, PE).

Notes: Two specimens collected by Handel-Mazzetti, i.e., *7853* and *7927*, were cited by Brotherus (1929). These should be regarded as syntypes. Vitt (1981) designated *7927* (H-BR) as the lectotype. Duplicates of the syntype (not clear of which one), bearing “*materia originalis*” collected by Handel-Mazzetti from the same place at the same time but without a collection number, were distributed as an exsiccate #286 to numerous herbaria around the world as Musci Selecti et Critici editit Fr. Verdoorn Exsiccate series VI (1939) with an indication (cf. Ann. Bryologici. Vol. XII), but information of the exsiccate had never been published. The duplicate of the syntype (exsiccate #286) was regarded to be an isosyntype or syntype by each herbarium that possesses this specimen (BM000982242, BM000982243, F-C0001638F, JE04005338, JE04008654, MICH526017, MO1146230, MO3365773, NY01202154, NY01475720, PC0135016, PC0135017, PC0147190). Lewinsky annotated one of them (JE04005338) as an isotype of *Florschuetziella scaberrima* in 1991, on the herbarium annotation label. Although we have not seen the lectotype, *Handel-Mazzetti 7927* (H-BR), two syntypes at MO (MO1146230, MO3365773) and specimen images of two isolectotypes (PC0135018, WU0046025), one syntype *Handel-Mazzetti 7853* (WU46024), and all of the above mentioned type material in various herbaria were seen through Jstor website at (https://plants.jstor.org/search?plantName=%22Orthotrichum+scaberrimum%22&syn=1). All of these specimens seem to be identical and bearing sporophytes. The plant habit, branching pattern of leafy stems and leaf outlines could be viewed clearly. With the Covid-19 pandemic situation affecting availability of herbarium loans, we could not borrow the lectotype for comparison. However, we feel confident that we can draw our conclusion based on the material we have seen.

Leratia scaberrima appears indistinguishable from the Mexican endemic *Florschuetziella steerei*, although Vitt (1981) alluded to, albeit unspecific, differences other than in capsule shape, which we have not perceived based on the recent collection from Yunnan of the former and the isotype material of the latter held in MO. At present we recommend retaining the two as distinct pending the discovery of more collections enabling more critical comparisons and ideally inferences also from DNA data. Our recommendation is motivated by the growing evidence of cryptic speciation in mosses, i.e., phylogenetic structure and differentiation within morphologically rather uniform lineages (e.g., Hedenäs *et al.* 2022), and the recent evidence following integration of morphometric analyses within a phylogenetic framework, that individual moss species are unlikely to span broad geographic ranges (e.g., Vigalondo *et al.*, 2019: Hanusch *et* *al.*, 2020). Our current molecular data clearly support a close relationship of the Chinese and Mexican taxa but are not adequate to reject the hypothesis of divergence, and the small sample size of Mexican populations, i.e., one, precludes acquired robust and meaningful data pertaining to a possible morphological differentiation.

Leratia steerei **(Vitt) Goffinet, S.He & Shevock, comb. nov.**

Basionym: *Florschuetziella steerei* Vitt, Bryologist 82: 16. 1979. **Type**: Mexico. Chiapas: 14 km South of San Cristobal, 2330 m, *R. Düll 13*, 9 Oct. 1966 (holotype, ALTA!; isotypes, MO2559762!, DUIS, MICH, NY, TENN, U).

Description: see Vitt (1979).

Distribution and habitat: Only known from the type locality in Mexico, epiphytic on tree trunk.

The species here included in *Leratia* were previously each treated as the sole member of a distinct genus (*Leratia neocaledonica*, *Florschuetziella steerei* sensu Vitt [1979] and *Bryomaltaea obtusifolia* sensu Goffinet & Vitt [1998]) or supraspecific taxon (*Orthotrichum* subg. *Exiguifolia* Vitt [1971: 705], *Zygodon* sect. *Obtusifolii* Malta [1923: 282] =*Zygodon* subg. *Obtusifolium* [Malta] Calabrese [2006: 469]) reflecting their isolation and hence the difficulties of accommodating them within traditional generic circumscriptions. Vitt (1973, p. 105), for example, considered *O. exiguum* “an isolated species of uncertain phyletic relations within the genus”. Crum (1987, p. 603) discussed the subfamilial intermediacy of *Leratia* (then including only *L. neocaledonica*) highlighting that it was obviously related to *Macromitrium* Bridel (1819: 132), but at the fringes of the Macromitrioideae, relatively close to the Orthotrichoideae. When describing *Florschuetziella*, Vitt (1979, p. 18) expressed his uncertainty about the subfamilial placement of the genus. These ambiguities in part reflect that affinities were not considered within a comprehensive systematic framework, preventing similarities and uniquely shared ancestry among these “isolated” taxa to be uncovered.

The extended circumscription of *Leratia* to include *Bryomaltaea* (or *Zygodon*) *obtusifolia* and *Orthotrichum exiguum*, is now accepted (e.g., Wang & Jia 2020; Plášek *et al*. 2021) but was not readily adopted by others. Calabrese (2006, p. 470) argued against the segregation of *Bryomaltaea* from *Zygodon* on the basis of “inconclusive molecular evidence” and that seta torsion and calyptra cell features were not good characters, although admittedly the calyptrae of *B. obtusifolia* were not studied. Wilbraham and Long (2005) recognized *Bryomaltaea* but argued against its merger with *Leratia* on a patristic ground: the two monospecific genera were significantly distinct morphologically to justify their separation. Systematic concepts should reflect – ideally uniquely (i.e., non-homoplasious) - shared traits. Arguably, generic concepts are subjective entities in the sense that no single criterion defines the rank (e.g., a temporal definition, see Kraichak *et al*. 2017), such that genera would be “equivalent” across the tree of life or at least within some of its branches. Recognizing genera solely on the basis of the perceived magnitude of their differences obscures phylogenetic relationships. All species here accommodated within *Leratia* exhibit striking differences, justifying their recognition as distinct species, but these species also share a unique ancestor (Fig. 2) and at least one unique trait, prorate papillose cells of the calyptra, which is congruent with accommodating them within a distinct supraspecific taxon, here genus. The species also share a similar overall Gestalt, of orthotropic stems with stout, erect and dull leaves composed of bulging and papillose laminal cells, which distinguish them macroscopically from sympatric taxa.

The geographic distribution of *Leratia* spans across subtropical-temperate regions of the globe but is most noticeably absent from the African continent. Three species are narrow endemics: *L. neocaledonica* to New Caledonia, *L. scaberrima* to southwestern China, and *L. steerei* to Mexico. *Leratia exigua* is disjunct between Eastern Asia and Eastern North America (Vitt 1971; Plášek *et al*. 2021), whereas *L. obtusifolia* is currently widely disjunctive occurring in the Neotropics (Allen 2002), Australasia (Lewinsky 1990), and Asia (Wilbraham & Long 2005).

Key to the species of *Leratia*

1.	Leaves erect-twisted; capsules smooth	*L. neocaledonica*
1.	Leaves erect-straight; capsules 8-ribbed	2
2.	Basal laminal hardly differentiated; capsules immersed or slightly emergent	*L. exigua*
2.	Basal laminal cells clearly differentiated from upper cells; capsules long exserted	3
3.	Plants usually less than 10 mm tall; basal laminal cells short, weakly differentiated from upper cells	*L. obtusifolia*
3.	Plants to 20 mm tall; basal cells clearly longer than mid and upper laminal cells	4
4.	Plants occurring in Asia, currently only known from China	*L. scaberrima*
4.	Plants occurring in Central America, currently only known from Mexico	*L. steerei*

Following the herein proposed merger of *Florschuetziella* with *Leratia*, the about 800 species of Orthotrichaceae are currently accommodated in 24 genera: *Atlantichella*, *Australoria*, *Cardotiella* Vitt (1981: 101), *Ceuthotheca*, *Codonoblepharon*, *Desmotheca*, *Groutiella* Steere (Crum & Steere 1950: 145), *Leiomitrium*, *Leratia*, *Lewinskya* F.Lara, Garilleti & Goffinet (Lara *et al*. 2016: 365), *Macrocoma*, *Macromitrium*, *Matteria*, *Nyholmiella, Orthotrichum*, *Pentastichella*, *Plenogemma*, *Pulvigera*, *Rehubryum*, *Schlotheimia* Bridel (1812: 16), *Sehnemobryum*, *Stoneobryum*, *Ulota*, and *Zygodon*.

Acknowledgements

BG acknowledges NSF grant DEB-1753811, that supported NP and OL. We thank Louis Thouvenot (France) for providing a duplicate of his recent collection of *Leratia neocaledonica*, which was made possible by permit N° 2825-2019/ARR/DENV delivered on May 23, 2019 by the president of the Assembly of the South Province of New Caledonia. We dedicate this contribution to Dr. Jeffrey Duckett in honor of his significant and continuous impact on advancing our understanding of bryophyte biology.

References

Allen, B.H. (2002) Moss Flora of Central America. Part 2. Encalyptaceae-Orthotrichaceae. *Monographs in Systematic Botany from the Missouri Botanical Garden* 90: 1–699.

Bridel, S.É.v. (1812) *Muscologiae Recentiorum Supplementum* 2. C. G. Ettinger, Gotha, 257 pp.

Bridel, S.É.v. (1819) *Muscologiae Recentiorum Supplementum* 4. C. G. Ettinger, Gotha, 220 pp.

Brotherus, V.F. (1905) *Pleurorthotrichum*, eine neue Laubmoosgattung aus Chile. *Öfversigt af Finska Vetenskaps-Societetens Förhandlingar* 47: 1–3.

Brotherus, V.F. (1909) Contribution à la flore bryologique de la Nouvelle Calédonie II. *Öfversigt af Finska vetenskaps-societetens förhandlingar* 51: 1–31.

Brotherus, V.F. (1910) Musci. *In*: Mildbraed, G.W.J. (Ed.) *Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition 1907–1908, Botanik*. Klinkhardt & Biermann, Leipzig, pp. 136–176.

Brotherus, V.F. (1929) *Musci*. Symbolae Sincae 4. Julius Springer, 147 pp.

Calabrese, G.M. (2006) A taxonomic revision of *Zygodon* (Orthotrichaceae) in southern South America. *The Bryologist* 109: 453–509. https://doi.org/10.1639/0007-2745(2006)109[453:ATROZO]2.0.CO;2

Chen, P.-C. (1978) *Genera Muscorum Sinicorum, Pars Secunda*. Science Press, Beijing, viii + 331 pp. Fig. 192–400.

Crosby, M.R., Magill, R.E., Allen, B.H. & He, S. (1999) *A Checklist of the Mosses*. Missouri Botanical Garden, St. Louis.

Crum. H.A. (1987) *Leratia* and its place in the Orthotrichaceae, subfamily Macromitrioideae. *Memoirs of the New York Botanical Garden* 45: 602–606.

Crum, H.A. & Steere, W.C. (1950) Additions to the moss flora of Panama. *The Bryologist* 53: 139–152.

Damsholt, K., Holmen, K. & Warncke, E. (1969) A list of the bryophytes of Denmark. *Botanisk Tidsskrift* 65: 163–183.

Draper, I., Garilleti, R., Calleja Alarcón, J.A., Flagmeier, M., Mazimpaka, V., Vigalondo, B. & Lara, F. (2021) Insights into the evolutionary history of the subfamily Orthotrichoideae (Orthotrichaceae, Bryophyta): new and former supra-specific taxa so far obscured by prevailing homoplasy. *Frontiers in Plant Science* 12: 629035 [1–18]. https://doi.org/10.3389/fpls.2021.629035

Draper, I., Villaverde, T., Garilleti, R., Burleigh, J.G., McDaniel, S.F., Mazimpaka, V., Calleja, J.A. & Lara, F. (2022) An NGS-based phylogeny of Orthotricheae (Orthotrichaceae, Bryophyta) with the proposal of the new genus *Rehubryum* from Zealandia. *Frontiers in Plant Science* 13: 882960 [1–13]. https://doi.org/10.3389/fpls.2022.882960

Drummond, A.J., Ashton, B., Cheung, M., Heled, J., Kearse, M., Moir, R., Stones-Havas, S., Thierer, T. & Wilson, A. (2007) Geneious v3.0.

Dusén, P. (1905) Musci nonnulli novi e Fuegia et Patagonia reportati. *Botaniska Notiser* 1905: 299–310.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Enroth, J. & Ji, M.-C. (2006) *Shevockia* (Neckeraceae), a new moss genus with two species from Southeast Asia. *Journal of the Hattori Botanical Laboratory* 100: 69–76.

Enroth, J., Shevock, J.R. & Ignatov, M.S. (2018) *Mawenzhangia thamnobryoides* (Bryophyta, Lembophyllaceae), a new moss genus and species from the Shangri-la region of Yunnan Province, China. *Phytotaxa* 346 (3): 237–246.
https://doi.org/10.11646/phytotaxa.346.3.3

Fife, A.J. (1982) *A generic revision of the Funariaceae (Bryophyta: Musci)*. Doctoral Dissertation. The University of Michigan.

Fife, A.J. (1985) A generic revision of the Funariaceae (Bryophyta: Musci) Part I. *Journal of the Hattori Botanical Laboratory* 58: 149–196.

Goffinet, B. (1997) *Circumscription and phylogenetic trends in the Orthotrichales (Bryopsida)*. Ph.D. dissertation. University of Alberta, Edmonton, Canada.

Goffinet, B. & Buck, W.R. (2011) *Physcomitridium readeri* is the correct name for *Physcomitrella readeri*. *The Bryologist* 114: 545–546.
https://doi.org/10.1639/0007-2745-114.3.545

Goffinet, B. & Vitt, D.H. (1998) A revised classification of the Orthotrichales (Bryopsida) based on comparative morphology and a rbcL based phylogeny. *In*: Bates, J.W., Ashton, N.W. & Duckett, J.G. (Eds.) *Bryology for the Twenty-First Century. Proceedings of the Centenary Symposium of the British Bryological Society*. Maney and The British Bryological Society, Leeds, pp. 143–159.

Goffinet, B., Vitt, D.H. & Bayer, R.J. (1998) Circumscription and phylogeny of the Orthotrichales (Bryopsida) inferred from rbcL sequence analyses. *American Journal of Botany* 85: 1324–1337.
https://doi.org/10.2307/2446642

Goffinet, B., Shaw, A.J., Cox, C.J., Wickett, N.J. & Boles, S.B. (2004a) Phylogenetic inferences in the Orthotrichoideae (Orthotrichaceae: Bryophyta) based on variation in four loci from all genomes. *Monographs in Systematic Botany from the Missouri Botanical Garden* 98: 270–289.

Goffinet, B., Shaw, A.J. & Cox, C.J. (2004b) Phylogenetic inferences in the dung-moss family Splachnaceae from analyses of cpDNA sequence data and implications for the evolution of entomophily. *American Journal of Botany* 91: 748–759.
https://doi.org/10.3732/ajb.91.5.748

Goffinet, B., Buck, W.R. & Shaw, A.J. (2009) Morphology and classification of the Bryophyta. *In*: Goffinet, B. & Shaw, A.J. (Eds.) *Bryophyte Biology*, 2nd edition. Cambridge University Press, pp. 55–138.

Grout, A.J. (1944) Preliminary synopsis North American Macromitriae. *The Bryologist* 47: 1–22.

Hanusch, M., Ortiz, E.M., Patiño, J. & Schaefer, H. (2020) Biogeography and integrative taxonomy of *Epipterygium* (Mniaceae, Bryophyta). *Taxon* 69: 1150–1171.
https://doi.org/10.1002/tax.12324

Hedenäs, L., Collart, F., Heras, P., Infante, M., Kooijman, A. & Kučera, J. (2022) Distributions and habitats of the two partly allopatric cryptic species of the vulnerable moss *Hamatocaulis vernicosus* (Bryophyta) in Europe. *Botanical Journal of the Linnean Society* 200: 233–254.
https://doi.org/10.1093/botlinnean/boac011

Hedwig, J. (1801) *Species Muscorum Frondosorum*. Joannis Ambrosii Barthii, Lipsiae, vi + 352 pp.

Hooker, W.J. (1819) *Musci Exotici* 2. Longman et al., London, 27 pp.

Hooker, W.J. & Taylor, T. (1818) *Muscologia Britannica*. Longman, Hurst, Rees, Orme, and Brown, London, xxxv + 152 pp.

Ignatov, M.S., Ignatova, E.A., Czernyadjeva, I.V., Goffinet, B., Kuznetsova, O.I. & Fedosov, V.E. (2015) *Afoninia*, a new moss genus of Funariaceae from Transbaikalia (East Siberia, Russia). *Arctoa* 24: 14–20.
https://doi.org/10.15298/arctoa.24.02

Jia, Y. (2005) Orthotrichaceae. *In*: Li, X.-J. (Ed.) *Flora Yunnanica: Tomus 19 (Bryophyta: Musci)*. Science Press, Beijing, pp. 33–59.

Jia, Y. & He, S. (2013) Orthotrichaceae. *Species Catalogue of China: Bryophytes*. Science Press, Beijing, pp. 230–235.

Jia, Y., He, S. & Guo, S.-L. (2011a) Orthotrichaceae. *In*: Wu, P.-C., Crosby, M.R. & He, S. (Eds.) *Moss Flora of China*. Vol. 5. *Erpodiaceae—Climaciaceae*. Science Press, Beijing & Missouri Botanical Garden, New York & St. Louis, pp. 22–117.

Jia, Y., Wang, Q.-H. & Yu, N.-N. (2011b) Orthotrichaceae. *In*: Wu, P.-C. & Jia, Y. (Eds.) *Flora Bryophytorum Sinicorum*. Science Press, Beijing, pp. 20–108.

Kraichak, E., Crespo, A., Divakar, P.K., Leavitt, S.D. & Lumbsch, H.T. (2017) A temporal banding approach for consistent taxonomic ranking above the species level. *Scientific Reports* 7: 1–7.
https://doi.org/10.1038/s41598-017-02477-7

Lara, F., Garilleti, R., Goffinet, B., Draper, I., Medina, R., Vigalondo, B. & Mazimpaka, V. (2016) *Lewinskya*, a new genus to accommodate the phaneroporous and monoicous taxa of *Orthotrichum* (Bryophyta, Orthotrichaceae). *Cryptogamie, Bryologie* 37: 361–382.
https://doi.org/10.7872/cryb/v37.iss4.2016.361

Lewinsky, J. (1990) *Zygodon* Hook. & Tayl. In Australasia: a taxonomic revision including SEM-studies of peristomes. *Lindbergia* 15:

109–139. [https://www.jstor.org/stable/20149718]

Lewinsky-Haapasaari, J. (1994) The genus *Pleurorthotrichum* Broth. *Lindbergia* 19: 11–24. [https://www.jstor.org/stable/20149858]

Lewinsky-Haapasaari, J. & Crosby, M.R. (1996) *Orthomitrium tuberculatum* (Orthotrichaceae), a new genus and species from Guizhou, China. *Novon* 6: 1–5.
https://doi.org/10.2307/3392203

Lewinsky-Haapasaari, J. & Hedenäs, L. (1998) A cladistic analysis of the moss genus *Orthotrichum*. *The Bryologist* 101: 519–555.
https://doi.org/10.2307/3244527

Lindberg, S.O. (1873) Remarks on *Mesotus*, Mitten. *Journal of the Linnean Society, Botany* 13: 182–185.
https://doi.org/10.1111/j.1095-8339.1872.tb02399.x

Liu, Y., Budke, J.M. & Goffinet, B. (2012) Phylogenetic inference rejects sporophyte based classification of the Funariaceae (Bryophyta): rapid radiation suggests rampant homoplasy in sporophyte evolution. *Molecular Phylogenetics and Evolution* 62: 130–145.
https://doi.org/10.1016/j.ympev.2011.09.010

Ma, W.-Z., Shevock, H.T. & Enroth, J. (2014) Rediscovery of the monospecific moss genus *Cyptodontopsis* (Cryphaeaceae) in China: a species restricted to flood plain habitats. *Acta Bryolichenologica Asiatica* 5: 141–149.

Ma, W.Z., Long, D.G., Kuznetsova, O.I., Ignatova, E.A. & Ignatov, M.S. (2018) *Rheoshevockia* (Symphyodontaceae, Bryophyta), a new rheophytic moss genus from Yunnan, China. *Arctoa* 27: 104–111.
https://doi.org/10.15298/arctoa.27.10

Ma, W.-Z., Shevock, J.R., He, S. & Liu, Y. (2020) *Entosthodon elimbatus* (Bryophyta, Funariaceae), a new species from the sub-alpine region in Yunnan and *E. physcomitrioides* new for mainland China. *Phytotaxa* 451 (2): 103–112.
https://doi.org/10.11646/phytotaxa.451.2.1

Malta, N. (1923) Studien über die Laubmoosgattung Zygodon 5–9. *Latvijas Universitâtes Raksti* 6: 273–285.

Medina, R., Johnson, M., Liu, Y., Wilding, N., Hedderson, T., Wickett, N. & Goffinet, B. (2018) Evolutionary dynamism in bryophytes: Phylogenomic inferences confirm rapid radiation in the family Funariaceae. *Molecular Phylogenetics and Evolution* 120: 240–247.
https://doi.org/10.1016/j.ympev.2017.12.002

Medina, R., Johnson, M.G., Liu, Y., Wickett, N.J., Shaw, A.J. & Goffinet, B. (2019) Phylogenomic delineation of *Physcomitrium* (Bryophyta: Funariaceae) based on nuclear targeted exons and their flanking regions rejects the retention of *Physcomitrella*, *Physcomitridium* and *Aphanorrhegma*. *Journal of Systematics and Evolution* 57: 404–417.
https://doi.org/10.1111/jse.12516

Mitten, W. (1879) Musci, Transit of Venus expeditions carried out by order of her Majesty's government in the years 1874–1875. *Philosophical Transactions of the Royal Society of London* 168: 388–396.
https://doi.org/10.1098/rstl.1879.0037

Mohr, D.M.H. (1806) Observations on *Orthotrichum* and *Neckera*, together with some other genera of mosses. *Annals of Botany* 2: 532–547, pl. 14.

Müller, C. (1845) Synopsis Macromitriorum hactenus cognitorum. *Botanische Zeitung* 3: 521–526.

Müller, C. (1897) Synopsis generis Harrisonia. *Oesterreichische Botanische Zeitschrift* 47: 417–422.
https://doi.org/10.1007/BF01791236

Norris, D.H. & Robinson, H.E. (1981) *Stoneobryum*, a new genus of Orthotrichaceae from South Africa and southern Queensland. *The Bryologist* 84: 95–99.
https://doi.org/10.2307/3242986

Ochyra, R. (1990) *Corynotheca*, a remarkable new genus of Funariaceae (Musci) from the Himalayas. *Polish Botanical Studies* 1: 59–65.

Ochyra, R. & Shevock, J.R. (2012) A fruiting plant of *Handeliobryum sikkimense* (Bryopsida, Thamnobryaceae) from Yunnan, China. *Nova Hedwigia* 94: 307–321.
https://doi.org/10.1127/0029-5035/2012/0021

Plášek, V., Sawicki, J., Ochyra, R., Szczecinska, M. & Kulik, T. (2015) New taxonomical arrangement of the traditionally conceived genera *Orthotrichum* and *Ulota* (Orthotrichaceae, Bryophyta). Acta Musei Silesiae. *Scientiae Naturales* 64: 169–174.
https://doi.org/10.1515/cszma-2015-0024

Plášek, V., Komínková, Z., Ochyra, R., Fialová, L., Guo, S.-L. & Mamtimin, S. (2021) A synopsis of *Orthotrichum* s. lato (Bryophyta, Orthotrichaceae) in China, with distribution maps and a key to determination. *Plants* 10: 499 [1–42].
https://doi.org/10.3390/plants10030499

Porebski, S., Bailey, L.G. & Baum, B.R. (1997) Modification of a CTAB DNA extraction protocol for plants containing high polysaccharide and polyphenol components. *Plant Molecular Biology Reporter* 15: 8–15.
https://doi.org/10.1007/BF02772108

Rambaut, A. (2018) Figtree v. 1.4.4. [http://tree.bio.ed.ac.uk/software/figtree/]

Redfearn Jr., P.L., Tan, B.C. & He, S. (1996) A newly updated and annotated checklist of Chinese mosses. *Journal of the Hattori Botanical Laboratory* 79: 163–357.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Sawicki, J., Plášek, V. & Szczecińska, M. (2010) Molecular studies resolve *Nyholmiella* (Orthotrichaceae) as a separate genus. *Journal of Systematics and Evolution* 48: 183–194. https://doi.org/10.1111/j.1759-6831.2010.00076.x

Schwägrichen, C.F. (1824) *Species Muscorum Frondosorum*. Supplementum Secundum 2 sect. 2, pages [87]–186 + plages 126–150. Barth, Leipzig.

Shevock, J.R., Ochyra, R. & Buck, W.R. (2006) Observations on the ecology and distribution of *Hydrocryphaea wardii*, a southeast Asian monospecific genus, reported new for China from Yunnan Province. *Journal of the Hattori Botanical Laboratory* 100: 407–418.

Shevock, J.R., Ochyra, R., He, S. & Long, D.G. (2011) *Yunnanobryon*, a new rheophytic moss genus from southwest China. *The Bryologist* 114: 194–203. https://doi.org/10.1639/0007-2745-114.1.194

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Sullivant, W.S. (1856) *Musci and Hepaticae*. George P. Putnam & Co., New York, pp. 607–702.

Vigalondo, B., Garilleti, R., Vanderpoorten, A., Patiño, J., Draper, I., Calleja, J.A., Mazimpaka, V. & Lara, F. (2019) Do mosses really exhibit so large distribution ranges? Insights from the integrative taxonomic study of the *Lewinskya affinis* complex (Orthotrichaceae, Bryopsida). *Molecular Phylogenetics and Evolution* 140: 106598. https://doi.org/10.1016/j.ympev.2019.106598

Vitt, D.H. (1971) The infrageneric evolution, phylogeny, and taxonomy of the genus Orthotrichum (Musci) in North America. *Nova Hedwigia* 21: 683–711.

Vitt, D.H. (1973) A revision of the genus *Orthotrichum* in North America, north of Mexico. *Bryophytorum Bibliotheca* 1: 1–208.

Vitt, D.H. (1979) New taxa and new combinations in the Orthotrichaceae of Mexico. *The Bryologist* 82: 1–19. https://doi.org/10.2307/3241962

Vitt, D.H. (1981) The genera *Leiomitrium* and *Cardotiella* gen. nova (Orthotrichaceae). *Journal of the Hattori Botanical Laboratory* 49: 92–113.

Vitt, D.H. (1982) The genera of the Orthotrichaceae. *Beheifte zur Nova Hedwigia* 71: 261–268.

Vitt, D.H. (1990) *Desmotheca* (Orthotrichaceae): Gondwanan fragmentation and the origin of a Southeast Asian genus. *Tropical Bryology* 3: 79–88. https://doi.org/10.11646/bde.3.1.10

Vitt, D.H. (1994) Orthotrichaceae. *Moss Flora of Mexico*. *Memoirs of the New York Botanical Garden* 69: 590–656.

Wang, Q.-H. & Jia, Y. (2020) A taxonomic study of the genus *Orthotrichum* (Orthotrichaceae, Musci) in China. *Acta Bryolichenologica Asiatica* 9: 1–166.

Wang, Q.-H., Dong, S.-S., Zhang, J.-L., Liu, Y. & Jia, Y. (2022) Phylogeny of *Orthotrichum* sl and *Ulota* sl (Orthotrichaceae, Bryophyta): Insights into stomatal evolution. *Journal of Systematics and Evolution* 60 (4): 876–900.

Werner, O., Ros, R.M. & Goffinet, B. (2007) A reconsideration of the systematic position of *Goniomitrium* (Funariaceae) based on chloroplast sequence markers. *The Bryologist* 110: 108–114. https://doi.org/10.1639/0007-2745(2007)110[108:AROTSP]2.0.CO;2

Wilbraham, J. & Long, D.G. (2005) *Zygodon* Hook. & Taylor and *Bryomaltaea* Goffinet (Bryopsida: Orthotrichaceae) in the Sino-Himalaya. *Journal of Bryology* 27: 329–342. https://doi.org/10.1179/174328205X72531

Yi, Y.-J., He, S. & Ma, W.-Z. (2015) *Hyophila flavolimbata*, a new species of Pottiaceae from northwestern Yunnan, China. *Phytotaxa* 231 (2): 182–186. https://doi.org/10.11646/phytotaxa.231.2.7

Yi, Y.-J., Zhang, J., Xiao, X.-X. & He, S. (2021) *Delongia flavolimbata* (S.He & Y.J.Yi) S.He & Y.J.Yi, an unusual species with elamellate laminae from China, newly combined in Polytrichaceae based on molecular data. *Journal of Bryology* 43: 313–320. https://doi.org/10.1080/03736687.2021.2004358