RESEARCH ARTICLE

Phylogenomics resolves the rediscovered Himalayan endemic *Brachymeniopsis gymnostoma* (Bryophyta, Funariaceae), as a species of *Entosthodon*, prompting also the transfer of *Clavitheca poeltii*

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Abstract Traits of the spore-bearing generation have historically provided the basis for systematic concepts across the phylogenetic spectrum and depth of mosses. Whether taxa characterized by a simple sporophytic architecture are closely related or emerged from independent reduction is often ambiguous. Phylogenomic inferences in the Funariaceae, which hold the model taxon *Physcomitrium patens*, revealed that several such shifts in sporophyte complexity occurred, and mostly within the *Entosthodon-Physcomitrium* complex. Here, we report the rediscovery of the monospecific, Himalayan endemic genera *Brachymeniopsis* and *Clavitheca*, after nearly 100 years and 40 years since their respective descriptions. The genera are characterized by, among other traits, their short sporophytes lacking the sporangial peristome teeth controlling spore dispersal. Phylogenomic inferences reveal that *Brachymeniopsis gymnostoma* arose within the clade of *Entosthodon* s.str., a genus with typically long-exserted capsules. We therefore propose to transfer *B. gymnostoma* to the genus *Entosthodon*, as *E. gymnostomus* comb. nov. Furthermore, *Clavitheca poeltii*, the sole species of the genus, is morphologically highly similar to *E. gymnostomus*, and should also be transferred to *Entosthodon*, but is retained as a distinct taxon, *E. poeltii* comb. nov., until additional populations allow for testing the robustness of the observed divergence in costa and seta length between the Nepalese and Chinese populations.

Keywords mosses; nomenclature; phylogenomic reference; taxonomy

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The life cycle of bryophytes in the broad sense, i.e., including hornworts, liverworts, and mosses, exhibits an alternation of two morphologically, developmentally, and physiologically complex generations (Crum, 2001), each facing selection forces that optimize their fitness. The gametophyte composes the vegetative and, by definition, the reproductive body: it represents the free-living generation that produces gametes, undergoes sexual reproduction, and supports the resulting zygote and sporophyte. In some mosses at least, the gametophyte also controls sporophyte development via the calyptra, which covers the sporophyte apex (Budke & al., 2011, 2012; Budke & Goffinet, 2016; Budke, 2019). The sporophyte is permanently attached, physiologically dependent on the maternal plant, and hence shorter-lived, and functionally limited to producing and dispersing spores to complete the cycle. Modifications of the morphological traits may be linked to habitat (e.g., Vitt, 1981; Huttunen & al., 2018) and may serve as phylogenetic markers informing on the shared ancestry of taxa (e.g., *Archidium* Brid.; Snider, 1975). The diversification of moss lineages may have resulted in species differing in their vegetative bodies but sharing a highly conserved sporophytic architecture (e.g., *Sphagnum*; Crum, 2001), or in congeneric taxa exhibiting distinct morphologies in both generations (e.g., *Lewinskya* F.Lara & al. in the Orthotrichaceae; Draper

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& al., 2021), or in taxa sharing a rather stenotypic vegetative body but differing in their morphologically divergent sporophytes (e.g., *Physcomitrium* (Brid.) Brid. in the Funariaceae; Liu & al., 2012; Medina & al., 2019).

Systematic concepts within the Funariaceae have traditionally reflected perceived phylogenetic structure in the variation of the sporophyte, and in particular the length of the seta, curvature, shape, and mode of dehiscence of the urn, and in the complexity of the peristome controlling spore dispersal (Fife, 1985). The first phylogenetic inferences derived from few discrete genetic loci (Liu & al., 2012) suggested that some of the genera defined by immersed and indehiscent capsules, such as *Physcomitrella* Bruch & Schimp. sensu Tan (1979) arose from within a lineage (i.e., *Physcomitrium*) with long exserted and dehiscent sporophytes. Further evidence against sporophytic trait-based generic concepts within the *Physcomitrium*-*Entosthodon* complex was gained from analyses of all organellar protein encoding genes (Medina & al., 2018) and hundreds of putative single-copy nuclear genes (Medina & al., 2019). These phylogenetic hypotheses suggest that transformations of the sporophyte are evolutionarily much more labile than previously assumed, a hypothesis congruent with sporophytic development perhaps being controlled by shifts in temporal expression of just a few genes (Kirbis & al., 2020).

The Funariaceae comprise an estimated 250 species, primarily distributed among four genera in the Funarioideae, namely *Entosthodon* Schwägr., *Funaria* Hedw., *Physcomitrellopsis* Broth. & Wager (see Wilding, 2015) and *Physcomitrium* (Fife, 1985; Crosby & al., 1999). Although the major splits in the evolution of the family occurred between approximately 80 and 60 million years ago, extant species emerged from diversification events within the last 25 million years (Medina & al., 2018). Some of the common (morpho-)species harbor populations with contrasting ploidies (Fritsch, 1991) assumed to reflect genome doubling (Patel & al., 2021). However, interspecific and even intergeneric hybridization gave rise to some species (Ostendorf & al., 2021) and may in fact be an underestimated mechanism underlying shift in ploidy, as for example the morphospecies *Physcomitrium pyriforme* (Hedw.) Brid. harbors at least three lineages, including two allopolyploids of distinct progenitor species (Patel & al., in press). So far only one species with an immersed capsule appears to be of hybrid origin, namely *P. immersum* Sull. (Medina & al., 2019; Patel & al., in press).

Recent phylogenomic inferences have clarified generic circumscriptions within the Funariaceae by merging genera with immersed capsules, i.e., *Aphanorrhegma* Sull., *Physcomitridium* G.Roth and *Physcomitrella* with *Physcomitrium* (Medina & al., 2018, 2019). Another taxon with a shortened seta, i.e., *Physcomitrium pygmaeum* James was resurrected from synonymy with *P. pyriforme* (Medina & al., 2022), further highlighting the extensive homoplasy in reduction of sporophytic complexity within *Physcomitrium*. Here, we assess the affinities of two other monospecific genera of the Funariaceae, namely *Brachymeniopsis* Broth. (Brotherus, 1929), and *Clavitheca* O.Werner & al. (Werner & al., 2007), the latter being a replacement name for the illegitimate *Corynotheca* Ochyra (1990). The latter is a homonym of *Corynotheca* F.Muell. ex Benth. (Bentham, 1878), a genus of Asphodelaceae (angiosperms) endemic to Australia (Barrett & al., 2021). *Brachymeniopsis* and *Clavitheca* are diagnosed by gametophytes with small imbricate leaves, mitrate calyptrae, and sporophytes composed of an elongated, operculate and gymnostomous capsule, elevated above the perichaetial leaves on a short seta.

Brachymeniopsis gymnostoma Broth. was described based on a single collection made by the Austrian botanist, H. Handel-Mazzetti in 1916 around Lidjiang (or Likiang, now Lijiang), in NE Yunnan (China), at ca. 2800 m a.s.l., on calcareous soil (Brotherus, 1929). Brotherus's decision to recognize the material at the generic level in the family appears to have been driven, in part, by its unusual gametophyte morphology, for which he presumably attributed the name *Brachymeniopsis*—because the small, erect, imbricate leaves resemble those in the genus *Brachymenium* Schwaegr. (and other bryaceous genera), rather than the larger, spreading leaves, which are more typical of Funariaceae. In his generic diagnosis of *Brachymeniopsis*, Brotherus (1929) acknowledges the affinity of the material to *Entosthodon*, probably because of the rectangular exothecial cell walls of the capsule and the presence of a persistent annulus, but he further noted that it differed by the mitrate (vs. cucullate) calyptra and a cup-like (vs. plane to planoconvex) operculum. While this combination of gametophytic and sporophytic traits is not present elsewhere in the family, placement of *Brachymeniopsis* in the Funariaceae is clearly indicated by its lax leaf areolation, and incompletely divided stomatal guard cells (Fife, 1982). Similarly, *Clavitheca* (as *Corynotheca*) was accommodated within the Funariaceae based on a similar suite of characters, including the antheridial paraphyses with enlarged, globose terminal cells, which are also diagnostic of the family (Ochyra, 1990). Given the similarities in morphology and habitat as well as the likelihood that they share a similar geographic distribution in the Himalayas, we suspected that the two species are at least closely related.

Until recently, *Brachymeniopsis gymnostoma* was only known from the type specimen collected in 1916 in Yunnan, China, and *Clavitheca poeltii* (Ochyra) O.Werner & al., only from a single specimen collected in 1986 by Joseph Poelt, in central Nepal, at 4300–4500 m a.s.l. Multiple expeditions in the area of the type locality of *B. gymnostoma*, including the neighboring provinces, yielded no new sightings or collections. Consequently, after almost a century since it was last collected, the species was officially classified as the only extinct bryophyte species in China according to the "China Biodiversity Red List" (see http://www.mee.gov.cn/gkml/hbb/bgg/201309/t20130912_260061.htm). In 2012, however, a population first considered reminiscent of *Brachymeniopsis* had been located by the senior author in an alpine shrubland at ca. 4045 m elevation in Yadong County, Xizang (Tibet; *Zhang 9430*; Fig. 1A), and another population was uncovered and sampled by W.-Z. Ma (*Ma 18-9837*; Fig. 1B) and

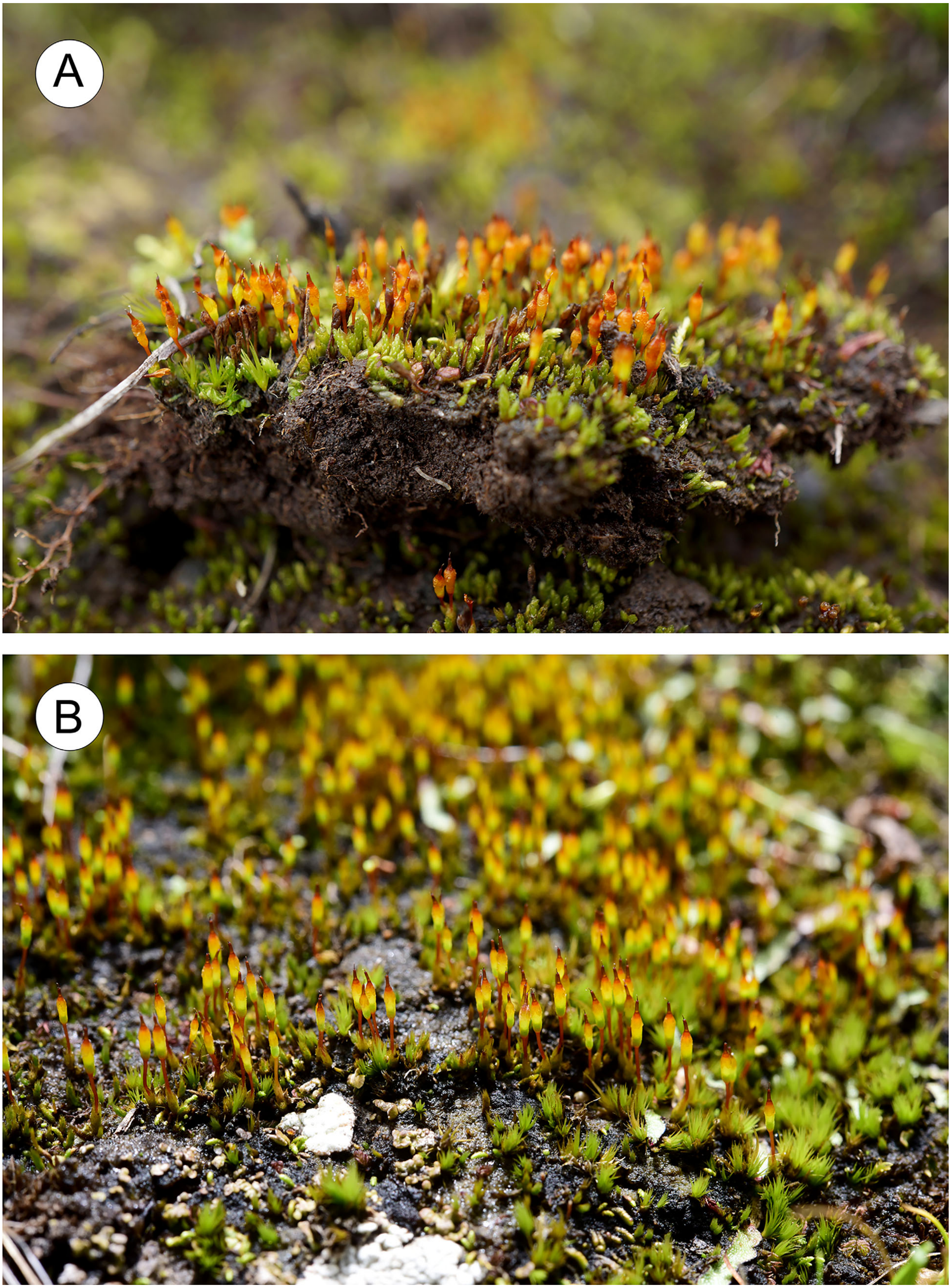

Fig. 1. Habit of *Entosthodon* species formerly assigned to *Clavitheca* or *Brachymeniopsis*. **A**, *Entosthodon poeltii* comb. nov., plants with sporophytes from Yadong, Xizang, China (by L. Zhang); **B**, *Entosthodon gymnostomus* comb. nov., plants with sporophytes from Dao-cheng, Sichuan, China (by W.-Z. Ma)

J. Shevock and W.-Z. Ma (*Shevock & Ma 52863*) in the province of Sichuan in 2018.

These recent collections provided an opportunity to assess variation in morphological traits and the distinction between *Brachymeniopsis gymnostoma* and *Clavitheca poeltii*, and to further assess their relationships and systematic position within a phylogenomic framework available for the Funariaceae.

■ MATERIALS AND METHODS

Morphological study. — We studied and compared morphological traits of the recent collections tentatively assigned to *Brachymeniopsis gymnostoma* (*Zhang 9430* – CONN, KRAM, SZG; *Ma 18-9837* – CAS, KUN, SZG; *Shevock & Ma 52863* – CAS, CONN, E, FH, KRAM, KUN, MO, NICH, NY, TAIE) as well as of the type collections of *B. gymnostoma* (E00011387, US00069674) and *Clavitheca poeltii* (KRAM).

DNA extraction and sequencing. — Targeted DNA sequencing of nuclear loci was carried out using similar protocols as in Medina & al. (2019). We extracted DNA from gametophyte tissue of *Zhang 9430* (CONN) and of *Shevock & Ma 52863* (CONN) using the modified CTAB/chloroform method (Doyle & Doyle, 1987). We checked DNA concentration using a Qubit fluorometer (Qiagen, Hilden, Germany). Only the extraction of the latter provided sufficient DNA to proceed. Genomic libraries were prepared with a NEBNext Ultra II FS DNA kit (New England Biosciences, Ipswich, Massachusetts, U.S.A.), which contains fragmentase for enzymatic shearing of DNA and SPRI beads for size selection of 500–750 bp inserts. We hybridized the prepared NEBNext library with custom RNA probes described in Medina & al. (2019) targeting 809 nuclear protein-coding genes using the MyBaits protocol v.3 (Arbor Biosciences, Ann Arbor, Michigan, U.S.A.). The *Brachymeniopsis* sample was pooled with other samples not included in the present study (i.e., no samples of *Entosthodon* were included in this sequencing, to avoid potential contamination) and sequenced on an Illumina MiSeq 2x300 PE (v.3 chemistry) at the Texas Tech Center for Bioinformatics and Genomics.

We trimmed raw, demultiplexed sequences using Trimmomatic v.0.39 (Bolger & al., 2014) to trim adapters, remove sequences with average quality score below 30 and reads less than 50 bp long. To extract gene sequences, we used HybPiper v.1.3.1 (Johnson & al., 2016) with both paired and unpaired trimmed reads and a nucleotide target gene reference from *Physcomitrium patens*. We also extracted "supercontig" sequences (coding sequence along with flanking non-coding sequence) with intronerate.py and identified potential polyploidy with the paralog_investigator.py script within HybPiper. Sequencing reads have been uploaded to the NCBI Sequence Read Archive (BioProject: PRJNA674709), and all sequences extracted from HybPiper are available on Dryad (https://doi.org/10.5061/dryad.j6q573nk3).

Molecular phylogenetic analyses. — We added the extracted nuclear sequences from *Brachymeniopsis* to the 648 single-gene alignments of Medina & al. (2019; https://doi.org/10.5061/dryad.8rq9465) using the "–add" function in MAFFT v.7.520 (Katoh & Standley, 2013). We generated two phylogenetic datasets: (1) an exon only based phylogeny of the Funariidae (Goffinet & al., 2009) using Timmiidae and Gigaspermidae as outgroups, and (2) a phylogeny of the *Entosthodon*-*Physcomitrium* complex (sensu Medina & al., 2018) based on "supercontigs", i.e., exon and the non-coding flanking regions. We inferred individual gene trees with the GTRCAT substitution model in RAxML v.8 (Stamatakis, 2014) along with 200 bootstrap replicates. To avoid biasing species tree inference with gene tree branches of low support, we collapsed any branch on the gene trees with less than 33% gene tree bootstrap support using DendroPy v.4.4.0 (Sukumaran & Holder, 2010). We inferred a species tree using the summary coalescent method ASTRAL-III (Zhang & al., 2017), and evaluated support via local posterior probability (LPP). We also summarized conflict among gene trees using PhyParts v.0.0.1 (Smith & al., 2015), which lists genes in concordance and in conflict with a given species phylogeny. We visualized the PhyParts bipartition summary using phypartspiecharts.py, available at github.com/mossmatters/phyloscripts.

To confirm the placement of *Brachymeniopsis*, we also conducted an analysis of plastid loci recovered from the "by catch" of the targeted nuclear loci. Using the same target file for organellar loci used by Medina & al. (2018), we extracted chloroplast loci using HybPiper. Extracted sequences from 31 of the 80 plastid loci were added to the corresponding gene alignments from Medina & al. (2018) using the "–add" feature in MAFFT. We concatenated the gene alignments using the fasta_merge.py script in HybPiper and conducted a partitioned analysis of chloroplast loci using RAxML along with 200 fast-bootstrap replicates. Extracted plastid loci sequences are also available in the Dryad repository.

■ RESULTS

Morphological study. — The type specimens of *Brachymeniopsis gymnostoma* and *Clavitheca poeltii* exhibit highly similar gametophytic (e.g., leaf shape and areolation) and sporophytic traits (Figs. 2A–H & 4A–G). They differ somewhat in (i) their perichaetial leaves, with a costa mostly excurrent in *B. gymnostoma* versus mostly ending below apex to percurrent in *C. poeltii* (Fig. 2I versus 4G, respectively), and (ii) the length of the seta relative to that of the perichaetial leaves, with the perichaetial leaves generally not reaching the middle of the seta in *B. gymnostoma*, versus extending to the base of the capsule in *C. poeltii*. The two recently discovered populations (*Ma 18-9837*, *Zhang 9430*) express the same traits (Figs. 3A–F,H–L versus 5A–H,K, respectively) and variation in perichaetial leaves, with the costae mostly excurrent in the former and mostly ending below apex to percurrent in the latter (Figs. 3G, 5I,J), as observed in the type material of *B. gymnostoma* and

C. poeltii, respectively. Henceforth, we will refer to *Ma 18-9837* and *Shevock & Ma 52863* as *B. gymnostoma* and *Zhang 9430* as *C. poeltii*.

Sequencing data. — The genome extraction from the collection *Zhang 9430* yielded insufficient DNA for library preparation and could not be processed further. The sequencing of enriched library for the collection by *Shevock & Ma 52863* (UCONN DNA # DNA 5271) generated 781,507 pairs of reads; 699,177 read pairs passed filter, along with 78,477 unpaired reads. Of the total of 1,747,626 reads, 61.6% mapped to one of the target genes. HybPiper produced a contig for all 809 nuclear genes, none of which produced warnings about potential paralogs, potentially indicative of allopolyploidy (see Patel & al., in press). A subset of 648 genes was used to infer the phylogenetic position of *Shevock & Ma 52863* by adding sequences of this sample to existing alignments from (Medina & al., 2019). A total of 843,009 bp were added to the exon alignment, and 2,292,892 bp to the supercontig alignment.

Phylogenetic inferences. — The overall exon-based topology of the Funarioideae (suppl. Fig. S1) and the supercontig-based phylogeny of the *Entosthodon-Physcomitrium* complex (Fig. 6) are fully congruent with those presented by Medina & al. (2019). Inferences from variation in exon sequences only (suppl. Fig. S1) resolve *Shevock & Ma 52863* (i.e., *Brachymeniopsis gymnostoma*) within the *Entosthodon*-*Physcomitrium* complex, a hypothesis supported by at least 423 gene trees (suppl. Fig. S1). Within this complex, the species seems most closely related to *Entosthodon lindigii* (Hampe) Mitt. (185 gene trees) forming a pair of putative sister taxa included in *Entosthodon* s.str. whose monophyly is only supported by a small plurality of loci (i.e., 26 or 7%). Inferences from the more variable supercontigs (Fig. 6), provide stronger support (i.e., 83 loci or 14%) for *Brachymeniopsis* being nested within *Entosthodon* s.str., with 307 gene trees (i.e., 54%) recovering its uniquely shared ancestry with *E. lindigii* (Fig. 6). No dominant alternative bipartition emerged in either PhyParts analyses. The phylogeny drawn from concatenated plastid loci also places *Brachymeniopsis* sister to *E. lindigii* with maximal support (suppl. Fig. S2).

■ DISCUSSION

The systematic position of *Brachymeniopsis*. — Recent phylogenomic inferences revealed that several monospecific genera of the Funariaceae are nested within more speciose lineages: *Cygnicollum* Fife, *Funariella* Sérgio and *Physcomitrellopsis* Broth. & Wager are nested within a lineage of *Entosthodon* Schwägr. (Wilding, 2015; Medina & al., 2018, 2019) and *Aphanorrhegma* Sull. and *Physcomitrella* Bruch

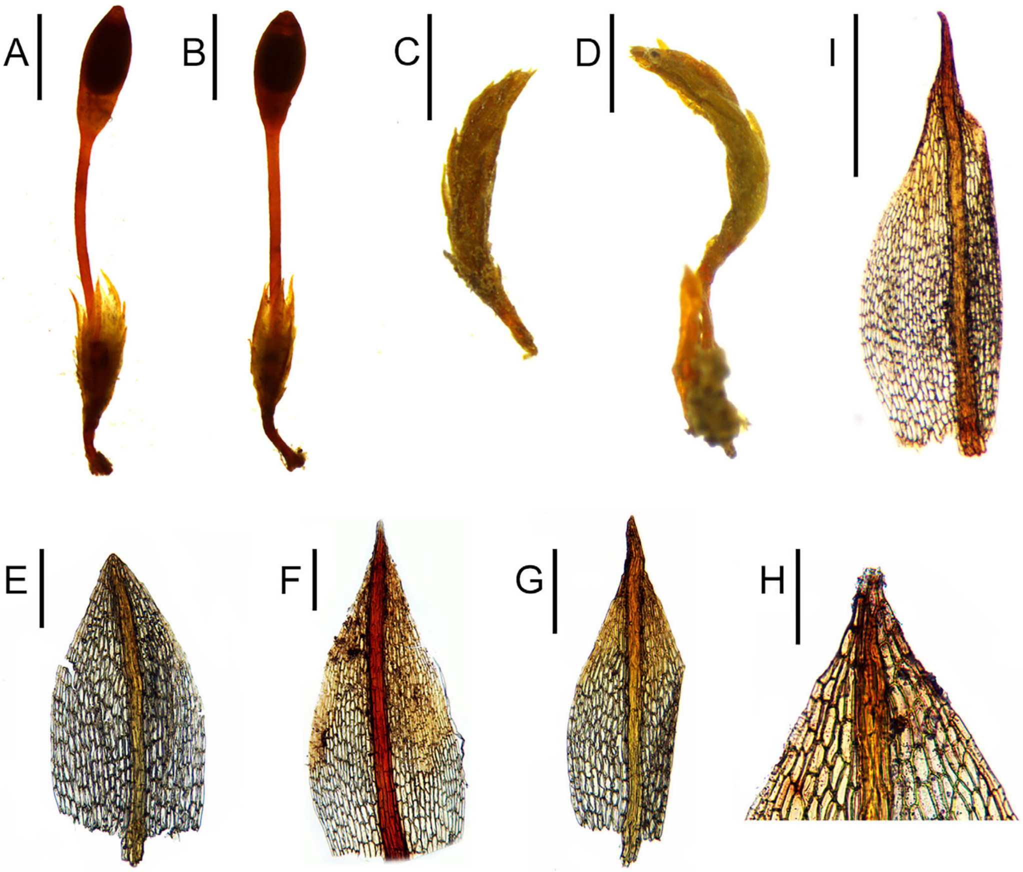

Fig. 2. *Entosthodon gymnostomus* comb. nov. Isotype of *Brachymeniopsis gymnostoma* (US!). **A & B**, Fertile plants; **C & D**, Vegetative plants; **E–G**, Vegetative leaves; **H**, Apex of vegetative leaf; **I**, Perichaetial leaf. — Scale bars: A & B = 1 mm, C–E = 500 μm, F–H = 200 μm, I = 100 μm.

& Schimp. (including *Physcomitridium* G.Roth.) are nested within *Physcomitrium*, whose circumscription was consequently broadened (Medina & al., 2018, 2019). Inferences from 648 nuclear loci (Fig. 6, suppl. Fig. S1) resolve the collection by *Shevock & Ma 52863* within *Entosthodon* s.str., i.e., the clade comprising the type *E. attenuatus* (Dicks.) Bryhn, a position congruent with that inferred from protein-coding plastid loci (suppl. Fig. S2) and phenetic analyses of morphological traits (Fife, 1985). Furthermore, the nuclear loci lack any signal of extensive heterozygosity indicative of a hybrid origin, as seen in other Funariaceae (McDaniel & al., 2010; Beike & al., 2014; Patel & al., in press). Thus, *Brachymeniopsis gymnostoma*, based on *Shevock & Ma* is a non-hybrid species that should be transferred to *Entosthodon*, and consequently the generic name *Brachymeniopsis* (Brotherus, 1929) should be considered a synonym of *Entosthodon* (Schwägrichen, 1823), given that the latter is the earliest name for the clade that holds the generic type *E. attenuatus*, which is the accepted name for the original type *E. templetonii* (Sm.) Schwägr. (fide Limpricht, 1895; Grout, 1935).

The circumscription of *Entosthodon* (*Brachymeniopsis*) *gymnostomus*. — *Brachymeniopsis gymnostoma* was described from a single collection made in Yunnan, China (Brotherus, 1929). Decades later, Ochyra (1990) established the genus *Corynotheca* (later renamed *Clavitheca* by Werner & al., 2007) for a single species, *C. poeltii*, also known from

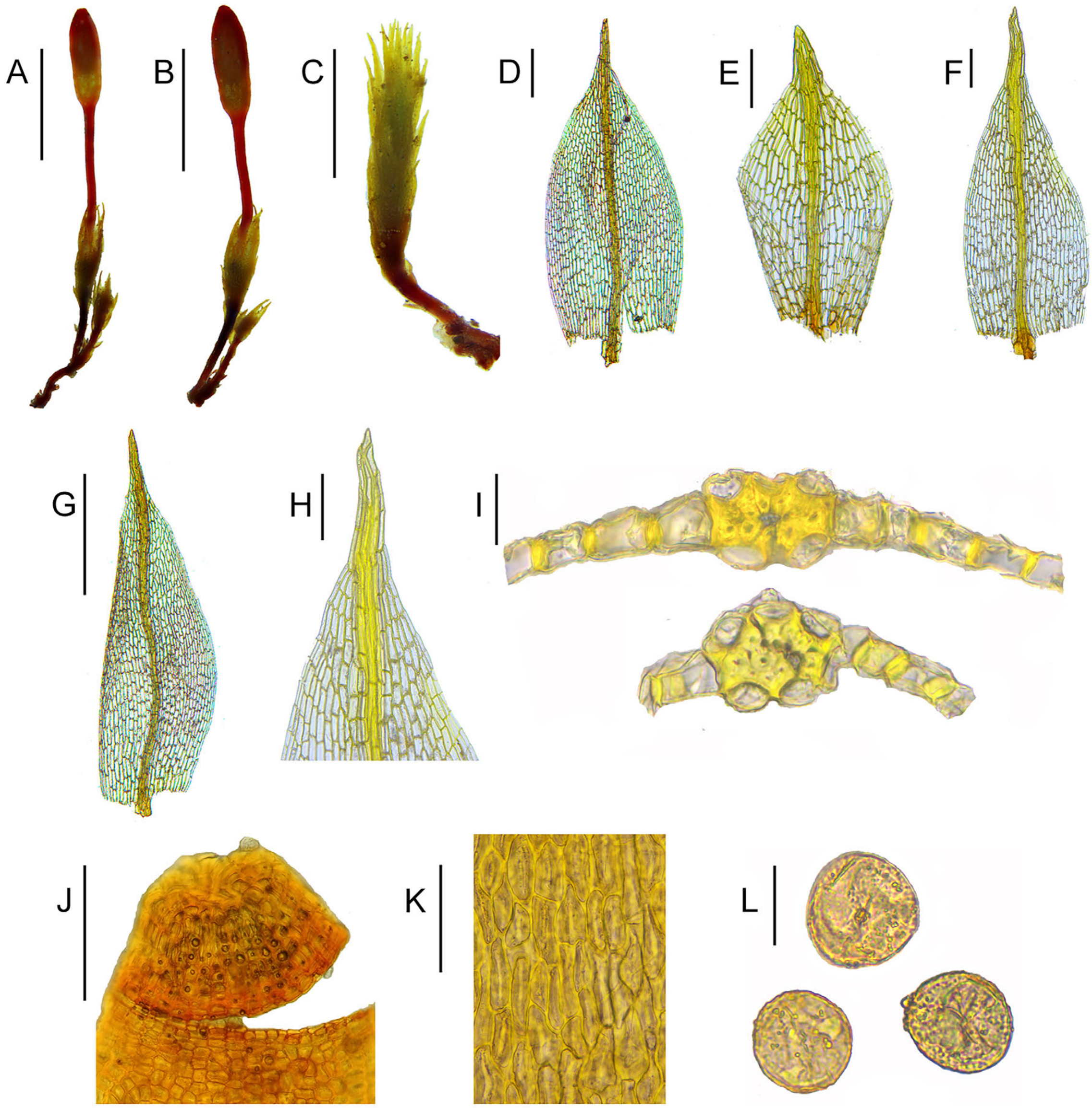

Fig. 3. *Entosthodon gymnostomus* comb. nov. **A & B**, Fertile plants; **C**, Vegetative plant; **D–F**, Vegetative leaves; **G**, Perichaetial leaf; **H**, Apex of vegetative leaf; **I**, Cross-sections of vegetative leaf; **J**, Part of a capsule, showing operculum and absence of peristome teeth; **K**, Median exothecial cells of capsule; **L**, Spores. — Scale bars: A & B = 1 mm, C = 1 mm, D = 200 μm, E & F = 100 μm, G = 500 μm, H = 200 μm, I = 20 μm, J = 200 μm, K = 50 μm, L = 20 μm. Based on *W.-Z. Ma 18-9837* (SZG).

a single collection from Nepal. The type material of *B. gymnostoma* in US and the isotype of *C. poeltii* in KRAM are morphologically highly similar, such that both taxa are at least closely related.

Type materials of the two taxa display the same characteristic traits: small erect plants with short imbricate leaves characterized by a stout costa, and short erect, gymnostomous sporophytes with a truncate-conic operculum. The major differences between the respective type specimens are primarily related to variation in leaf traits and the length of the seta. The isotype in US of *Brachymeniopsis gymnostoma* (Fig. 2) has plane (when moist), ovate to shortly ovate-lanceolate leaves, usually with acute to acuminate apices, perichaetial leaves and vegetative leaves mostly with shortly excurrent costae, and relatively long setae (up to 2.5 mm versus 5 mm in the protologue). The isotype in KRAM of *Clavitheca poeltii* (Fig. 4) has leaves that are similar in shape, but they are more or less concave when moist, with obtuse to subacute apices and costae that mostly ending below apex to percurrent both in perichaetial and vegetative leaves, and the setae are shorter (up to 1.3 mm). The collection *Ma 18-9837* (Fig. 3) and *Shevock & Ma 52863* resemble the isotype of *B. gymnostoma*, whereas *Zhang 9430* (Fig. 5) is similar to *C. poeltii*.

The few populations sampled so far differ only slightly in the length of the costa and the seta, and could be accommodated in two, albeit phenotypically very similar species. In a somewhat similar case, He & al. (2022) proposed to retain *Leratia scaberrima* (Broth.) Goffinet & al., another Chinese endemic species rediscovered after nearly a century, as distinct from *L. steerei* (Vitt) Goffinet & al., which is also known only from its type from Central America. Although the Asian and Neotropical samples are morphologically identical, He & al. (2022) argued that the transoceanic disjunction may be indicative of a phylogenetic divergence and that pending the discovery and study of additional populations, the two species should conservatively be retained. Furthermore, recent studies in the Funariaceae (Medina & al., 2018, 2019; Patel & al., in press) have highlighted that current morphological species concepts in *Physcomitrium* did not reflect phylogenetic structure and diversity, as the *P. pyriforme* (Hedw.) Brid. or the *P. sphaericum* (C.Ludw.) Brid. morphotypes were shared by several, including non-sister, sympatric and even haploid and allopolyploid lineages.

Brachymeniopsis gymnostoma is robustly resolved within the genus *Entosthodon* and given that *Clavitheca poeltii* is morphologically highly similar to *B. gymnostoma*, it is likely also a member of this clade. At present each putative species is only known from one historical and one recent collection, and the two species can be distinguished, albeit only by the length of the costa in the perichaetial leaves. Given the paucity of collections but the availability of two epithets, we propose

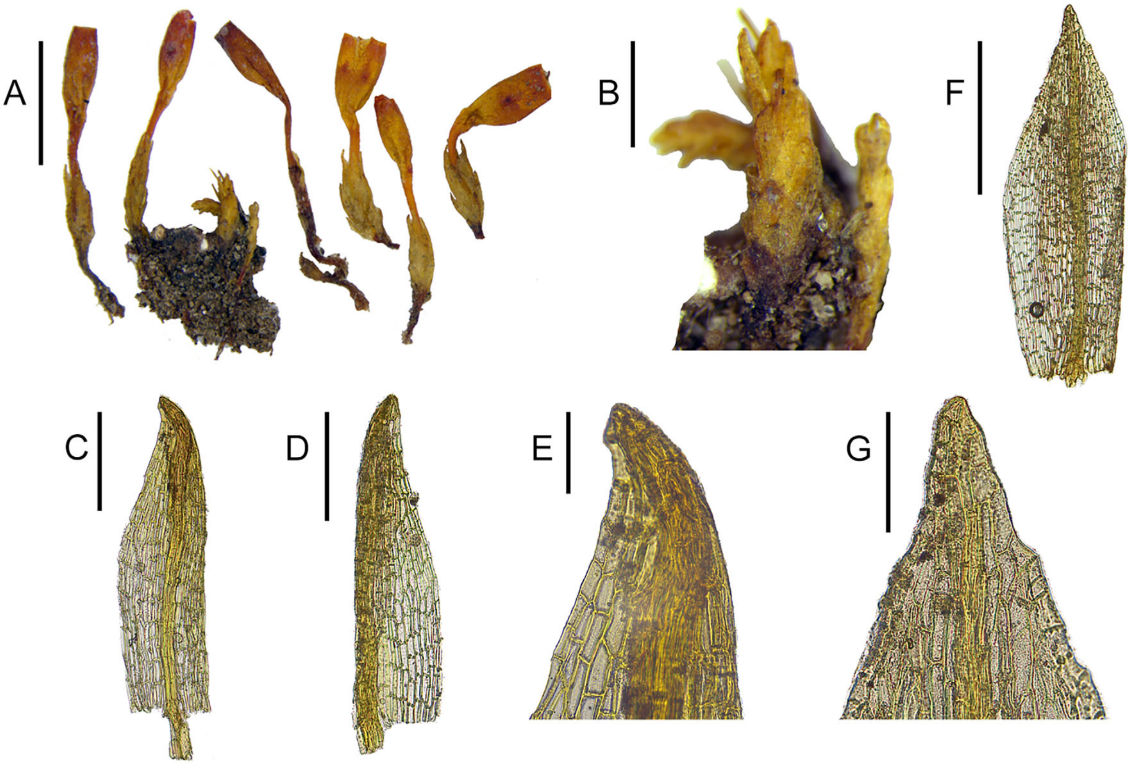

Fig. 4. *Entosthodon poeltii* comb. nov. Isotype of *Corynotheca poeltii* (KRAM!). **A**, Fertile plants; **B**, Vegetative plants; **C & D**, Vegetative leaves; **E**, Apex of vegetative leaf; **F**, Perichaetial leaf; **G**, Apex of perichaetial leaf. — Scale bars: A = 2 mm, B = 500 µm, C & D = 200 µm, E = 50 µm, F = 500 µm, G = 100 µm.

to remain conservative and retain the two species as distinct, following their transfer to *Entosthodon*, as *E. gymnostomus* and *E. poeltii*.

■ TAXONOMIC TREATMENT

Entosthodon Schwägr., Sp. Musc. Frond. Suppl. 2(1): 44. 1823 – Type: *Entosthodon templetonii* (Sm.) Schwägr.

= *Brachymeniopsis* Broth. in Handel-Mazzetti, Symb. Sin. 4: 48. 1929 – Type: *Brachymeniopsis gymnostoma* Broth., **syn. nov.**

= *Corynotheca* Ochyra in Polish Bot. Stud. 1: 60. 1990, nom. illeg., non F.Muell. ex Benth., Fl. Austral. 7: 49. 1878 ≡ *Clavitheca* O.Werner, Ros & Goffinet in Bryologist 110: 113. 2007 – Type: *Clavitheca poeltii* (Ochyra) O.Werner, Ros & Goffinet, **syn. nov.**

Entosthodon gymnostomus (Broth.) Li Zhang & Goffinet, **comb. nov.** ≡ *Brachymeniopsis gymnostoma* Broth. in Handel-Mazzetti, Symb. Sin. 4: 48, t. 1, fig. 13. 1929 – **Lectotype (designated here):** China, Prov. Yünnan bor.-occid.: In regionis calide temperatae prope urbem Lidjiang („Likiang“) agris derelictis siccis supra vicum Semioba in via Djiuho ducente. Substr. calceo alt. s. m. ca. 2800 m., 25 Sep 1916, *Dr. Heinr. Frh. v. Handel-Mazzetti. Nr. 10.061* (Diar. Nr. 1900) (W No. 1925-0004810; isolectotypes: BM barcode BM000983327, E barcode E00011387!, G barcode G00051036, H-BR barcode H3011758, PC 2D-barcode PC0135544, US barcode 00069674!, WU No. WU0045984).

Figs. 1B, 2, 3.

Description. – Plants ca. 4–6 mm high (with sporophytes), yellowish green, dull. Stems erect, 1.0–2.4 mm high. Leaves imbricate, appressed in both vegetative and fertile plants, plane to more or less concave when moist, ovate to shortly ovate-lanceolate, acute, acuminate or sometimes subacute at apex; margins plane, entire; costa single, occasionally ending below the apex, percurrent to mostly shortly excurrent, bulges both adaxially and abaxially in cross-section; lamina cells smooth, thin-walled, rhomboidal, rectangular or subhexagonal, median cells 30–73 μm long, 10–18 μm wide, basal cells laxer. Autoicous. Perichaetial leaves similar but larger than the vegetative leaves, reaching the middle of the seta, usually with acuminate apices and excurrent costae. Seta short, erect, yellowish red to reddish brown, 1.9–2.5(–5) mm long. Capsule erect, club-shaped, 1.2–2.2 mm long, operculum truncate-conic, sometimes pitted atop; annulus persistent; median exothecial cells rectangular to oblong-hexagonal, slightly thick-walled; peristome teeth absent.

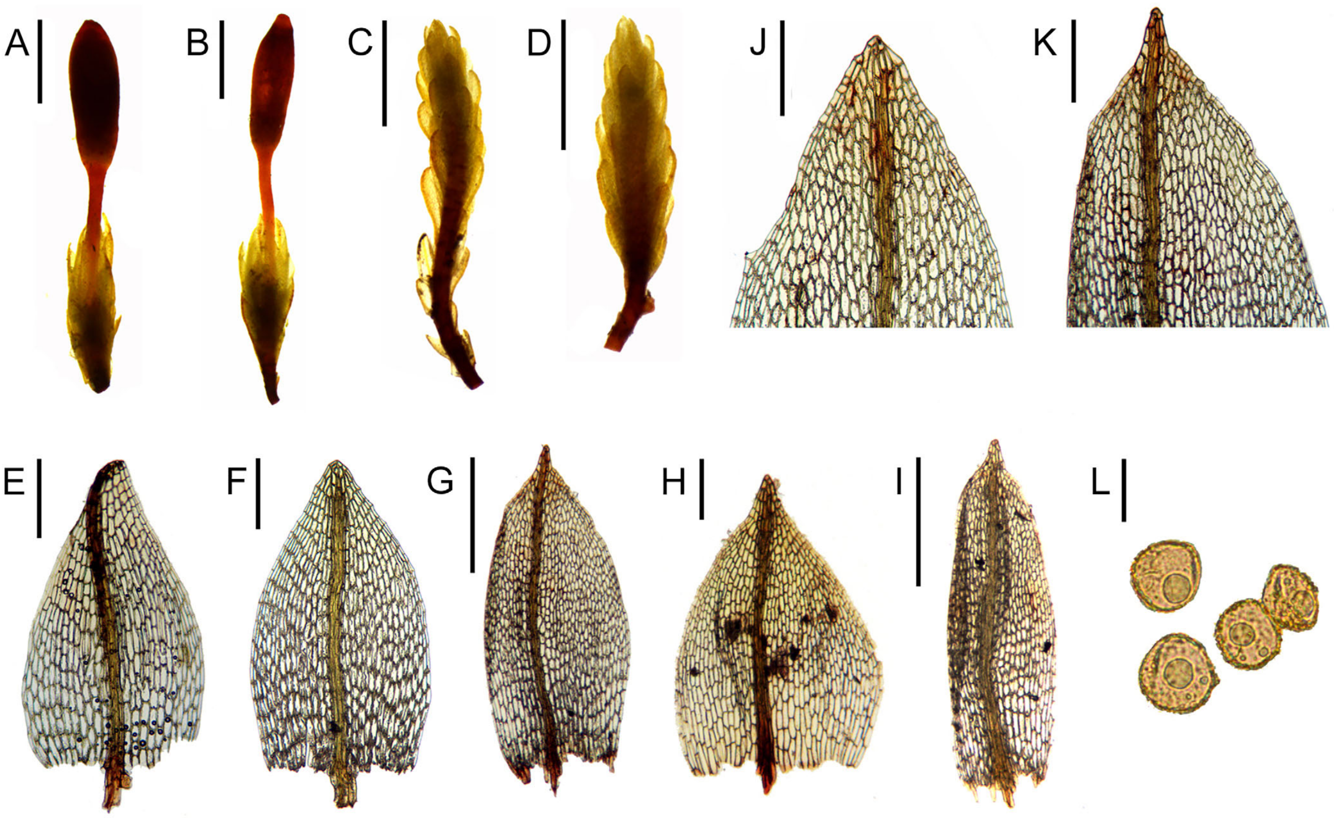

Fig. 5. *Entosthodon poeltii* comb. nov. **A & B**, Fertile plants; **C & D**, Vegetative plants; **E–H**, Vegetative leaves; **I**, Perichaetial leaf; **J**, Apex of perichaetial leaf; **K**, Apex of vegetative leaf; **L**, Spores. — Scale bars: A–D = 1 mm, E & F = 200 μm, G = 500 μm, H = 200 μm, I = 500 μm, J = 200 μm, K = 200 μm, L = 20 μm. From *L. Zhang 9430* (SZG).

Calyptra mitrate, long rostrate. Spores spherical, dark brown to light brown, 19–26 μm, smooth or with fine granular ornamentation.

Distribution. – Currently only known from one locality above 2800 m in each of the Chinese provinces of Sichuan and Yunnan.

Specimens examined. – CHINA, Sichuan, Dao-Cheng Co., Sheng-Mu Xiang, near Ge-Wa village at the south side of Dao-Cheng River, 29°01′57″N, 100°23′53″E, on soil crust in open, regenerating forest, elev. 3750 m, 28 Aug 2018, *W.Z. Ma 18-9837* (CAS, KUN, SZG); idem, off of concrete road eastward of Dao Cheng city along the Dao Cheng River, about 10 km down river from Dao Cheng city, 29°02′01.6″N, 100°24′06.0″E, elev. 3750 m, granitic boulder field with *Rhododendron* and *Berberis* shrubs along cascading stream, on soil crusts with humus in sun, 28 Aug 2018, *Shevock & Ma 52863* (CAS, CONN [CONN00233144], E, FH, KRAM, KUN, MO, NICH, NY, TAIE).

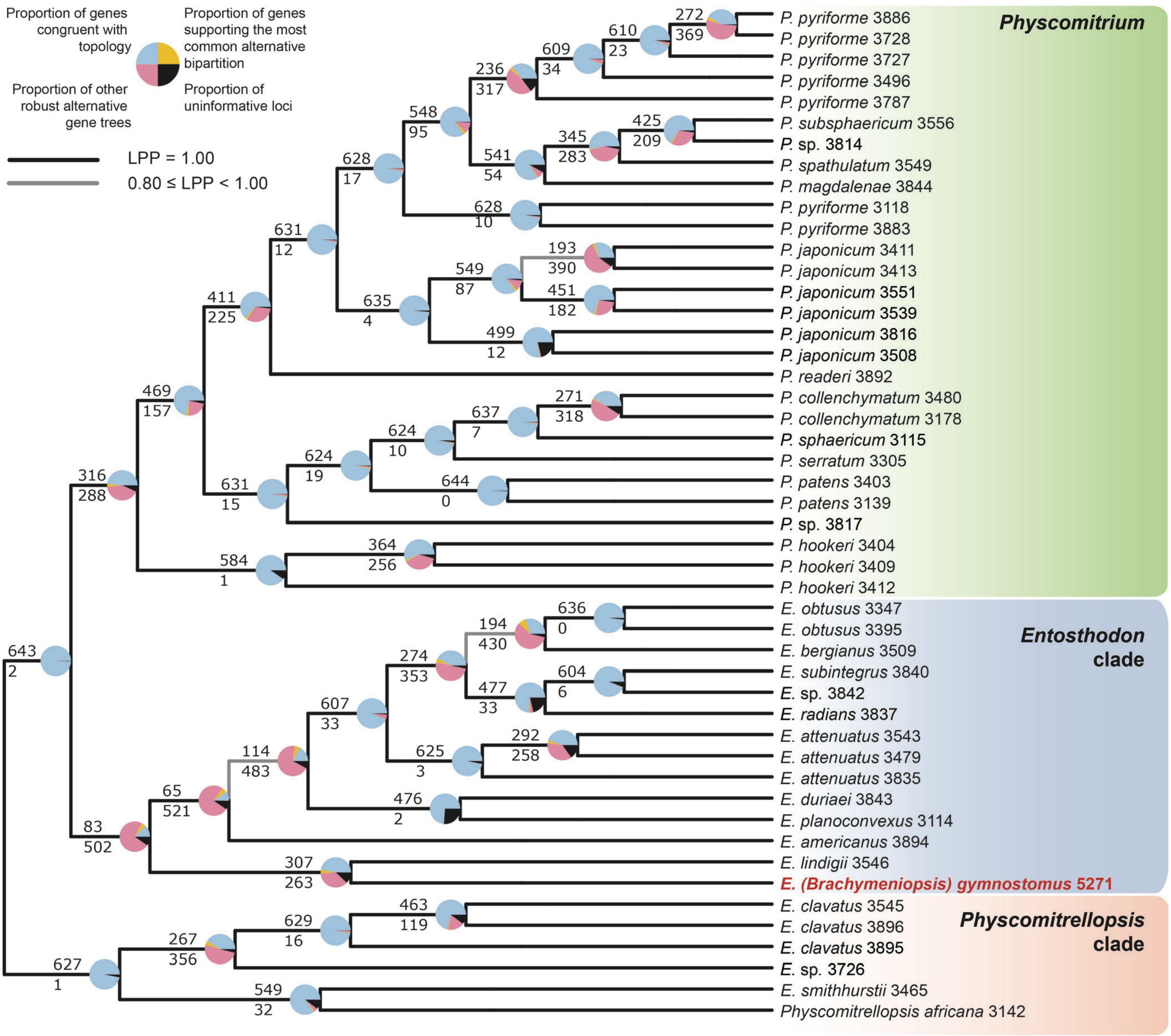

Fig. 6. Phylogenomic inferences for the *Entosthodon-Physcomitrium* complex (sensu Medina & al., 2018) based on 648 nuclear loci. Astral tree summarizing inferences from single-locus trees, with loci being exons and their flanking regions. Color of branches reflects local posterior support, with black referring to maximally supported branches and grey to branches with LPP values lower than 1 but greater or equal to 0.80. Pie diagrams on the nodes reflect the percentage of gene trees that are concordant with the topology (blue), support the most common alternative bipartition (orange), support all other alternative bipartitions (red) or are uninformative for each bipartition (black). The number above the branch is the number of gene trees with the topology and the number below the branch is the total number of gene trees with a supported (>33% bootstrap) discordant topology.

Note on typification. – A specimen of *Brachymeniopsis gymnostoma* deposited in H-BR was annotated as the holotype by Allan Fife in December 1980. The specimen is, however, composed of only the scraps (Ryszard Ochyra, pers. comm. 30 Jan 2023), and as such is not representative, as it lacks some essential details, for example the operculum, which is unique in this taxon. The original specimens were returned to Vienna as requested by Handel-Mazzetti, on the basis that the original material was presented as a unicate (Koponen, 2010). Cao Tong in his annotation of the specimen in H-BR in August 2000 suspected that "there must be more material according to Brotherus' description and illustration". Indeed, Handel-Mazzetti did ultimately distribute duplicates to various herbaria, as evidenced by the various isotypes, retaining a collection in his herbarium, which is now held in W. Furthermore, this collection, unlike the one in H-BR, has many shoots with complete sporophytes and calyptrae, thus exhibiting the diagnostic traits of the species, and therefore the specimen in W should be chosen as the lectotype and the material in H-BR should be treated as an isolectotype. Although the collection in W is labeled "lectotype" by Prof. Ryszard Ochyra (see https://www.jacq.org/detail.php?ID=305512), this designation is not effective according to Art. 7.10 of the *International Code of Nomenclature for algae, fungi, and plants* (Turland & al., 2018), and hence the lectotype is formally designated here.

Entosthodon poeltii (Ochyra) Li Zhang & Goffinet, **comb. nov.** ≡ *Corynotheca poeltii* Ochyra in Polish Bot. Stud. 1: 60, fig. 1–32. 1990 ≡ *Clavitheca poeltii* (Ochyra) O.Werner, Ros & Goffinet in Bryologist 110: 113. 2007 – Holotype: Nepal, Central Himalayas. Upper Langtang Valley, on N slope above Nubama Dang, 28°10′N, 85° 20′E, elev. 4300–4500 m; on soil in pasture on moraines; 13 Sep 1986, *Poelt s.n.* (GZU barcode GZU000282660; isotype: KRAM B No. B165343!), **syn. nov.**
Figs. 1A, 4, 5.

Description. – Plants ca. 4–5 mm high (with sporophytes), yellowish green, dull. Stem erect, 0.8–2.4 mm high. Leaves 0.5–0.6 mm long, and 0.15 mm wide at the base, imbricate, distinctly keeled in vegetative plants, usually appressed to slightly keeled above in fertile plants, more or less concave when moist, ovate to oblong-ovate, obtuse, subacute, or slightly apiculate, sometimes cucullate at apex; margins plane, entire; costa single, percurrent or failing 3 to 4 cells below the apex, bulges both adaxially and abaxially in cross-section; lamina cells smooth, thin-walled, rhomboidal, rectangular or subhexagonal, median cells 30–65 µm long, 12–22 µm wide, basal cells laxer. Autoicous. Perichaetial leaves slightly larger and more concave than the vegetative leaves, extending more than half of the setae, usually with subacute, acuminate, apiculate to cuspidate apices, with costae mostly ending below the apex to percurrent. Seta short, erect, yellowish red to reddish brown, 1.0–1.7 mm long. Capsule erect, club-shaped, 1.6–2.0 mm long, operculum truncate-conic, pitted atop; annulus persistent; median exothecial cells rectangular to oblong-hexagonal, slightly thick-walled; peristome teeth absent. Calyptra mitrate, long rostrate. Spores spherical, yellow to brown, 19–28 µm, smooth or with fine granular ornamentation.

Comments. – The gametophyte morphology of the above two species, while uncommon, is not unique in the family. Gametophytes bearing imbricate, oblong-ovate leaves can be observed in two other species, *Entosthodon jamesonii* (Taylor) Mitt. and *E. productus* Mitt., both thought to be closely related to *E. gymnostomus* (Fife, 1982, 1985), although neither of these possess the stout costa observed in *E. gymnostomus*, which bulges both adaxially and abaxially in cross-section vs. only abaxially in all other Funariaceae (Fife, 1982). It is also worth mentioning that *E. lindigii*, the most closely related taxon in the molecular dataset, shares with *E. gymnostomus* and *E. poeltii* an imbricate foliage (Hampe, 1865) and excurrent costae (Fife, 1987; Wilding, 2015), a rare trait in the genus. Like many other species in the Funariaceae, *E. gymnostomus* and *E. poeltii*, are annual species, and are most readily noted in the field by their sporophytes that mature in mid-summer to early fall. Although currently rare, targeted seasonal searches may prove critical to assess the distribution and the frequency of populations. Previous reports of *E. gymnostomus* from Guizhou Province in China by Peng & Zhang (2007) and Xu & al. (2021) proved not to be Funariaceae but be a mixture of *Bryum argenteum*, *B.* cf. *dichotomum*, *B.* cf. *turbinatum*, and *Didymodon constrictus* (*T. Peng 050517012B*, GNUB) or of *Anomobryum yasudae*, *Barbula indica*, *Bryum argenteum*, *B.* cf. *dichotomum, Didymodon ditrichoides*, and *D. perobtusus* (*Xu & al. 20201001026*, GNUB).

Distribution. – Currently only known from two localities above 4000 m, one in Nepal and one in Xizang Province of China, from where it was first reported as *Brachymeniopsis gymnostoma* by Zhang & Zuo (2015).

Specimens examined. – CHINA, Xizang, Yadong Co., Shangyadong, rear mount of Rubinggangcun, 27°31′36.5″N, 88°56′31.0″E, 4045 m, on soil covering rock in sparse shrubland, 12 Aug 2012, *L. Zhang 9430* (CONN [CONN00233143], KRAM, SZG).

■ AUTHOR CONTRIBUTIONS

LZ and BG designed the study. LZ, W-ZM and JRS collected the material. QZ and LZ lead the morphological study. NP, RM and MJ completed the sequencing and phylogenetic analyses. LZ and BG wrote the manuscript, with contributions from NW and other co-authors. The manuscript was reviewed and accepted by all the authors. — LZ, https://orcid.org/0000-0002-0745-3841; QZ, https://orcid.org/0000-0002-1061-081X; W-ZM, https://orcid.org/0000-0003-3144-001X; JRS, https://orcid.org/0000-0003-1283-0709; NP, https://orcid.org/0000-0002-3504-7314; MJ, https://orcid.org/0000-0002-1958-6334; RM, https://orcid.org/0000-0001-5629-1503; NW, https://orcid.org/0000-0003-4029-5387; BG, https://orcid.org/0000-0002-2754-3895

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■ LITERATURE CITED

Barrett, R.L., Macfarlane, T.D. & Keighery, G.J. 2021. Taxonomic revision of *Corynotheca* (Hemerocallidaceae/Asphodelaceae). *Telopea* 24: 7–52. https://doi.org/10.7751/telopea14693

Beike, A.K., von Stackelberg, M., Schallenberg-Rüdinger, M., Hanke, S.T., Follo, M., Quandt, D., McDaniel, S.F., Reski, R., Tan, B.C. & Rensing, S.A. 2014. Molecular evidence for convergent evolution and allopolyploid speciation within the *Physcomitrium-Physcomitrella* species complex. *B. M. C. Evol. Biol.* 14: 158. https://doi.org/10.1186/1471-2148-14-158

Bentham, G. 1878. *Flora Australiensis: A description of the plants of the Australian territory*, vol. 7. London: Reeve. https://doi.org/10.5962/bhl.title.16515

Bolger, A.M., Lohse, M. & Usadel, B. 2014. Trimmomatic: A flexible trimmer for Illumina sequence data. *Bioinformatics* 30: 2114–2120. https://doi.org/10.1093/bioinformatics/btu170

Brotherus, V.F. 1929. Musci. In: Handel-Mazzetti, H. (ed.), *Symbolae Sinicae: Botanische Ergebnisse der Expedition der Akademie der Wissenschaften in Wien nach Südwest-China, 1914/1918*, part 4. Wien: Springer. https://doi.org/10.5962/bhl.title.878

Budke, J.M. 2019. The moss calyptra: A maternal structure influencing offspring development. *Bryologist* 122: 471–491. https://doi.org/10.1639/0007-2745-122.3.471

Budke, J.M. & Goffinet, B. 2016. Comparative cuticle development reveals taller sporophytes are covered by thicker calyptra cuticles in mosses. *Frontiers Pl. Sci. (Online journal)* 7: 832. https://doi.org/10.3389/fpls.2016.00832

Budke, J.M., Goffinet, B. & Jones, C.S. 2011. A hundred-year-old question: Is the moss calyptra covered by a cuticle? A case study of *Funaria hygrometrica*. *Ann. Bot. (Oxford)* 107: 1279–1286. https://doi.org/10.1093/aob/mcr079

Budke, J.M., Goffinet, B. & Jones, C.S. 2012. The cuticle on the gametophyte calyptra matures before the sporophyte cuticle in the moss *Funaria hygrometrica* (Funariaceae). *Amer. J. Bot.* 99: 14–22. https://doi.org/10.3732/ajb.1100311

Crosby, M., Magill, R., Allen, B. & He, S. 1999. *A checklist of the mosses*. St. Louis: Missouri Botanical Garden Press.

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

Doyle, J.J. & Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.

Draper, I., Garilleti, R., Calleja, 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 Pl. Sci. (Online journal)* 12: 427. https://doi.org/10.3389/fpls.2021.629035

Fife, A.J., 1982. *A generic revision of the Funariaceae (Bryophyta: Musci)*. Dissertation. University of Michigan, Ann Arbor, Michigan, U.S.A.

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

Fife, A.J. 1987. A revision of the Andean species of *Entosthodon*. *Mem. New York Bot. Gard.* 45: 301–325.

Fritsch, R. 1991. Index to bryophyte chromosome counts. *Bryophyt. Biblioth.* 40: 1–352.

Goffinet, B., Buck, W.R. & Shaw, A.J. 2009. Morphology and classification of the Bryophyta. Pp. 55–138 in: Goffinet, B. & Shaw, A.J. (eds.), *Bryophyte biology*, 2nd ed. Cambridge: Cambridge University Press.

Grout, A.J. 1935. *Moss flora of North America North of Mexico*, vol. 2(2). Newfane, Vermont: published by the author.

Hampe, E. 1865. Musci. In: Prodromus florae Novo-Granatensis: ou Énumération des plantes de la Nouvelle-Grenade, avec description des espèces nouvelles, par M. m. Triana et J. E. Planchon. Musci. *Ann. Sci. Nat., Bot.*, sér. 5, 3: 337–376.

He, S., Shevock, J.R., Patel, N., Lemieux, O. & Goffinet, B. 2022. Rediscovery of *Florschuetziella scaberrima* (Bryophyta, Orthotrichaceae) a century after its description leads to its transfer to *Leratia*. *Bryophyte Diversity Evol.* 45: 188–198. https://doi.org/10.11646/bde.45.1.12

Huttunen, S., Bell, N. & Hedenäs, L. 2018. The evolutionary diversity of mosses – Taxonomic heterogeneity and its ecological drivers. *Crit. Rev. Pl. Sci.* 37: 128–174. https://doi.org/10.1080/07352689.2018.1482434

Johnson, M.G., Gardner, E.M., Liu, Y., Medina, R., Goffinet, B., Shaw, A.J., Zerega, N.J. & Wickett, N.J. 2016. HybPiper: Extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. *Applic. Pl. Sci.* 4: 1600016. https://doi.org/10.3732/apps.1600016

Katoh, K. & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molec. Biol. Evol.* 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kirbis, A., Waller, M., Ricca, M., Bont, Z., Neubauer, A., Goffinet, B. & Szövényi, P. 2020. Transcriptional landscapes of divergent sporophyte development in two mosses, *Physcomitrium* (*Physcomitrella*) *patens* and *Funaria hygrometrica*. *Frontiers Pl. Sci. (Online journal)* 11: 747. https://doi.org/10.3389/fpls.2020.00747

Koponen, T. 2010. Compilation of *Musci* in *Symbolae Sinicae* in the light of H. Handel-Mazzetti's letters to V. F. Brotherus. *Bryobrothera* 10: 1–78.

Limpricht, K.G. 1895. *Dr L. Rabenhorst's Kryptogamen-Flora von Deutschland Oesterreich und der Schweiz*, 2nd ed., vol. 4, *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz*, 2. Abt., *Bryineae (Stegocarpae [Acrocarpae, Pleurocarpe excl. Hypnaceae])*. Leipzig: Kummer.

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. *Molec. Phylogen. Evol.* 62: 130–145. https://doi.org/10.1016/j.ympev.2011.09.010

McDaniel, S.F., von Stackelberg, M., Richardt, S., Quatrano, R.S., Reski, R. & Rensing, S.A. 2010. The speciation history of the *Physcomitrium—Physcomitrella* species complex. *Evolution* 64: 217–231.https://doi.org/10.1111/j.1558-5646.2009.00797.x

Medina, R., Johnson, M., Liu, Y., Wilding, N., Hedderson, T.A., Wickett, N. & Goffinet, B. 2018. Evolutionary dynamism in bryophytes: Phylogenomic inferences confirm rapid radiation in the family Funariaceae. *Molec. Phylogen. Evol.* 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 targeted sequencing of nuclear exons and their flanking regions rejects the retention of *Physcomitrella*, *Physcomitridium* and *Aphanorrhegma*. *J. Syst. Evol.* 57: 404–417. https://doi.org/10.1111/jse.12516

Medina, R., Johnson, M.G., Patel, N., Tocci, G.E., Toren, D.R. & Goffinet, B. 2022. Vindication of *Physcomitrium pygmaeum*:

An elusive and endangered moss from North America's Great Basin. *Bryologist* 125: 528–540. https://doi.org/10.1639/0007-2745-125.4.528

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

Ostendorf, A.K., Van Gessel, N., Malkowsky, Y., Sabovljevic, M.S. & Rensing, S.A. 2021. Polyploidization within the Funariaceae—A key principle behind speciation, sporophyte reduction and the high variance of spore diameters? *Bryophyte Diversity Evol.* 43: 164–179. https://doi.org/10.11646/bde.43.1.13

Patel, N., Medina, R., Johnson, M. & Goffinet, B. 2021. Karyotypic diversity and cryptic speciation: Have we vastly underestimated moss species diversity? *Bryophyte Diversity Evol.* 43: 150–163. https://doi.org/10.11646/bde.43.1.12

Patel, N., Medina, R., Willliams, L.D., Lemieux, O., Goffinet, B. & Johnson, M.J. In press. Frequent allopolyploidy with distant progenitors in the moss genera *Physcomitrium* and *Entosthodon* (Funariaceae) identified via subgenome phasing of targeted nuclear genes. *Evolution.*

Peng, T. & Zhang, Z. 2007. New records of the bryophytes in Xiangzhigou Scenic Spot, Guizhou Province. *J. Guizhou Norm. Univ. (Nat. Sci.)* 25: 20–24.

Schwägrichen, C.F. 1823. *Species muscorum frondosorum, Supplementum secundum*, vol. 1(1). Lipsiae [Leipzig]: sumtu Ioannis Ambrosii Bartii. https://doi.org/10.5962/bhl.title.26

Smith, S.A., Moore, M.J., Brown, J.W. & Yang, Y. 2015. Analysis of phylogenomic datasets reveals conflict, concordance, and gene duplications with examples from animals and plants. *B. M. C. Evol. Biol.* 15: 150. https://doi.org/10.1186/s12862-015-0423-0

Snider, J. 1975. A revision of the genus *Archidium* (Musci). *J. Hattori Bot. Lab.* 39: 105–201.

Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Sukumaran, J. & Holder, M.T. 2010. DendroPy: A Python library for phylogenetic computing. *Bioinformatics* 26: 1569–1571. https://doi.org/10.1093/bioinformatics/btq228

Tan, B.C. 1979. A new classification for the genus *Physcomitrella*. *J. Hattori Bot. Lab.* 46: 327–336.

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.H., Li, D.Z., Marhold, K. & May, T.W. (eds.) 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books. https://doi.org/10.12705/Code.2018

Vitt, D.H. 1981. Adaptive modes of the moss sporophyte. *Bryologist* 84: 166–186. https://doi.org/10.2307/3242820

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

Wilding, N. 2015. *Systematics, biogeography and morphological evolution in Entosthodon Schwägr. (Bryopsida, Funariaceae) with a revision of the genus in Africa*. Ph.D. Dissertation. University of Cape Town, Cape Town, South Africa.

Xu, S., Zhang, Z.-H. & Wang, Z.-H. 2021. Effects of heavy metals on moss diversity and analysis of moss indicator species in Nancha manganese mining area, Southwestern China. *Global Ecol. Conservation* 28: e01665. https://doi.org/10.1016/j.gecco.2021.e01665

Zhang, C., Sayyari, E. & Mirarab, S. 2017. ASTRAL-III: Increased scalability and impacts of contracting low support branches. Pp. 53–57 in: Meidanis, J. & Nakhleh, L. (eds.), *Comparative genomics*. Cham: Springer International.

Zhang, L. & Zuo, Q. 2015. The rediscovery and the phylogenetic position of *Brachymeniopsis* Broth. (Funariaceae, Bryophyta). P. 26 in: *International Association of Bryologists (IAB) Conference, January 11–15, 2015: Program and Abstracts.*