Phytotaxa 689 (1): 015–026
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.689.1.2

The neglected Brazilian moss, *Hyophila loxorhyncha* (Pottiaceae, Bryophyta), re-emerges as *Trichostomum loxorhynchum*

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Abstract

The ongoing morphological and molecular analyses of the genus *Trichostomum* in South America has allowed us to study some specimens from Brazil, Bolivia, and Paraguay that do not match with any Pottiaceae species presently recognized in these countries. We originally identified them as *Hyophila loxorhyncha*, a neglected taxon known only from the type locality and a few others Brazilian localities. The phylogenetic position of this species is inferred based on the new specimens by the nuclear ITS sequences. This analysis resolves the species in the clade corresponding to the genus *Trichostomum*, supporting its new combination as *T. loxorhynchum*. We present a complete description of this species, its distribution map, and its main distinctive morphological characters. Lectotypes are also proposed for *Hyophila loxorhyncha* and *Gymnostomum jamesonii*. *Trichostomum loxorhynchum* is newly reported from Bolivia and Paraguay. The distribution of *Tainoa subcucullata* is here updated excluding South America.

Key words: *Hyophila*, Pottiaceae, South America, Taxonomy, *Trichostomum*

Introduction

The Pottiaceae (Bryophyta) is by far the most species-rich moss family, consisting of 108 accepted genera and 1255 accepted species (Brinda & Atwood 2024). The identification of the species in this family is often considered difficult due to the reduced size of the plants, polymorphic morphological traits, and the high taxonomic importance of anatomical characters that are sometimes difficult to observe. Additionally, sporophytes are absent or rare in many specimens, and there is a lack of regional manuals for correct identification, particularly in tropical areas (Zander 1993, Cárdenas 1995). Despite its complexity, numerous authors have conducted extensive taxonomic studies on this family in the past two decades, with molecular analyses providing abundant data on the phylogenetic relationships of many genera (e.g., Kučera *et al.* 2013, Alonso *et al.* 2019, Cano *et al.* 2022a, Jiménez *et al.* 2022). Preliminary studies of this family in South America have shown problems in the circumscription of some species within the family. The ongoing morphological and molecular analyses of the genus *Trichostomum* Bruch in South America has allowed us to study material of this genus deposited in the main European and American herbaria and our own collections kept at MUB. We have found some *Trichostomum* specimens from Brazil, Bolivia, and Paraguay that do not match with any species currently recognised in the latest checklists or treatments from these countries (O'Shea & Price 2008, Churchill *et al.* 2009, Costa 2016). The specimens were tentatively placed in the genus *Hyophila* Brid., based on the epapillose ventrally bulging upper laminal cells and the poorly differentiated small area of short basal laminal cells near the insertion. However, the shape of the leaves and absence of propagula, together with the costa anatomy and the differentiation of bulging laminal cells in one recently described species, *Trichostomum mammillosum* R.H. Zander (Zander 2023), suggested their inclusion within *Trichostomum*. Mainly due to the large number of species in this genus and its remarkable morphological diversity, the taxonomic delimitation of *Trichostomum* has been a challenge for taxonomists (Alonso *et al*. 2016). This work presents a taxonomic study based on morphological and molecular phylogenetic data, considering the possibility that the diversity of the South American subfamily Trichostomoideae

Accepted by Vítězslav Plášek: 27 Jan. 2025; published: 20 Feb. 2025

is still underestimated. Its aims were: 1. study the types of previous names described in Trichostomoideae in South America to explore possible available names applicable to newfound plants, 2. provide a complete morphological description of these specimens, and 3. resolve its phylogenetic position within the Pottiaceae.

Materials and methods

Taxon sampling

For morphological delimitation and characterization of the species, we studied approximately 500 specimens of *Trichostomum* from 7 herbaria (BM, FH, JE, L, MO, MUB, NY, S), including the types of the genera *Hyophila* and *Trichostomum* described from South America, as well as material collected by the authors in the field. Index Herbariorum (2024) acronyms are used for designation of herbaria. Nomenclature follows Brinda & Atwood (2024) except for *Scopelophila cataractae* (Mitt.) Broth. and *Neotrichostomum crispulum* (Bruch) R.H. Zander which follow Zander (1993, 2023).

To determine the phylogenetic position of the controversial specimens, representative genera of Trichostomiodeae were sampled: the tribe Hyophileae M. Fleisch. (*Hyophila* and *Plaubelia* Brid.), the tribe Pleuroweisieae Limpr. (*Gymnostomum* Nees & Hornsch., *Anoectangium* Schwägr., *Tuerckheimia* Broth., *Molendoa* Lindb., *Hymenostylium* Brid., *Hymenostyliella* E.B. Bartram, *Reimersia* P.C. Chen, *Gyroweisia* Schimp., and *Leptobarbula* Schimp.), the tribe Trichostomeae Dixon (*Trichostomum*, *Neotrichostomum* R.H. Zander, *Weissia* Hedw., *Aschisma* Lindb., *Ephemerum* Hampe, *Chionoloma* Dixon, *Pachyneuropsis* H.A. Mill., *Eucladium* Bruch & Schimp., *Tortella* (Müll. Hal.) Limpr., *Pleurochaete* Lindb., *Streptocalypta* Müll. Hal., and *Pottiopsis* Blockeel & A.J.E. Sm.), and a group of four *Hydrogonium* (Müll. Hal.) A. Jaeger species. This selection is based on previous phylogenetic studies within the subfamily Trichostomoideae (Werner *et al.* 2004, 2005, Alonso *et al.* 2016, Inoue & Aung 2021). *Scopelophila cataractae* was used to root the phylogeny. Specimen data are listed in Table 1.

DNA extraction, amplification and sequencing

Plants were placed under a stereo microscope and the green distal portion of a few gametophores per specimen were dissected. Total genomic DNA was extracted using the method of Suzuki *et al.* (2013) with some minor modification. The shoots were ground with 80 µl extraction buffer (TE) using a polypropylene pestle in a 1.5 ml microcentrifuge tube. Once ground, a further 80 µl of extraction buffer (TE) was added, mixed gently and stored at –20°C until the polymerase chain reaction (PCR) was carried out. We selected the nuclear internal transcribed spacers 1 and 2 (ITS1-5.8S-ITS2). The ITS1 and ITS2 were either amplified and sequenced separately or in a single amplification. This locus has been shown to be useful for phylogenetic reconstruction in the Pottiaceae (Cano *et al*. 2009, Alonso *et al.* 2016, Cano *et al.* 2022b, Gallego *et al.* 2022, Jiménez *et al.* 2022, Cano *et al.* 2024). The primer pairs used were ITS1-F/ITS1-R (Sawicki & Szczecińska 2011) and seqITS2 (Olsson 2009). Amplification reactions were performed using an Eppendorf Mastercycler in a 25 µL volume containing 10 µL Supreme NZYTaq II 2x Green Master Mix (Nzytech, Lisbon, Portugal), 2 µL of each primer (10 µM), and 1 µL of the DNA extract. Thermocycling conditions were as follows: 4 min at 95 °C, 35 cycles of 1 min at 94 °C, 1 min at 55 °C and 1 min 30 sec at 72 °C, and a final 7 min extension step at 72 °C. PCR products were visualized on a 1% agarose gel. Successful amplifications were purified using the GenElute PCR Clean-Up kit (Sigma-Aldrich, St. Louis, MO, USA), and sequenced at Macrogen Spain (Madrid, Spain). Nucleotide sequence contigs were edited and assembled for each DNA region using Geneious 9.1.8 (Kearse *et al*. 2012). Consensus sequences were aligned using default parameters of MUSCLE (Edgar 2004) implemented in Geneious with subsequent manual adjustments. Regions of partially incomplete data in the beginning and end of the sequences were identified and were excluded from subsequent analyses. Insertions and deletions (indels) were coded using SeqState v.1.4.1 (Müller 2005) using a simple coding model as suggested by Simmons & Ochoterena (2000). We present the analyses with the indels included since these provided additional phylogenetic evidence.

Phylogenetic analysis

Phylogenetic relationships were estimated using maximum likelihood (ML) in IQ-TREE v.2.3.4 (Minh *et al*. 2020) under the best-fit substitution model automatically selected by the software according to Bayesian information criterion

(BIC) (Kalyaanamoorthy *et al*. 2017). Branch support was obtained through 1000 replicates of ultrafast bootstrap (UFBoot) (Hoang *et al*. 2018), and additionally, we performed a Bayesian-like transformation of the approximate likelihood ratio test [aLRT] (aBayes) (Anisimova *et al.* 2011). An ultrafast bootstrap support (UFBoot) ≥ 95% and aBayes support ≥ 0.95 were considered strong support. Phylogenetic rooting was done using midpoint methodology (Hess & De Moraes Russo 2007). Trees were visualized and partially edited in FigTree v. 1.4.4 (Rambaut 2018).

Morphological-anatomical analysis

The samples were studied with the typical anatomical and morphological methods applied for the Pottiaceae (Zander 1993). Microscopic examinations and measurements were taken with an Olympus BH-2 light microscope and microphotographs were obtained with a Jenoptik ProgRes C7 camera mounted on the microscope. Laminal cells measurements and types of basal laminal cells followed Alonso (2018). Chemical color reaction of the lamina was observed using 2% potassium hydroxide (KOH), which increases index of refraction and generates a distinctive color reaction in many Pottiaceae taxa (Zander 1993).

Results

Nomenclaural assessment

Examination of the type material for the published names of South American Trichostomoideae revealed that *Gymnostomum jamesonii* Arn. and *Hyophila loxorhyncha* Müll. Hal. ex Ångstr. are conspecific, both exhibiting the morphological characters found in our controversial specimens (see taxonomy section). *Hyophila loxorhyncha* was originally described by Ångström (1876) from a single locality in Brazil (Caldas) and later reported from a few others Brazilian localities (Brotherus 1894, 1895, 1924). Subsequently, the species has not been documented anew, nor is it identified among the species treated by Costa (2016) within the family. *Gymnostomum jamesonii* was described by Arnott (1824) and later transferred to *Weissia* Hedw. by Mitten (1869) as the illegitimate *W. jamesonii* (Arn.) Mitt., and finally to *Hymenostomum* by Hampe (1879) as *H. jamesonii* (Arn.) Hampe. Among the synonyms of the latter, Hampe (1879) also considered a specimen collected by Salzmann in Bahia described by Duby (1836) as *Gymnostomum bahiense* Salzm. ex Duby. Through the courtesy to the staff of Geneva Herbarium (G) we have been able to study images of its original material. Although these images did not allow us to confirm the identity of the species with certainty, they have helped us to rule out conspecificity between *G. bahiense* and *G. jamesonii*. Consequently, the first published epithet would have priority but cannot be used under *Trichostomum* due to the existence of *Trichostomum jamesonii* (Taylor) Mitt. Therefore, we propose here a new combination to be used hereafter, *Trichostomum loxorhynchum* (Müll. Hal. ex Ångrst.) M.J. Cano, M.T. Gallego & O. Rodríguez, *comb. nov.*

Phylogenetic analyses of ITS sequences

The ITS sequence matrix is 1498 bp long (2493 bp including indels). The differences between *Trichostomum loxorhynchum* and the nearest related taxa according to ITS are quite extensive in both ITS1 and ITS2 spacers and include dozens of substitutions and many indel events ranging from 1 to 36 bp in length. The topology of the ML tree is shown (Fig. 1), with ultrafast bootstrap support (UFBoot) and aBayes support values. The results of the analyses conducted using this method were found to be largely in agreement, with node support consistently high for both the ultrafast bootstrap (UFBoot) and the Bayesian-like transformation of aLRT (aBayes). However, there were some exceptions where aBayes exhibited higher node support.

The phylogenetic tree (Fig. 1) shows a well-supported clade of *Hydrogonium* (aBayes = 0.99; UFBoot = 96). After that, a strongly supported clade (aBayes = 1; UFBoot = 100) includes species of the tribe Hyophileae. The tribes Pleuroweisieae (aBayes = 0.98; UFBoot = 79) and Trichostomeae (aBayes = 0.98; UFBoot = 89) are only well supported by aBayes. Within Trichostomeae, two well-supported subclades are resolved. One clade with *Pottiopsis* sister to *Streptocalypta*, *Pleurochaete*, *Tortella*, *Eucladium*, *Pachyneuropsis*, and *Chionoloma* (aBayes = 1; UFBoot = 98), and another with *Ephemerum* sister to *Aschisma*, *Weissia*, *Neotrichostomum*, and *Trichostomum* (aBayes = 1; UFBoot = 99). *Trichostomum* is resolved only with aBayes support (aBayes = 1; UFBoot = 67), with *Neotrichostomum* and *Weissia* grouped as sisters (aBayes = 0.99; UFBoot = 71). *Trichostomum loxorhynchum* is fully supported (aBayes

= 1; UFBoot = 100) within *Trichostomum* clade, with *T. antillarum* R.H. Zander as sister (aBayes = 1; UFBoot = 100). In turn, this clade is significantly distant from the Hyophileae tribe.

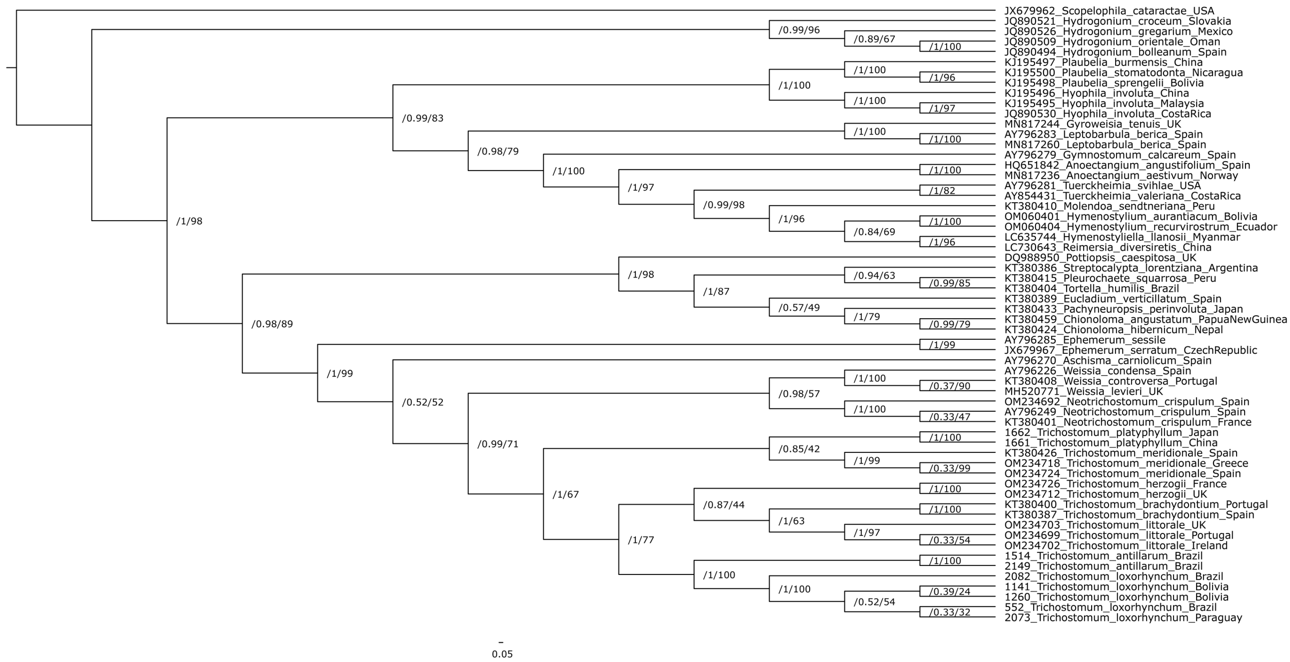

FIGURE 1. Maximum likelihood topology as estimated by IQ-TREE v.2.3.4 showing the phylogenetic relationships of *Trichostomum loxorhynchum* and the related genera within the subfamily Trichostomoideae based on ITS data. Numbers at nodes (from left to right) indicated bootstrap values from aBayes support and ultrafast bootstrap support (%).

Taxonomy

Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez, *comb. nov.* Fig. 2

Basionym:—*Hyophila loxorhyncha* Müll. Hal. ex Ångstr., Öfvers. Kongl. Vetensk. -Akad. Förh. 33(4): 9. 1876 (Ångström 1876). Type citation: "Regnell sub No: 39 p.p. misit". Type:—BRAZIL. Minas Gerais, Caldas, *A.F. Regnell 39 pp*. (lectotype, designated here: S B185598!; isolectotypes: BM000872464-image!, S B123936!). ≡ *Syrrhopodon loxorhynchus* (Müll. Hal. ex Ångstr.) Paris, Index Bryol.: 1250. 1898 (Paris 1898).

= *Gymnostomum jamesonii* Arn., Soc. Hist. Nat. Paris 1(2): 347. 1824 (Arnott 1824) *syn. nov.* Type citation: "In collibus in Rio de Janeiro". Type:—BRAZIL. Rio de Janeiro, 1822, *M.N. Jameson s.n.* (lectotype, designated here: BM000872360!; isolectotypes: BM000872361!, BM000872362! and E00428848-image!). ≡ *Weissia jamesonii* (Arn.) Mitt., J. Linn. Soc., Bot., 12: 132. 1869 (Mitten 1869) *nom. illeg.* ≡ *Hymenostomum jamesonii* (Arn.) Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn, ser. 4, 1–2: 84. 1879 (Hampe 1879).

Description:**—***Plants* 5–10 mm high, forming dense tufts, bright light green. *Stems* 3.2–9.3 mm high, erect, not or scarcely tomentose, simple or scarcely branched; in cross-section rounded, sometimes oval, (120)160–210 µm in diameter, with hyalodermis, sclerodermis differentiated by 1–2(3) layers of thicker-walled cells; central strand present; axillary hairs filiform, 4–9 hyaline cells, 60–110 µm long. *Rhizoids* red-brown, smooth. *Leaves* twisted or incurved and crispate when dry, erect or erect-patent when moist, elliptical to oblong-elliptical, (1.4)1.6–2.4 mm length, 0.3–0.4 mm wide at base, 0.3–0.5 mm wide at the middle, 0.1–0.3 mm wide at apex, canaliculated from midleaf to apex, base hyaline, not seated, usually slightly undulate above the basal part, constricted in the upper base, sometimes fragile; lamina unistratose throughout, yellow-orange in KOH reaction; *margins* entire, slightly incurved in upper third, plane otherwise, unbordered; *apex* acute, sometimes obtuse; *costa* 60–84 µm wide at base, 26–36 µm wide at apex, excurrent in a straight mucro, 24–44(–60) µm long, brownish, ventral surface cells quadrate to short rectangular, sometimes oblate, and smooth from base to apex, dorsal surface cells linear and smooth from base to apex, in cross-section plano-convex, with 4–5 guide cells at base and midleaf, and 2–3(–4) guide cells distally, 2–4(–5) layers of ventral stereids and 2–4 layers of dorsal stereids at midleaf, ventral surface cells rounded to quadrate or short-rectangular, (4)6–10 ×

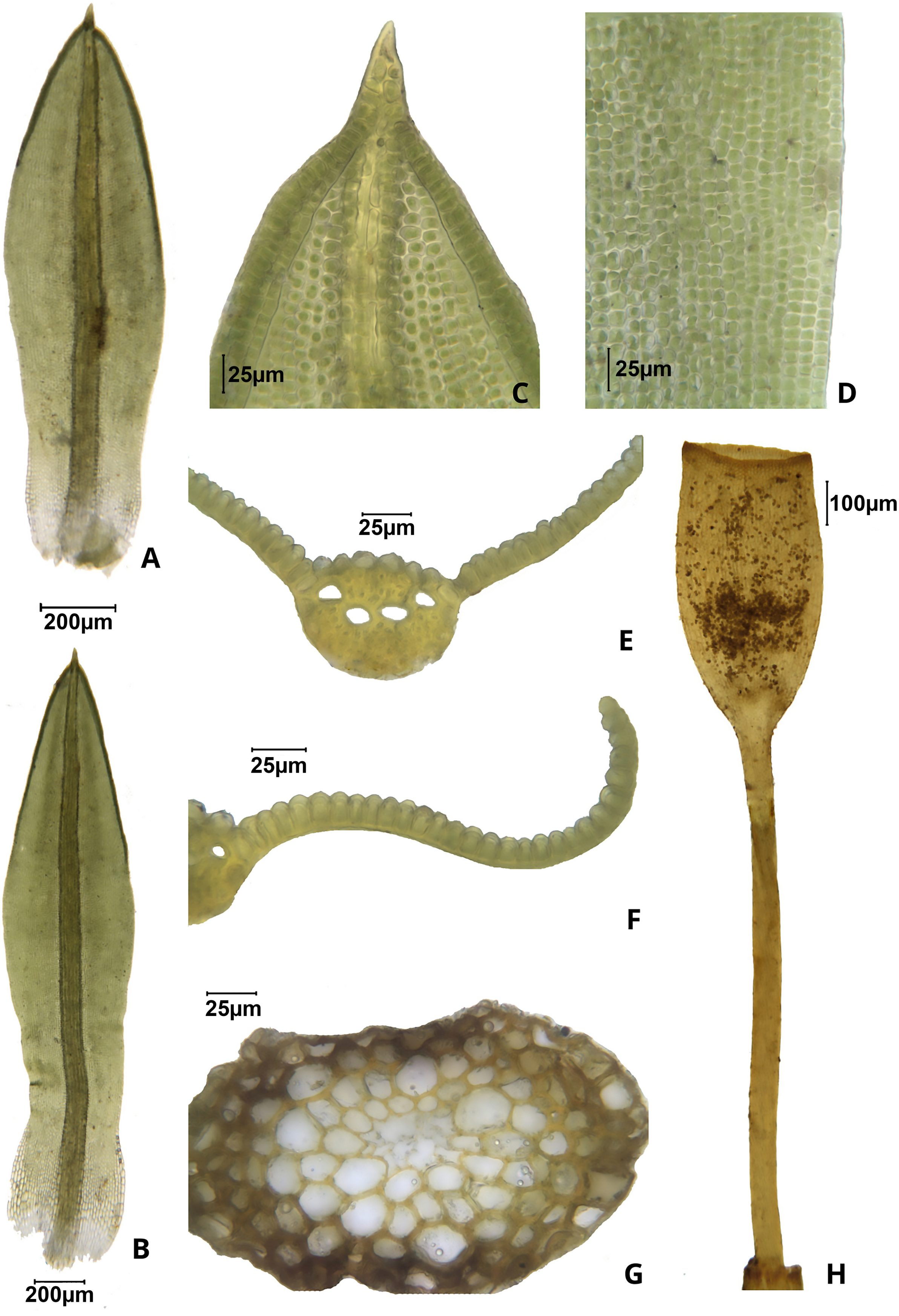

FIGURE 2. *Trichostomum loxorhynchum*. A–B: leaves, C: leaf apex, D: middle laminal cells, E–F: cross-sections at midleaf, G: cross-section of the stem, H: sporophyte. A–D from *Soares et al. 2214* (MUB); E–G from *Churchill & Florentín 20159a* (MUB); H from *Dialer s.n.* (S).

(4)6–8(10) µm, smooth, occasionally with inconspicuous papillae, dorsal surface cells rounded, 4–8(10) × 4–6 µm, smooth; *upper and midleaf laminal cells* mostly rounded or rectangular, sometimes hexagonal or oblate, (2–)4–8(–10) × (2–)4–8 µm, slightly thick-walled, ventrally strongly bulging, dorsally flat, smooth; *upper and midleaf marginal cells* oblate or quadrate, 2–4 × 4–6(–8) µm, slightly thick-walled, smooth, or sometimes with low papillae dorsally; *lower basal cells* rectangular or oblong, (14–)18–28 × 6–10(–12) µm, thin-walled, smooth; *marginal basal cells* rectangular, 22–36(–42) × 8–14(–18) µm, thin-walled, smooth; *central basal cells* oblong or rectangular, (14–)18–48(–52) × 6–10 µm, thick-walled, smooth; *juxtacostal cells* rectangular, (8–)10–36(–44) × 6–12 µm, thick-walled, smooth; *transitional cells* mostly rectangular or quadrate, sometimes irregular, (4–)6–14(–18) × 4–8 µm, thick-walled, smooth. Specialized asexual reproduction absent. *Dioicous*. *Perichaetial leaves* undifferentiated. *Seta* 2.7–3.6 (5.1) mm long, twisted to the left from the middle to the upper part, brownish. *Capsule* stegocarpous, erect and exserted; *Theca* (urn) obloid, 0.5–1.2 × 0.36–0.7 mm, light brown; *exothecial cells* subquadrate to rounded, 6–8 × 6–10 µm, thin-walled; *annulus* not seen. *Peristome* absent. *Operculum* subulate, 0.6–0.8 mm. *Calyptrae* cucullate, 1.2–1.8 mm, smooth. *Spores* 10–16 µm in diameter, brown, coarsely granulose.

Habitat:—On clay or rocky soils, sometimes on poorly drained soils or landscaped areas, in Cerrado, Chaco and Caatinga biome; 150–1168 m a.s.l.

Distribution:—Bolivia, Brazil and Paraguay (Fig. 3).

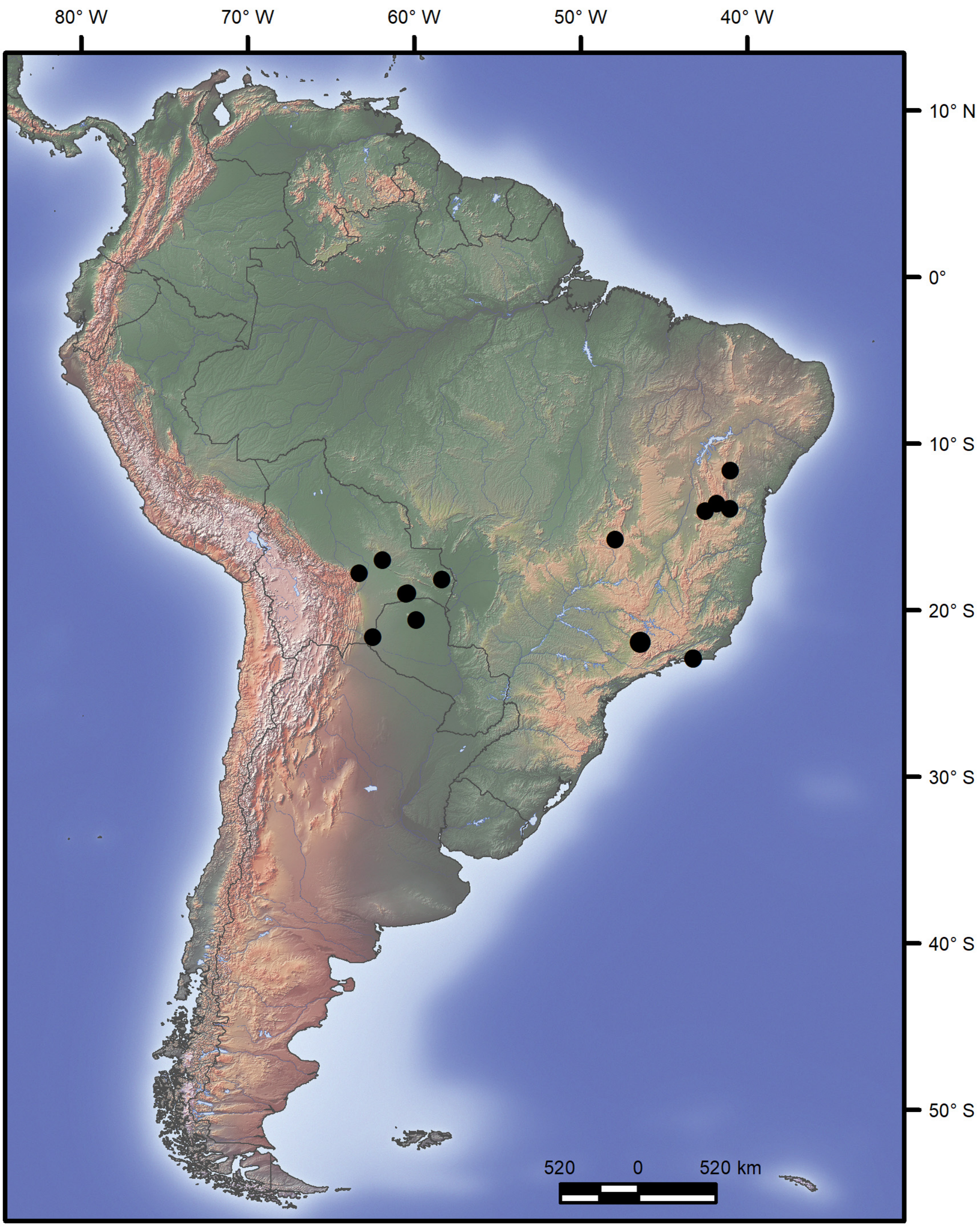

FIGURE 3. Geographical distribution of the studied specimens of *Trichostomum loxorhynchum*.

Remarks:—*Hyophila loxorhyncha* was described by Ångström (1876) based on a single gathering collected by A. F. Regnell in Caldas (Brazil). We have located three syntypes of this material deposited in S and BM. All duplicates coincide with the protologue and they do not contradict the guidelines in the ICN. Material from S: B185598 is here chosen as lectotype to prioritize the author´s herbarium. *Gymnostomum jamesonii* was described by Arnott (1824) based on a specimen collected by M. N. Jameson in Rio de Janeiro (Brazil). We found four syntypes of this material deposited in BM and E. Material from BM: BM000872360 is here chosen as lectotype because it has the most material with sporophytes.

Specimens examined:—Bolivia. Santa Cruz: Andrés Ibáñez, laguna Capibara, km 6 antigua carretera a Cochabamba, 3 km al N laguna Capibara, 3 December 1993, *Fuentes 292a,* MO (5913997); Nuflo de Chavez, Pascana San Miguelito, 31 July 1995, *Fuentes 1009*, MUB (40334); Germán Busch, localidad de Bocaina, camino a Rincón del Tigre (a 100 m del camino), 26 September 2005, *Linneo & Parada 168*, MUB (40335); Cordillera, entrando por Robore, 25 km pasando el puesto de guardaparques del parque Kaa Iya, de ida al puesto Abaroa (Fortín), 12 November 2013, *Linneo & Villarroel 3792* MUB (58588); same data as for preceding, 14 November 2013, *Linneo & Villarroel 3830*, MUB (58583); Tarija: Gran Chaco, La Reserva Natural El Corbalán, few kms north of Esmeralda (border with Paraguay), 13 May 2008, *Abrahamczyck 6*, MUB (29237).

Brazil. Bahia: Caetité, June 1914, *Dialer s.n.*, S (B185597); ca. 20km E of Morro do Chapéu, road to Mundo Novo, 21 February 1971, *Irwin et al. 30740*, MUB (41353); Livramento do Brumado, 3–6 km da cidade na estrada para Rio de Contas, 5 December 1988, *Harley 27069a,* MO (5285129); Mun. Tremedal, km 72 on BA 262 between Vitoria da Conquista and Brumado, 21.5 km WNW of Anajé, 29 km SE of Aracatu, 19 July 1991, *Vital & Buck 20368b*, MUB (63547); Contendas do Sincorá, Floresta Nacional de Contentas do Sincorá, Trilha das Grotas, 3 December 2009, *Peralta & Perez-Maluf 10291*, MUB (44439); Distrito Federal: Brasilia, 13 May 2012, *Soares et al. 2214*, MUB (43300); Rio de Janeiro: s.loc., s.d., *Doellinges s.n*, L (L 0789547); Catumbi, 23 June 1873, *Mosén 198*, S (B185600); Catumbi, 22 June 1873, *Mosén s.n.*, S (B185596); Comprido, January 1887, *Schenk 4822*, S (B195599); Corcovado, 23 August 1888, *Schwacke 6358*, L (L 0473906).

Paraguay. Alto Paraguay: Madrejón, en Parque Nacional Defensores del Chaco, March 2000, *Churchill & Florentín 20159a,* MUB (21809).

Discussion

The integration of morphological and molecular data of this study provides evidence to recognize our controversial specimens as a new combination within the genus *Trichostomum*. The specimens of *T. loxorhynchum* included in the molecular study appear in a well-supported clade within the genus *Trichostomum*, which indicates a considerable phylogenetic distance with the species of *Hyophila*. *Trichostomum loxorhynchum* is characterized by oblong-elliptical, (1.4)1.6–2.4 mm long leaves, constricted near the base, with acute to obtuse apices, entire, unbordered and usually incurved margins in the upper third, and the costa excurrent in a straight, short mucro. But the most striking feature is the bulging laminal cells and the apparent absence of papillae on the entire lamina, although sometimes inconspicuous papillae may develop dorsally on the upper and middle marginal cells of the leaf and on the ventral surface cells of the costa.

Morphologically, *T. loxorhynchum* shares traits with the genus *Hyophila*, such as the strongly bulging upper and midleaf cells ventrally and capsules eperistomates, but differs by its excurrent costa as a mucro, unbordered margins and absence of gemmae. *Hyophila* has a percurrent costa ending in a short apiculus, leaf margins sometimes differentiated as a thickened border, and gemmae produced in leaf axils.

Our results suggest that *T. loxorhynchum* is related to *T. antillarum*, a species distributed in Cuba, Brazil, Guadeloupe Island, Mexico, Puerto Rico, the United States (Texas), the Virgin Islands, and the Windward Islands (Zander 2023). *Trichostomum loxorhynchum* differs from the latter mainly by the bulging and smooth laminal cells on the ventral side and the absence of a border, as *T. antillarum* has papillose leaf cells and distinct leaf borders. The recently described *T. mammillosum* from the Dominican Republic also lacks papillae on the leaves and the upper and middle laminal cells are ventrally bulging, as in *T. loxorhynchum*, but differs in the size and shape of the leaves: elliptical, sometimes oblong, (1.4–)1.6–2.4 mm long in *T. loxorhynchum*, and long-lanceolate to long-elliptical, 2.5–3(–4) mm long in *T. mammillosum*.

Two specimens of *T. loxorhynchum* from Bolivia (*Linneo & Parada 168*, MO 592279) and Brazil (*Harley 27069a,* MO 5285129) were previously identified as *Tainoa subcucullata* (R.S. Williams) R.H. Zander by Zander

(2023). *Tainoa subcucullata* differs from *T. loxorhynchum* mainly by a ventrally papillose costa and upper laminal cells papillose on both sides. Therefore, *Tainoa subcucullata* must be excluded from South America and its distribution restricted to Cuba and Trinidad and Tobago.

TABLE 1. Alphabetical list of taxa used for the phylogenetic analyses with vouchers and GenBank accession numbers. Newly obtained accession number is shown in bold.

	Voucher information	GenBank accesion no.	Reference
Anoectangium angustifolium Mitt.	Spain, *Köckinger s.n.* (CBFS)	HQ651842	Köckinger & Kučera (2011)
Anoectangium aestivum (Hedw.) Spruce	Norway, *Kučera 15892* (CBFS)	MN817236	Ignatova *et al*. (2019)
Aschisma carniolicum (F. Weber & D. Mohr) Lindb.	Spain, *Cano et al. s.n.* (MUB)	AY796270	Werner *et al*. (2005)
Chionoloma angustatum (Mitt.) M. Menzel	Papua New Guinea, *Norris 62286* (S)	KT380459	Alonso *et al*. (2016)
Chionoloma hibernicum (Mitt.) M. Alonso, M.J. Cano & J.A. Jiménez	Nepal, *Long 30538* (E)	KT380424	Alonso *et al*. (2016)
Ephemerum serratum (Schreb. ex Hedw.) Hampe	Czech Republic, *Košnar 692* (CBFS)	JX679967	Kučera *et al*. (2013)
Ephemerum sessile (Bruch) Müll. Hal.	Location and collection data unknown (MUB)	AY796285	Alonso *et al*. (2016)
Eucladium verticillatum (With.) Bruch & Schimp.	Spain, *Cano 6702* (MUB)	KT380389	Alonso *et al*. (2016)
Gymnostomum calcareum Nees & Hornsch.	Spain, *Guerra et al. s.n.* (MUB)	AY796279	Werner *et al*. (2005)
Gyroweisia tenuis (Hedw.) Schimp.	United Kingdom, *Blockeel 42/036*	MN817244	Ignatova *et al*. (2019)
Hydrogonium bolleanum (Müll. Hal.) A. Jaeger	Spain, *Kučera 13670* (CBFS)	JQ890494	Kučera *et al*. (2013)
Hydrogonium croceum (Brid.) Jan Kučera	Slovakia, *Kučera 1087* (CBFS)	JQ890521	Kučera *et al*. (2013)
Hydrogonium gregarium (Mitt.) Jan Kučera	Mexico, *Eckel 188986* (DUKE)	JQ890526	Kučera *et al*. (2013)
Hydrogonium orientale (F. Weber) Jan Kučera	Oman, *Rothfels 2763* (DUKE)	JQ890509	Kučera *et al*. (2013)
Hymenostyliella llanosii (Müll. Hal.) H. Rob.	Myanmar, *Inoue 7547* (TNS)	LC635744	Inoue & Aung (2021)
Hymenostylium aurantiacum Mitt.	Bolivia, *Churchill et al. 23336* (MUB)	OM060401	Cano *et al*. (2022b)
Hymenostylium recurvirostrum (Hedw.) Dixon	Ecuador, *Cano and Gallego 2905a* (MUB)	OM060404	Cano *et al*. (2022b)
Hyophila involuta (Hook.) A. Jaeger	China, *Zhang 9797* (SZG)	KJ195496	Mao *et al*. (2014)
Hyophila involuta (Hook.) A. Jaeger	Costa Rica, *Hauer s.n.* (CBFS)	JQ890530	Kučera *et al*. (2013)
Hyophila involuta (Hook.) A. Jaeger	Malaysia, *Zhang 8636* (SZG)	KJ195495	Mao *et al*. (2014)
Leptobarbula berica (De Not.) Schimp.	Spain, *Cano 1014* (MUB)	AY796283	Werner *et al*. (2005)
Leptobarbula berica (De Not.) Schimp.	Spain, *Kučera 13640* (CBFS)	MN817260	Ignatova *et al*. (2019)
Molendoa sendtneriana (Bruch & Schimp.) Limpr.	Peru, *Cano and Jiménez 5333* (MUB)	KT380410	Alonso *et al*. (2016)
Neotrichostomum crispulum (Bruch) R.H. Zander	Spain, *Ros s.n.* (MUB)	AY796249	Werner *et al*. (2005)
Neotrichostomum crispulum (Bruch) R.H. Zander	Spain, *Ros and Werner s.n.* (MUB)	OM234692	Ros *et al*. (2022)
Neotrichostomum crispulum (Bruch) R.H. Zander	France, *Cano 6521* (MUB)	KT380401	Alonso *et al*. (2016)
Pachyneuropsis perinvoluta (Tixier) M. Alonso, M.J. Cano & J.A. Jiménez	Japan, *Yamaguchi 24446* (HIRO)	KT380433	Alonso *et al*. (2016)
Plaubelia burmensis (B.C. Tan & Z. Iwats.) S. He & Li Zhang	China, *Mao 101* (HIRO)	KJ195497	Mao *et al*. (2014)
Plaubelia sprengelii (Schwägr.) R.H. Zander	Bolivia, *Linneo and Nee LN203* (HIRO)	KJ195498	Mao *et al*. (2014)
Plaubelia stomatodonta (Cardot) R.H. Zander	Nicaragua, *Zhang 9797* (HIRO)	KJ195496	Mao *et al*. (2014)
Pottiopsis caespitosa (Bruch ex Brid.) Blockeel & A.J.E. Sm.	United Kingdom, *Long 30986* (BCB)	DQ988950	Ros & Werner (2007)
Reimersia diversiretis (Broth. ex Hand.-Mazz.) Shevock, W.Z. Ma, S. He & D.G. Long	China, *Shevock and Ma 50685* (TNS)	LC730643	Inoue & Aung (2023)
Scopelophila cataractae (Mitt.) Broth.	USA, *Shaw s.n.* (CBFS)	JX679962	Kučera *et al*. (2013)

......*continued on the next page*

TABLE 1. (Continued)

	Voucher information	GenBank accesion no.	Reference
Streptocalypta lorentziana Müll. Hal.	Argentina, *Cano et al. 4181* (MUB)	KT380386	Alonso *et al*. (2016)
Tortella humilis (Hedw.) Jenn.	Brazil, *Soares et al. 1728* (MUB)	KT380404	Alonso *et al*. (2016)
Trichostomum antillarum R.H. Zander	Brazil, *Athayde Filho s.n.* (MUB)	**PV053390**	This study
Trichostomum antillarum R.H. Zander	Brazil, *Câmara 2163* (MUB)	**PV053391**	This study
Trichostomum brachydontium Bruch	Portugal, *Cano 6569* (MUB)	KT380400	Alonso *et al*. (2016)
Trichostomum brachydontium Bruch	Spain, *Cano 792* (MUB)	KT380387	Alonso *et al*. (2016)
Trichostomum herzogii Ros, O. Werner & R.D. Porley	France, *Hugonnot s.n.* (MUB)	OM234726	Ros *et al*. (2022)
Trichostomum herzogii Ros, O. Werner & R.D. Porley	United Kingdom, *Blockeel 50/064* (MUB)	OM234712	Ros *et al*. (2022)
Trichostomum littorale Mitt.	Portugal, *R.D. Porley 41* (MUB)	OM234699	Ros *et al.* (2022)
Trichostomum littorale Mitt.	United Kingdom, *Norton 130211* (MUB)	OM234703	Ros *et al*. (2022)
Trichostomum littorale Mitt.	Ireland, *Hodgetts 11181* (MUB)	OM234702	Ros *et al*. (2022)
Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez	Brazil, *Soares et al. 2214* (MUB)	**PV053394**	This study
Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez	Brazil, *Peralta and Perez-Maluf 10291* (MUB)	**PV053396**	This study
Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez	Bolivia, *Linneo and Villarroel 3830* (MUB)	**PV053393**	This study
Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez	Bolivia, *Linneo and Villarroel 3792* (MUB)	**PV053392**	This study
Trichostomum loxorhynchum (Müll. Hal. ex Ångstr.) M.J. Cano, M.T. Gallego & O. Rodríguez	Paraguay, *Churchill and Florentín 20159a* (MUB)	**PV053395**	This study
Trichostomum meridionale Ros, O. Werner & R.D. Porley	Spain, *Cano 6745* (MUB)	KT380426	Alonso *et al.* (2016)
Trichostomum meridionale Ros, O. Werner & R.D. Porley	Spain, *Ros s.n.* (MUB)	OM234724	Ros *et al.* (2022)
Trichostomum meridionale Ros, O. Werner & R.D. Porley	Greece, *T.L. Blockeel 47/027* (MUB)	OM234718	Ros *et al.* (2022)
Trichostomum platyphyllum (Broth. ex Ihsiba) P.C. Chen	China, *Shevock and Yang 41653* (MUB)	**PV053389**	This study
Trichostomum platyphyllum (Broth. ex Ihsiba) P.C. Chen	Japan, *Orgaz s.n.* (MUB)	**PV053388**	This study
Tuerckheimia svihlae (E.B. Bartram) R.H. Zander	Costa Rica, *Anderson 24791* (DUKE)	AY796281	Werner *et al*. (2005)
Tuerckheimia valeriana (E.B. Bartram) R.H. Zander	Costa Rica, Bryotheca Goettingensis Fasc. 9, No. 38 (GOET)	AY854431	Grundmann *et al*. (2006)
Weissia condensa (Voit) Lindb.	Spain, *Ros and Werner s.n.* (MUB)	AY796226	Werner *et al*. (2005)
Weissia controversa Hedw.	Portugal, *Cano 6259* (MUB)	KT380408	Alonso *et al*. (2016)
Weissia levieri (Limpr.) Kindb.	United Kingdom, *Callaghan s.n.* (Priv. Herb. D.A. Callaghan)	MH520771	Callaghan *et al*. (2019)

Acknowledgments

This research was supported by the grants numbers PID2019-103993GB-I00 funded by MCIN/AEI/10.13039/501100011033 and by FSE+ and PID2023-147459NB-I00, funded by MCIU/AEl/10.13039/501100011033/FEDER, UE. We thank the curators of the herbaria cited in the text for sending the type and non-type specimens. We also thank K.

Watson (curator of Botany at Glasgow Museums) for his quick response and information on where to find some type material, and Michelle J. Price, Isabella Valette, and Mathilde Ruche from Geneva Conservatory and Botanical Garden (G) for providing images of the type material of *Gymnostomum bahiense*. MJC is grateful to Paulo E.A.S. Câmara and its bryology group for logistical support and help while conducting fieldwork in Brazil. OR is also grateful to Lars Hedenäs and Irene Bisang for their support and expertise during the stay at the Stockholm Museum of Natural History. Thanks are also given to Terry McIntosh for checking and correcting the English.

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