The *Trematodon longicollis* complex, widely distributed taxa?

Emanuelle LAIS DOS SANTOS[1] & Denilson Fernandes PERALTA[2]

[1] *Pós Graduação em Biodiversidade Vegetal e Meio Ambiente. Instituto de Pesquisas Ambientais, Av. Miguel Stéfano 3687 - CEP 04301902 São Paulo, SP, Brasil. E-mail: emanuellelais.s@gmail.com*

[2] *Instituto de Pesquisas Ambientais, Av. Miguel Stéfano 3687 - CEP 04301902 São Paulo, SP, Brasil. E-mail: denilsonfperalta@gmail.com*

Abstract: Lais dos Santos, E. & Peralta, D.F. (2026). The *Trematodon longicollis* complex, widely distributed taxa? *Frahmia*. 47:1 – 12.*

The revaluation of the type specimens corresponding to *Trematodon longicollis* Michx. and their respective synonyms resulted in the recognition of two species and one variety: *T. longicollis* var. *reflexus*, a new combination occurring in South America; *T. africanus* synonymized with *T. borbonicus*, which occurs in Africa and was recognized as a valid species; and *T. longicollis*, which has 14 species reduced to synonymy, with *T. aureus* and *T. humilis* becoming new synonyms. A description, with emphasis on spores, distribution, and taxonomic comments, were presented. Because this is a cosmopolitan species with variation in the gametophyte and sporophyte characters, observation of spore ornamentation and cross sections of the leaves are essential for determining a correct identification.

Keywords: cosmopolitan moss, ornate perina, estegocarpic.

1. Introduction

Approximately 86 species have been described for the genus *Trematodon* Michx. worldwide (Tropicos 2025) and the current global taxonomic review delimits 54 species, including *T. longicollis* (Santos & Peralta 2021 (in prep.). Recent classifications include the genus *Trematodon* in the family Bruchiaceae (Goffinet et al. 2009), but there is a need to include molecular analyses to characterize and delimit the species of the genus *Trematodon* and their relationships with other genera.

Trematodon Michx. (Bruchiaceae, Bryophyta) is a haplolepid moss, as it has peristome teeth composed of a row of cells. Distributed worldwide, mainly in temperate regions, it is found in highly altered regions (Colloti et al. 2003, Ramsay et al. 2018, Belkina & Vilnet, 2019, Ramsay et al. 2020), has terrestrial habits, and occurs on soil or rocks.

The first time the name *Trematodon* appeared in literature was in the Flora Boreal Americana in 1803, with the type species *Trematodon longicollis* Michx. (1803, 289), and in this work it was not placed in any family. *Trematodon* means: tremato (perforated) + odon (tooth), this characteristic being evident in the teeth of the

* Published online: January 9, 2026

peristome that have vertical grooves, horizontal trabeculae, and in the rectilinear tooth, perforations at the central line.

Trematodon longicollis was well illustrated for eastern North America, the type region, in Crum & Anderson (1981) and Zander (2007). In other studies, *T. longicollis* is evaluated with superficial observations of the spores, considering characteristics such as size (given as large, medium, small, etc.), coloration (Bruch et al. 1836[-1855], Briton 1913) and, less frequently, spore ornamentation. However, from this information, it is not possible to delimit the species. Another very common characteristic is the observation of the size of the neck in relation to the capsule (Roth 1911), which is very variable and does not allow a good differentiation between species.

The genus morphologically closest to *Trematodon* is *Bruchia*, which was revised by Rushing (1986). It is characterized by a long seta, a long neck in the capsule, and ornate spores. This author points out the difficulty of separating some species and refers to the works of Brown and Lemon (1981); Buck (1979); Rushing (1985, 1986), and Rushing and Snider (1985), agreeing that the differentiation of Bruchiaceae from other families should be made by spore morphology, even though this is not uniform within the family.

McClymont (1954) proposed that *Bruchia* species can be delimited or identified solely by spore morphology, and Rushing (1985) grouped them into four types of ornamentation: 1. warty, with a distinction between the proximal and distal poles, with the apertural region poorly defined; 2. perforated; 3. spiny; and 4. reticulate. Types 2, 3, and 4 also present a distinction between the proximal and distal poles, with a well-defined apertural region.

McClymont (1955) evaluated *T. longicollis* (January 1916, El Salvador, A. Kovare) and described it with the following characteristics: Well-defined proximal pole with triangular apertural region, surrounded by a ring. Spiny-baculate ornaments (ca. 1.5> alt), two rings around the aperture, with similar elements. Rushing (1985) described that the ornamentation of the spores follows a geographic pattern, in which the species of *Bruchia* in South America have spiny spores and for *Trematodon* it presents the warty spore type. Luizi Ponzo (1995) and Luizi-Ponzo & Barth (1998) described the ornamentation of the spores of Bruchiaceae, and characterized *T. longicollis* by presenting gemoid-type elements, which consists of medium-sized spores, radial symmetry, with a perina formed by pili and buds and the proximal pole with an apertural region with a trilobate contour and delimited by a ring.

Considering that *T. longicollis* is found on all continents (Tropicos 2025), and also regarding the divergence between descriptions of the species, this review aims to reevaluate the species already included as synonyms, and compare the type materials based on spores (Santos & Peralta 2021 (in prep.), which is the characteristic that allows a better delimitation of the species.

2. Materials and methods

Type species from the herbaria BM, PC, SP, and R were evaluated, and permanent slides were prepared using glycerine gelatine (Erdtman 1952) with all sporophyte and gametophyte structures, which are available within each exsiccate analysed. Illustrations were created from photographs obtained with a stereoscopic and optical microscope, and the plates presented include the diagnostic characters of each species.

Furthermore, spore morphology was evaluated, using the Wodehouse method (1935) to evaluate sporoderm characteristics (Luizi-Ponzo & Barth 1998). The spores were characterized using scanning electron microscopy (SEM) (Philips XL-20). The sporophyte capsules were ruptured and dispersed on stubs containing adhesive tape, and metallized using Bal-Tec SCD 050 (Sputter Coater). The nomenclature adopted for size in the equatorial view, shape, and description of ornamental elements was based on Crum & Anderson (1981), McClymont (1954), Rushing & Snider (1985), Luizi-Ponzo & Barth (1998), and Punt et al. (2007).

The species reduced to synonymy are cited for each of their respective continents. Thus, the definition of *Trematodon longicollis* for each continent is discussed, as the distribution is cosmopolitan.

3. Results

Taxonomic treatment

Trematodon longicollis Michx. var. ***longicollis***, Fl. Bor.-Amer. 2: 289. 1803, non *Trematodon longicollis* Wilson & Mitt., Bot. Zeitung (Berlin) 22: 350, 1864, late homonym. *Trematodon ambiguus* var. *longicollis* (Michx.) Arn., Mém. Soc. Linn. Paris 5: 252, 1827. Type: U.S.A. North Carolina "In arenosis Carolinae" [sin col. s.n.] (K [ac.001127507], PC) (not located). (Figures 1, 2 A-B.)

= *Cynontodium trematodum* P. Beauv., Prodr. Aethéogam. 52. 1805, inval. name cited in synonym, synonymized by *Wijk et al.* (1959).

= *Trematodon baileyi* Broth., Ofvers. Finska Vetensk.-Soc. Forh. 33: 91, 1891, non *Trematodon braileyi* Broth., Nat. Pflanzenfam. (ed. 2) 10: 176. 1924, orthographic variant. Type: [AUSTRALIA] Im Jahre 1889, entdeckt und auch in [Bellenden] den Ker Range gesammelt, *von F.M. Bailey [s.n.]* (lectotypo H[bc.H4270023 (hb.Broth.)], designated by Ramsay *et al.* (2018), isolectotypes PC[bc.PC0131486], PC[bc.PC0131487], BM![bc.BM000964905], BM![bc.BM000964906, BM![bc.BM000964907], BM![bc.BM000964908!). [AUSTRALIA] In Queensland am Mulgarve River, [ubi in terra anno 1889, *F. M. Bailey 670*] (syntype), synonymized by Ramsay *et al.* (2018).

= *Trematodon capillipes* Müll. Hal. ex G. Roth, Aussereur. Laubm. 304. 28 f. 6. 1911. Type: [FILIPINAS] Auf der Philippinen Insel Luzon in 5000 Fub resp. ca. 2500 m, *von W. Micholitz [s.n.]* (BM![bc.BM000964890], BM![bc.BM000964891], PC[bc.PC0101574]), synonymized by Norris & Koponen (1990).

= *Trematodon ceylonensis* Müll. Hal., Botanische Zeitung (Berlin) 22: 350. 1864. Type: [SRI LANKA] Auf der Insel Ceylon bei Matale, *von Dr. Gander [s.n.]* (syntypes BM000964900!, BM000964898!, BM000964899!, G00116148). [SRI LANKA] auch von Nietner bei Punduloya in 2500 m, bey Mercara im Sudlichen Indien gesammelt, *von Dr. Walker [s.n.]* (syntype), synonymized by Kumar (1985[1986]).

= *Trematodon drepanellus* Besch., J. Bot. (Morot) 12: 283. 1898. Type: E.U.A. North Carolina "In arenosis Carolinae" *Jean Faurie 12716* (lectotype BM![bc.BM000964854], designated by Gao Chien (1994), isolectotypes K[bc.K001127507], PC); Syntype: HOKKAIDO. Prov. Oshima: Yakumo [s.n.] (UF10211[2], BM!) , synonymized by Cao & Gao (1988).

= *Trematodon flexifolius* Müll. Hal., Flora 69: 278. 1886. Type: [ILHA SÃO TOMÁS] Auf der Insel St. Thomas in Afrika bei Cachoeira do rio Manuel Jorge, ca. S. Nicolau in 850-880 m von dem Universitats gartner zu Coimbra im Juli 1884 gesammelt, *A. Moller [s.n.]* (S[bc.S-B179674], S[bc.S-B179675], JE[bc.JE04007972], PC[bc.PC0029192], PC[bc.PC0075494], BM![bc.BM000870256]), synonymized by Magill (1981 [1982]).

= *Trematodon humilis* Mitt., J. Linn. Soc., Bot. 12: 47, 1869. Type: ECUADOR, In den Andes Quitenses ad Flusse Bombonasa, [ocis cultis (1200 ped.), von *Spruce 44b* (lectotype BM![bc.BM000724627] here designated; isolectotypes NY[bc.NY01086146], BM![bc.BM000724626], , E[bc.E00165005]); [ECUADOR] ad fl. Napo, *Jameson [s.n.]* (syntypes NY[bc.NY01086147], BM![bc.BM000879105], BM![bc.BM000879106]). CUBA, *Wright 22* (syntype BM![bc.BM000879104]), *syn. nov.*

= *Trematodon solmsii* Bolle, Verh. Bot. Vereins Prov. Brandenburg 7: 30 1865. Type: [ITALIA] Ischia, 1865, *C. Bolle [s.n.]* (BM![bc.BM000964845], BM![bc.BM000964847], BM![bc.BM000964846], GOET[bc.GOET013617]), synonymized by Wijk *et al.* (1969).

= *Trematodon stricticalyx* Dixon, Honk Kong Naturalist, Supplement 2: 3. 1 f. 1. 1933. Type: [CHINA] Hang Chow, Chekiang Province, june.1922, *E.D. Merril [s.n.]* (hb. Dixon 11520) (G[bc.B00114481], NY[bc.NY01086178], BM![bc.BM000964860]), synonymized by Cao & Gao (1988).

= *Trematodon tenellus* Schimp. Ex Besch, Ann. Sci. Nat. Bot. VI, 3. 178. 1876. Type: Auf GUADELOUPE an Felsen *[s.col.s.n.]* (Herb. Husnot 194) (syntypes BM![bc.BM000879099], BM![bc.BM000879100], BM![bc.BM000879101], BM![bc.BM000879102], BM![bc.BM00087910, PC[bc.PC0150578],

PC[bc.PC0736974], NY[bc.NY00615244], NY[bc.NY00615245], F[bc.F0001886]), synonymized by Sharp et al. (1994).

= *Trematodon uncinatus* Müll.Hal., Linnaea 38: 628. 1874. Type: MÉXICO, Mirador: *Sartorius [s.n.]* (hb. C. Mohr et Schimper) (NY[bc.NY00596992], syn. fide Sharp *et al.* (1994).

= *Trematodon brachyphyllus* Müll.Hal., Hedwigia 37: 109, 1898. Type: AUSTRALIA tropical, Queensland, *F.M. Bailay [s.n.]* (B, H[hb.Broth.]), synonymized by Ramsay *et al.* (2018).

= *Trematodon longifolius* Broth. & Paris, Oefvers. Förh. Finska Vetensk.-Soc. 51 A(17): 1, 1909. Type: [NOVA CALEDONIA] Von Le Rat in Neu-Caledonien Gesammelt, [s.col.s.n.] (BM![bc.BM000964923], H[hb.Broth.], PC[bc.PC0101581]), synonymized by Ramsay *et al.* (2018).

= *Trematodon longescens* Müll. Hal., Hedwigia 37: 109, 1898. Type: [AUSTRALIA], Queensland: Moreton; Beenleigh, Brisbane, C.J. Wild, Aug 1887 [*F.M. Bailey Hb. 440*] (lectotype H (hb.Brotherus) [bc.H4274008], designated by Ramsay *et al.* (2018); isolectotype: BRI-AQ 0733989). [AUSTRALIA] In Australien, in Neu Sudwales bei Sydney 1872 [1975], *von Frau Kayser [s.n.]* (hb. Geheeb) (syntype BM![bc.BM000964910], BM[bc.BM000964911]). [AUSTRALIA] Auch am Richmond River von Capt. Stackhouse [in Melbourne 1881] [*von Frau Kayser s.n.*]; epitype: New South Wales: Murwillumbah, x.1900, *T. Forsyth 656* (NSW 754650), synonymized by Ramsay *et al.* (2018).

Description: The leaf shape is oblong-lanceolate, with an obtuse apex and a thick percurrent costa. In cross-section of the apex, it has guide cells and a double margin. In cross-section of the base, it has guide cells and undifferentiated cells. The outer peristomial teeth differ from the inner ones, with a thick, wavy base and a papillary apex. Equatorial view: planoconvex with grouped pili. Diameter: 15 to 20 µm. At the outer view, the surface covering is densely distributed with pili. At the inner view, it presents a lobed, triangular apertural region, densely distributed with smaller elements, characterized by pili and buds.

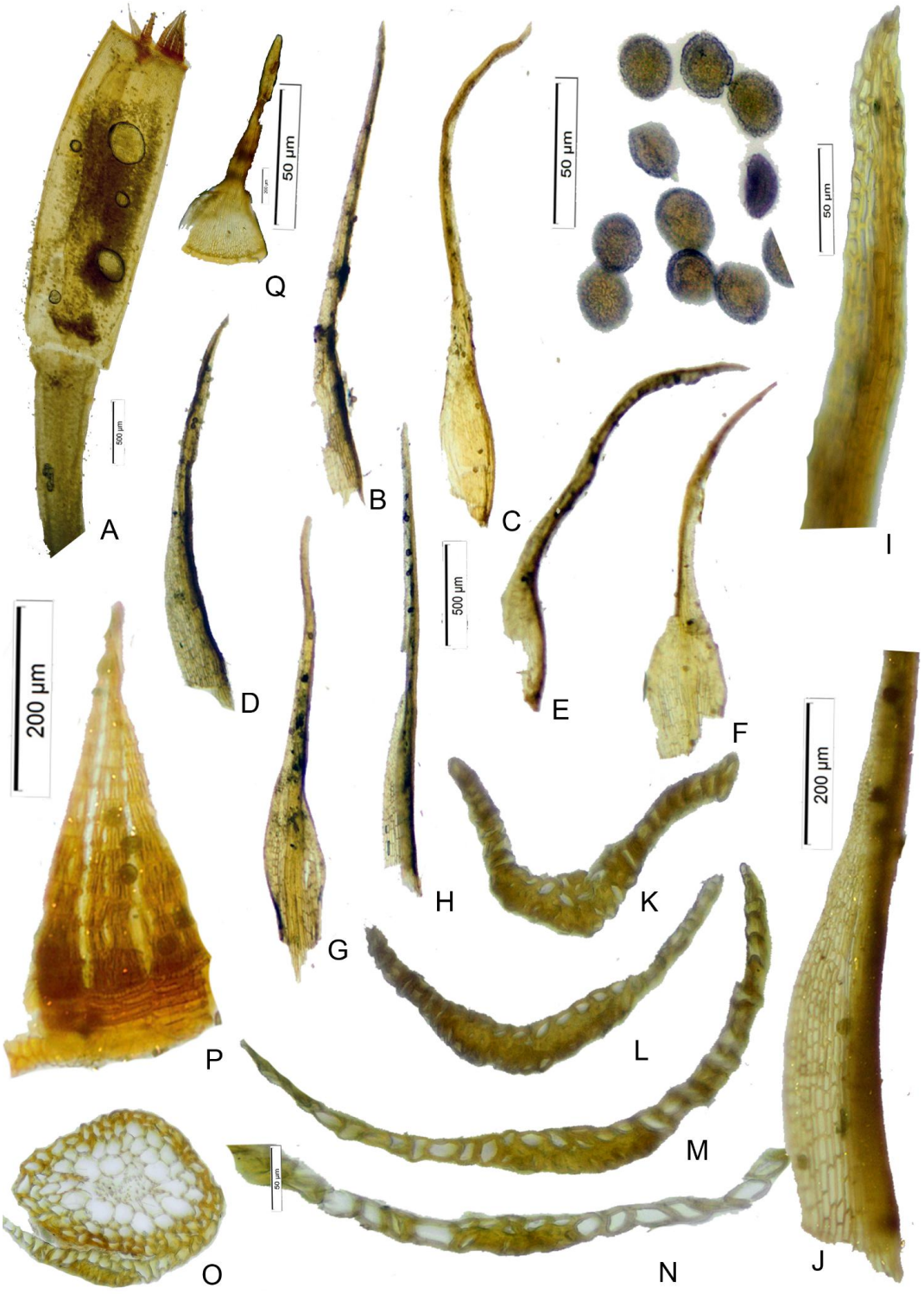

Figure 1: *Trematodon longicollis* (from the syntype *Yakumo [s.n.])*. Morphological characterization of the gametophyte and sporophyte. A. Detail of capsule; B-H. Leaf; I. Leaf apex; J. Leaf base; K-L. Cross section through the median region of leaf; M-N. Cross section through the base of leaf; O. Cross section of stem; P. Peristome teeth; Q. Operculum.

Comments: The protologue of *T. longicollis* includes characters such as a long, tortuous neck, a conical, rostrate operculum, and a peristome with perforated teeth; however, the collection site citation refers to materials collected and analyzed by Andre Michaux. The type locality is indicated in the protologue, and only the Tropicos database (2025) compiles this data. According to Taxonomic Literature (Stafleu & Cowan 1981), the material collected by Andre Michaux is deposited in the PC collection (https://www.sil.si.edu/DigitalCollections/tl-2/browse.cfm?vol=3#page/472), and the Paris herbarium website indicates the existence of the aforementioned collector's collection, which is separated in the historical collections' library (https://www.mnhn.fr/fr/explorez/dossiers/orchidees-colombie-pas-humboldt-bonpland/collections-historiques-museum). However, it was not possible to find this specific material, which may not be digitized, or may have been lost in the shipwreck suffered by the author of the species off the German coast, in which many materials were lost.

When analysing the label of the *T. drepanellus* material, it is noted that researcher Tong Cao correctly designates Urbain Jean Faurie's sample, no. 12716 (BM000964854!) as the lectotype of the *T. drepanellus*, since the species protolog lists several materials without a holotype being designated. This species was evaluated in this study, and the characteristics of the sporophyte and gametophyte match the description presented for the *T. drepanellus* lectotype.

We evaluated this species and observed that the spore, under SEM, has a distal pole with a densely distributed surface covering of pili, and the proximal pole presents a triangular, lobed apertural region. This description resembles the analysis made by McClymont (1955), who evaluated the spores of *T. longicollis* (January 1916, El Salvador, A. Kovare) and observed: Well-defined proximal pole with triangular apertural region, surrounded by a ring, spinous-baculate ornamentation elements (ca. 1.5> alt).

Regarding synonyms, we observed that *T. aureus* and *T. humilis* correspond to the same species, maintaining these species as synonyms of *T. longicollis*, and without any variation. The species T. tenellus, observed under optical microscopy, also matches the characteristics of *T. aureus*, thus reaffirming the synonymy.

The description of the protolog of *T. humilis* notes the similarity to the filidium of *T. reflexus*, and Churchill (1998) noted a note by R. S. Williams in New York, which accompanies the type collection of *T. humilis,* stating that T. reflexus is essentially identical to *T. humilis*, thus concluding the reduction of these names to the synonymy *T. longicollis*.

Geographical distribution: *T. longicollis* occurs in Europe (Ignatov et al. 2006, Belkina and Vilnet 2019), North America, Central America and South America (Herzog 1926; Delgadillo-Moya 1994; Allen 1998; Crosby et al. 1999; Colotti et al. 2003 and Yano 2011), in Asia (Schwarz 2014), Africa (O'shea 1995; Dandotiya et al. (2011), and in Oceania (Ramsay et al. 2018; 2020).

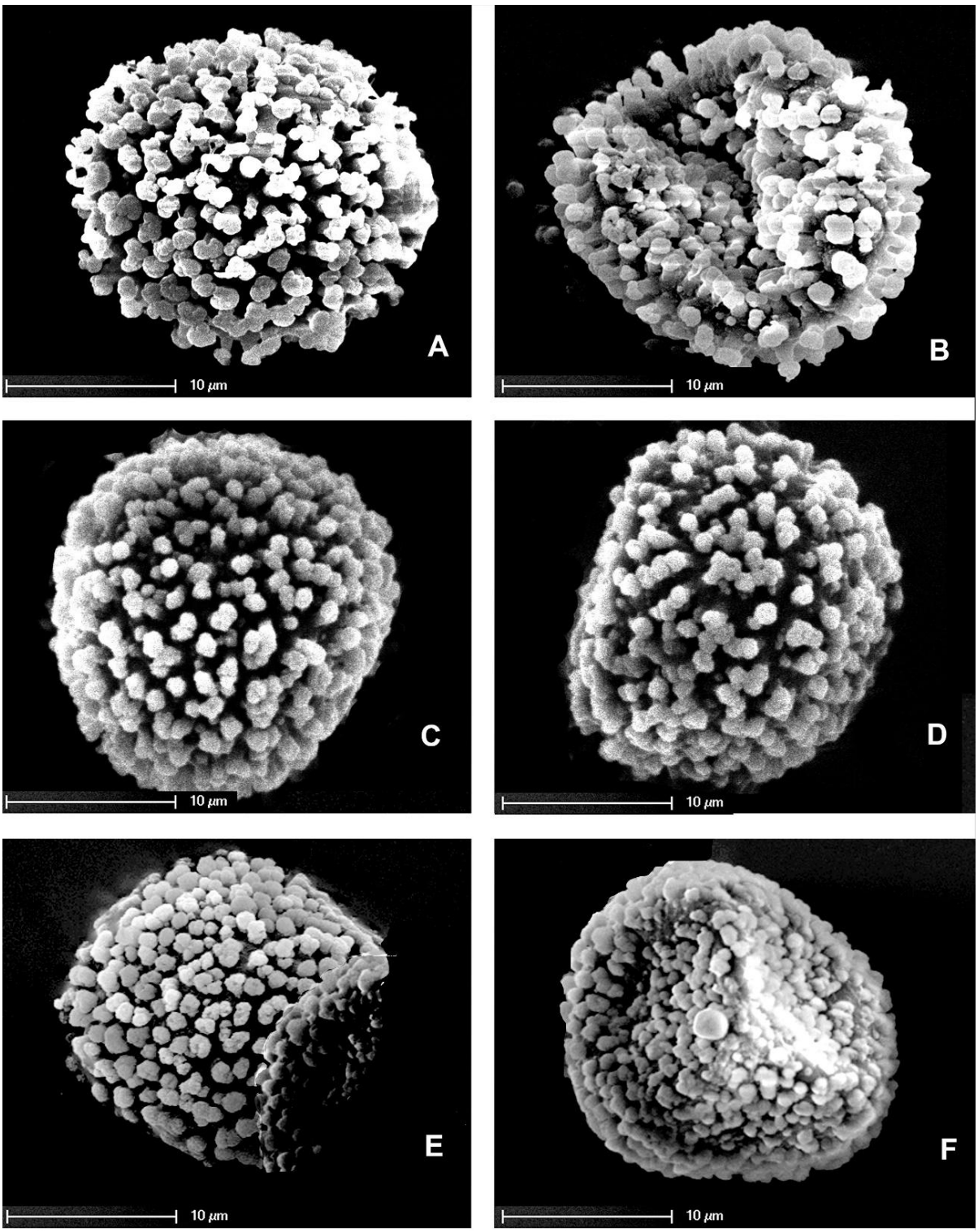

Figure 2: *Trematodon longicollis* (from the syntype *Yakumo [s.n.]*). Scanning microscopy of the spore morphology. A. Spore outer view; B. Spore inner view; *Trematodon longicollis* var. *reflexus* (from the isotype of *T. aureus* - *E. Ule 15*) C. Spore outer view; D. Spore inner view; *Trematodon africanus* (from the isotype of *T. borbonicus* - *Gaudichaud-[Beaupré] [s.n.]*). E. Spore outer view; F. Spore inner view.

Trematodon longicollis var. ***reflexus*** (Müll.Hal.) E.L. Santos & D.F. Peralta, *comb. nov.*

Basionym: *Trematodon reflexus* Müll.Hal., Synopsis Muscorum Frondosorum omnium hucusque Cognitorum, 1: 459. 1849. Type: [BRAZIL] Auf sandgem Boden in Brasilien, Prov. Santa Catharina, von Pabst, und auf dem Berge Corcovado von Gardner, sowie von Weinio und anderen bei Rio de Janeiro gesammelt, Brasília, ab *Hagendorf s.n.* (JE[bc.JE04007959 [URL - https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.je04007959]). (Figure 2C-D.)

= *Trematodon aureus* Müll.Hal. ex G. Roth, Die Aussereur. Laubm. 278, 1911. Type: BRAZIL. Santa Catarina, Tubarão, Nov.1889, *E. Ule 15* (BM![bc.BM000879121], BM![bc.BM000879122], G[bc.G00116147], GOET[bc.GOET013621], JE[bc.JE04007962], JE[bc.JE04007963], MICH[bc.MICH526512], PC[bc.PC0150582], R![bc.R000080399], H[hb.Broth.]), *syn. nov.*

Description: Leaves oblong-lanceolate, distal portion long, lanceolate, apex rounded to acute, with a crenate to dentate margin, percurrent costa thin to thick. In cross-section of the apex, it has guide cells and a double margin present. In cross-section of the base, it has guide cells that may be present or absent, and undifferentiated cells present or absent. The outer surface of the peristome teeth differs from the inner surface, with the outer part having a smooth base, the distal portion bearing papillae, and the entire inner part papillary. The base of the peristome has thin, wavy to thick, wavy cells; the apex of the peristome may have few papillae, being smooth with spiral ornamentation, or with many papillae. In equatorial view, the spore has a plano-convex or concave-convex shape. Spore diameter: 20–25 µm. The outer view has a sparse sporoderm covering, as it presents unornamented exine spaces. The elements are grouped in two or more groups with rounded tips, but they are not uniform. At the inner view, the exine is more exposed, without a ring delimitation, and the apertural region consists of a subtriangular area formed by buds in the centre, the same size as the other elements.

Comments: We evaluated the species cited as *T. longicollis* in South America and found that it differs from known patterns. *T. longicollis* was not illustrated in Roth's (1911) study, only described. The lectotype of *T. drepanellus* is synonymous with *T. longicollis*, and spore analysis reveals a different pattern from that analyzed for the species identified as *T. longicollis*. The work of Colloti et al. (2003) and Luizi-Ponzo and Barth (1998) corroborates the description and images of what we define as *T. longicollis* in South America, consisting of sporoderm elements classified as gemmoid. Furthermore, the species can be characterized by its cross-section, with a row of 3–5 guide cells separating the steroid strata, and spores between 15–21 µm in diameter, in agreement with that presented by Colloti et al. (2003). Regarding the SEM images of the spores presented by Colloti et al. (2003), they have a lot of noise in the image, but even so, we can visualize the gemmoid-type elements predominating in the sporoderm. However, as this species is widely distributed but does not match the characteristics of the lectotype, we can propose a variety of *T. longicollis* for South America.

Geographical distribution: This is the most cited species for Brazil (Yano 2011), and extensively described and illustrated in the literature on the name *T. longicollis*.

Trematodon africanus Wager & Dixon, Trans. Roy. Soc. South Africa 4: 4. 16. 1914. Type: [ÁFRICA DO SUL] Habit: Natal and Tzaneen, Transvaal *[s.col.s.n.]* (BM [bc.BM000870262!], PC[bc.PC0736947], PC[bc.PC0736946]). (Figure 2E-F.)

= *Trematodon borbonicus* Besch., Ann. Sci. Nat., Bot., sér. 6, 9: 307, 1880. Type: [ILHA REUNIÃO] G. de I´Isle und anderen auf La Reunion gesammelt, *Gaudichaud-[Beaupré] [s.n.]* (BM![bc.BM000866301], BM![bc.BM000866302], BM![bc.BM000866303], BM![bc.BM000866304], BM![bc.BM000866305], BM![bc.BM000866306], PC[bc.PC0029203], PC[bc.PC0736944], PC[bc.PC0736945], JE[bc.JE04007968], PC[bc.PC0029180], PC[bc.PC0074238], PC[bc.PC0074239]). *syn. nov.*

= *Trematodon pallidens* Müll. Hal., Linnaea 40: 242. 1876. Type: [COMORES] Auf den Comoren auf der Insel Anjouan im Mai 1850 von Boivin entdeckt, sowie auch, *von Hildebrandt [s.n.]* (sintype). [ANJOUAN] auf der Insel Johanna daselbst in 300 m 1875 in der Gesellschaft, *von Tr. Hildebrandt [s.n.]* (BM![bc.BM000870244]), synonymized by Magill (1981 [1982]).

Description: Leaves are oblong-lanceolate, with an obtuse apex and a thick percurrent costa. In cross-section of the apex, it has a double margin, but no guide cells were visible. The base has guide cells and undifferentiated cells. The outer peristome teeth differ from the inner, with a thick base and a papillary apex. In equatorial view, it has a planoconvex shape and clustered buds. Diameter: 20–24 µm. The spores are gemmoid, with the outer view densely distributed with buds and concreted buds, and the inner veiw with a slight trilete projection and densely distributed buds.

Comments: Initially, the synonymy of *Trematodon longicollis* was reduced, but the morphology of *T. africanus* evaluated in SEM has gemmoid ornamentation, thus differing from the lectotype of *T. drepanellus* (free or concretized pili and buds at the proximal pole), which occurs in Asia and presents ornamentation elements characterized as elongated processes. It does not correspond to the species found in South America, which has gemmoid elements. This species has similarities to *T. crispatissimus* due to the characteristics seen in the spores. Based on this analysis, this name was removed from the synonymy of *T. longicollis*. *Trematodon borbonicus* was identified as *T. longicollis*, as stated in the notes of the samples seen in BM!. Samples BM000866302 and BM000866305 have a greater amount of material and correspond to the type locality. Sample BM000866301 (1836-37 Ile de Borbon) does not correspond to the Type; and BM000866306 corresponds to the sample from the 1880 publication in La Reunion, and the information sheet is uninformative. Based on the morphology of the peristome, the urn-like neck relationship, spore size, stem and leaves with the same anatomy, bi extratose (double) margins on the subula; leaf apex denticulated by projecting cell ends; and spores evaluated under SEM that have ornamentation characterized by pili and concreted buds, as well as the lectotype spore. *Trematodon pallidens*, initially reduced to a synonym of i, was evaluated and has spores in equatorial view that appear in development, not being conclusive for the synonymy. It was also possible to observe the characteristics of the gametophytes, which have oblong-lanceolate leaves, with an acute apex and a toothed margin, a thick percurrent costa, in a cross-section of the apex, guide cells and a double margin present, and at the base, undifferentiated cells present. The teeth of the peristome appear in development, with a papillose base and apex.

Geographical distribution: This species only occurs in the type locations (South Africa, Comores Islands and Reunion), but it was treated as a synonym of *T. longicollis* for a long time.

Doubtfull names

Trematodon acutus Müll. Hal., Syn. Musc. Frond. 1: 458. 1848. Type: [JAVA] Auf feuchter Erde an Wegen und mit Erde bedeckten Mauern in Java verbretet, besonders am Gedeh in 1300 m, auch um buitenzorg in 300 m, bei Tjibodas, Tjipannas usw in West-wie Ostjava *[s.col.s.n.]* (BM000964889, BM000964901! BM000964902!)?), syn. by Norris & Koponen (1990).
Comments: The samples deposited in B did not have sporophytes, and the leaves were very degraded, thus making cross-sections impossible.

Trematodon atrovirens Broth., Öfvers. Finska Vetensk.-Soc. Förh. 62A(9): 1. 1921. *Trematodon longicollis* fo. *atrovirens* (Broth.) Takaki, J. Hattori Bot. Lab. 25: 271, 1962. Type: [JAPÃO] Tokio, terricola, 2-VI-1908, *K. Sakurai 480* (B?, H[hb.Broth.], PC-foto! PC0736975), *syn. by* Noguchi & Iwatsuki (1987).
Comments: The sample analysed corresponds to the type and does not have sporophytes, making the analysis restricted.

Trematodon cubensis Müll. Hal., Hedwigia 37: 228. 1898. Type: [CUBA] Auf der Insel Cuba von 1856 entdeckt, *Charles Wright [s.n.]* (BM![bc.BM000879098 e BM![bc.BM000879097)?), syn. by Sharp et al. (1994).
Comments: The samples seen do not present sporophytes, and in the gametophyte, there are few leaves, making the analysis restricted.

Trematodon paucifolius Müll. Hal., Syn. Musc. Frond. 1: 459. 1848. Type: [JAVA] Am Pangerango in Java von Taysmann in fast 3000 m Meereshohe entdeckt, sowie von Zollinger bei Tjipannas und von im Berggatern von Tjibodas auf Java in 1450 m in 1900 gesammelt, *M. Fleischer [s.n.]* (BM000964892!, BM000964893!, PC0101579, BM000964901?), synonymized by Cao & Gao (1988) e Norris & Koponen (1990).
Comments: The materials seen in the BM are without sporophytes and with degraded leaves.

Trematodon reineckei Müll. Hal., Bot. Jahrb. Syst. 23: 320. 1896. Type: [POLINÉSIA] Nord Sawaii: Juni 1894, *Tuafa (n. 133)* (syntype B?); [POLINÉSIA] Upolu, Marz 1895, uber *Vailele (n.135)* (syntype B?), synonymized by Schultze-Motel (1974).
Comments: Type specimens were not found.

4. Discussions

Our studies and conclusions about the *Trematodon* complex worldwide are based on morphological details and anatomical analyses, including the evaluation of types, when available, and comparison with descriptions and illustrations of *T. longicollis* from other regions of the world. Most herbarium collections are very old, but the materials always contained spores, which allowed them to be evaluated by scanning electron microscopy and improved species delimitation.

This re-evaluation of the type specimens corresponding to *Trematodon longicollis* and their respective synonyms resulted in the recognition of two species, one variety, and the designation of a lectotype. *T. longicollis* var. *reflexus*, a new combination occurring in South America, *T. africanus*, previously synonymized with *T. borbonicus*, which occurs in Africa, was recognized as a valid species, and *T. longicollis*, which has 14 species, was reduced to synonymy, with *T. aureus* and *T. humilis* becoming new synonyms. However, there is a need to include molecular analyses to characterize and delimit the species of the genus *Trematodon* and their relationships with other genera, allowing for a better determination of their geographic distribution based on their characteristics.

5. New Taxa and Combinations

- *Trematodon longicollis* var. *reflexus* (Müll.Hal.) E.L. Santos & D.F. Peralta, *comb. nov*.

6. Acknowledgements

I would like to express my gratitude to the CNPq (313574/2023-5) for the Grant of the second author.

7. Bibliography

ALLEN, B. (1998) The genus *Trematodon* (Musci: Bruchiaceae) in Maine. *Evansia* 15(3): 99-103.

BELKINA, O.A. & VILNET, A.A. (2019) *Trematodon laetevirens* Hakelier & J.-P. Frahm and T. *brevicollis* Hornsch. (Bruchiaceae, Bryophyta) in Russia. *Cryptogamie, Bryologie* 40(19): 247-258. https://doi.org/10.5252/cryptogamie-bryologie2019v40a19

BRITTON, E.G. (1913) Bruchiaceae. North American Flora 15(1): 47-54.

BROWN, R.C. & LEMMON, B.E. (1981) Aperture development in spores of the moss *Trematodon longicollis* Mx. *Protoplasma* 106: 273-287.

BRUCH, P., W. P. SCHIMPER & T. GÜMBEL. (1836[–1855]). Bryol. Eur. 5 vols. E. Schweizerbart, Stuttgart.

BUCK, W.R. (1979) A re-evaluation of the Bruchiaceae with the description of a new genus. *Brittonia* 31: 469-473.

CAO, T. & GAO, C. (1988) Studies of Chinese bryophytes (2). *Trematodon* Michx. (Musci, Dicranaceae). *Journal of the Hattori Botanical Laboratory* 65: 323-334.

COLOTTI, M.T., SCHIAVONE, M.M. & MATTERI, C.M. (2003) El género *Trematodon* (Bruchiaceae, Musci) en el noroeste de Argentina. *Boletín de La Sociedad Argentina De Botánica* 38: 255-263.

CROSBY, M.R., MAGILL, R.E., ALLEN, B. & HE, S. (1999) Checklist of the Mosses. Missouri Botanical Garden, St. Louis, 306 pp.

CRUM, H.A. & ANDERSON, L.E. (1981) Mosses of Eastern North America. Columbia University Press, New York, 663 pp.

DANDOTIYA, D., GOVINDAPYARI, H., SUMAN, S. & UNIYAL, P.L. (2011) Checklist of the bryophytes of India. *Archive für Bryology* 88: 1-126.

DELGADILLO-MOYA, C. (1994) Endemism in the neotropical moss flora. *Biotropica* 26: 12-16

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. An Introduction to Palynology I. Almqvist & Wiksells. Stockholm, 539 pp

GOFFINET, B., W. R. BUCK & A. J. SHAW. (2009 [2008]) Morphology, anatomy, and classification of the Bryophyta. Pp. 55–138. In B. Goffinet & A. J. Shaw (eds.) Bryoph. Biol. (ed. 2). Cambridge University Press, Cambridge, U.K.

HERZOG, T. (1926) Beiträge zur Moosflora Westpatagoniens. *Hedwigia* 46: 79-92.

IGNATOV, M.S., AFONINA, O.M. & IGNATOVA, E.A. 2006[2007]. Check-list of mosses of East Europe and North Asia. *Arctoa* 15: 1-130.

KUMAR, S.S. (1985[1986]) Taxonomic studies of west Himalayan mosses - II. The genus *Trematodon*. *Nova Hedwigia* 42: 9-18.

LUIZI-PONZO, A.P. (1995) Morfologia de esporos da família Dicranaceae (Bryopsida-Bryophyta). Dissertação de Mestrado. Universidade Federal do Rio de Janeiro, Museu Nacional, Rio de Janeiro, 123 pp.

LUIZI-PONZO, A.P. & BARTH, O.M. (1998) Spore morphology of some Bruchiaceae species (Bryophyta) from Brazil. *Grana* 37: 222-227.

MAGILL, R.E. (1981) Mosses. Part 1, Fascicle 1. Sphagnaceae to Grimmiaceae. Flora of South Africa, Bryophyta. 291 pp.

MCCLYMONT, J.W. (1954) Spores of the Musci: their Structure and Significance in Systematic Research. University of Michigan, Ann Arbor, 185 pp

MCCLYMONT, J.W. (1955) Spore studies in the musci, with special reference to the genus *Bruchia*. *The Bryologist* 58(4): 287-306.

NOGUCHI, A. & IWATSUKI, Z. (1987) Ilustrated Moss Flora of Japan. Hattori Botanical Laboratory, Nichinan, 242 pp.

NORRIS, D.H. & KOPONEN, T. (1990) Bryophyte flora of the Huon Peninsula, Papua New Guinea. XXXV. Dicranaceae and Dicnemonaceae (Musci). *Acta Botanica Fennica* 139: 1-64.

O'SHEA, B. (1995) Checklist of the mosses of sub-Saharan Africa. *Tropical Bryology* 10: 91-198.

PUNT, W., HOEN, P. P., BLACKMORE, S., NILSSON, S., & LE THOMAS, A. (2007). Glossary of pollen and spore terminology. Review of palaeobotany and palynology, 143(1-2), 1-81. DOI: https://doi.org/10.1016/j.revpalbo.2006.06.008

RAMSAY, H. P., SEPPELT, R. D., & DOWNING, A. J. (2018) *Trematodon* (Bryopsida: Bruchiaceae) in Australia: unravelling the conundrum. *Telopea*, 21, 101-119. DOI: http://dx.doi.org/10.7751/telopea12444

RAMSAY, H., DOWNING, A., & SEPPELT, R. (2020). The moss family Bruchiaceae in Australia: Introduction and the genus Trematodon. *Telopea*, 23, 1-19. DOI: http://dx.doi.org/10.7751/telopea12856

ROTH, G. (1911) Die außereuropäischen Laubmoose. Band I. Enthaltend die Andreaeaceae, Archidiaceae, Cleistocarpae und Trematodonteae. Verlag von C. Heinrich, Dresden, 374 pp.

RUSHING, A.E. (1985) Spore morphology in the genus Bruchia Schwägr. (Musci). *American Journal of Botany 72: 75-85.*

RUSHING, A.E. (1986) A revision of the genus *Bruchia* Schwägr. (Musci). *Journal of the Hattori Botanical Laboratory* 60: 35-83.

RUSHING, A.E. & SNIDER, J.A. (1985) A natural hybrid between Bruchia microspora Nog. and Trematodon longicollis Michx. *Monographs in systematic botany from the Missouri Botanical Garden* 11: 121-132.

SCHULTZE-MOTEL, W. (1974) Die Moose der Samoa-Inseln. *Willdenowia* 7: 333–408.

SCHWARZ, U. (2014) Bruchiaceae collected in Karnataka, India, with a synopsis of the family in India. *Frahmia* 10: 1-9.

SHARP, A.J., CRUM, H. & ECKEL, P.M. (1994) The moss flora of Mexico. *Memoirs of The New York Botanical Garden* 69: 1-1113.

STAFLEU, F.A. & COWAN, R.S. (1981) Taxonomic literature: a selective guide to botanical publications with dates, commentaries and types. *Regnum Vegetabile* 52: 1-556.

TROPICOS (2025) Available from: <https://www.tropicos.org> (accessed: 11 Oct 2025).

WIJK, R.V.D., MARGADANT, W.D. & FLORSCHÜTZ, P.A. (1969) Regnum Vegetabile (vol. 65). Index Muscorum (vol. 5 T- Z). International Bureau for Plant Taxonomy and Nomenclature of the International Association for Plant Taxonomy, Utrecht, 922 pp.

YANO, O. (2011) New records of bryophytes for the States of Brazil. *Boletim do Instituto de Botânica* 21: 19-45.

ZANDER, R.H. (2003) Glycerin jelly as a substitute for Hoyer's solution mountant. Res Botanica: Methods. Available from: (accessed 4 June 2019).