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Novelties on *Tortella* (Pottiaceae, Bryophyta) from South America

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ABSTRACT
During recent botanical surveys undertaken in South America (Uruguay and Paraguay) some of the samples collected were identified as *Tortella fruchartii* (Müll. Hal.) R. H. Zander and *T. lilliputana* (Müll. Hal. ex G. Roth) R. H. Zander, two autoicous species of the genus with distribution area restricted to the New World. The former is re-described based on recent collections from Uruguay, where it has not been found since its original description in 1888; while the latter is recorded for the first time from Paraguay. Detailed descriptions, illustrations in LM and SEM, and a distribution map of the two species are here presented.

KEY WORDS
Autoicous species, Barbula, Bryophyta, cleistocarpous, Paraguay, stegocarpous, Uruguay.

RÉSUMÉ
Deux nouveaux signalements dans le genre Tortella *(Pottiaceae, Bryophyta) pour l'Amérique du Sud.*
Lors de récentes excursions botaniques en Amérique du Sud (Uruguay et Paraguay), *Tortella fruchartii* (Müll.Hal.) R. H. Zander et *T. lilliputana* (Müll.Hal. ex G.Roth) R. H. Zander ont été récoltées, deux espèces autoïques du genre dont la distribution est restreinte au Nouveau Monde. *Tortella fruchartii* est redécrit sur la base de récentes récoltes d'Uruguay, où il n'avait pas été retrouvé depuis sa première description en 1888, tandis que *T. lilliputana* est signalé pour la première fois au Paraguay. Les deux espèces sont décrites en détail, avec des illustrations en microscopie optique et à balayage, et une carte de distribution des deux espèces est donnée.

MOTS CLÉS
Espèces autoïques, Barbula, Bryophyta, cléistocarpes, Paraguay, stégocarpes, Uruguay.

INTRODUCTION

The southernmost extent of South America includes Argentina, southern Brazil, Chile, Paraguay and Uruguay. This area is known as "Cono Sur" and it extends south of parallel 20°S from the Atlantic Ocean to the Pacific Ocean. This territory covers a total of 4 708 617 km², which represent 26% of the total surface of South America (Zuloaga *et al.* 2008). Despite the geographic size and biodiversity richness, the bryoflora of the area is still poorly known. The extant floras and checklists of the mosses from South America (Bartram 1949; Delgadillo *et al.* 1995; Boggan *et al.* 1997; He 1998; Churchill *et al.* 2000, 2009; Gradstein *et al.* 2001; Matteri 2003, 2004; O'Shea & Price 2008; Müller 2009; O'Shea 2010) in addition to recent discoveries on mosses (e.g. Ellis *et al.* 2011, 2012a, b; Suárez & Schiavone 2013; Flores & Suárez 2014; Suárez *et al*. 2014, 2017; Cañiza *et al.* 2017; Jimenez & Suárez 2017, among others) have highlighted the importance and singularity of the regional flora, especially in Uruguay and Paraguay where references on mosses are scanty and disperse.

The main objective of this paper is to increase the knowledge of the bryophyte flora in South America. We also particularly hope to illuminate the distributions of two very odd much reduced species of the genus *Tortella* (Müll. Hal.) Limpr.

Particular objectives includes: i) to describe in detailed the species found in Uruguay and Paraguay; and ii) to illustrate in detail by using light microscopy (LM) and scanning electron microscopy (SEM) the diagnostic characters of the taxa, and iii) to delimit its current range of distribution.

MATERIAL AND METHODS

Several botanical surveys were undertaken by the second author in Uruguay and Paraguay during 2011-2012 within the framework of a major project entitled "Study of the bryophytes of Southern South America (Systematics and Phylogeny)".

The specimens were studied morphologically following classical techniques for bryophytes, and mounted in Hoyer's solution (Anderson 1954). Microscopic characters were analyzed by using LM Leica Model CME, and SEM JEOL 5800 LV operating at 20 KV. Characters illustrated using SEM were obtained from samples fixed in Formaldehyde-acetic acid-alcohol-water (FAA), critical-point dried, mounted on double-sided tape and coated with gold-palladium. Spores were obtained from mature capsules, removed with FAA, mounted directly on aluminum stubs and subsequently coated with gold-palladium. Spores were described following the concepts of McClymont (1955) and Punt *et al.* (2007).

The samples are kept in the herbaria of the Instituto de Botánica del Nordeste, Corrientes, Argentina (CTES), Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (LIL) and Missouri Botanical Garden, St. Louis, Missouri, USA (MO).

RESULTS

Within the samples collected, two of them matched with two autoicous species of the genus *Tortella*: *T. fruchartii* (Müll. Hal.) R. H. Zander and *T. lilliputana* (Müll. Hal. *ex* G. Roth) R. H. Zander. The former was recorded in Uruguay and the second in Paraguay.

For both species detailed descriptions, illustrations with LM and SEM are here given, as well as world distribution data.

Tortella fruchartii (Müll. Hal.) R. H. Zander (Figs 1; 2)

In Bulletin of the Buffalo Society of Natural Sciences 32: 104 (1993). — *Phascum fruchartii* Müll. Hal., *Flora* 71: 4 (1888). — *Systegium fruchartii* (Müll. Hal.) Kindb., *Enumeratio Bryinearum Exoticarum, Supplementum* 95. (1889) — *Astomum fruchartii* (Müll. Hal.) Broth., *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 26 Afd. 3(7): 19 (1900). — Type: **Uruguay**, Montevideo, en la terra, VIII.1874: *Arechavaleta 205*, in Hb. Lund. (syn-, H!, NY!)

Astomum latifolium Broth., *Aussereur. Laubm.* 190. 17 f. 8 (1910). — Type: Brazil, Porto Allegre (Brasilien), bei der Vorstadt Saõ Joaõ, auf Erdböschungen, *E. M. Reineck & J. Czermak 222,* 23.V.1899 (iso-, BM!).

Specimen examined.— **Uruguay**. Rocha, Parque Fortaleza Santa Teresa, 33°58'39"S, 53°32'17"W, 33 m, sobre suelo, 3.I.2011, *G. Suárez 1047* (CTES, LIL, MO).

Geographical distribution. New World species described by Müller (1888) from Uruguay and later reported from Brazil (Roth [1910-] 1911; Yano 1981), Mexico (Delgadillo & Cárdenas 1996) and Paraguay (Brotherus 1900; Buck 1985; O'Shea & Price 2008) (Fig. 3). This is the second record in Uruguay collected 135 years after original collection in 1874.

Description

Plants

Loosely caespitose forming low turfs, yellowish green above, brown below.

Stems

0.2-0.3 cm long, erect, simple, in cross section rounded to rounded-pentagonal, central strand well-developed, sclerodermis present but usually weak, hyalodermis present, composed of cells that are little collapsed when mature, weakly radiculose, reddish brown rhizoids, axillary hairs ca. 110 µm long, 5-6 cells in length, all hyaline.

Leaves

Evenly distributed along the stem, erect-flexuose, convolute when dry, spreading when moist, ligulate to lanceolate, 1.7-2.2 × 0.3-0.4 mm, margins plane, entire at base, weakly crenulate to dentate with projecting papillae below midleaf, apex obtusely mucronate; base oblong, weakly differentiated in shape; costa 106-112 µm in width near base, short excurrent as a mucro, in cross section ovate, ventral and dorsal stereid bands well developed, 6-8 guide cells in 1(-2) layers, hydroid strand absent, ventral epidermis present from base

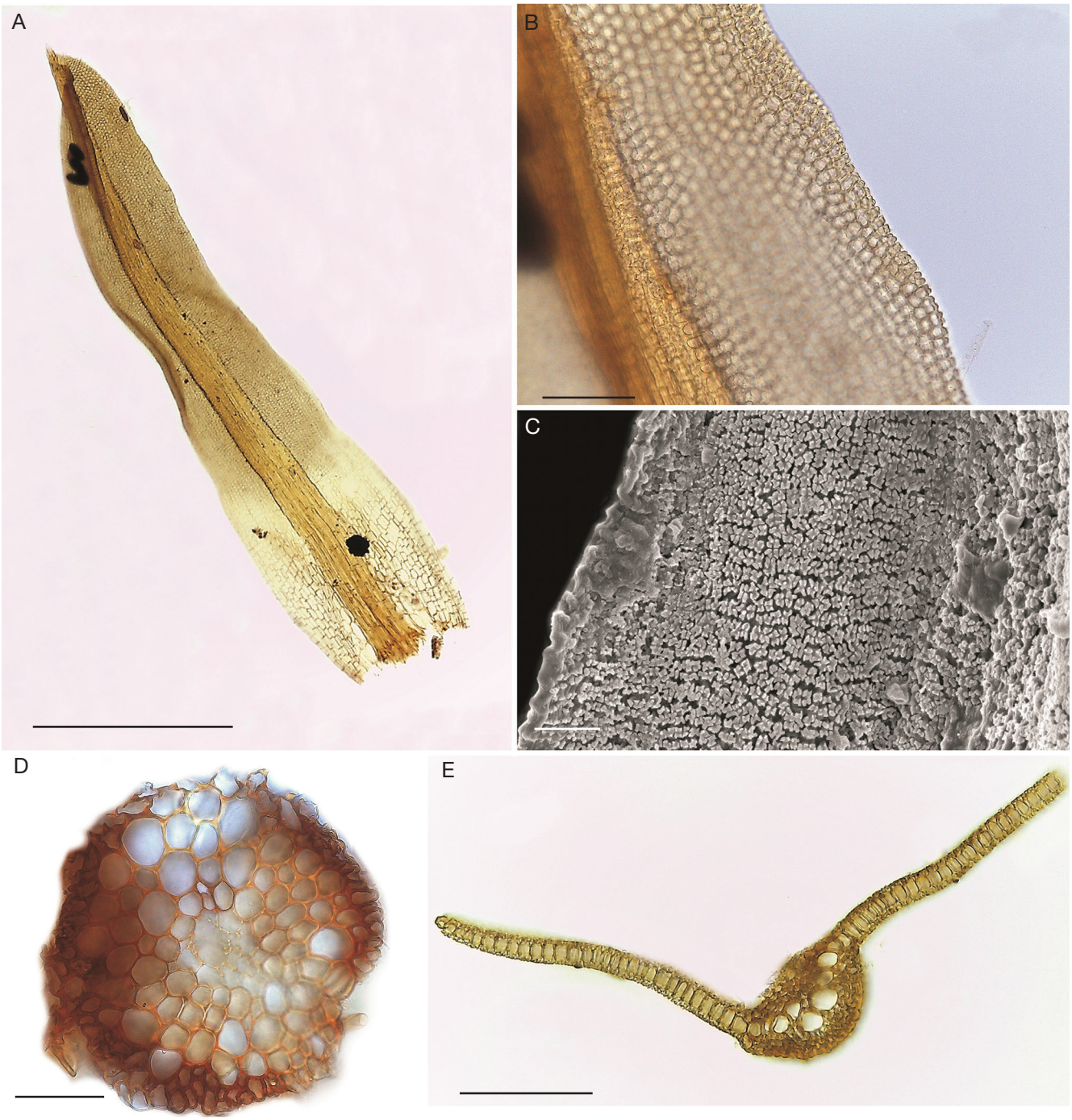

Fig. 1.— *Tortella fruchartii* (Müll. Hal.) R. H. Zander gametophyte micrographs: **A**, Vegetative leaf; **B**, **C**, Laminal cells at the middle of the leaf; **D**, Stem cross section; **E**, Leaf cross section at the middle part (A, B, D, E made with LM and C with SEM). Scale bars: A, 0.5 mm; B, C, E, 100 µm; D, 50 µm (all from Suárez 1047, CTES).

to apex, dorsal weakly developed to absent from base to apex; upper laminal cells quadrate to hexagonal, 8.3-9.9 × 4.9-6.6 µm, walls thin, superficially convex on both sides, papillose, papillae bifid, 3-4 per lumen, basal cells differentiated across leaf in a V-shape, extending ⅓ above the base, well differentiated from the upper cells, long-rectangular to linear, 24-41 × 3.3-8.3 µm, walls thin, smooth, gradual transition in a V-shaped.

Autoicous

Perichaetia
Terminal. Perichaetial leaves little differentiated, lanceolate, 0.7-0.9 × 0.1-0.3 mm.

Perigonia
Not seen.

Seta
Less than 0.1 cm long.

Theca
Immersed, ellipsoidal to cylindric, long rostrate, reddish brown; exothecial cells mostly short-rectangular, 54-69 × 23-28 µm, stomata absent, annulus absent, dehiscence by irregular rupture, peristome absent.

Calyptra
Cucullate.

Spores
Bilateral, concave-convex in shape, 16-18 µm, brown to yellowish brown, rugulate, with long rugulae in distal view, turning short towards proximal view appearing wide verrucae. Laminal KOH reaction yellow.

Tortella lilliputana (Müll. Hal. *ex* G. Roth) R. H. Zander (Figs 4; 5)

In Bulletin of the Buffalo Society of Natural Sciences 32: 104 (1993). — *Phascum lilliputanum* Müll. Hal. *ex* G. Roth., *Aussereuropäischen Laubmoose* 212. pl. 20: 3 (1911). — *Tetrapterum lilliputanum* (Müll. Hal. *ex* G. Roth) Broth., *Natürlichen Pflanzenfammilien (ed. 2)* 10: 253. (1924). — Type: **Brazil**, S. Catharina, Tubarão, ad terram, VIII.1890, (iso-, [E. Ule 133], NY!, S!)

Specimen examined. — **Paraguay**. 3 km al Norte de Paraguarí, Cerro Hú, 25°36'20"S, 57°08'08"W, 135 m, sobre suelo, 03.VIII.2012, *G. Suárez 1488* (CTES, LIL, MO).

Geographical distribution. — It is a New World species described from Brazil (Roth [1910-] 1911), and later reported from Panama (Crum & Arzeni 1953). Here is recorded as new to Paraguay (Fig. 3).

Description
Plants
Forming low turfs, greenish brown below.

Stems
0.4-0.5 cm long, erect, branching occasionally, in cross section rounded-pentagonal, central strand well-developed, sclerodermis present but usually weak, hyalodermis present, composed of cells that are little collapsed when mature, weakly radiculose, reddish brown rhizoids; axillary hairs 110-150 µm long, 7-8 cells in length, all hyaline.

Leaves
Often crowded, erect incurved, somewhat contorted when dry, spreading when moist, ligulate to long-lanceolate, 1.5-3.1 × 0.1-0.3 mm, lamina channeled across leaf, margins incurved, entire at base, weakly crenulate to dentate with projecting papillae below midleaf, apex subulate; base oblong, not differentiated in shape; costa 68-74 µm in width near base, short excurrent as a mucro, in cross section rounded, ventral and dorsal stereid bands well-developed, 4-6 guide cells in 1 layer, hydroid strand absent, ventral epidermis present from base to apex, dorsal epidermis weakly-developed to absent; upper laminal cells quadrate to hexagonal, 6.6-8.3 × 4.9-8.3 µm, walls thin, superficially convex on both sides, papillose, papillae 3-4 per lumen, basal cells differentiated across leaf in a weak V-shape, extending 1/3 above the base, well differentiated from the upper cells, long-rectangular, 28-59 × 8-16 µm, walls thin, smooth, gradual transition in a V-shaped.

Autoicous

Perichaetia
Terminal, gemmiform. Perichaetial leaves lanceolate, 1.5-1.9 × 0.1-0.3 mm, the inner smaller than the outer.

Perigonia
Terminal, gemiform. Perigonial leaves lanceolate, 0.4-1.1 × 0.1-0.3 mm, the inner smaller than the outer. *Seta* 0.4-0.5 cm, twisted clockwise below.

Theca
Exserted, ellipsoidal, reddish brown; exothecial cells mostly rectangular to long-rectangular, 41-68 × 24-31 µm, stomata at base of theca, phaneropore, annulus absent or weak and non-functional, dehiscence by the fall of the long rostrate operculum, peristome absent.

Calyptra
Cucullate

Spores
Bilateral, concave-convex in shape, 19-24 µm, yellowish-brown, papillose, papillae low and blunt homogenously distributed on both views.

Laminal
KOH reaction yellow.

DISCUSSION

The name *Tortella* was first used by Müller (1849) for a section in the genus *Barbula* Hedw. (*Barbula* section *Tortella* Müll. Hal.) and later elevated to the generic level by Limpricht (1888). The morphological traits that define *Tortella* include the presence of a well-developed hyalodermis, the chlorophyllose, quadrate upper laminal cells distinctly differentiated from the usually hyaline, rectangular basal leaf cells, which run up the basal margin in a V-shaped pattern (Zander 1993; Eckel 1998; Allen 2002). Nevertheless Werner *et al.* (2014) showed by molecular phylogenetic analyses that the V-shaped line of demarcation between the basal hyaline cells and the distal chlorophyllose cells cannot be used to refer all species of *Tortella*, and that the characterization of the genus based on this character is inaccurate.

The genus *Tortella* includes both cleistocarpic and stegocarpic species, condition not necessarily infrequent in Pottiaceae (Werner *et al.* 2002; Flores & Suárez 2017). Despite sporophytic characters have been widely used to

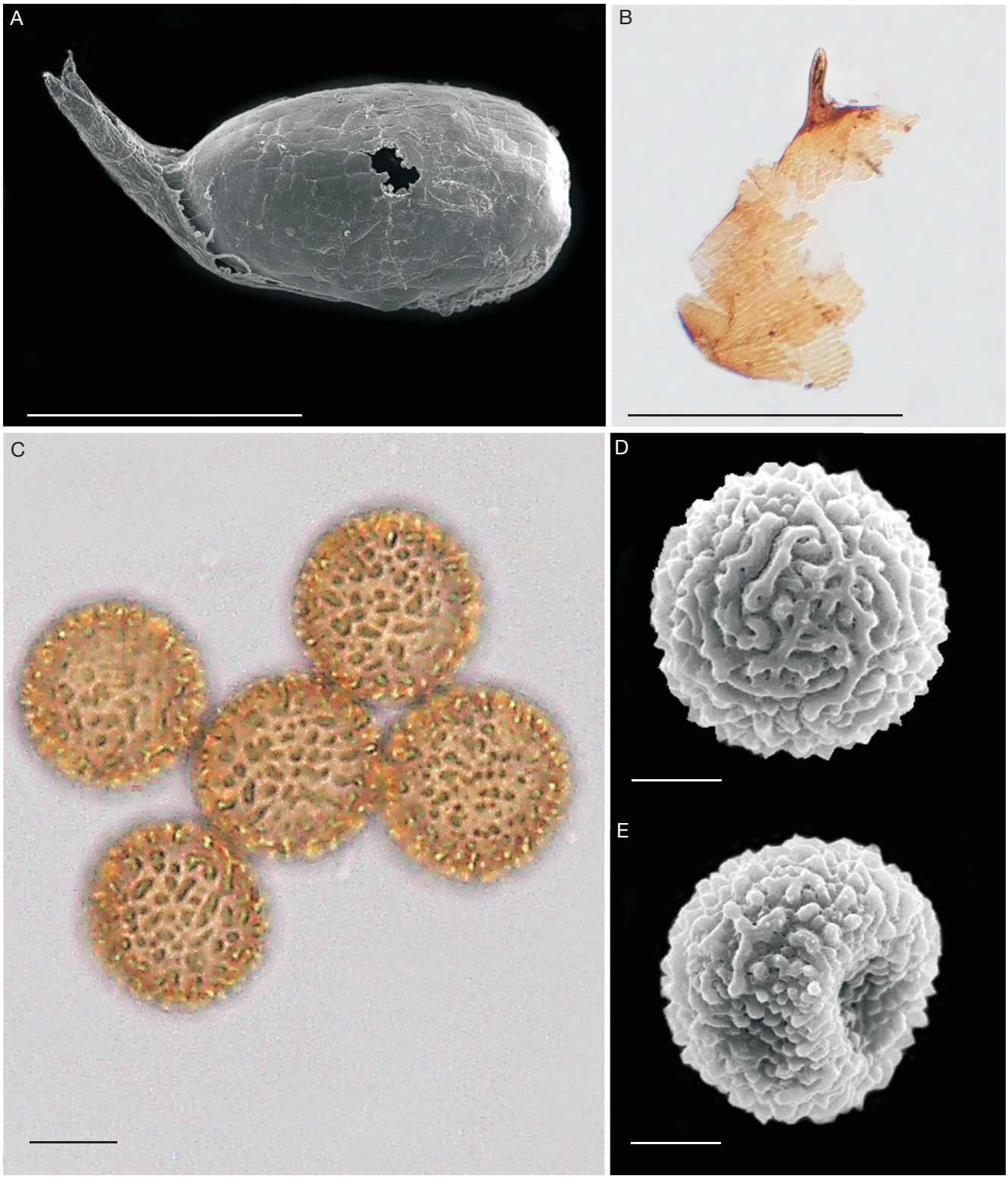

Fig. 2.— *Tortella fruchartii* (Müll. Hal.) R. H. Zander sporophyte and spores micrographs: **A**, Capsule showing apicule covered by the calyptra; **B**, Capsule irregularly ruptured; **C**, Spores; **D**, Spore detail in distal view; **E**, Spore detail in proximal view (A, D, E made with SEM and B, C with LM). Scale bars: A, B, 0.5 mm; C, 10 µm; D, E, 5 µm (all from Suárez 1047, CTES).

define relations at high levels, Zander (1993) emphasized the information content of the characters of the gametophyte and generalizes the use of sporophytic characters at specific levels.

Tortella fruchartii and *T. lilliputana* have been described as being cleistocarpic, been considered this character diagnostic for the distinction from all other members of *Tortella* (Zander 1993; Allen 2002). Nevertheless, the study of the

Fig. 3.— Distribution map of *Tortella fruchartii* (Müll. Hal.) R. H. Zander and *T. lilliputana* (Müll. Hal. ex G. Roth) R. H. Zander. **Black circles**, previously known records of *T. fruchartii* in Brazil, Mexico, Paraguay and Uruguay; **empty circle**, rediscovery of *T. fruchartii* in Uruguay; **black squares**, previously known records of *T. lilliputana* in Brazil and Panama; **empty square**, new record of *T. lilliputana* in Paraguay.

newly recorded South American samples of both species showed that in *T. lilliputana* an operculum exists that can be detached by a weak annulus. In the case of *T. fruchartii*, it is confirmed that the dehiscence of the capsule is due to irregular rupture.

Both *Tortella* species are mainly distinguished from each other by sporophytical traits that include: 1) the length of the seta (< 1 mm in *T. fruchartii* vs 4-5 mm in *T. lilliputana*); 2) the dehiscence mechanism of the capsule, cleistocarpous in *T. fruchartii* vs stegocarpous in *T. lilliputana*; 3) the presence of phaneropore stomata in the capsule of *T. lilliputana*, which are absent in *T. fruchartii*. Adittionally, some spore details obtained by LM and SEM also differ between both taxa: 4) spore diameter, 16-18 µm in *T. fruchartii* vs 19-24 µm in *T. lilliputana*; and 5) spore ornamentation, being rugulate in *T. fruchartii* and papillose in *T. lilliputana* (Table 1).

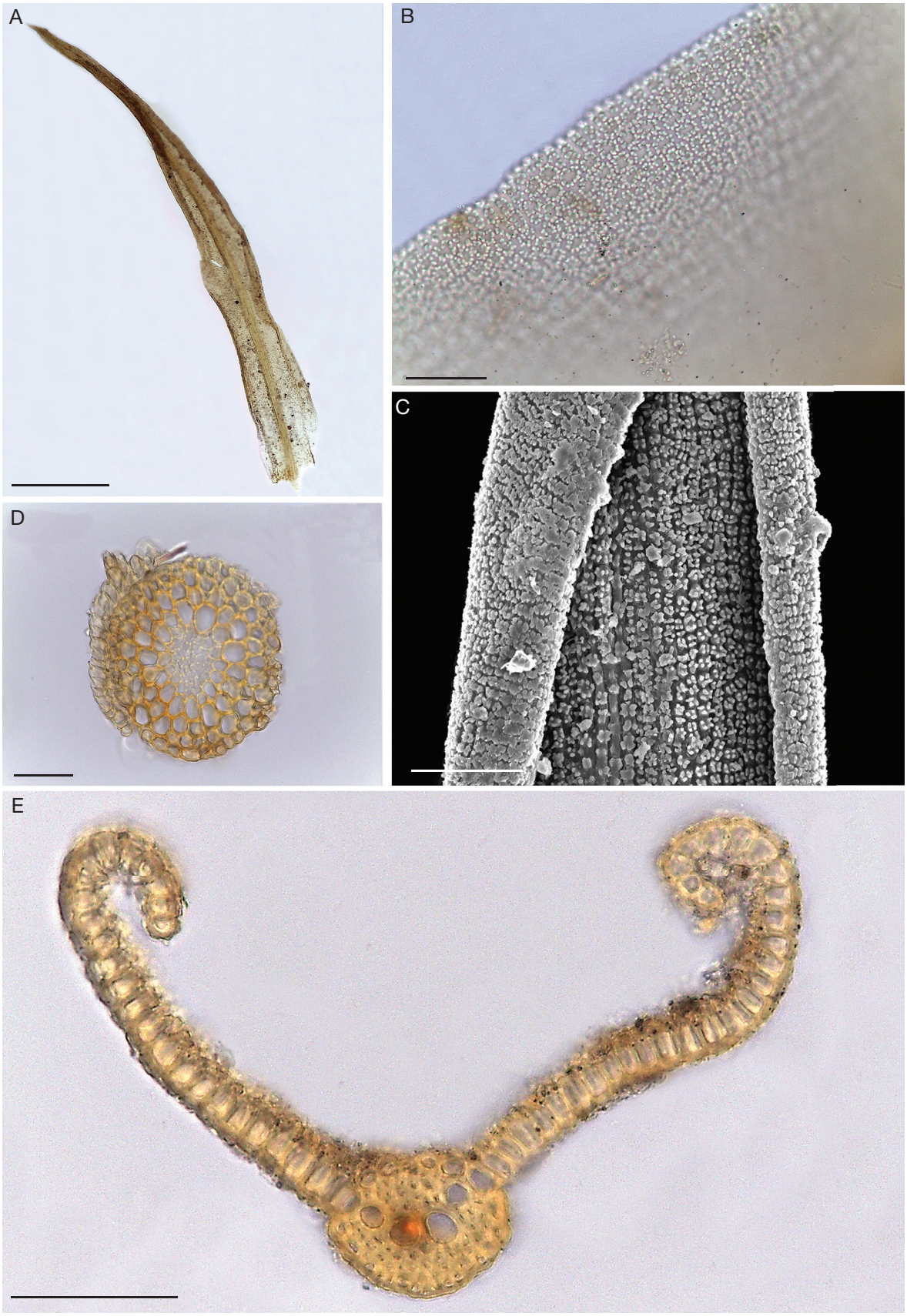

Fig. 4.— *Tortella lilliputana* (Müll. Hal. ex G. Roth) R. H. Zander gametophyte micrographs: **A**, Vegetative leaf; **B**, **C**, Laminal cells at the middle of the leaf; **D**, Stem cross section; **E**, Leaf cross section at the middle part (A, B, D, E made with LM and C with SEM). Scale bars: A, 0.5 mm; B-E, 50 µm (all from Suárez 1488, CTES).

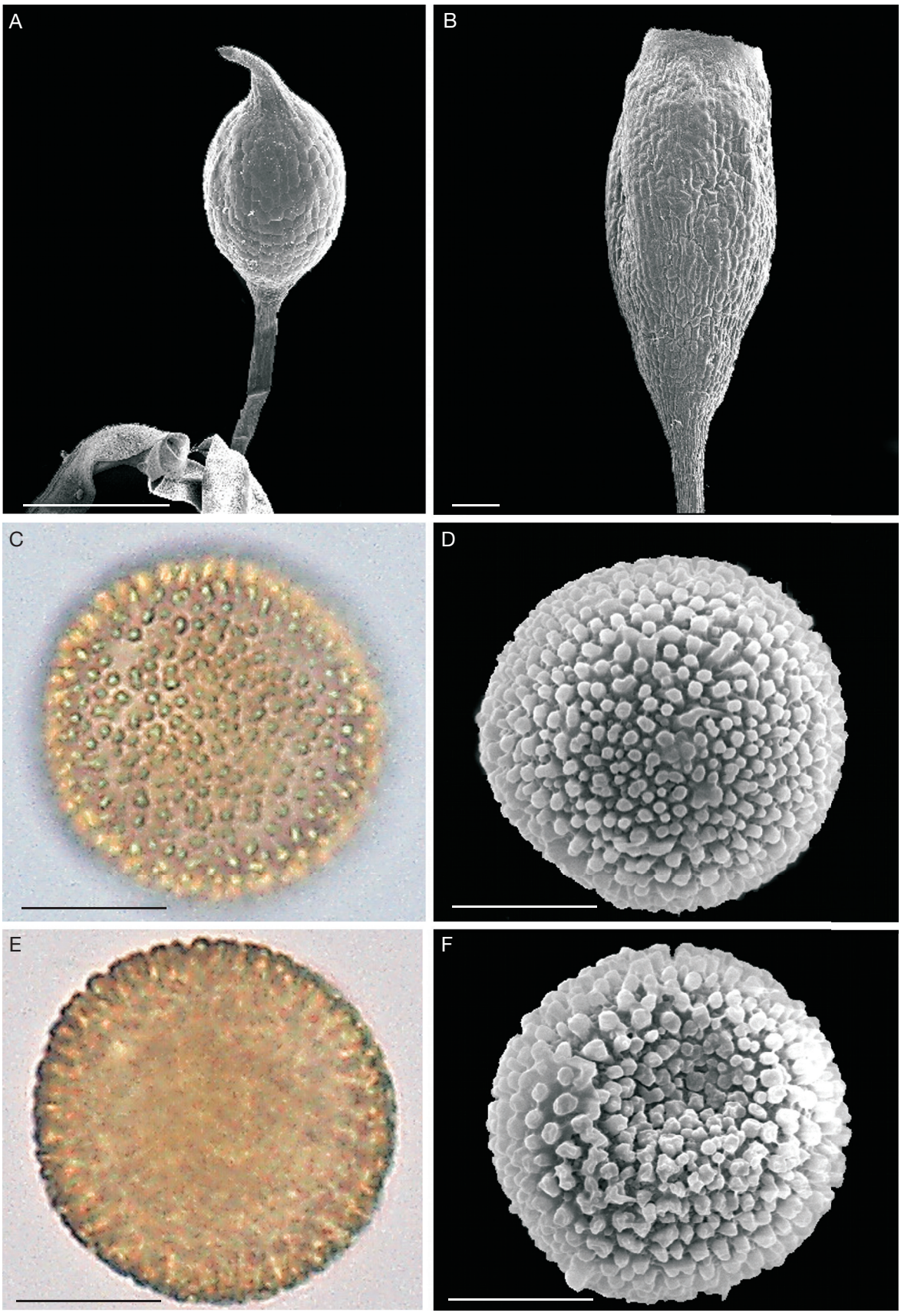

Fig. 5.— *Tortella lilliputana* (Müll. Hal. ex G. Roth) R. H. Zander sporophyte and spores micrographs: **A**, Sporophyte showing complete capsule; **B**, Deoperculate capsule; **C**, **D**, Spores in distal view; **E**, Spore in optical view; **F**, Spore in proximal view (A, B, D, G made with SEM and C, E with LM). Scale bars: A, B, 0.5 mm; C-F, 10 µm (all from Suárez 1488, CTES).

TABLE 1.— Comparative diagnostic characters for *Tortella fruchartii* (Müll. Hal.) R. H. Zander and *T. lilliputana* (Müll. Hal. ex G. Roth) R. H. Zander.

	Tortella fruchartii	***Tortella lilliputana***
Lenth of seta	<1 mm	4-5 mm
Capsule dehiscence	Cleistocarpous	Stegocarpous
Capsule stomata	Absent	Present (phaneropore)
Spore diameter	16-18 µm	19-24 µm
Spore ornamentation	Rugulate	Papillose
Leaves on dry condition	Erect-flexuose, convolute	Erect-incurved, somewhat contorted
Margin of leaves	Plane	Incurved

Despite some authors consider *T. fuchartii* and *T. lilliputana* as possibly conspecific taxa (Zander 1993; Allen 2002), during this work we observed some gametophytic characters that contribute to separate them: 6) leaves on dry condition erect-flexuose, convolute in *T. fruchartii* vs erect incurved, somewhat contorted in *T. lilliputana;* 7) margins of leaves, plane in *T. fruchartii* vs incurved in *T. lilliputana* (Table 1).

Tortella fruchartii was included in a molecular study using nrITS sequences by Werner *et al.* (2005). It was resolved in a clade including also *Tortella inflexa* (Bruch) Broth., *Trichostomum sweetii* (E.B. Bartram) L.R. Stark, *Trichostomum caespitosum* (Bruch *ex* Brid.) Jur., and *Weissia triumphans* (De Not.) M.O. Hill, occurred at a distance of four nodes from a clade with a number of other species of *Tortella.* Between these two clades were found several pecies of *Oxystegus* (Limpr.) Hilp., *Pseudosymblepharis* Broth. and *Chionoloma* Dixon, what lead to Werner *et al.* (2005) to questioned the belonging of *T. fruchartii* to the genus *Tortella.* The cladogram of these authors may be interpreted in an evolutionary context (Zander 2017) as a basal clade of a few surviving species of an old, now much reduced *Tortella* lineage separated from a more modern branch of *Tortella* by a third clade of well-developed genera descendant from an ancient *Tortella* line. Critical is the hypothesis that *T. fruchartii* (and *T. lilliputana*) are specialized, reduced (small size, or sometimes with weak, non functional annulus) remnants of a now mostly extinct lineage of an ancient branch of what is clearly *Tortella*. It has been empirically demonstrated (Zander 2016, 2017) that there may be anywhere from one to four descendant species from any one progenitor, it would take a distance of at least five contiguous nodes for a morphological or molecular phylogenetic tree to be reliable as to evolutionary distance between taxa.

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