Notes on the genus *Syntrichia* with a revised infrageneric classification and the recognition of a new genus *Syntrichiadelphus* (Bryophyta, Pottiaceae)

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ABSTRACT

A revised infrageneric classification of the genus *Syntrichia* Brid. is proposed that includes the segregation of a new genus *Syntrichiadelphus* for the species currently known as *Syntrichia flagellaris* (Schimp.) R.H. Zander. In addition, a synopsis of *Syntrichia* for Madagascar is presented with new synonymy, lectotypifications, and *Syntrichia ammonsiana* (H.A. Crum & L.E. Anderson) Ochyra newly reported from the island. *Published online* ***www.phytologia.org*** *Phytologia 103(4): 90-103 (December 22, 2021). ISSN 030319430.*

KEY WORDS: infrageneric classification, Madagascar, Pottiaceae, *Syntrichia*, *Syntrichiadelphus*

INFRAGENERIC CLASSIFICATION OF *SYNTRICHIA*

A recent investigation into the molecular phylogenetics of *Syntrichia* Brid. (Mishler et al. in prep.) found several smaller, closely related genera to be nested within it. Recognition of a somewhat broader circumscription for *Syntrichia* requires many updates to nomenclature. The complete molecular results will be presented separately and space constraints would prohibit a detailed accounting of the nomenclature at the same time. Therefore, we present a revised infrageneric classification here including nine sections, and formally establish the new names for use in forthcoming publications. In the following discussion we list 'representative species' for groups that were supported by our molecular analyses and morphological studies. For this purpose, we have chosen mostly well-known species whose placement remained relatively stable across different loci and analyses. This is not meant to be a complete or final list of the constituents of each section, but instead aims to characterize those clades morphologically.

Syntrichia Brid., J. Bot. (Schrader) 1(2): 299. 1801. (Bridel 1801)
=*Streptopogon* Wilson ex Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 51. 1851. (Mitten 1851), *syn. nov.*
=*Willia* Müll. Hal., Int. Polarforsch., Deutsch. Exped. 2: 311. 1890. (Müller 1890), *syn. nov.*
=*Calyptopogon* (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 419. 1902. (Brotherus 1902), *syn. nov.*
=*Sarconeurum* Bryhn, Nyt Mag. Naturvidensk. 40(3–4): 204. 1902. (Bryhn 1902), *syn. fide* Ochyra & Zander (2007)
=*Sagenotortula* R.H. Zander, Phytologia 65: 429. 1989. (Zander 1989), *syn. nov.*

Type: *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr (lectotype designated by Zander [1989: 432])

A genus of roughly 85 species and with a worldwide distribution. Species of *Syntrichia* are frequent and often dominant members of cryptogamic communities in arid ecosystems. They can be found in diverse habitats ranging from cold arctic deserts and temperate Mediterranean chaparral to tropical high elevation paramo. The genus is also diverse morphologically and can be divided into at least nine sections, as outlined below.

Syntrichia Brid. sect. ***Syntrichia***
≡*Tortula* sect. *Syntrichia* (Brid.) Lam. & DC., Syn. Pl. Fl. Gall. 100. 1806.
≡*Tortula* subg. *Syntrichia* (Brid.) Chevall., Fl. Gén. Env. Paris 2: 52. 1827.
≡*Barbula* sect. *Syntrichia* (Brid.) Müll. Hal., Syn. Musc. Frond. 1: 632. 1849.
≡*Barbula* subg. *Syntrichia* (Brid.) Schimp., Bryol. Eur. 2: 10 (fasc. 46–47 Consp. 2: III). 1851.
=*Tortula* [unranked] *Rurales* De Not., Mem. Reale Accad. Sci. Torino 40: 286. 1838.
=*Barbula* [unranked] *Rurales* Bruch & Schimp., Bryol. Eur. 2: 101 (fasc. 13–15 Mon. 39). 1842.
=*Barbula* sect. *Syntrichiae* Lesq. & James, Man. Mosses N. America 130. 1884, *nom. illeg.*
=*Barbula* [unranked] *Ruraliformes* Kindb., Eur. N. Amer. Bryin. 2: 245. 1897, *nom. illeg.*

Type: *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr

Other representative species:
Syntrichia antarctica (Hampe) R.H. Zander
Syntrichia calcicola J.J. Amann
Syntrichia campestris (Dusén) R.H. Zander
Syntrichia caninervis Mitt.
Syntrichia cavallii (G. Negri) Ochyra
Syntrichia handelii (Schiffn.) S. Agnew & Vondr.
Syntrichia latifolia (Bruch ex Hartm.) Huebener
Syntrichia montana Nees
Syntrichia norvegica F. Weber
Syntrichia rigescens (Broth. & Geh.) Ochyra
Syntrichia virescens (De Not.) Ochyra

The type section of *Syntrichia* mostly contains the well-known and widely distributed species centered around *S. ruralis*. These species are described and illustrated in numerous publications (e.g., Kramer 1980, Kramer 1988, Zander 1993, Gallego 2005). Another species that apparently belongs here is *Syntrichia squarripila*. That name has never been validly published despite appearing in several floristic works (Herzog 1954; Cano & Gallego 2008; Müller 2009; Ireland et al. 2010, 2017). We correct this oversight here:

Syntrichia squarripila (Thér.) Herzog ex Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Tortula squarripila* Thér., Revista Chilena Hist. Nat. 21: 10. 1917. (Thériot 1917)

Syntrichia sect. ***Streptopogon*** (Wilson ex Mitt.) Brinda, Jáuregui-Lazo & Mishler *comb. nov.*
Basionym: *Streptopogon* Wilson ex Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 51. 1851. (Mitten 1851)
=*Streptopogon* sect. *Calymperella* Broth., Hedwigia 33: 128. 1894. (Brotherus 1894)
=*Streptopogon* sect. *Streptopogonella* Demaret & P. de la Varde, Bull. Jard. Bot. État Bruxelles 26: 270. 1956. (Demaret & Potier de la Varde 1956)
=*Syntrichia* sect. *Collotortula* R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 264. 1993. (Zander 1993), *syn. nov.*

Note: *Streptopogon* was monotypic when published and the sectional autonym was generated by the publication of *Streptopogon* sect. *Calymperella* Broth. (Brotherus 1894).

Type: *Syntrichia erythrodonta* (Taylor) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Barbula erythrodonta* Taylor, London J. Bot. 5: 50. 1846. (Taylor 1846)
≡*Tortula erythrodonta* (Taylor) Wilson, London J. Bot. 5: 454. 1846.
≡*Streptopogon erythrodontus* (Taylor) Wilson ex Mitt., Hooker's J. Bot. Kew Gard. Misc. 3: 51. 1851.
≡*Tayloria erythrodonta* (Taylor) Spruce, J. Proc. Linn. Soc., Bot. 5: 48. 1860.

The genus *Streptopogon* was revised by Casado (2000), who reduced some species to synonymy. The remaining species are here transferred to *Syntrichia*:

Syntrichia brasiliensis (Casado ex D.P. Costa) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon brasiliensis* Casado ex D.P. Costa, Syst. Bot. 37(3): 584. 2012. (Costa 2012)

Syntrichia calymperes (Müll. Hal.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon calymperes* Müll. Hal., Abh. Naturwiss. Vereins Bremen 7: 207. 1881. (Müller & Geheeb 1881)

Syntrichia cavifolia (Mitt.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon cavifolius* Mitt., J. Linn. Soc., Bot. 12: 180. 1869. (Mitten 1869)

Syntrichia clavipes (Spruce) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Tayloria erythrodonta* var. *clavipes* Spruce, J. Proc. Linn. Soc., Bot. 5: 49. 1860. (Spruce 1861)
≡*Streptopogon clavipes* (Spruce) Mitt., J. Linn. Soc., Bot. 12: 178. 1869.

Syntrichia lindigii (Hampe) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon lindigii* Hampe, Ann. Sci. Nat., Bot., sér. 5, 3: 351. 1865. (Hampe 1865)

Syntrichia matudiana (H.A. Crum) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon matudianus* H.A. Crum, Bryologist 55: 51. 1952. (Crum 1952)

Other representative species:
Syntrichia aculeata (Wilson) R.H. Zander
Syntrichia ammonsiana (H.A. Crum & L.E. Anderson) Ochyra
Syntrichia amphidiacea (Müll. Hal.) R.H. Zander
Syntrichia andicola (Mont.) Ochyra
Syntrichia angustifolia (Herzog) M.J. Cano
Syntrichia bogotensis (Hampe) Mitt. ex R.H. Zander
Syntrichia chisosa (Magill, Delgad. & L.R. Stark) R.H. Zander
Syntrichia fragilis (Taylor) Ochyra
Syntrichia gemmascens (P.C. Chen) R.H. Zander
Syntrichia kingii (H. Rob.) M.T. Gallego & M.J. Cano
Syntrichia obtusissima (Müll. Hal.) R.H. Zander
Syntrichia sinensis (Müll. Hal.) Ochyra
Syntrichia submontana (Broth.) Ochyra

One of the less intuitive results of the molecular phylogenetic analyses was that *Streptopogon* is nested in *Syntrichia*. While it is possible that not all currently recognized *Streptopogon* species belong in *Syntrichia*, the type species was studied and found to be closely related to *S. amphidiacea*. In herbaria

one can find specimens where bryologists have mistaken *S. amphidiacea* for *S. calymperes* or vice versa. The two species bear a superficial similarity and both share the conspicuous production of clavate, multicellular gemmae on the leaves. In many ways, both *S. amphidiacea* and *S. gemmascens* (two species included in *Syntrichia* sect. *Collotortula* by Zander [1993]) present character states intermediate between those more typical of *Syntrichia* and those found in *Streptopogon*. For example, both show a trend towards loss of papillae, more rounded costal cross-section with some development of a dorsal epidermal layer, copious production of gemmae, and somewhat elongated laminal cells. Some of these features might be explained as adaptations to the epiphytic habit, which is common in this group.

In addition, the rosette-forming, gemmiferous habit seems to have arisen independently in more than one lineage of *Syntrichia* and is a common feature of those species that inhabit both rock and wood substrates (e.g., *S. amphidiacea*, *S. chisosa*, *S. fragilis*, *S. latifolia*, *S. pagorum*). Their superficial similarity is at least in part due to convergent evolution and their facultative epiphytism may have facilitated the transition to this niche in several lineages. *Syntrichia* species that are more exclusively epiphytic show some trends in morphology that parallel those found in unrelated groups (Fedosov et al. 2020), such as the strongly differentiated perichaetial leaves found in *Willia* and *Calyptopogon* below.

Syntrichia sect. ***Willia*** (Müll. Hal.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Willia* Müll. Hal., Int. Polarforsch., Deutsch. Exped. 2: 311. 1890. (Müller 1890)

Note: The sectional autonym for *Willia* was generated by the publication of *Willia* sect. *Schistidiella* Müll. Hal. (Müller 1901[1900]).

Type: *Willia grimmioides* Müll. Hal. (monotypic when published, =*Willia austroleucophaea* (Besch.) Broth. [see below])

The transfer of *Willia* to *Syntrichia* requires the following combinations:

Syntrichia austroleucophaea (Besch.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Grimmia austroleucophaea* Besch., Bull. Soc. Bot. France 32: LX. 1885. (Bescherelle 1885)
≡*Willia austroleucophaea* (Besch.) Broth., Nat. Pflanzenfam. I(3): 453. 1902.
=*Willia grimmioides* Müll. Hal., Int. Polarforsch., Deutsch. Exped. 2: 311. 1890, *syn. fide* Bell (1974)

Syntrichia brachychaete (Dusén) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Tortula brachychaete* Dusén, Bot. Not. 1905: 300. 1905. (Dusén 1905)
≡*Willia brachychaete* (Dusén) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 236. 1993.

Note: The designation 'Syntrichia brachychaete' was printed on exsiccatae distributed by Dusén & Brotherus (Sayre 1975) but the name has never been validly published. These were cited as "M. Am. austr. n. 761" by Paris (1906).

Syntrichia calobolax (Müll. Hal.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Barbula calobolax* Müll. Hal., Bot. Jahrb. Syst. 5: 80. 1883. (Müller 1883)
≡*Willia calobolax* (Müll. Hal.) Lightowl., J. Bryol. 13: 370. 1985.

Zander (1993) has commented on the close relationship between *Willia* and *Syntrichia* and suggested that *Willia* may be only a section of the latter. We agree and note that the morphological features that characterize *Willia* are also present to varying degrees in other members of *Syntrichia*, including the strong constriction of the leaf and differentiated perichaetial leaves. Therefore, we have made the transfer without any change in circumscription. Zander also pointed out that it is rather close

to section *Aesiotortula* (see below) and the molecular phylogenetic analyses also support this relationship. For the moment, we do not have enough evidence to join the two.

Syntrichia sect. ***Calyptopogon*** (Mitt.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Streptopogon* [unranked] *Calyptopogon* Mitt., Philos. Trans. 168: 33. 1879. (Mitten 1879, Salmon 1903)
≡*Streptopogon* sect. *Calyptopogon* (Mitt.) Paris, Index Bryol. Suppl. 86. 1900.
≡*Calyptopogon* (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 419. 1902.

Type: *Syntrichia mnioides* (Schwägr.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Barbula mnioides* Schwägr., Sp. Musc. Frond., Suppl. 4: pl. 310b. 1842. (Schwägrichen 1842)
≡*Tortula mnioides* (Schwägr.) Mont., Fl. Chil. 7: 150. 1850.
≡*Streptopogon mnioides* (Schwägr.) Mitt., Fl. Tasman. 2: 376. 1859.

Other representative species:
Syntrichia papillosa (Wilson ex Spruce) Spruce
Syntrichia subpapillosa (Cardot & Broth.) Matteri

Zander (1993) commented on similarities between *S. papillosa* and *Calyptopogon* and Matteri (1994) noted the same for *S. subpapillosa* which is even more reminiscent of *Calyptopogon* because of its partial leaf border.

Syntrichia sect. ***Vallidens*** (Müll. Hal.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Barbula* sect. *Vallidens* Müll. Hal., Linnaea 43: 432. 1882. (Müller 1882)
=*Sarconeurum* Bryhn, Nyt Mag. Naturvidensk. 40(3–4): 204. 1902, *syn. nov.*

Type: *Syntrichia percarnosa* (Müll. Hal.) R.H. Zander

Other representative species:
Syntrichia breviseta (Mont.) M.J. Cano & M.T. Gallego
Syntrichia lithophila (Dusén) Ochyra & R.H. Zander
Syntrichia magilliana L.E. Anderson
Syntrichia phaea (Hook. f. & Wilson) R.H. Zander
Syntrichia sarconeurum Ochyra & R.H. Zander

Ochyra & Zander (2007) considered *Sarconeurum* to be synonymous with sect. *Aesiotortula*, but in our phylogenetic analysis *S. sarconeurum* is one member of a well-supported clade of small blackish-green plants with plane leaf margins, a short proportion of differentiated basal cells in relation to leaf length, and occasionally modified, caducous leaf apices. *Barbula* sect. *Vallidens* was listed incorrectly in *Index Muscorum* as not validly published (Wijk et al. 1959). They also provided an incorrect place of publication and this no doubt contributed to the error. Müller (1882) validated the name and designated the type in his discussion following the description of *Barbula characodonta* Müll. Hal. (a synonym of *S. percarnosa* fide Cano & Gallego 2008).

Syntrichia sect. ***Sagenotortula*** (R.H. Zander) Brinda, Jáuregui-Lazo & Mishler, *comb. & stat. nov.*
Basionym: *Sagenotortula* R.H. Zander, Phytologia 65: 429. 1989.

Type: *Syntrichia quitoensis* (Taylor) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Tortula quitoensis* Taylor, London J. Bot. 6: 332. 1847. (Taylor 1847)
≡*Barbula quitoensis* (Taylor) Müll. Hal., Syn. Musc. Frond. 1: 627. 1849.

≡*Sagenotortula quitoensis* (Taylor) R.H. Zander, Phytologia 65: 430. 1989.

Other representative species:
Syntrichia princeps (De Not.) Mitt.
Syntrichia scabrella (Dusén) R.H. Zander

Zander (1993) noted the similarities between *Sagenotortula* and *Syntrichia*. Despite the unusual traits of its type species, *Sagenotortula* shares with *Syntrichia* the red reaction to KOH in addition to the costa with a (weakly) reniform stereid band and no abaxial epidermis. The core species of this section also share a strong central strand in the stem, hydroids in the costa, and larger laminal cells. While this last character is highly exaggerated in *S. quitoensis*, it is also commonly used to differentiate *S. princeps* from other *Syntrichia* species. Synoicous specimens of the widely distributed and well-known *S. princeps* reliably clustered with each other in our analyses suggesting that sexuality is possibly a more informative character in *Syntrichia* than in some other groups. However, since *S. princeps* may have evolved the synoicous condition through polyploidy and/or hybridization our conclusions are tentative pending further studies. While *Sagenotortula* and *S. princeps* are both relatively isolated, in most of our analyses they do form a well-supported clade. For these reasons we have decided to group them under the existing name rather than describe an additional section for *S. princeps* that might later prove to be superfluous. It is an interesting problem that we hope to explore further.

Syntrichia sect. ***Aesiotortula*** R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 264. 1993. (Zander 1993)

Type: *Syntrichia pagorum* (Milde) J.J. Amann

Other representative species:
Syntrichia anderssonii (Ångstr.) R.H. Zander
Syntrichia buchtienii (Herzog) M.J. Cano & M.T. Gallego
Syntrichia costesii (Thér.) R.H. Zander
Syntrichia epilosa (Broth. ex Dusén) R.H. Zander
Syntrichia glacialis (Kunze ex Müll. Hal.) R.H. Zander
Syntrichia lacerifolia (R.S. Williams) R.H. Zander
Syntrichia laevipila Brid.
Syntrichia saxicola (Cardot) R.H. Zander
Syntrichia serripungens (Lorentz & Müll. Hal.) R.H. Zander

Our circumscription of sect. *Aesiotortula* differs from that outlined by Zander (1993), but we have retained both the type, *S. pagorum*, and *S. epilosa* as core species, so the name is still applicable. The species of this section usually have plane (often bordered) margins and relatively short, smooth hair points. In the dioicous species, there is also a strong tendency towards asexual reproduction either by minute, leaf-like propagules or by fragile leaves. In contrast with some other 'tortuloid' genera, *Syntrichia* does not contain any species with highly reduced sporophytes and cleistocarpous capsules (e.g., *Phascum* Hedw., *Pottia* Ehrh. ex Fürnr., etc.) Zander (1993) noted that *Phascopsis* I.G. Stone could represent one example of this and may be related to sect. *Aesiotortula*, but the sole species of *Phascopsis* is rare and was not analyzed molecularly.

Syntrichia sect. ***Magnisyntrichia*** Brinda, Jáuregui-Lazo & Mishler, *sect. nov.*

Diagnosis: Differs from the typical section by the lanceolate leaves with denticulate to serrate distal margins and strongly sheathing bases made up of rather narrow and highly elongated cells. In addition, the apices lack elongated hairpoints and the costa is percurrent to short-excurrent. (Fig. 1).

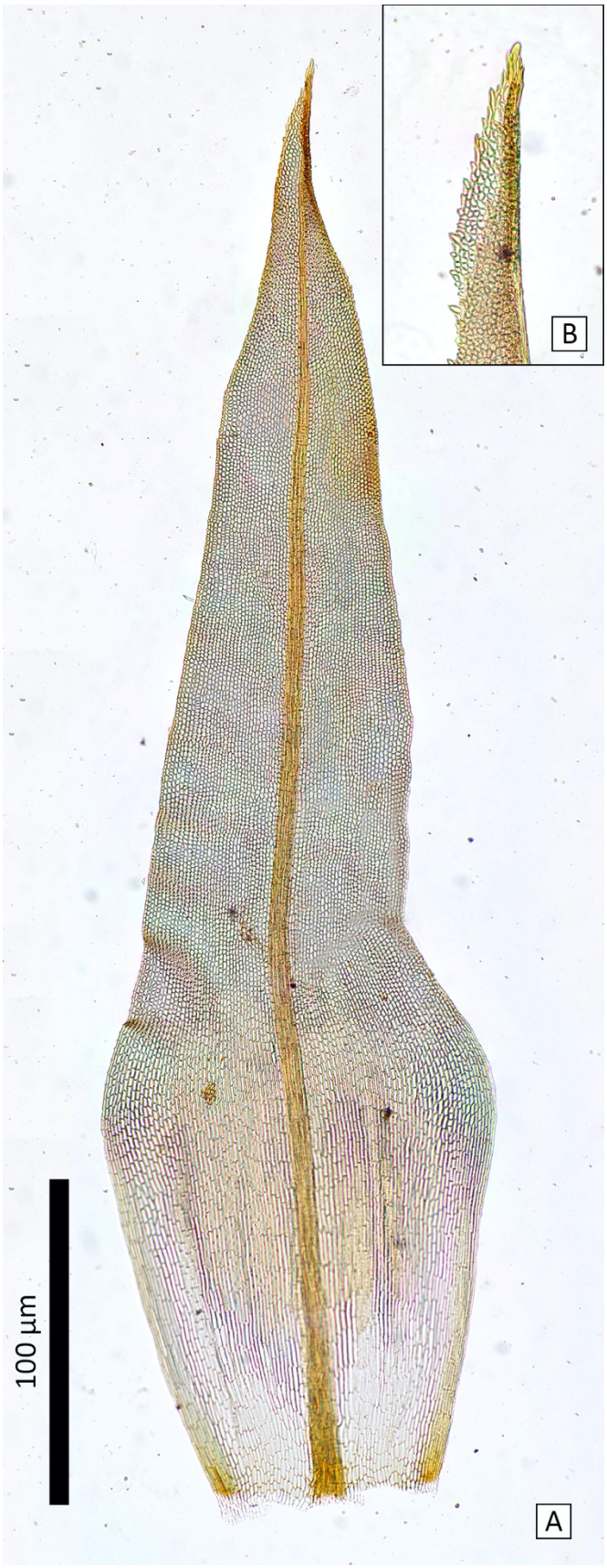

Figure 1. *Syntrichia robusta* (Chile, *Larraín 38586*, MO). A. Surface view of leaf emphasizing the lanceolate shape, serrulate margin, and sheathing leaf base. B. Close-up of marginal teeth.

Type: *Syntrichia robusta* (Hook. & Grev.) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 269. 1993.

Other representative species:
Syntrichia geheebiaeopsis (Müll. Hal.) R.H. Zander
Syntrichia rubra (Mitt.) R.H. Zander

Syntrichia robusta was included in sect. *Collotortula* by Zander (1993). However, our analyses show that it is part of a unique clade that is relatively easily differentiated by the characters given above. The sectional name is derived by combining the Latin prefix magni-, meaning large, with the genus name. It refers to the robust growth forms of the constituent species, especially the type, *S. robusta*.

Syntrichia sect. ***Eosyntrichia*** Brinda, Jáuregui-Lazo & Mishler, *sect. nov.*

Diagnosis: Differs from the typical section by the stoutly mucronate leaves, sharply spinose-dentate leaf margins, and strongly sheathing bases (Fig. 2A). The mucro is strongly serrate and may exceed 1 mm in length but remains ± rigid and reddish-orange throughout its length. The marginal teeth are large, frequently multicellular, and smooth, contrasting starkly with the adjacent papillose laminal cells (Fig. 2C and 3).

Figure 2. *Syntrichia pseudorobusta* (Chile, *Ireland & Bellolio 35943*, MO). A. Side view of leaf showing the strong marginal teeth, sheathing base, and stoutly mucronate apex. B. Cross-section of costa. C. Close-up of marginal teeth.

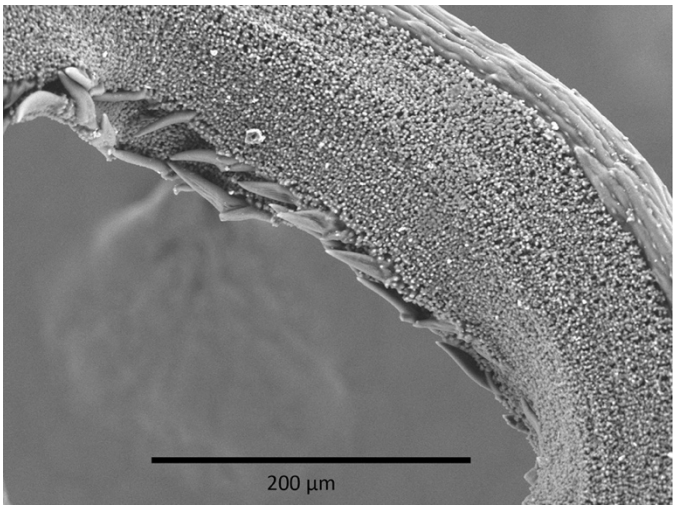

Figure 3. Scanning electron microscope image of *Syntrichia pseudorobusta* (Chile, *Ireland & Bellolio 35943*, MO), showing the sharp, strong teeth along the leaf margin.

Type: *Syntrichia pseudorobusta* (Dusén) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 269. 1993.

Other representative species:
Syntrichia serrata (Dixon) R.H. Zander

This section (like the preceding one) is exclusive to the southern hemisphere and hints at the origins of the genus. Therefore, we have given it a name derived from the Greek word ἠώς (eos), meaning dawn. The marginal teeth in well-developed *S. pseudorobusta* are striking and unlike any other *Syntrichia* except for *S. serrata* where they are somewhat less pronounced.

Syntrichiadelphus Brinda, Jáuregui-Lazo & Mishler, *gen. nov.* (Fig. 4)

Diagnosis: Similar to *Syntrichia* except for basal cells that gradually transition into the laminal cells while retaining simple or branching papillae nearly throughout the hyaline region (Fig. 4F), broadly reflexed (Fig. 4B) and ± undulate leaf margins (Fig. 4D), and the frequent presence of flagellate stems (Fig. 4A).

Type: *Syntrichiadelphus flagellaris* (Schimp.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*
Basionym: *Barbula flagellaris* Schimp., Ann. Sci. Nat., Bot., sér. 2, 6: 146. pl. 10. 1836. (Schimper 1836)
≡*Tortula flagellaris* (Schimp.) Mont., Fl. Chil. 7: 147. 1850.
≡*Syntrichia flagellaris* (Schimp.) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 269. 1993.

Syntrichiadelphus flagellaris is an unusual species that seems morphologically out of place in *Syntrichia*. In *Syntrichia* the basal cells are usually more strongly differentiated, the costal stereid band (Fig. 4C) is usually stronger, undulate leaf margins are uncommon, and the leaf recurvature (when present) is usually narrower. At the same time there is no other genus into which *S. flagellaris* might fit comfortably. Molecular phylogenetic analyses confirmed its isolated position well outside of *Syntrichia*, so we provide a new genus for it here. The name is derived by combining *Syntrichia* with the Greek word ἀδελφός (adelphos), meaning brother, in recognition of their close resemblance. The genus is monotypic making the characters of the genus the same as those of its only species. The sole species seems to be endemic to the Mediterranean climatic region of Chile, occurring in dry to mesic habitats there.

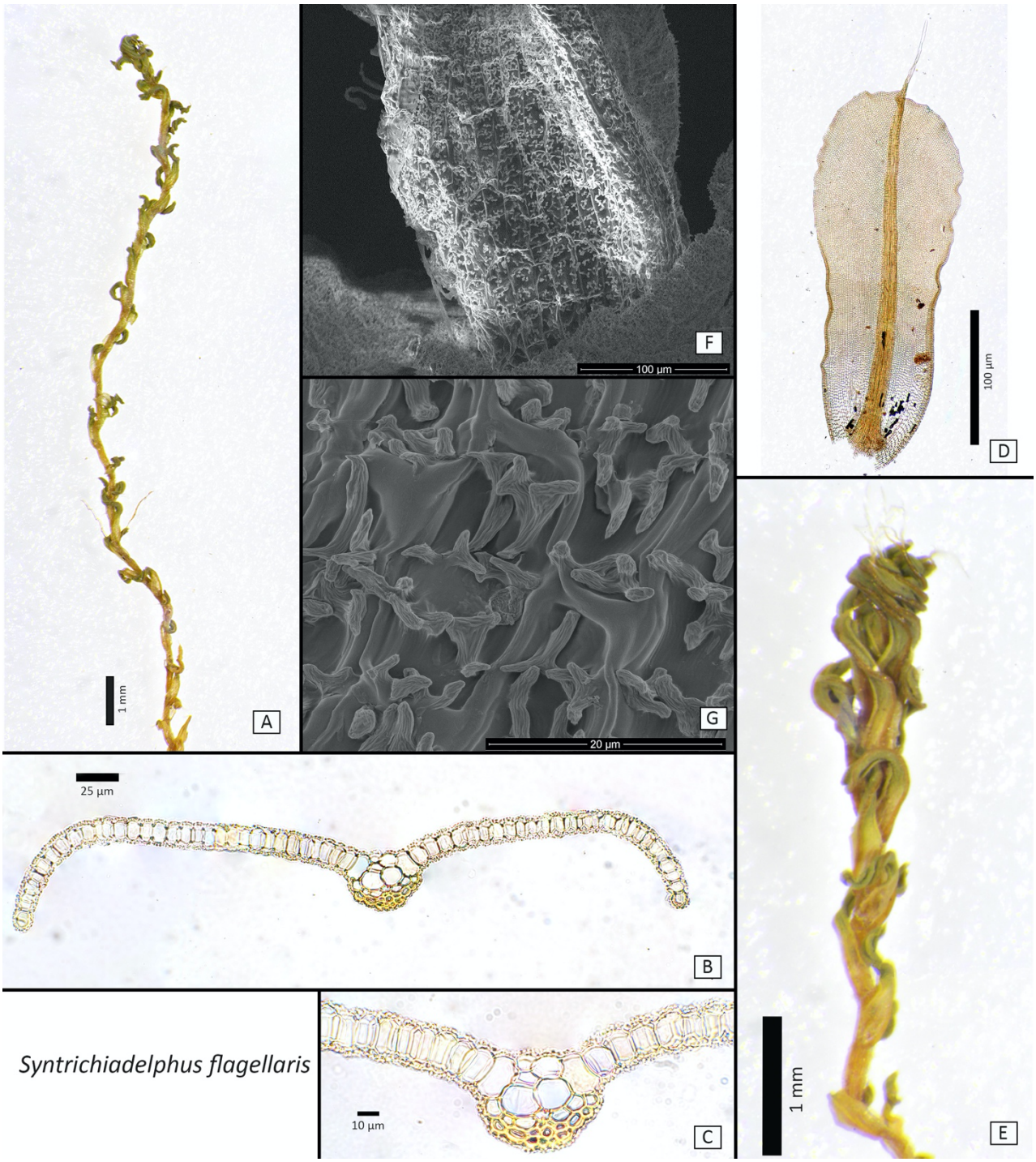

Figure 4. *Syntrichiadelphus flagellaris* (Chile, *Jáuregui-Lazo 66*, UC). A. Flagellate stem. B. Cross-section of leaf showing the broadly reflexed margin. C. Cross-section of costa. D. Abaxial surface of leaf. E. Dried habit of typical stem. F. Scanning electron microscope image illustrating the leaf attachment and papillose basal cells. G. Close-up of bifurcated papillae of basal cells.

SYNOPSIS OF *SYNTRICHIA* IN MADAGASCAR

While revising some collections from Madagascar as part of the MadBryo project (www.madbryo.org), JCB had the opportunity to examine type material for some names of Pottiaceae described from that region. No *Syntrichia* species are listed for Madagascar by either O'Shea (2006) or Marline (2012), but at least five species do indeed occur there. Two of these are formerly *Streptopogon* species, another two have been reported under names in *Tortula* Hedw. that are synonyms, and finally the fifth is apparently newly reported here.

Syntrichia ammonsiana (H.A. Crum & L.E. Anderson) Ochyra — *New to Madagascar*
Specimens examined: *Crosby* 7356 (!MO-6239661), *Crosby* 7359 (!MO-6897724), *Crosby* 7375A (!MO-6897723) all collected in Ramiova Forest, Andringitra Massif, 3 November 1972.

Syntrichia amphidiacea (Müll. Hal.) R.H. Zander
=*Tortula omissa* Thér., Recueil Publ. Soc. Havraise Études Diverses 93: 46. 1926, *syn. nov.*
Note: 'Barbula omissa' is an error for *T. omissa* that appears in *Index Muscorum* (Wijk et al. 1959).
Specimens examined: *Decary 145 p.p.* (!PC0099693 lectotype [here designated] of *Tortula omissa*), *Magill & Pócs 12927B* (!MO-6897764), *Magill & Pócs 13106A* (!MO-6969073), *Magill & Pócs 13138A* (!MO-6897765), *Onraedt 71.M.5146* (!PC0787153), *Onraedt 74.M.2028* (!PC0787173), *Tixier 9189* (!PC0661684);
Additional note — *new to Comoros*, W slope of Mt. Kartala, Grande Comore, *Magill & Pócs 11137* (!MO-4429065)

Syntrichia calymperes (Müll. Hal.) Brinda, Jáuregui-Lazo & Mishler
Specimens examined: *Crosby 6643* (!G00048882; !MO-3111648)

Syntrichia erythrodonta (Taylor) Brinda, Jáuregui-Lazo & Mishler
=*Streptopogon hildebrandtii* Müll. Hal., Gen. Musc. Frond. 422. 1900.
=*Streptopogon subelimbatus* Cardot, Hist. Phys. Madagascar, Mousses 222. 1915.
Specimens examined: *Hildebrandt 2098* (!G00048873; !G00048872; !G00048871; !PC0099023; BM000867580 lectotype [here designated] of *Streptopogon hildebrandtii fide* Casado [2000] and JSTOR Global Plants <https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bm000867580>), *Hildebrandt 2118* (!G00048881), *Sikora s.n.* (!PC0073075 lectotype [here designated] of *Streptopogon subelimbatus*)

Syntrichia fragilis (Taylor) Ochyra
=*Barbula subrufa* Renauld & Cardot, Suppl. Prodr. Fl. Bryol. Madagascar 45. 1909, *nom. illeg.*, *syn. nov.* (non *Barbula subrufa* Broth. ex Müll. Hal., Gen. Musc. Frond. 444. 1900.)
=*Tortula subrufa* Cardot, Hist. Phys. Madagascar, Mousses 223. 1915, *syn. nov.*
Specimens examined: *Drouhard s.n.* (!G00048884; !PC0660781; !PC0787151; !PC0787159), *Onraedt 71.M.5051* (!PC0787166), *Tixier 8165* (!PC0661678), *Villaume s.n.* [1904] (!PC0099936), *Villaume s.n.* [1905] (!PC0099933 lectotype [here designated] of *Barbula subrufa* [≡*Tortula subrufa*]; !PC0099934; !PC0134945; !PC0099935)

Tóth (1987: fig. 3) reported *S. fragilis* from the region including Madagascar without any details, presumably after examining specimens of *T. subrufa*. Another older and poorly known species, *Barbula rufa* Schimp. ex Besch., is also a *Syntrichia* as was pointed out by O'Shea (2008). This species is apparently known only from the small type collection made on the island of Mauritius — *Ayres s.n.* (!PC0109923 lectotype [here designated] of *Barbula rufa*; !PC0074368; !PC0767998; !PC0767999). The leaves are faintly bordered and have costae with hydroids. These and other characters are suggestive of the widespread southern hemisphere species *S. antarctica* and therefore the following synonymy is proposed:

Syntrichia antarctica (Hampe) R.H. Zander
=*Barbula rufa* Schimp. ex Besch., Ann. Sci. Nat., Bot., sér. 6, 9: 344. 1880, *syn. nov.*
=*Tortula rufa* (Schimp. ex Besch.) Broth., Nat. Pflanzenfam. I(3): 435. 1902, *nom. illeg.*, *syn. nov.* (non *Tortula rufa* (Lorentz) Braithw., J. Bot. 9: 293. 1871.)
=*Syntrichia rufa* (Schimp. ex Besch.) O'Shea, Trop. Bryol. 29: 5. 2008, *syn. nov.*

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LITERATURE CITED

Bell, B. G. 1974. A synoptic flora of South Georgian mosses. V. *Willia* and *Racomitrium*. British Antarctic Survey Bulletin 38: 73–101.

Bescherelle, É. 1885. Mousses nouvelles de l'Amérique australe. Bulletin de la Société Botanique de France 32: liv–lxix.

Bridel, S. É. 1801. Animadversiones in Muscologiae Recentiorum Tomum secundum, ab ipso auctore propositae. Journal für die Botanik 1800(2): 268–299.

Brotherus, V. F. 1894. Musci Schenckiani. Hedwigia 33: 127–136.

Brotherus, V. F. 1902. Bryales, in part. Pp. 385–432. In: H. G. A. Engler & K. Prantl, Die Natürlichen Pflanzenfamilien I(3). Engelmann, Leipzig.

Bryhn, N. 1902. *Sarconeurum*, genus novum. *Sarconeurum antarcticum* sp. nov. Nyt Magazin for Naturvidenskaberne 40(3): 204–207.

Cano, M.J. and M.T. Gallego. 2008. The genus *Tortula* (Pottiaceae, Bryophyta) in South America. Botanical Journal of the Linnean Society 156(2): 173–220.

Casado, C. M. 2000. A Taxonomic Revision of *Streptopogon* Wils. (Pottiaceae). Master's thesis, University of Missouri-St. Louis. 66 pages.

Costa, D. P. da. 2012. Validation of the new species of *Streptopogon* (Pottiaceae, Bryophyta) and a synopsis of the genus for Brazil. Systematic Botany 37(3): 583–586.

Crum, H. A. 1952. Two new species of Mexican mosses collected by Aaron J. Sharp. The Bryologist 55: 51–58.

Demaret, F. and R. A. L. Potier de la Varde. 1956. Quelques taxa nouveaux de mousses du Ruwenzori (Congo belge). Bulletin du Jardin Botanique de l'État à Bruxelles 26: 265–275.

Dusén, P. 1905. Musci nonnulli novi e Fuegia et Patagonia reportati. Botaniska Notiser 1905(7): 299–310.

Dusén, P. 1906. Beiträge zur Bryologie der Magellansländer, von Westpatagoien und Südchile. 4. Arkiv för Botanik 6(8): 1–40, 12 pl.

Fedosov, V.E., A.V. Fedorova, J. Larraín, M.B. Santos, M. Stech, J. Kučera, J.C. Brinda, D.Y. Tubanova, M. von Konrat, E.A. Ignatova and M.S. Ignatov. 2020. Unity in diversity: phylogenetics and taxonomy of Rhabdoweisiaceae (Dicranales, Bryophyta). Botanical Journal of the Linnean Society 195: 545–567.

Gallego, M. T. 2005. A taxonomic study of the genus *Syntrichia* Brid. (Pottiaceae, Musci) in the Mediterranean region and Macaronesia. Journal of the Hattori Botanical Laboratory 98: 47–122.

Hampe, E. 1865. Prodromus florae Novo-Granatensis ou énumération des plantes de la Nouvelle-Grenade, avec description des espéces nouvelles, par M. m. Triana et J. E. Planchon. Musci. Annales des Sciences Naturelles; Botanique, série 5, 3: 337–376.

Herzog, T. 1954. Zur Bryophytenflora Chiles. Revue Bryologique et Lichénologique 23(1-2): 27–99.

Ireland, R. R., G. Bellolio, J. Larraín and R. Rodríguez. 2010. Studies on the moss flora of the Bío-Bío region of Chile: Part 2. Tropical Bryology 32: 39–44.

Ireland, R. R., G. Bellolio, J. Larraín and R. Rodríguez. 2017. Studies on the moss flora of the Bío-Bío Region of Chile: Part 3. PhytoKeys 77: 1–20.

Kramer, W. 1980. *Tortula* Hedw. sect. *Rurales* De Not. (Pottiaceae, Musci) in der östlichen Holarktis. Bryophytorum Bibliotheca 21: 1–165.

Kramer, W. 1988. Beiträge zur Systematik und Bryogeographie einiger Sippen von *Tortula* Hedw. Sect. *Rurales* De Not. (Pottiaceae, Musci) unter besonderer Berücksichtigung der Südhemisphäre. Journal of the Hattori Botanical Laboratory 65: 81–144.

Marline, L., R. L. Andriamiarisoa, J. Bardat, M. Chuah-Petiot, T. A. J. Hedderson, C. Reeb, D. Strasberg, N. Wilding and C. Ah-Peng. 2012. Checklist of the bryophytes of Madagascar. Cryptogamie, Bryologie 33(3): 199–255.

Matteri, C. M. 1994. *Tortula subpapillosa* and *T. papillosa* in southern South America with a new combination in *Syntrichia*. Journal of the Hattori Botanical Laboratory 75: 33–40.

Mitten, W. 1869. Musci Austro-Americani. Journal of the Linnean Society, Botany 12: 1–659.

Mitten, W. 1879. Musci in Transit of Venus expeditions carried out by order of her Majesty's government in the years 1874–1875. Philosophical Transactions of the Royal Society of London 168(extra vol.): 388–396.

Mönkemeyer, W. 1927. Die Laubmoose Europas. Akademische Verlagsgesellschaft, Leipzig.

Müller, C. 1851. Synopsis Muscorum Frondosorum Omnium Hucusque Cognitorum, Pars Secunda. Alb. Foerstner, Berlin.

Müller, C. and A. Geheeb. 1881. Laubmoose. Pp. 203–214 in F. Buchenau. Reliquiae Rutenbergianae. III. (Botanik, Fortsetzung.) Abhandlungen herausgegeben vom Naturwissenschaftlichen Vereins zu Bremen 7(2): 198–214.

Müller, C. 1882. Prodromus bryologiae Argentinicae II, seu musci Lorentziani Argentinici. Linnaea 43(5–6): 341–486.

Müller, C. 1890. Bryologia Austro-Georgiae. Pp. 279–322. In: G. B. v. Neumayer, Die Internationale Polarforschung 1882–1883, Die Deutschen Expeditionen... 2. A. Asher & Co., Berlin.

Müller, C. 1901. Genera Muscorum Frondosorum. Eduard Kummer, Leipzig.

Müller, F. 2009. An updated checklist of the mosses of Chile. Archive for Bryology 58: 1–124.

Ochyra, R. and R. H. Zander. 2007. Is *Tortula lithophila* conspecific with *Sarconeurum glaciale* (Bryopsida: Pottiaceae)? Fragmenta Floristica et Geobotanica, Series Polonica 14: 209–212.

O'Shea, B. J. 2006. Checklist of the mosses of sub-Saharan Africa (version 5, 12/06). Tropical Bryology Research Reports 6: 1–253.

O'Shea, B. J. 2008. Name changes for 13 African mosses with invalid names. Tropical Bryology 29: 4–5.

Paris, E. G. 1906. Index Bryologicus sive Enumeratio Muscorum, Editio Secunda, Vol. V. Paris: Librairie Scientifique A. Hermann.

Salmon, E. S. 1903. Bryological notes (continued). The Journal of Botany, British and Foreign 41(482): 46–51.

Sayre, G. 1975. Cryptogamae Exsiccatae—An Annotated Bibliography of Exsiccatae of Algae, Lichenes, Hepaticae, and Musci: V. Unpublished Exsiccatae. I. Collectors. Memoirs of the New York Botanical Garden 19(3): 277–423.

Schimper, W. P. 1836. Muscorum chilensium species novas descripsit. Annales des Sciences Naturelles; Botanique, série 2, 6: 145–149.

Schwägrichen, C. F. 1842. Species Muscorum Frondosorum, Supplementum Quartum Sect. 1, plates 301–325. Barth, Leipzig.

Spruce, R. 1861. Mosses of the Amazon and Andes. Journal of the Proceedings of the Linnean Society, Botany 5: 45–51.

Taylor, T. 1846. The distinctive characters of some new species of Musci, collected by Professor William Jameson, in the vicinity of Quito, and by Mr. James Drummond at Swan River. London Journal of Botany 5: 41–67.

Taylor, T. 1847. Descriptions of new Musci and hepaticae, collected by Professor William Jameson on Pichincha, near Quito. London Journal of Botany 6: 328–342.

Thériot, I. 1917. Contribution à la flore bryologique du Chili (2.e article). Revista Chilena de Historia Natural 21(1-2): 6–37.

Tóth, Z. 1987. A phytogeographic review of *Tortula* Hedw. Sect. *Rurales* De Not. (Pottiaceae Musci) in Hungary. Acta Botanica Hungarica 33(3–4): 249–278.

Wijk, R. van der, W. D. Margadant and P. A. Florschütz. 1959. Index Muscorum. Volume I (A–C). Regnum Vegetabile 17: 1–548.

Zander, R. H. 1989. Seven new genera in Pottiaceae (Musci) and a lectotype for *Syntrichia*. Phytologia 65: 424–436.

Zander, R. H. 1993. Genera of the Pottiaceae: mosses of harsh environments. Bulletin of the Buffalo Society of Natural Sciences 32: 1–378.