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 

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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)  
= *Calyphtopogon* (Mitt.) Broth., Nat. Pflanzenfam. 1(3): 419. 1902. (Brotherus 1902), syn. nov.  
= *Sarconeurn* Bryhn, Nyt Mag. Naturvidensk. 40(3–4): 204. 1902. (Bryhn 1902), syn. fide Ochyra & 

Zander (2007)  
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*


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.*

**Syntrichia** sect. *Streptopogon* (Wilson ex Mitt.) Brinda, Jáuregui-Lazo & Mishler *comb. nov.*
≡*Streptopogon* sect. *Calympeterella* Broth., Hedwigia 33: 128. 1894. (Brotherus 1894)
Note: *Streptopogon* was monotypic when published and the sectional autonym was generated by the publication of *Streptopogon* sect. *Calymerella* 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)

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.*


*Syntrichia cavifolia* (Mitt.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*

*Syntrichia clavipes* (Spruce) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*

*Syntrichia lindigii* (Hampe) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*


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.


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.*


*Syntrichia brachychaete* (Dusén) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*


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).


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.


Type: *Syntrichia mnioides* (Schwägr.) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*

≡*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 *Calyp;topogon* and Matteri (1994) noted the same for *S. subpapillosa* which is even more reminiscent of *Calyp;topogon* because of its partial leaf border.


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).


Type: *Syntrichia quitoensis* (Taylor) Brinda, Jáuregui-Lazo & Mishler, *comb. nov.*


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.


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., Phasum Hedw., Pottia Ehrh. ex Führ., 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, Larrain 38586, MO). A. Surface view of leaf emphasizing the lanceolate shape, serrulate margin, and sheathing leaf base. B. Close-up of marginal teeth.

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.

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 ἡώς (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.
≡*Tortula flagellaris* (Schimp.) Mont., Fl. Chili. 7: 147. 1850.

*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.

Note: 'Barbula omissa' is an error for T. omissa that appears in Index Muscorum (Wijk et al. 1959).
Specimens examined: Decary 145 p.p. (!PC0099023 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

Syntrichia fragilis (Taylor) Ochyra
Specimens examined: Drochard s.n. (!G00048884; !PC0660781; !PC0787151; !PC0787150), Onraedt 71.M.5051 (!PC0787166), Tixier 8165 (!PC0661678), Villaume s.n. [1904] (!PC099036), Villaume s.n. [1905] (!PC0099933 lectotype [here designated] of Barbula subrufa [=Tortula subrufa]; !PC099034; !PC0134945; !PC099035).

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; !PC074368; !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

=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.)

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LITERATURE CITED


