A SYNOPSIS OF RECENT LITERATURE ON THE GENUS SYNTRICHIA IN THE NORTHERN HEMISPHERE

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Abstract: A compilation of recent literature on the genus Syntrichia in the northern hemisphere is presented with complete synonymies, descriptions, geographic distributions, and discussion of species delineations by various authors is presented. A key to taxa presently known from the northern hemisphere and accepted by recent authors is included.

Keywords: Syntrichia, Tortula, Pottiaceae

The genus Syntrichia was first described by Bridel in 1801, but until very recently, most authors (Lawton 1971, Flowers 1973, Smith 1978, Kramer 1980, Crum & Anderson 1981, Mishler 1985, 1985a, 1994) have included it in the genus Tortula Hedwig. Many of the taxa were originally described in the genus Barbula Hedwig and others were transferred into that genus by other workers. Ochyra (1992) and Zander (1989, 1993) have spearheaded Syntrichia’s resurrection based largely on Kramer’s (1980) seminal work. Werner et al (2002) have presented convincing genetic evidence demonstrating that Syntrichia is clearly separate from Tortula. Most recently, Gallego (2002) and a group of associates (2000, 2002a, 2002b, 2004) have been producing excellent work sorting out the Mediterranean taxa of the genus.

It is at best, a complex genus. The student must examine plants for a large number of characters, many of which take a lot of time to determine. Furthermore, in all of the cited references, taxa are defined by a combination or suite of characters. Because of these difficulties, the genus has remained a confusing one. During an initial study of the California taxa in the genus I realized that I knew only Mishler’s interpretations. Largely through the help of Maria Gallego, I became aware of a much larger body of work. Because California and the Mediterranean area share a lot of species in general, Kramer’s and Gallego’s work were quite relevant to my study. The same could be said for Mishler’s (1994) treatment of Mexican Tortulas. Unfortunately, there was no single reference for all of the taxa that might be found in California, and I felt the need to assemble the information in one place. This paper has grown from that need.

This synopsis and key is a compilation of the recent literature on the genus Syntrichia for the northern hemisphere. I have relied most heavily on modern works because many of the original and early descriptions did not include the characters that have since been found most useful to separate the taxa. The skeletal structure of the key is taken from Gallego (2002) and Gallego et al. (2002a), with taxa not included in their studies added in appropriate places. As much as possible, characters have been chosen that represent agreement between the various authors. Where a character is used that is described by only one author, that reference is noted in brackets in the key or species description.
With the remarkable correlation between the bryofloras of Southern Europe and California (Koch 1956, Schofield 1988) it is quite possible that any of these taxa might be found outside of its presently known range. Therefore, so as not to influence key decisions, I have left out geographical distributions in the key. Instead, at the end of the key, there is a list of the included species descriptions annotated with each taxa’s presently known range, and references with illustrations.

Species description is accomplished by a list of characters with the appropriate description for that taxon of that character. The list of characters are the same for each taxon, and were chosen by relying on the various authors discussion of the important differences between taxa. Most often, I have used Gallego and her co-authors as the basis of the descriptions, as her measurements and descriptions are the most thorough. However, I have expanded her data where other authors describe the plants differently.

There is one appendix: a list of heterotypical synonymies. This is included only as an aid to track older names for a particular taxon that have been dropped as synonyms. The complete list of synonymies is included under each taxa in the main body of the paper.

It is important to emphasize that I am acting as only a compiler, and that this synopsis is not a product of study of specimens of each species, especially the European and Asian taxa. All of the data presented here are from the available literature, and reflect the taxonomic opinions and concepts of each of the authors. Conflicts between interpretations and synonymies are discussed after the species descriptions. For that purpose, I used Magill (1990), the AltaVista Babel Fish on line translator (http://babelfish.altavista.com), and Translat, a botanical latin translator program (http://www.geocities.com/Athens/Oracle/2821/Translat.html). Patricia Eckel also translated latin on several plants that had no modern treatments. Where I have used her translations, I have noted it in the text following the description.

There are three African and one Asian taxa listed in Zander (1993) that are very poorly known: S. alpestris (Dixon in Herzog) Zander; S. brandisii (C. Müller Hal) Zander; S. mollis (C. Müller Hal) Zander; S. subaristata (C. Müller Hal) Zander. I was unable to find any treatment save the original descriptions for any of these four. As these descriptions are minimal, I was unable to gather enough characters to make meaningful distinctions between these plants and the others in the genus without examining the type specimens. This is beyond the scope of this study. I have, therefore, included them as accepted species, but I have not included them in the key, nor have I attempted to fill in the descriptions beyond that information from translations of the original latin description.

Use of the key:

For the proper use of this key, leaf sections in the distal 1/3 of the leaf must be made of all collections, as there is no reliable shortcut to determine the presence of hydroids in the costa, or the nature of the stereid band. This procedure also helps in determining the stratosity of the lamina, which the often dense papillae make difficult to determine in surface view. Sections are also useful in measuring medial cell width, as the surface view is often obscured by dense papillae. Surface mounts of non-gemmiferous leaves are most useful with the dorsal side up, so as to see the ornamentation of the costa.

The presence of hydroids in the costa, along with a central strand in the stem, is a major breakpoint in the key. Both of these characters can be subtle and deserve a short discussion here.
The central strand does not have to be a well defined, or sharply delineated bundle of cells. In this genus, it more often appears as cells that gradually get smaller in diameter, so that the central cells are, as a group, smaller than most of the other cells in the stem. (See Zander 1993, plate 109, figure 1) It is helpful to note that plants without a stem central strand may have one or two smaller cells in the center, but in general, most of the cells are the same size. Of course, a transverse section of the stem must be made to see this. Hydroids may be found immediately dorsal to the centermost guide cells. They are a group of cells that often disintegrate in age, leaving an irregular, polygonal or star-shaped gap. (See Mishler 1994 figures 249g, 252e, 256f) It is in this condition that they are most easily recognized. I suggest that to check for hydroids in the costa, sections be made of older leaves slightly below the apex. In plants without hydroids, there is sometimes a band of smaller diameter cells between the guide cells and the stereids. (See Zander 1993, plate 105 figure 7 or Mishler 1994 figure 259e) These are rounded or elliptical, and show none of the sharp angularity so typical of the degraded hydroid strand. However, these “sub-guide cells” can also collapse, leaving the question unclear. Cross checking the presence of a stem central strand can add further evidence, as Zander (1993) states that plants that consistently lack stem central strands never have hydroid strands in the costa.

An explanation of two other characters is also necessary for clarity. Constricted at midleaf refers to the shape of the leaf margin. When midleaf constriction exists, the outline of the leaf is shaped at least somewhat like a violin. Basal to leaf length % is simply a measurement of the hyaline basal area compared to the total leaf length. This character is used by Kramer and Gallego, but is quantified only by Gallego. Gallego (2005) measures the basal area to the top of the curved line of differentiation, but the wide infraspecific variation indicates that a precise measurement is not critical.

As with all keys, this key should only be used as a starting point in the identification process. Determinations should be confirmed first by referring to the literature (see the species descriptions), and second by comparison to reliably named specimens.

Also, it is important to remember that Mishler (1985) demonstrated that many of the characters used in this key are variable with different growing conditions. The user should not be surprised therefore, that any one, or maybe even two characters would not match the described “ideal” plant of each taxa. As an example, Gallego (2002) describes both S. princeps and S. echinata with midleaf constriction. Heyn & Herrnstadt (2004) key these plants with the following statement: “Leaves not or indistinctly constricted at middle, or constricted only on one side...”. Another example: Smith (2004) describes S. ruralis with midleaf cells measuring 12-16 μm wide, but Gallego et al. (2002a) claims the median cells measure (5)7.5-10(12.5) μm wide.

There are also a large number of specimens that are intermediate between two taxa, and these are difficult to place. Some authors respond to this intergradation by synonymizing plants. For instance, Smith (2004) uses this rationale to synonymize S. calcicola with S. ruralis. Both Kramer (1980) and Gallego et al. (2002a) accept both taxa. Gallego et al. (2004) subsumes S. pagorum into S. laevipila with a lengthy and convincing discussion of the intergradation of the two forms. One possible explanation for this confusing array of interpretation is that a trait that is stable (and therefore a reliably useful character for taxonomic decisions) in one geographical area may not be stable in another location. (Gallego personal communication) Whether or not this morphological plasticity is a reflection of genetic diversity awaits major genetic study.

A final caveat is illuminated in Mishler (1986). Many mosses, especially those of the genus Tortula in the widest sense, develop primitive leaves at the base of a new stem or innovation. These leaves never develop into leaves that display the true characters of the moss.
In many cases these primitive leaves illustrate the characters of the ancestors of the taxon. However, if one were to examine these primitive leaves with the purpose of identification, confusion would be the inevitable outcome. Therefore, it is best to examine the leaves near the middle of the latest year’s growth. This would avoid the primitive leaves, as well as the developing (sometimes perichaetial) leaves at the extreme apex.

**Syntrichia** Bridel *J. Bot. (Schrader)* 1: 299 1801.
*Tortula* sect. **Syntrichia** (Brid.) Lam. & Cand. 1806
*Tortula* subg. **Syntrichia** (Brid.) Chev. 1827
*Tortula* sect. **Rurales** De Not. 1838
*Barbula* sect. **Rurales** B.S.G. 1842
*Barbula* sect. **Syntrichia** (Brid.) Müll. Hal. 1849
*Barbula* subg. **Syntrichia** (Brid.) B.S.G. 1851
*Barbula* sect. **Vallidens** Müll. Hal. 1879
*Barbula* sect. **Syntrichiae** Lesq. & James nom. illeg. 1884
*Barbula* sect **Ruraliformes** Kindb. nom. illeg. 1897
*Syntrichia* sect. **Eusyntrichia** Moenk. nom. illeg. 1927

The following description and discussion is adapted from Zander (1993)

Plants large or small, scattered or more often forming turfs or cushions; green, often reddish brown or blackish. Stems branching occasionally, 0.9-4(12) cm long, central strand present or not. Rhizoids present, often dense. Leaves appressed to weakly spreading, often somewhat twisted when dry, erect to squarrose when moist; narrowly ligulate to broadly spatulate, occasionally broadly lanceolate; 1.5-5(7) cm long including awn; upper lamina broadly channeled to keeled, often narrowly grooved along costa; margins plane to recurved, rarely broadly incurved, entire or toothed near apex, sometimes bordered with thick-walled, less papillose cells; apex acute, shortly acuminate, more often rounded obtuse or emarginate. Costa prominent dorsally, smooth or prorate or toothed, ventrally covered with short, papillose cells, ending below the apex or excurrent as a mucro or a long, often hyaline and toothed, awn; in section round, occasionally elliptical or semicircular, ventral cells similar to laminal cells, no ventral stereid band, guide cells in 2-4 layers, hydroids present or not, dorsal stereid band crescent shaped, without a differentiated epidermal layer. Upper laminal cells rounded-quadrate, shortly rectangular or irregularly hexagonal, walls various, sometimes collenchymatous, in section bulging on both surfaces, with 1-12 usually bifid, occasionally simple or stellate-branched papillae. Basal cells differentiated across the base, usually rectangular and thin walled, hyaline, smooth, 16-30 µm wide, 2-6:1. Basal marginal cells in 2-6 rows, often shorter, green or hyaline, and thicker walled than the interior basal cells. Propagula sometimes present: leaf shaped and borne near the apex of the plant or multicellular and elliptical, spherical or clavate; borne on the surface of the lamina or on the costa, or on the rhizoids. Dioicus or monoicus. Perichaetia terminal, with perichaetal leaves little differentiated. Perigonia gemmate, terminal or lateral as stalked buds. Seta elongate, (0.8)1-3 cm long, 1(2) per perichaetium, reddish-brown, twisted. Capsule, erect or slightly inclined. cylindrical or ovate-cylindrical, 2-6 mm long, reddish-brown. Exothecial cells quadrate or rectangular; stomates at base of capsule, superficial. Annulus of 2-4 rows of vesiculose cells, persistent. Peristome teeth 32, densely spiculose, twisted ½-2 turns, ca. 1-2 mm long from a united, tessellated basal membrane of 3-42 rows of cells, 0.1-0.8 mm long. Operculum conical, smooth 1-2.25 mm long, cells twisted. Calyptra cucullate, smooth, rather long. Spores 8-15 µm in diameter, spherical, light-brown, papillose.
KOH reaction brick-red. Chromosome numbers 6+m, 12, 12+m, 13, 13+m, 24, 24+m, 26, 28, 32+2m, 48.

Syntrichia is characterized by the costa generally round in section, without a ventral stereid band, the crescent shaped dorsal stereid band without an epidermal layer, quadrate marginal cells, enlarged, clear basal cells that end above in an inverted “U”, the red KOH reaction, sporophytes not reduced, and the peristome teeth at least somewhat twisted from a united basal membrane.

*Syntrichia* is separated from *Tortula* by the red KOH reaction, the marginal cells not elongate, the crescent-shaped dorsal stereid band without a differentiated epidermis, and the sporophyte not in a reduction series within the genus. In general the plants of *Syntrichia* are larger than those of *Tortula* or *Hennediella*, but this is not a hard and fast rule.

Zander (1993) described two sections in addition to the typical section:

**sect. Collotortula** Zand. 1993

Differentiated from the typical section by at least somewhat collenchymatous upper laminal cells, leaf margins usually recurved, papillae sometimes simple, and gemmae when present clavate or elliptical. Sometimes, the upper medial cells have round central pores. Upper margins are usually serrate, and there is no stem central strand.

Northern hemisphere plants included in this section by Zander (1993) are: *S. alpestris*, *S. amphidacea*, *S. andicola* (the type species), *S. bogotensis*, *S. cainii*, *S. gagemascens*, *S. mollis*, *S. papilloso*, and *S. subaristata*.

**sect. Aesirotortula** Zand. 1993

Differs from the typical section by plants small for the genus, margins plane, papillae bifid, and (when present) leaf-shaped propagulae borne near the leaf apex. The type species is *Syntrichia pagorum* (Milde) Amann, which has since been synonymized with *S. laevipila* by Gallego, Cano & Guerra (2004).

Northern hemisphere plants included in this section by Zander (1993) are: *S. ammonians*, *S. bartramii*, and *S. chisosa*. Indicative of the great controversy generated by the *S. laevipila*-*S. pagorum* group (for an overview see Gallego, Cano & Guerra 2004), Zander does not include *S. laevipila* var. *laevipila* in this section, but states that “Certain of the infraspecific taxa of *S. laevipila* may also belong here,…”. If one accepts the opinion of Gallego, Cano & Guerra (2004), then *S. laevipila* should also be included in this section, and the description broadened somewhat to include weakly recurved leaf margins. One form of *S. fragilis*, originally described by Bartram (1924) as *Tortula fragilifolia* also has leaf shaped propagules. Since the leaf margins of *S. fragilis* are also weakly recurved, an argument could be made that this plant also belongs in this section, and buttressing the expansion of the sectional concept.

**A KEY TO THE NORTHERN HEMISPHERE TAXA OF SYNTRICHIA**

1. Plants with gemmae or brood-leaves ................................................................. 2
1. Plants without propagules ......................................................................................... 14

*Plants with propagules*
2. Propagules leaf-shaped, papillose, with or without costa, clustered near the apex of the plant.................................................................3
2. Gemmae somewhat spherical, scattered over the leaf lamina or on the costa, or rhizoidal, or on branched filaments.............................................6

3. Lamina unistratose .................................................................................................4
3. Lamina bistratose, apex apiculate, margins plane .................................. S. chisosa

4. Propagules borne on the leaf margins.................................................................S. laevipila var. gemmifera
4. Propagules borne on the apex of the stem or in the upper leaf margins or on branched stalks in the axils of the upper leaves.........................5

5. Margins of upper leaves generally broken and irregular. .................. S. fragilis
5. Margins of upper leaves generally intact and either entire, or crenulate.................................................................6

6. Leaf margins plane, unbordered, with several small teeth near the apex; apex apiculate. Propagules borne on branched stalks in the axils of the upper leaves. On rock. [Crum & Anderson 1981] .................................................. S. ammonsiana
6. Leaf margins plane to recurved at midleaf, sometimes bordered with up to 6 rows of smoother, thicker walled, sometimes colored cells; apex with a smooth or weakly toothed awn. Propagules in a rosette at the apex of the stem or in the axils of the upper leaves. On tree bark, rarely on rock...............................................................S. laevipila

7. Gemmae on branched stalks clustered at the apex of the stem. ........... S. caninervis var. astrakhanica
7. Gemmae laminal, rhizoidal, or restricted to the costa .........................8

8. Leaves without awns, gemmae scattered over lamina or rhizoidal ...........9
8. Leaves with hyaline awn, gemmae on the upper costa.........................12

9. Gemmae rhizoidal [Smith 1978]. Leaves bordered with smaller, less papillose, thick walled cells, often yellow.................................................S. amplexa
9. Gemmae scattered over ventral lamina. Leaf margins bordered or not .................................................................................................10

10. Leaves often with a border of smaller, thicker walled cells; apex acute or mucronate. Medial laminal cells often collenchymatous .................11
10. Leaves without a border, apex rounded-obtuse, without a mucro or awn. Margins plane or weakly recurved at most to the middle of the leaf. Laminal papillae dense.........................................................S. latifolia

11. Upper cells with low, weak papillae. Upper margins entire to crenulate, at most remotely serrulate. Leaf apex apiculate or mucronate. Gemmae borne on the distal half of the leaf. .........................S. amphidacea
11. Upper laminal cells with dense papillae. Upper margins serrate. 
Leaf apex acute. Gemmae in leaf axils or on leaf lamina. ..................................S. gemmascens

12. Upper leaf cells with 1-2 simple (rarely bifid) papillae, only on 
the adaxial surface. Awn smooth, rarely weakly spinulose .....................S. papillosa 
12. Upper leaf cells with 4-6 bifurate papillae on both surfaces of 
the leaf. Awn spinulose. ..................................................................................13

13. Margins recurved throughout the basal ¾ of the leaf. Costa with 
3-5 dorsal stereid rows and hydroids, with pedicellate, bi-trifurcate, 
stellately branched papillae on the dorsal surface. Lamina irregularly 
bistratose in distal half of leaf. .................................................................S. rigescens 
13. Margins plane to weakly recurved to midleaf. Costa with 1-2(3) 
dorsal stereid rows, without hydroids, with non-pedicellate, simple 
or bifurcate papillae on the dorsal surface. Lamina strictly 
unistratose .................................................................................................S. virescens

Plants without propagules

14. Lamina bistratose in distal ½ .................................................................15 
14. Lamina unistratose or bistratose in streaks in upper 1/3..............19

Without propagules; leaves bistratose

15. Margins plane.........................................................................................S. chisosa 
15. Margins recurved to at least 2/3 the leaf length.........................16

16. Distal dorsal costal surface strongly papillose with simple, or 
bifurcate papillae. Leaves not constricted near the middle, margins 
recurved to near the apex ..........................................................S. handelii 17 
16. Upper dorsal costal surface weakly papillose, with warty 
papillae. Leaves sometimes narrowed near the middle. Margins 
recurved in basal 2/3. S. handelii ........................................18

17. Plants short, to 11 mm tall. Costa 75-115 μm wide at midleaf. 
Abaxial upper costa with simple or bi to trifurcate or pedicellate and 
branched papillae [Gallego et al (2002a)] ..................................................S. caninervis var. caninervis 
17. Plants taller, 2.5-7 cm tall. Costa 120-135 μm wide at midleaf. 
Abaxial upper costa with pedicellate and branched papillae 15-25μm 
tall. [Gallego et al (2002a)] ...........................................................................S. pseudohandelii

18. Leaves with awn, costa mostly without substereids ....................S. handelii var. handelii 
18. Leaves without awn, costa mostly with substereids. Extremely 
rare ..............................................................................................................S. handelii var. ferganensis
19. Leaves without awn, sometimes mucronate. ..............................................20
19. At least the perichaetal leaves with an awn, sometimes short. .................26

Without propagules; leaves unistratose at midleaf, without awn

20. Costa not reaching the apex of the leaf. ...............................................21
20. Costa reaching the mucronate leaf apex. ..............................................23

21. Leaf apex rounded..................................................................................22
21. Leaf apex abruptly narrowed, pinched and reflexed with the costa often dying in the short apiculus, thus appearing percurrent. Margins recurved in the lower ½ to 2/3. Laminal cells 12-18 μm wide with 3-5 low c-shaped papillae per cell. [Crum & Anderson 1981] ..........................................................S. cainii

22. Leaf apex cucullate. Lamina sometimes bistratose in streaks. Margins sometimes bistratose, without a border, plane or weakly recurved at base. Basal marginal cells thick-walled and short-rectangular contrasting sharply with the enlarged inner basal cells. Costa with substereids [Allen 2002]..................................................................S. percarnosa
22. Leaf apex never cucullate. Lamina strictly unistratose. Leaf margin bordered by cells that are smaller, often yellower, less papillose, and thicker walled in comparison to medial cells. ..................S. amplexa

23. Leaves short-ovate. Lamina bistratose in streaks in upper third, unistratose at midleaf. Extremely rare .........................................................S. caninervis var. abrancheii
23. Leaves longer, lingulate or spatulate. Lamina strictly unistratose. ............24

24. Costa without hydroids, and with the stereid band dying below the apex of the leaf. Medial laminal cells large, generally >18μm in diameter. ..................................................................................S. norvegica var. calva
24. Costa with hydroids, the stereid band reaching the apex of the leaf. Medial laminal cells smaller, generally less than 17.5 μm. .......................25

25. Leaf margin usually fragile and erose or fragmented. Medial laminal cells 12.5-15 μm wide..................................................S. fragilis
25. Leaf margin not erose or fragmented except on very old leaves. Medial laminal cells 5-10(12.5) μm wide..............................................S. montana var. calva

Without propagules; leaves unistratose at midleaf, with awn

26. Leaf apex acute to acuminate, sometimes with teeth..............................27
26. Leaf apex mostly rounded, never with teeth.........................................31
27. Costa weak above as stereid bands end. Median cells 12-20(25) μm wide. .................................................................29
27. Costa strong to the apex. Median cells smaller.........................................................28

28. Awn smooth. Cells 6-9 μm wide ..............................................S. cavallii
28. Spinose, hyaline awn present on most leaves and decurrent onto lamina. Median cells 10-12 μm wide. ...............................................S. ruralis var. ruraliformis

29. Upper cells collenchymatous, apical margins sometimes with teeth. Marginal recurvature various. Leaves 3-6 mm long. .......................30
29. Upper cells not collenchymatous, apical margins only very rarely with teeth. Awn typically reddish or orange throughout. Margins weakly recurved to midleaf, sometimes to 2/3, rarely plane. Leaves 2.2-3.5 mm long. ................................................S. norvegica

30. Leaf margins plane to weakly reflexed, costa with 1-2 rows of stereids. Teeth at leaf apex occasional ........................................S. bogotensis
30. Leaf margins strongly revolute to about ¾, teeth common at apex
[Mishler 1994] .................................................................S. andicola

31. Costa without hydroids, stem without central strand..........................32
31. Costa with hydroids, stem with central strand..............................................40

Without propagules; leaves unistratose, with awn; costa without hydroids, stem without central strand

32. Awn usually reddish throughout. Upper back of costa appearing similar to lamina as the dorsal stereid band dies out, or with stereid band reaching the apex. Cells generally >18 μm..............................S. norvegica
32. Awn hyaline, although sometimes reddish at the base. Dorsal stereid band strong to the apex of the leaf. Cells smaller .........................33

33. Costa with 1-2(3) rows of stereids. Margins recurved at most to mid-leaf. ........................................................................................................34
33. Costa with (2)3-6 rows of stereids. Margins recurved from ca 2/3 the leaf length to near the apex ..........................................................35

34. Median laminal cells with 4-6(8) (c-shaped in surface view) bifurcate papillae without pedicels ca 2.5 μm tall. Medial leaf cells 12.5-15 μm wide. Saxicolous. ......................................................S. virescens
34. Median laminal cells with 1 pedicellate, branched, star-shaped or antleroid papilla,10-15(17.5) μm tall. Medial leaf cells (7.5) 10-12.5 μm wide. Epiphytic. ..........................................................S. minor
35. Leaves with margins recurved to ca 2/3 the length of the leaf, rarely only to midleaf. ................................................................. 36
35. Leaves with margins recurved to near the leaf apex. ................................. 37

36. Median cells 9-10 μm wide; awn long and spiny .................................. S. rupicola
36. Median cells 12.5-17.5 μm wide, awn short and spinulose ......................... S. calcicola

37. Papillae low (around 2.5 μm tall) and without pedicels ............................ 38
37. Papillae pedicellate 5-12.5 (15)μm tall .................................................. 39

38. Plants large, leaves squarrose when moist ........................................ S. ruralis var. ruralis
38. Plants smaller, leaves erect-scaping when moist .................................... S. densa

39. Medial cells with 1 branched, stellate or antleroid papilla, papillae at back of upper costa stellate-branched or bifurcate, rarely simple, 2.5-7.5 μm tall ........................................................... S. papillosissima
39. Medial cells with more than 1, usually bifurcate, rarely stellate-branched. Papillae on the back of the upper costa simple, 2.5-5 μm tall ........................................................... S. subpapillosissima

Without propagules; leaves unistratose, with awn; costa with hydroids, stem with central strand

40. Awn smooth or weakly spinulose .......................................................... 41
40. Awn strongly toothed. ........................................................................... 45

41. Awn strong, (0.2) 0.4-0.9(1.6) mm long. Margins plane or weakly recurved near the middle of the leaf (See notes under S. sinensis and S. longimucronata). ................................................................. 42
41. Awn short, 0.1-0.5 mm long. Marginal recurvature various. .................... 44

42. Leaves sometimes with a marginal border of less papillose, thicker walled and colored cells. Awn hyaline except at base. Laminal cells with 4-6(8) bifurcate papillae ......................................................... 43
42. Leaves never with a marginal border. Awn reddish or brownish. Laminal cells with (6) 8-12 bifurcate papillae ......................................................... S. sinensis

43. Plants at most 2 cm tall. Peristome basal tube 200-600 μm. Primarily epiphytic ................................................................................. S. laevipila
43. Plants robust, 3-5 cm tall. Peristome basal tube very short, less than ¼ the length of the teeth. Primarily on rock or soil ............................... S. longimucronata

44. Plants dioicous. Margins recurved to near the apex. Leaves lingulate, rounded apically ................................................................. S. submontana
44. Plants monoicous. Peristome basal tube 90-160 µm long. Leaves usually oblong-ovate, rarely lingulate, decreasing in width approaching the apex. Marginal recurvature at most to 2/3 the leaf length [Kramer 1980] or to the basal 1/3 [Gallego 2002] (See notes under S. sinensis) ................................................................. S. sinensis

45. Irregularly bistratose in the upper third of the leaf (unistratose at midleaf). Leaf ovate to ovate-lanceolate, recurved to near the apex. .......... S. caninervis var. gypsophila

46. Medial cells with 1-4 pedicellate papillae, at least 8 µm tall .................. 47
46. Medial cells with 4-6(8) low, bifurcate papillae .................................. 48

47. Medial cells (10)15-17µm wide, with 1 papilla; synoicous .................. S. echinata
47. Medial cells 10-12(15) µm wide, with 1-4 papillae; dioicous .............. S. sucrosa

48. Margins plane, awn short and stout, upper dorsal costa strongly toothed ................................................................. S. bartramii
48. Margins recurved 2/3 the leaf length to near the apex, awn usually flexuose, leaves ± constricted in width near the middle ...................... 49

49. Mean medial leaf cell width 18 µm, back of upper costa not spinose or prorate ................................................................. S. obtusissima
49. Mean medial leaf cell width smaller, 10-15 µm, back of upper costa variously spinose or prorate. ............................................ 50

50. Median leaf cell width 10 µm. Leaves 1.5-3.3 mm long. Dioicous .......... S. montana
50. Median leaf cell width 15 µm. Leaves 2.6-5.0 mm long. Synoicous or dioicous. ................................................................. S. princeps

**SPECIES DESCRIPTIONS**

The accepted taxa are listed by alphabetical order with all synonyms. The basionym is listed first, along with the publication where it was described. Other synonyms are listed by publication date. Please note that only one new synonymy is made here (S. laevipila var. gemmifera).

In the vast majority of cases, the specific epithet of any given taxon is the same in *Tortula* and *Syntrichia*. Even though many of the cited authors worked in *Tortula*, their conclusions as to a particular taxon apply equally well independent of its placement in either genus. Therefore, to save space in the discussions following the species descriptions, I have used the genus that the cited author used, with the immediate implication that the statement applies to that taxon in *Syntrichia*. The same concept applies to the list of references with illustrations, i.e. that the student should look under *Tortula* if the author did not recognize *Syntrichia*. 
**Syntrichia alpestris** (Dixon in Herzog) Zander 1993

- **Moist leaf stance:** erect
- **Leaf Dimensions:** 3-4 mm long
- **Leaf shape:** broadly oblong-ovate, concave
- **Constricted at midleaf?** not described
- **Shape of apex:** broadly rounded
- **Awn:** smooth hyaline cusp scarcely equaling ½ the leaf width
- **Marginal recurvature:** usually strongly revolute throughout
- **Marginal border?** marginal cells are scarcely smaller than median cells
- **Basal to leaf length %:** not described
- **Medial cell width:** 12-18 μm
- **Medial cell papillae:** low coarse
- **Hydroids present?** not described
- **Dorsal stereid band:** not described
- **Upper dorsal costal ornamentation:** not described
- **Laminal stratosity:** not described
- **Propagules:** not described
- **Sexuality:** apparently dioicous
- **Peristome:** not described
- **Habitat:** not described
- **Range:** Africa

**Illustrations:** none

Translation from the original Latin description by Eckel.
Dixon’s (1935) original account describes differentiated perichaetial leaves that are larger than the cauline leaves, acuminate, with the costa excurrent as a pale, smooth arista, and convolute.
Zander (1993) includes this species in section *Collortortula* indicating at least somewhat collenchymatous upper laminal cells.

**Syntrichia ammonsiana** (Crum & Anderson) Ochyra 1992
*Tortula ammonsiana* (Crum & Anderson) *The Bryologist* 82: 469. 1979

- **Moist leaf stance:** spreading
- **Leaf Dimensions:** 1-1.5mm
- **Leaf shape:** Oblong to lingulate
- **Constricted at midleaf?** not described
- **Shape of apex:** Acute to obtuse or rounded obtuse, generally toothed near apex
- **Awn:** concolorous apiculus ending in a yellowish or reddish
- **Marginal recurvature:** plane
- **Marginal border?** none
- **Basal to leaf length %:** not described
- **Medial cell width:** not described
- **Medial cell papillae:** several inconspicuous c-shaped
- **Hydroids present?** not described
Dorsal stereid band: reaching apex, but # of rows not described
Upper dorsal costal ornamentation: not described
Laminal stratosity: 1
Propagules: leaf shaped, costate, borne on branched stalks in axils of upper leaves.
Sexuality: not described
Peristome: not described
Habitat: Damp stone walls
Range: Eastern North America, South Africa, South America (Gallego et al 2006)

*S. ammonsiana* is known by the leaf-shaped propagulae borne on branched stalks, and the apiculate, toothed leaf apex. It can be separated from *S. chisosa*, which also bears leaf-shaped gemmae on branched stalks, because *S. chisosa* has leaves that are mostly bistratose. The gemmae on *S. laevipila* are not borne on branched stalks.

**Syntrichia amphidacea** (C. Müller) Zander 1993

*Tortula caroliniana* Andr. 1920
*Tortula tanganyikae* Dix. 1938
*Tortula novoguineensis* Bartr. 1945

Moist leaf stance: erect-spreading
Leaf Dimensions: 2-3 mm
Leaf shape: oblong-obovate
Constricted at midleaf? not described
Shape of apex: acute, entire
Awn: apiculus, costa subpercurrent
Marginal recurvature: ½-2/3
Marginal border? occasional
Basal to leaf length %: not described
Medial cell width: (8)11-15 (20) μm; walls at least somewhat collenchymatous
Medial cell papillae: pleuripapillose
Hydroids present? not described
Dorsal stereid band: 6 rows (from illustration only)
Upper dorsal costal ornamentation: smooth
Laminal stratosity: 1
Propagules: ± cylindrical, multicellular, on 1 or both surfaces of upper half of leaf.
Sexuality: Dioicus
Peristome: irregularly twisted from a short basal tube
Habitat: Bark of hardwood trees, occasionally on rotting logs and rocks
Range: Central America, West Indies, North America, South America, Africa, Asia


Zander (1993) describes this plant as having interior laminal cells with occasional, large, round central pores. This might be seen by staining transverse sections of the leaf. The collenchymatous walls, and the multicellular, non-leaf shaped gemmae, mark this plant as belonging to section *Collotortula*. 
**Syntrichia amplexa** (Lesquereux) Zander 1993  
*Tortula amplexa* (Lesq.) Steere in Grout 1940

Moist leaf stance: erect-spreading  
Leaf Dimensions: 1.7-3.8 mm  
Leaf shape: oblong to lingulate  
Constricted at midleaf? ±  
Shape of apex: obtuse to obtusely-acute, entire  
Awn: costa percurrent or forming a short mucro  
Marginal recurvature: plane or recurved  
Marginal border? 2-4 rows of yellowish thicker-walled, less papillose cells in one layer  
Basal to leaf length %: not described  
Medial cell width: (12)15-25(28) μm  
Medial cell papillae: 0-3-5  
Hydroids present? not described  
Dorsal stereid band: 2 rows  
Upper dorsal costal ornamentation: not described  
Laminal stratosity: 1  
Propagules: 1-3 thick-walled cells, borne on rhizoids  
Sexuality: Dioicous  
Peristome: papillose, twisted from a short basal tube  
Habitat: on soil in lowlands, usually near springs or washes  
Range: North America, Europe  

The rhizoidal gemmae are reported as always present by Smith (1978) but are not reported by any North American author. However, Side and Whitehouse (1974) report specimens from North America with the rhizoidal gemmae.  

The species is recognized by the percurrent or shortly excurrent costa, and the marginal border. Other species with a marginal border are *S. laevipila, S. gemmascens*, and *S. longimucronata*. *S. gemmascens* also has a percurrent costa, but the upper margin is serrate contrasting with the entire margin of *S. amplexa*. *S. laevipila* and *S. longimucronata* have long awns, making separation easy.  

Side and Whitehouse (1974) are the only authors to report differentiated perichaetal leaves that are erect, elongated and clasping the seta for most of their length. This description is from North American material. They believe that this differentiation occurs only after fertilization, as the sterile British plants have undifferentiated perichaetal leaves.

**Syntrichia andicola** (Montagne) Ochyra 1992  
*T. lemniscata* Zand.

Moist leaf stance: spreading to squarrose-recurved  
Leaf Dimensions: 3-6 x 1-2 mm  
Leaf shape: oblong-ligulate  
Constricted at midleaf?
Shape of apex: acute, usually with several sharp yellow or hyaline teeth
Awn: red-brown to hyaline, spinulose, up to ¼ the leaf length
Marginal recurvature: recurved in the basal ¾ of the leaf
Marginal border? none
Basal to leaf length %: not described
Medial cell width: 12-22(26) μm, collenchymatous
Medial cell papillae: 4-8 bifurcate
Hydroids present? not described
Dorsal stereid band: ending in the apical 1/8
Upper dorsal costal ornamentation: short, simple or branched papillae
Laminal stratosity: 1
Propagules: none
Sexuality: dioicous
Peristome: 1-1.5 mm, yellow-brown to red, twisted ¼-1 full turn, from a very low base
Habitat: on moist soil or soil over rock at high elevations
Range: Mexico, Western South America
Illustrations: Mishler (1994)

*S. andicola* is known by the strongly recurved margins, the sharp teeth that are usually present at the base of the awn, and the costa that is red only below, as the colored stereid band dies out. [Mishler (1994)]. Zander (1993) names this plant as the type species of section *Colotortula*, indicating that the upper laminal cells are at least somewhat collenchymatous. Zander (1993) describes this plant as having interior laminal cells with occasional, large, round central pores. This might be seen by staining transverse sections of the leaf.

**Syntrichia bartramii** (Steere in Grout) Zander 1993

Moist leaf stance: wide spreading
Leaf Dimensions: 1.25-2(3) x 0.5-0.75 mm
Leaf shape: lingulate to spatulate
Constricted at midleaf? yes
Shape of apex: acute to truncate, occasionally emarginate
Awn: serrate, 0.1-0.6(1.0) mm
Marginal recurvature: plane, very rarely recurved to midleaf [Steere in Grout (1939)]
Marginal border? never
Basal to leaf length %: not described
Medial cell width: 9-13 μm
Medial cell papillae: 4-6 bifurcate
Hydroids present? yes
Dorsal stereid band: reaching the leaf apex, in 4-6 rows
Upper dorsal costal ornamentation: sparsely to densely spinulose
Laminal stratosity: 1, sometimes bistratose in patches
Propagules: none
Sexuality: Dioicous, perigonia unknown
Peristome: capsules unknown
Habitat: on dry soil and rocks
Range: North America, Mexico

*S. bartramii* can be distinguished from the non-bordered, non-propagulous forms of *S. laevipila* by the plane leaf margins and the more strongly toothed awn. The upper dorsal costa is also at least somewhat spinulose in *S. bartramii*, but smooth in *S. laevipila.*

Personal observations:

*Syntrichia bartramii* fits in a complex association of other taxa in the genus. *S. ruralis* has a form in Arizona that macroscopically mimics *bartramii* almost perfectly, with short spiny awns, toothing on the abaxial distal costa, and small plants. It has no hydroids, very numerous and dense papillae, and margins that recurve in the basal 2/3, a reduction of the regular recurve to near the leaf apex.

I believe that *S. sinensis*, *laevipila*, and *bartramii* form a clinal triangle

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*Syntrichia bogotensis* (Hampe) Mitten ex Zander 1993
*Tortula bogotensis* (Hampe) Mitt.
*Tortula guatemalensis* Bartr.

Moist leaf stance: loosely squarrose recurved
Leaf Dimensions: (2)3-4(6)x1-1.5 mm
Leaf shape: lingulate to ovate-lanceolate
Constricted at midleaf? not described
Shape of apex: acute
Awn: varying from a short apiculus to an awn ¼ the leaf length; weakly spinulose
Marginal recurvature: plane or occasionally recurved near midleaf
Marginal border? none
Basal to leaf length %: not described
Medial cell width: (10)12-20(25) μm; collenchymatous
Medial cell papillae: 4-7 bifurcate, low
Hydroids present? not described
Dorsal stereid band: ending before the apex in 2-3 rows (from drawings)
Upper dorsal costal ornamentation: smooth or occasionally with low papillae
Laminal stratosity: 1
Propagules: none
Sexuality: Dioicus
Peristome: 1 mm long, twisted ½ turn from a short base
Habitat: usually on bark, rarely on rock. 1800-4000 m.
Range: Mexico, Central America, Western South America

Zander (1993) describes this plant as having interior laminal cells with occasional, large, round central pores. This might be seen by staining transverse sections of the leaf. The collenchymatous walls mark this plant as belonging to section *Colloportula.*

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*Syntrichia brandisii* (C. Müller Hal.) Zander 1993
*Barbula brandisii* Müll. Hal. *Flora* 61:82. 1878
*Tortula brandisii* (Müll. Hal.) Broth.
Moist leaf stance: not described
Leaf Dimensions: not described
Leaf shape: spathulate-oblong, deeply concave
Constricted at midleaf? not described
Shape of apex: acute, somewhat cucullate due to inrolled margins
Awn: short mucro
Marginal recurvature: distinctly revolute, but here and there only somewhat revolute.
Marginal border? none
Basal to leaf length %: not described
Medial cell width: not described
Medial cell papillae: not described
Hydroids present? not described
Dorsal stereid band: not described
Upper dorsal costal ornamentation: scabrous at the extreme apex
Laminal stratosity: not described
Propagules: not described
Sexuality: monoicous
Peristome: not described
Habitat: not described
Range: Central Asia
Illustrations: none

Translation from the latin description by P. Eckel.
Zander(1993) states that this species has a weakly differentiated dorsal epidermis, seen as somewhat wider lumens in costal section. This is contrary to the usual definition of the genus.
Interestingly, Müller, in his original description of Barbula brandisii, places it between Barbula inermis (Brid.) C. Müll. Hal (Tortula inermis (Brid.) Mont.) and Barbula subulata (Hedw.) C. Müll. Hal. (Tortula subulata Hedw.) Both of these species have been excluded from Syntrichia by Werner et al. (2002, 2003)

Syntrichia cainii (Crum & Anderson) Zander 1993

Moist leaf stance: spreading with recurved tips
Leaf Dimensions: 1.5-2 mm
Leaf shape: oblong or oblong-ovate
Constricted at midleaf? no
Shape of apex: obtuse, abruptly contracted to a short, stout, folded apiculus
Awn: costa ending in the folded mucro, but appearing percurrent
Marginal recurvature: 1/2-2/3
Marginal border? none
Basal to leaf length %: not described
Medial cell width: 12-18
Medial cell papillae: 3-5 low c-shaped
Hydroids present? not described
Dorsal stereid band: 2 (from drawing)
Upper dorsal costal ornamentation: papillose
Laminal stratosity: 1
Propagules: none
Sexuality: dioicus
Peristome: capsules not known
Habitat: limestone
Range: Eastern North America

The pinched leaf tips without awns are diagnostic.

**Syntrichia calcicola** Amann *Fl. mousses Suisse* 2:119. 1918
*Tortula calcicola* Grebe nom. illeg. 1909
*Syntrichia montana* Nees ssp. *calcicola* (Amann) Amann 1918
*Syntrichia ruralis* var. *calcicola* (Amann) Mönk. 1927
*Tortula ruralis* ssp. *calcicola* (Amann) Giacom. 1947
*Tortula ruralis* var. *calcicola* (Amann) Barkmann 1958
*Tortula calcicolens* Kramer 1980
*Tortula ruralis* var. *calcicolens* (Kramer) Düll. 1984
*Syntrichia ruralis* ssp. *calcicolens* (Kramer) Düll. 1992

Moist leaf stance: spreading or patent
Leaf Dimensions: 1.7-3.8x 0.6-1.6 mm
Constricted at midleaf? no
Shape of apex: rounded-obtuse or rounded-acute
Awn: 0.2-1.7 mm, hyaline, spinulose
Marginal recurvature: recurved in the basal 2/3 of leaf
Marginal border? none
Basal to leaf length %: 19-25(33)%
Medial cell width: 12.5-15(17.5) μm
Medial cell papillae: 4-6(8), bifurcate, 2.5-7.5 μm tall
Hydroids present? no
Dorsal stereid band: (2)3-5
Upper dorsal costal ornamentation: low, simple or bifurcate papillose
Laminal stratosity: 1
Propagules: none
Sexuality: dioicus
Peristome: 0.6-0.8 mm, with a basal membrane consisting of 11-25 rows of cells
Habitat: on soil or rock
Range: Europe, North America [Kramer 1988]

The species is known by its generally short, spinulose awn, the short basal area, the margins recurved in the basal 2/3 of the leaf, and the lack of hydroids in the costa. It is generally thought of as somewhat less opaque than other members of the genus. Frahm & Sabovljević (2006) state that this species has a stem central strand, while all other authors state that it has no hydroids.


*Barbula caninervis* (Mitt.) Jaeger 1873
*Tortula desertorum* Broth. 1888
Barbula desertorum (Broth.) Par. 1894
Tortula bornmuelleri Schiffn. 1897
Barbula bornmuelleri (Schiffn.) Par. 1900
Tortula caninervis (Mitt.) Broth. 1902
Tortula desertorum Podp. hom. illeg. 1923
Tortula saharae Trab. 1927
Syntrichia desertorum (Broth.) Amann 1933
Tortula bistratosa Flow. 1951
Tortula pseudodesertorum Fröhl 1964
Syntrichia pseudodesertorum (Fröhl) Agnew & Vondr. 1975

Moist leaf stance: usually patent or spreading, only very rarely squarrose
Leaf Dimensions: 1.5-2.6 x 0.6-1.2 mm
Leaf shape: ovate or ovate-lingulate, often appearing pinched above
Constricted at midleaf? no
Shape of apex: rounded, acuminate, somewhat cucullate; rarely hyaline and tapering to the awn
Awn: very long (0.6-2.3 mm) and spinose
Marginal recurvature: from near the base to near the apex
Marginal border? often unistratose, but otherwise similar to lamina
Basal to leaf length %: 28-38%
Medial cell width: 7.5-10 μm
Medial cell papillae: 4-6 low, bifurcate
Hydroids present? yes, but often difficult to see if substereids are present
Dorsal stereid band: (1)2-4(5) rows, reaching the apex of the leaf, substereids common
Upper dorsal costal ornamentation: varies from low and bifurcate to tall and branched
Laminal stratosity: bistratose in distal third to half
Propagules: none
Sexuality: dioicous
Peristome: basal membrane of 10-12 rows of cells, 0.3-0.4 mm, teeth twisted 0.7-0.8 mm long
Habitat: usually on calcareous rock or basic soil
Range: Western North America, Mexico, Europe, Middle East

The small plants (0.4-1.1 mm tall), short, ovate leaves, bistratose lamina, usually very long awn in relation to the patent or spreading leaves, separate S. caninervis var. caninervis from all other members of the genus. It shares many characters with S. pseudohandelli, but that species has much larger plants and leaves, and its leaves are recurved when moist. For a discussion on the merits of S. c. var. pseudodesertorum see the notes under S. pseudohandelli.

var. abranchesii (Luisier) Zander 1993
Syntrichia montana ssp. abranchesii (Luisier) Podp. 1954
Tortula caninervis var. abranchesii (Luisier) Kramer 1980
Syntrichia abranchesii (Luisier) Ochyra 1992

Habitat: on soil
Range: Spain
Illustrations: Kramer (1980), Gallego et al (2002a)

Differs from the typical variety by the lack of an awn. It can be distinguished from S. montana var. calva by the bistratose leaves, the lack of midleaf constriction, and the bifurcate or
branched papillae of the upper dorsal costa. It is apparently only known from the type specimen (fide Gallego et al. (2002))

**var. astrakhanica** (Ignatov, Ignatova & Suragina) Arctoa 11:333-336 2002

**Habitat:** on dry soil, sand or rock outcrops
**Range:** Asia
**Illustrations:** Ignatov et al. (2002), Ignatov & Ignatova (2003)

Differs from the typical variety by the presence of gemmae born on branched filaments in the axils of the upper leaves, and variable leaf forms, with some leaves unistratose, weakly papillose or smooth cells, and no awn, while others are bistratose in streaks, cells with bifurcate papillae, and a definite awn.

**var. gypsophila** (Amann ex Roth) Ochyra

*Tortula ruralis* (Hedw.) var. *gypsophila* Amann ex Roth. 1915
*Tortula gypsophila* Amann ex Roth nom. inval. 1915
*Tortula spuria* Amann 1916
*Syntrichia spuria* (Amann) Amann 1918
*Tortula ruralis* ssp. *spuria* (Amann) Giacom 1947
*Syntrichia ruralis* (Hedw.) Web. & Mohr var. *pseudodesertorum* Podp. 1950
*Syntrichia ruralis* var. *spuria* (Amann) Podp. nom. illeg. 1954
*Syntrichia hadacii* Vondr. 1965
*Tortula caninervis* ssp. *spuria* var. *gypsophila* (Amann ex Roth) Kramer 1980
*Syntrichia caninervis* var. *spuria* (Amann) Zand. 1993

**Habitat:** on rock or soil, often calcareous
**Range:** Europe, Middle East, North Africa
**Illustration:** Kramer (1980), Gallego et al (2002a)

This variety has a shorter, weaker awn than the typical variety, and it is only irregularly bistratose in the distal third of the leaf and unistratose at midleaf.

**Syntrichia cavallii** (Negri) Ochyra 1992

*Tortula cavallii* Negri Ann. Bot. (Roma) 7:164. 1908

**Moist leaf stance:** erect or erect-patent
**Leaf Dimensions:** 4.9-5.5 x 1.0-1.2 mm
**Leaf shape:** lanceolate, ligulate with a decurrent base
**Constricted at midleaf?** not described
**Shape of apex:** acute, somewhat channeled
**Awn:** smooth, flexuose hairpoint, 1.0 mm long
**Marginal recurvature:** from above the base to near the apex
**Marginal border?** none
**Basal to leaf length %:** not described
**Medial cell width:** 6-9 μm (see note below)
**Medial cell papillae:** densely papillose and opaque
**Hydroids present?** not described but none in the drawing in Zander (1993)
**Dorsal stereid band:** 3-4 (from drawing in Zander (1993))
**Upper dorsal costal ornamentation:** not described
Laminal stratosity: 1
Propagules: none
Sexuality: not described
Peristome: not described
Habitat: on rock, soil over rock, and on tree bark at high elevation [Chuah-Petiot (2003)]
Range: Africa

Negri (1908) in his original description of the plant calls the leaves fragile when dry. It is not clear whether this fragility is comparable to S. fragilis. Dixon (1935) also mentions this fragility in comparison to Tortula alpestris. No illustration shows any marginal erosion or fragmentation.

Negri (1908) also states that the leaves have a decurrent base, although this is not discussed or illustrated in any other reference.

Zander (1993) illustrates and discusses this species at some length. He is the only author who mentions differentiated perichaetial leaves, and uses this character as a basis for a possible future new section or even genus for this plant. Eckel’s illustration in Zander (1993) shows the perichaetial leaves longer than the cauline leaves and with an awn. Her drawings of the cauline leaves are meticulous. This is possibly in conflict with the original description by Negri who described the plant from sterile material. Negri’s account makes no distinction between cauline and perichaetial leaves, and describes the leaves with a smooth hyaline awn. Chuah-Petiot (2003) more or less agrees with Negri, stating “Nerve strong, usually excurrent. …inner perichaetial leaves similar to upper stem leaves”. Illustrations in Chuah-Petiot (2003) show leaves with awns.

There is also some conflict between the description in Chuah-Petiot (2003) and the original description by Negri. Negri describes small upper cells (6-9 μm) while Chuah-Petiot discusses very large midleaf cells (30-35μm!) This latter figure must surely be an error, as these would be by far the largest medial cells in the genus, and the accompanying illustration does not show the medial cells to be ½ the size of the basal cells which are described as 60-65 μm long. Dixon (1935), again in comparison to Tortula alpestris, describes the cells of T. cavallii as “much smaller” (translation by Eckel). Perhaps Chuah-Petiot was referring to the transitional cells between the small upper cells and the basal cells.

Neither of the descriptions mentions the presence or absence of either a central strand in the stem, or costal hydroids, but Eckel’s very careful drawings in Zander (1993) show no hydroids. Therefore I reluctantly assume the smaller cell size for S. cavallii, and include it in the key based on that assumption. I leave the matter of the hydroids and the differentiated perichaetial leaves as undetermined.

Syntrichia chisosa (Magill, Delgado & Stark) Zander 1993

Moist leaf stance: erect-spreading
Leaf Dimensions: 1.2-2.3 x 0.5-0.8(1.0) mm
Leaf shape: spathulate
Constricted at midleaf? not described
Shape of apex: acute to truncate
Awn: a short mucro
Marginal recurvature: plane
Marginal border? no
Basal to leaf length 8-13
Medial cell width: 8-12(13) μm
Medial cell papillae: 3-5, low, bifurcate
Hydroids present? yes
Dorsal stereid band: 4-7
Upper dorsal costal ornamentation: tall, simple
Laminal stratosity: 2 with occasional unistratose patches
Propagules: leaf-shaped, borne on stalks in axils of upper leaves
Sexuality: dioicous
Peristome: capsules not known
Habitat: on soil or soil over rock in desert scrub
Range: Mexico, North America, Southern Africa

The combination of spatulate, bistratose, mucronate leaves with plane margins, and the usual presence of leaf-shaped gemmae borne on stalks, define the species. It is often found with S. bartramii (Magill et al. 1983). It is obviously closely related to S. ammonsi ana and S. laevipila.

Syntrichia densa (Velen) J. P. Frahm 2001

Moist leaf stance: erect-spreading
Leaf Dimensions: 3.5-4 mm
Leaf shape: not keeled
Constricted at midleaf? no
Shape of apex: obtuse or rounded
Awn: hyaline often with reddish base, spiny
Marginal recurvature: recurved in basal 3/4 of leaf to near apex
Marginal border? no
Basal to leaf length %: not described, but drawn as 25-30%
Medial cell width:
Medial cell papillae:
Hydroids present? no
Dorsal stereid band:
Upper dorsal costal ornamentation:
Laminal stratosity: 1
Propagules: none
Sexuality:
Peristome:
Habitat: on limestone rock but more commonly on walls and roofs
Range: Central Europe,
Illustrations: Frahm (1994)

Note that Gallego et al. (2002) synonymizes S. densa (Velen.) Frahm with S. calcicola, but Kramer (1980) synonymizes Tortula densa with T. ruralis. Frahm & Sabovljević (2006) use DNA evidence to disprove both synonymies, but use very small sample sizes for the analysis. In the same work they also state that S. glabra is a juvenile form of S. densa. Work needs to be done to compare this plant with S. rupicola Allen.

Frahm & Sabovljec (2006) state that the major differences between S. densa and S. ruralis are smaller size, leaves erect-spreading when moist, and leaves densely inserted on the stem in S. densa vs. larger size, leaves squarrose when moist, and leaves remotely inserted on the stem in S. ruralis.
Syntrichia echinata (Schiffner) Herrnst. & Ben-Sasson 1982
Syntrichia princeps subsp. echinata (Schiffn.) Podp. 1954
Tortula princeps var. echinata (Schiffn.) Bizot 1956
Tortula princeps subsp. echinata (Schiffn.) Kramer 1980
Syntrichia princeps var. echinata (Schiffn.) Zand. 1993.

Moist leaf stance: spreading or patent
Leaf Dimensions: 2.6-4.5 x 1.0-1.6 mm
Leaf shape: lingulate, lingulate-spatulate, ovate-lingulate
Constricted at midleaf? yes
Shape of apex: obtuse or rounded
Awn: hyaline, spinose or spinulose, 0.4-2.3 mm
Marginal recurvature: recurved in basal 2/3 of leaf
Marginal border? no
Basal to leaf length %: 30-41%
Medial cell width: (12.5)15-17 μm
Medial cell papillae: 1, variously branched or forked, pedicellate, (10)15-17.5(22.5) μm tall
Hydroids present? yes
Dorsal stereid band: 3-7
Upper dorsal costal ornamentation: bifurcate, 2.5 μm tall
Laminal stratosity: 1
Propagules: none
Sexuality: synoicous
Peristome: spirally twisted teeth, 0.6-1.4 mm long; basal membrane of 17-23 rows of cells, 0.5-1.0 mm tall
Habitat: on rock from 1100-2000 m
Range: Western Mediterranean Europe, Middle East

As the synonymy and the description above illustrates, this plant is very similar to S. princeps, except for the single pedicellate papilla per cell. Most of the above description is from that given to me from M. T. Gallego (personal communication), and from Heyn & Herrnstadt (2004).

Syntrichia fragilis (Taylor) Ochyra 1992
Tortula fragilis Taylor London J. Bot. 6:333 1847
Barbula fragilis (Tayl.) Müll. Hal. 1849
Barbula schmidii Müll. Hal. 1853
Barbula trianae Müll. Hal. 1857
Syntrichia schmidii (Müll. Hal.) Mitt. 1859
Barbula alpina (B.S.G.) var. inermis Mild.1862
Tortula trianae (Müll. Hal.) Mitt. 1867
Tortula alpina (B.S.G.) Bruch var. inermis (Mild.) De Not. 1869
Barbula erubescens Müll. Hal. 1872
Barbula hildebrandtii Müll Hal. 1876
Syntrichia alpina (B.S.G.) Jur. var. inermis (Mild.) Jur. 1882
Barbula brachyaichme Müll. Hal. 1899
Barbula brevimucronata Müll. Hal. 1899
Barbula exesa Müll. Hal. 1899
Barbula mac-owaniana Müll. Hal. 1899
Barbula oranica Müll. Hal. 1899
Tortula brachyaichme (Müll Hal) Broth. 1902
Tortula brevimucronata (Müll Hal) Broth. 1902
Tortula erubescens (Müll Hal) Broth. 1902
Tortula exesa (Müll. Hal.) Broth. 1902
Tortula hildebrandtii (Müll Hal) Broth. 1902
Tortula macowaniana (Müll. Hal.) Broth. 1902
Tortula oranica (Müll. Hal.) Broth. 1902
Tortula subspathulata (Müll. Hal.) Broth. 1902
Tortula schmidii (Müll. Hal) Broth. 1902
Tortula chiapensis Broth. ex Card. 1909
Tortula confusa Card. 1909
Tortula parva Card. 1909
Tortula pringlei Card. 1909
Tortula brevitubulosa Broth. 1913
Tortula fragilifolia Bartram 1924
Tortula irregularis Sim 1926
Tortula parva var. latifolia Thér. 1931
Tortula alpina (B.S.G.) Bruch ssp. inermis (Mild.) Giac. 1947
Syntrichia mutica Giac. 1950

Moist leaf stance: erect-patent to spreading or wide spreading.
Leaf Dimensions: 1.7-3.7 x 0.6-1.4 mm
Leaf shape: oblong-ligulate to lingulate to spatulate
Constricted at midleaf? no
Shape of apex: acute, truncate or obtuse
Awn: none or more commonly a short mucro
Marginal recurvature: recurved in the lower 1/3 to 1/2 of the leaf
Marginal border? none, but Mishler (1994) reports some populations with thick-walled marginal cells
Basal to leaf length %: 22-30%
Medial cell width: (9)12.5-15(17.5)
Medial cell papillae: 3-8
Hydroids present? yes
Dorsal stereid band: 3-5, reaching the apex of the leaf
Upper dorsal costal ornamentation: simple or bifurcate, low, 2.5 μm tall
Laminal stratosity: 1
Propagules: The leaf fragments act as asexual reproductive agents. Plants in southwest U.S.A have been described with “reduced branches bearing ecostate, ovate-acuminate, verrucose propagules in the form of imbricated brood leaves are found sparingly in the axils of the upper stem leaves.” [Bartram 1924]
Sexuality: dioicus
Peristome: teeth twisted ca 1/2 turn, 0.2-0.5 mm long, base, 5-10 cells and 0.1-0.3 mm tall
Habitat: on bark of trees, basic or acidic rock, soil
Range: Southern North America, Central America, Caribbean, South America, Southern Europe, Africa, Asia

As can be inferred from the synonymy, this plant is quite variable and quite widespread. Cardot published four names for this taxa in 1909 and Müller published nine others between 1853 and 1899!
It is characterized by the fragile lamina, weak marginal recurvature, and the mucronate apex. Mishler (1994) cautions against relying on the fragile leaves, as virtually all Syntrichias have older leaves in some form of decay, and S. fragilis can be found with its leaves intact. In fact, Crum & Anderson (1981) state that “…unbroken leaves are often sectioned in polygonal areas marking lines of weakness and fragmentation.” All other authors, however, stress the fragility.

**Syntrichia gemmascens** (Chen) Zander 1993

*Didymodon gemmascens* Broth. *hom. illeg.* 1929.
*Desmatodon gemmascens* Chen *Hedwigia* 80:297. 1941

Moist leaf stance: spreading, erect-patent

**Leaf Dimensions:** ca 3 x 0.8 mm

**Leaf shape:** oblong-obovate to oblong-elliptic, narrowed at the base

**Constricted at midleaf?** no

**Shape of apex:** abruptly acute to apiculate, serrate.

**Awn:** costa subpercurrent

**Marginal recurvature:** usually none

**Marginal border?** 1-2(several) thicker-walled, yellowish, smoother cells.

**Basal to leaf length %:** not described

**Medial cell width:** 17-20 μm, with moderately thick-walled, collenchymatous cells

**Medial cell papillae:** several low, bifurcate, non-pedicellate

**Hydroids present?** not described

**Dorsal stereid band:** not described

**Upper dorsal costal ornamentation:** smooth

**Laminal stratosity:** 1

**Propagules:** abundant, multicellular, clavate to ellipsoid borne in leaf axils or on the surface of the lamina

**Sexuality:** all known collections are sterile

**Peristome:** capsules are unknown

**Habitat:** tree trunks, rocks or soil

**Range:** Eastern Asia

**Illustrations:** Zander (1993), as *Desmatodon gemmascens*: Chen (1941), Li et al (2001.)

Included in section *Collotortula* by Zander (1993), this species is recognized by the collenchymatous upper leaf cells, abundant gemmae, the serrate upper margins with differentiated limbidium, and the acute, muticous apex. Zander also describes this plant as having interior laminal cells with occasional, large, round central pores. This might be seen by staining transverse sections of the leaf. The serrate distal margins are unique in the genus, and only the characteristic costal stereid band maintains its position in the genus.

**Syntrichia handelii** (Schiffn.) Agnew & Vondracek

*Syntrichia montana* Nees ssp. *handelii* (Schiffn.) Podp. 1954
*Tortula intermedia* (Brid.) De Not. ssp. *handelii* (Schiffn.) Wijk. *ex Marg.*

Moist leaf stance: generally patent, rarely squarrose
Leaf Dimensions: 2.4-2.8 x 0.4-0.8 mm
Leaf shape: lingulate or lingulate-lanceolate
Constricted at midleaf? sometimes
Shape of apex: rounded or obtuse or acute, sometimes emarginate
Awn: hyaline, strongly spinose, 0.5-1.5 mm long
Marginal recurvature: recurved in basal 2/3 of the leaf,
Marginal border? none
Basal to leaf length %: 26-36%
Medial cell width: 5-7.5(10) μm
Medial cell papillae: 4-6 bifurcate, non-pedicellate, 2.5 μm tall
Hydroids present? yes
Dorsal stereid band: (2)3-4, reaching the apex, generally without substereids
Upper dorsal costal ornamentation: simple, verrucose, 2.5 μm tall
Laminal stratosity: 2 sometimes 3 in patches in distal 1/3, irregularly bistratose at midleaf
Propagules: none
Sexuality: dioecious
Peristome: twisted teeth 0.6-0.8 mm long; basal membrane of 12-17 rows of cells, 0.3-0.6 mm tall
Habitat: on rock, rarely on tree bark
Range: Mediterranean Europe, Middle East, North Africa

**var. ferganensis** (Laz.) Ochyra
Tortula ferganensis Laz. Ukrain. Bot. Zhurn.4:64. 1928
Syntrichia ferganensis (Laz.) Laz. 1938
Tortula handelii var. ferganensis (Laz.) Kramer 1978
Habitat: on limestone rock
Range: Central Asia
Illustrations: Kramer (1980), Gallego et al (2002a)

This variety differs from the typical variety by its lack of a hairpoint, and the presence in the costa of substereids. It is only known from the type specimen.

**Syntrichia laevidula** Bridel Muscol. Recent.Suppl.4:98. 1818
Tortula laevidula (Brid.) Schwägr. 1823
Tortula rurals var. laevidula (Brid.) Hook. & Grev. 1824
Syntrichia rurals var. laevidula (Brid.) Spreng. 1827
Barbula laevidula (Brid.) Garov. 1840
Barbula laevidula var. meridionalis Schimp. 1860
Tortula laeviduliformis De Not. 1862
Barbula pagorum Milde 1862
Tortula laevidula var. marginata Lindb. 1864
Tortula laevidula var. propagulifera Lindb. 1864
Tortula saccardoauna De Not. 1869
Tortula pagorum (Milde) De Not.) 1869
Syntrichia laevidula var. propagulifera (Lindb.) Jur. 1882
Syntrichia laevidula var. meridionalis (Schimp.) Jur. 1882
Syntrichia laeviduliformis (De Not.) Card. 1883
Barbula saccardoauna (De Not.) Grav. 1883
Barbula laevidula var. laeviduliformis (De Not.) Husn. nom. illeg. 1886
Barbula laevidula var. pagorum (Milde) Husn. nom. illeg. 1886
Moist leaf stance: spreading or patent, rarely weakly recurved-squarrose

Leaf Dimensions: 1.0-3.8 x 0.3-1.3 mm

Leaf shape: lingulate or spatulate

Constricted at midleaf? yes, sometimes weakly

Shape of apex: rounded, obtuse, or emarginate

Awn: weakly spinulose or smooth; hyaline, sometimes brown at base; (0.2)0.4-0.9(1.6) mm long

Marginal recurrency: plane or weakly recurved near midleaf, very rarely recurved in basal 2/3

Marginal border? variable; when present, consisting of up to 4 rows of smoother, thicker-walled cells than the rest of the lamina, yellowish or brownish.

Basal to leaf length %: 20-38%

Medial cell width: (7.5)10-15(17.5) μm

Medial cell papillae: 4-6(8); bifurcate

Hydroids present? yes

Dorsal stereid band: 3-5(7)

Upper dorsal costal ornamentation: smooth

Laminal stratosity: 1

Propagules: variable; when present, leaf shaped, with or without costa, papillose, with or without a smooth mucro, 30-100 μm long; borne in clusters in the upper leaf axils or rarely on upper leaf margins

Sexuality: autoicous or dioicous

Peristome: teeth 0.4-1.3 mm long; basal membrane of 11-16 cellular rows, 0.2-0.6 mm long

Habitat: generally on the bark of hardwood trees, occasionally on rock

Range: North America, Europe, Asia, North Africa, India, Middle East


The sexuality, the presence or absence of the marginal border, and the leaf-shaped propagules (and combinations of the latter two characters) has lead to a great deal of taxonomic confusion and discussion in the last two centuries. Barkman (1963) recognized seven varieties of Tortula laevipila, based on combinations of the presence or absence of the leaf border and propagules, as well as the papillosity of the propagule’s apical cell. Those seven varieties are summarized as follows:

var. laevipila.........leaf without a border; plants without propagules

var. meridionalis......leaf with a border; plants without propagules

var. wachteri.........leaf without a border; plants with apical propagules; propagules with an acute, smooth apical cell.
var. *saccardoana*.....leaf with a border; plants with apical propagules; propagules with an acute, smooth apical cell.

var. *propagulifera*......leaf without a border; plants with apical propagules; propagules with stunted, papillose apical cell. Barkman indicated that this taxa is synonymous with *Tortula pagorum var. notarisii*............leaf with a border; plants with apical propagules; propagules with a stunted, papillose apical cell.

var. *gemiifera*............leaf without a border; plants with propagules on the leaf margins; apical cell not described

It is important to note that Barkman recognized that there were many intermediate forms between var. *propagulifera* and var. *wachteri*, between var. *wachteri* and var. *saccardoana*, between var. *laevipila* and var. *meridionalis*, and between var. *laevipila* and var. *saccardoana*.

Lawton (1971) discussed two species. *T. laevipila* is described as “sometimes bordered” and implies that the presence of propagulae varies. She briefly described two varieties, and accepts *T. pagorum*:

* T. l. var. *laevipila*.......border not discussed, plants without propagules, awns long

* T. l. var. *meridionalis*...border not discussed, plants with costate, mucronate propagules, awns short.

* T. pagorum*.................not described, but differentiated from *T. l. var. meridionalis* by ecostate propagules.

Smith (1978) does not discuss *T. pagorum*, but describes two varieties within *T. laevipila*:

* var. *laevipila*.............leaves bordered or not; plants without propagules; autoicous

* var. *laevipiliformis* (sic)...leaves bordered, plants with propagules (characters of the propagules not discussed); dioicous.

Crum & Anderson (1981) and Mishler (1994) describe *T. pagorum* as having ecostate, mucronate propagules, and the leaves without a border. Crum and Anderson do summarize Barkman’s concept, but do not accept it.

Heyn & Herrnstadt (2004) considered two varieties of *T. laevipila* present in Israel. *T. laevipila* var. *laevipila* is described as autoicous with leaves ca. 2.5 mm long, with a marginal border usually present (at least above midleaf) consisting of 1-2 rows of weakly papillose, slightly incrassate cells, with the lumen distinctly wider than long. *T. laevipila* var. *meridionalis* is described as dioicous, with leaves ca. 3.5 mm long, with a distinct marginal border of up to four rows of smooth, strongly incrassate yellowish cells, with lumens only a little wider than long.

It is clear that this complex is exceedingly variable. To make matters worse, it seems that no two authors can agree on the characteristics of the varietal names.

After closely examining a large number of specimens, Gallego et al. (2004) lumped virtually all of the taxa discussed above, including *Syntrichia pagorum*, into *S. laevipila*. They found a wide range of intermediate forms, and a poor correlation of characters. In particular, they found the type material of *T. laevipila* var. *laevipila* to have some plants with bordered leaves, and some plants with unbordered leaves; and they found plants that had both costate and ecostate propagules on the same plant!

These same authors theorize that the propagules are a response to air pollution or nitrification of the substrate. This is supported by anecdotal evidence in California, where propagulous forms of are known from city parks, or near well traveled roads,(Kellman 2003). At first reading, the work of Studlar et al. (1984) seems to support this theory by demonstrating the ability of *T. pagorum* to produce propagules under a wide variety of conditions that would be present in urban settings. They demonstrate that *T. pagorum* is a very tolerant plant, producing gemmiferous rosettes in a wide variety of conditions. However, this very tolerance might also be interpreted as evidence against pollution being the trigger for propagule formation. If propagules are formed so readily, why are they not as common in less urban situations? This question might be answered by studies looking into competition between propagulous and non-propagulous plants under varying conditions. The answer might have interesting taxonomic implications.
Because of lack of material to study, Gallego et al. (2004) hinted at, but did not formally synonymize *T. laevipila* var. *gemmifera* Squivet with *S. laevipila*. Interestingly, these authors did not include *S. ammonsiana* or *S. chisosa* in their study, in spite of the obvious relation to this group. As a result, I have included all three taxa as separate from typical *S. laevipila*, in spite of the future possibility that they too, might be found under the *S. laevipila* umbrella.

*Syntrichia laevipila* var. *gemmifera* (Squivet) Kellman *comb. nov.*


**Habitat:** tree bark

**Range:** Europe

**Illustrations:** none

The description of *T. laevipila* var. *gemmifera* is sparse at best (Squivet de Carondelet 1962). The entire paper discusses plants with leaf-shaped gemmae at the apex of the stem, and then discusses pluricellular propagules sometimes occurring on the margins of the leaves instead of at the apex of the stem. One has to assume that these marginal propagules are also leaf-shaped, and that this is the only difference between var. *gemmifera* and the typical variety. Barkman (1963) confirms this interpretation and I have applied that assumption to the key. The placement of the gemmae is the only character delineating this variety. I have found no worker who has brought this variety into the genus *Syntrichia*, making the new combination necessary.

*Syntrichia latifolia* (Bruch ex C. J. Hartman) Hübener 1833


*Syntrichia laevipila* var. *mutica* Schultz 1823

*Syntrichia ruralis* var. *latifolia* Arnott nom. illeg. 1827

*Barbula latifolia* (Bruch ex Hartm.) Hueb. hom. illeg. 1833

*Tortula mutica* (Schultz) Lindb. hom. illeg. 1879

**Moist leaf stance:** generally spreading or patent

**Leaf Dimensions:** 1.8-2.6 x 0.6-0.8 mm

**Leaf shape:** spatulate or lingulate-spataulate

**Constricted at midleaf?** yes

**Shape of apex:** rounded or obtuse, sometimes emarginate

**Awn:** costa sub-percurrent to percurrent: no awn, apiculus, or mucro

**Marginal recuration:** plane or weakly recurved near midleaf

**Marginal border?** none

**Basal to leaf length %:** 18-26%

**Medial cell width:** 12.5-17.5 μm

**Medial cell papillae:** 4-6, bifurcate, non-pedicellate, ca 2.5 μm tall

**Hydroids present?** yes

**Dorsal stereid band:** 2-3 layers

**Upper dorsal costal ornamentation:** simple, ca 2.5 μm tall

**Laminal stratosity:** 1

**Propagules:** multicellular, spherical or ovoid, 25-45 x 25-37.5 μm, sessile, green or brown, smooth, borne on the ventral surface of the lamina

**Sexuality:** dioicous

**Peristome:** teeth ca 1 mm tall; basal membrane of 16-18 rows of cells, 0.5-0.7 mm tall

**Habitat:** generally on tree bark or rotting wood, rarely on moist rock.
Range: North America, Europe,
The plant is characterized by the complete lack of awn, the abundant gemmae scattered on the ventral laminal surface, and the weak recurvature of the leaves.

_Syntrichia longimucronata_ (X.-j. Li) Zander 1993

Moist leaf stance: spreading or sometimes reflexed
Leaf Dimensions: not described
Leaf shape: oblong-elliptic to oblong-ligulate
Constricted at midleaf? not described, but none shown in drawings
Shape of apex: broadly acute
Awn: awn “long, hyaline”, denticulate.
Marginal recurvature: “often recurved”
Marginal border? usually present as several rows of thick-walled, yellowish or brownish, sometimes elongate cells
Basal to leaf length %: not described
Medial cell width: not described
Medial cell papillae: “densely covered with several c-shaped papillae”
Hydroids present? see notes below
Dorsal stereid band: 4 (from drawings only)
Upper dorsal costal ornamentation: “costa often denticulate on the back” drawn with simple papillae.
Laminal stratosity: 1
Propagules: none described
Sexuality: autoicous
Peristome: drawn with teeth twisted ca 1 turn from a short base 4-7 cells tall. Basal tube less than ¼ the length of the teeth.
Habitat: “on boulders, flooded plains, forest ground, or grasslands”
Range: China
Illustrations: Li (1981) Li Xing-jiang et al. (2001)

All quotes in the description above are from Li et al. 2001.
Tan and Yu (1997) synonymize _S. longimucronata_ with _S. ruralis_. However, Li et al (2001) recognize the species, with descriptions that differ in several respects from _S. ruralis_, including the presence of a stem central strand and a marginal border. I have therefore accepted _S. longimucronata_.
Li’s descriptions do not include mention of hydroids in the costa (in fact, the drawings in Li et al. 2001 show none). However, there is a strong correlation between a stem central strand and costal hydroids. Because this is a major breakpoint in the key, I have assumed that hydroids do exist in _S. longimucronata_.
The species is defined by the combination of the differentiated marginal border, the long denticulate (=spinulose?) awn, the wide spreading leaf stance, and the robust plants (3-5 cm tall). The latter character should separate _S. longimucronata_ from _S. laevipila_, but confirmation will be found in the peristome. Per Li et al. (2001) the basal membrane is very short in _S. longimucronata_ (less than ¼ the length of the teeth), contrasting very strongly with the much longer basal tube in _S. laevipila_ (ca 1/2 the length of the teeth Gallego(2002).

Separating this plant from _S. princeps_ should be possible based on the marginal border, the denticulate awn, the short persistome basal tube, and the more spreading leaf stance of _S. longimucronata_.

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However, more information on the size of the medial cells, the degree and variability of the marginal recurvature, and the components of the costa would increase the level of confidence.

_Syntrichia minor_ (Bizot) Gallego et al. 2000
_Tortula papillosissima_ var. _minor_ Bizot Rev. Bryol. Lichénol. 23:268. 1954
_Tortula laevipila_ var. _minor_ (Bizot) Bizot 1956
_Tortula bizotii_ Laz. nom. inv. 1960
_Tortula virescens_ ssp. _bizotii_ (Laz.) Kramer nom. inv. 1980
_Tortula virescens_ ssp. _minor_ (Bizot) Ochyra 1988
_Tortula virescens_ ssp. _bizotiana_ Kramer nom. inv. 1988
_Syntrichia virescens_ var. _minor_ (Bizot) Ochyra 1992
_Syntrichia virescens_ var. _bizotiana_ (Kramer) Zand. nom. illeg. 1993

Moist leaf stance: recurved
Leaf Dimensions: 1.2-2.5 x 0.4-0.9 mm
Leaf shape: lingulate
Constricted at midleaf? yes
Shape of apex: rounded
Awn: spinulose, hyaline, 0.3-1.0 mm long
Marginal recurvature: plane or slightly recurved at midleaf
Marginal border? none
Basal to leaf length %: 25-45%
Medial cell width: (7.5)10-12.5 μm
Medial cell papillae: 1 pedicellate, branched papilla per cell, 10-15(17.5) μm tall
Hydroids present? no
Dorsal stereid band: 1-3 layers with ±substrereids
Upper dorsal costal ornamentation: simple or bifurcate papillae, ca 2.5 μm tall
Laminal stratostraty: 1
Propagules: none
Sexuality: dioicous
Peristome: teeth twisted, 0.5-0.6 mm long; basal membrane of 10-13 rows of cells, 0.2-0.3 mm tall
Habitat: on tree bark
Range: Mediterranean Europe

This species is one of the three known taxa with a single pedicellate, branched papilla per cell. It can be distinguished from _S. echinata_ by the lack of hydroids in the costa, and from _S. papillosissima_ by the smaller leaf size, the weaker marginal recurvature, and the narrower stereid band in the costa.

_Syntrichia mollis_ (Bruch & Schimp. _ex_ Müll. Hal) Zander 1993
_Tortula mollis_ (Bruch & Schimp. _ex_ Müll. Hal.) Broth. 1902

Moist leaf stance: erect-spreading, closely imbricate
Leaf Dimensions: not described
Leaf shape: oblong-ovate
Constricted at midleaf? not described
Shape of apex: not described
Awn: smooth, hyaline
Marginal recurvature: distinctly revolute
Marginal border? not described
Basal to leaf length %: not described
Medial cell width: rather small
Medial cell papillae: thinly papillose
Hydroids present? not described
Dorsal stereid band: not described
Upper dorsal costal ornamentation: not described
Laminal stratosity: not described
Propagules: not described
Sexuality: monoicous
Peristome: long, on a long base
Habitat: moist rocks
Range: Central Africa
Illustrations: none

Translation from the original latin description by Eckel.

The original account by Müller describes a plant similar to *Barbula laevipila* (Brid) Gerov. (= *S. laevipila*), but with distinctly revolute margins, and differentiated perichaetial leaves. The outer perichaetial leaves are described as very broad at the base, with a lax areolation, and a long acuminate apex with an awn. The inner perichaetial leaves are much shorter and pellucid.

**Syntrichia montana** Nees *Flora* 2:301. 1819

*Syntrichia intermedia* Brid. 1826
*Tortula intermedia* (Brid.) De Not. 1838
*Tortula ruralis* var. *crinita* De Not. 1838
*Barbula ruralis* Hedw. var. *rupestris* B.S.G. *nom. illeg.* 1842
*Tortula ruralis* var. *minor* Wils. *nom. illeg.* 1855
*Tortula ruralis* var. *rupestris* Wils. 1855
*Barbula intermedia* (Brid.) Walth. et Mol. 1868
*Barbula intermedia* var. *rupestris* Mild. *nom. illeg.* 1869
*Barbula pulvinata* Jur. var. *rupestris* Mild. 1871
*Barbula ruralis* var. *intermedia* (Brid.) Limpr. 1876
*Tortula montana* (Nees) Lindb. *nom. illeg.* 1879
*Barbula ruralis* ssp. *intermedia* (Brid.) Boul. 1884
*Barbula montana* (Nees) Corb. *nom. illeg.* 1889
*Barbula leptotricha* Müll Hal. et Kindb. 1892
*Tortula montana* var. *planifolia* Fleisch. et Warnst. 1896
*Barbula pulvinata* ssp. *leptotricha* (Müll Hal. et Kindb.) Kindb. 1897
*Barbula intermedia* var. *planifolia* (Fleisch. et Warnst.) Par. 1900
*Syntrichia montana* var. *planifolia* (Fleisch. et Warnst.) Podp. 1954
*Tortula intermedia* var. *planifolia* (Fleisch. et Warnst.) Wijk et Marg. 1959

Moist leaf stance: patent or spreading
Leaf Dimensions: 1.5-3.3 x 0.5-1.5 mm
Leaf shape: lingulate or lingulate-spatulate
Constricted at midleaf? yes, sometimes weakly
Shape of apex: rounded, obtuse, emarginate or mucronate, not ascending to the awn
Awn: hyaline, spinose, (0.3)0.7-2.4 mm long; sometimes reduced to a mucro 20-60 μm long
Marginal recurvature: in the basal half or 2/3 of the leaf
Marginal border? none
Basal to leaf length %: 20-34%
Medial cell width: 5-10(12.5)μm
Medial cell papillae: 4-6(8), bifurcate, non pedicellate
Hydroids present? yes
Dorsal stereid band: (4)5-9
Upper dorsal costal ornamentation: simple or bifurcate papillae ca 2.5 μm tall
Laminal stratosity: 1
Propagules: none
Sexuality: dioicous
Peristome: teeth 0.5-1.3 mm tall; basal membrane of 14-24 rows of cells, 0.2-0.7 mm tall
Habitat: generally on rock or soil over rock, rarely on tree bases
Range: North America, Europe

Syntrichia montana was first described in 1819 by Nees. It was later described (1826) as S. intermedia by Bridel. The first mention of their synonomy that I found was in Steere (1939), but in (1940) he wrote as if they were already synonymized, and he was just cleaning up authority. Although most authors call this species Tortula intermedia, the correct epithet in Syntrichia is montana.

Mishler (1985) and Crum & Anderson (1981) synonymized Tortula intermedia with T. ruralis (Hedw.) Gaertn. Meyer & Scherb. This is contradicted by the fact that the former has a central strand in the stem, and hydroids in the costa, whereas the latter lacks both characters. Nonetheless, using Mishler’s stated logic, T. intermedia should rather be synonymized with T. princeps De Notaris. However, most other authors feel that the combination of dioicous sexuality, smaller leaves and smaller laminal cells is sufficient grounds to separate the two taxa.

var. calva (Durieu & Sagot ex Bruch & Schimper) J. Amann 1918
Barbula ruralis var. calva Durieu & Sagot ex Bruch & Schimp Bryol. Europ. 2:113. 1851

Habitat: on rock or soil, generally basic
Range: Europe
Differing from typical S. montana by the reduction of the awn to a short mucro, 20-60μm long.

Syntrichia norvegica Weber Arch. Syst. Naturgesch. 1: 130. 1804
Tortula ruralis var. alpina Wahlenb. 1815
Syntrichia ruralis var. norvegica (Web.) Strud. 1824
Barbula aciphylla B.S.G. 1842
Tortula aciphylla (B.S.G.) Hartm. 1849
Barbula norvegica (Web.) Lindb. 1863
Syntrichia aciphylla (B.S.G.) Jur. 1882
Barbula ruralis ssp. aciphylla (B.S.G.) Boul. 1884
Tortula brachyangia Müll. Hal. & Kindb. 1892
Barbula rufipila Card. & Thér. 1900
Tortula rufipila (Card. & Thér.) Broth. 1902
Tortula brachyangia (Müll. Hal. & Kindb.) Broth. 1902
Tortula ruralis var. pseudoaciphylla Wint. 1910
Tortula ruralis ssp. norvegica (Web.) Dix. 1924
Tortula rubripila Dix. 1930
Tortula remotifolia Tak. 1951
Syntrichia ruralis var. pseudoaciphylla (Wint.) Podp. 1954

Moist leaf stance: recurved or spreading
Leaf Dimensions: 2.2-3.5 x 0.8-1.3
Leaf shape: lingulate or ovate-lingulate
Constricted at midleaf? no
Shape of apex: acuminate, acute, or obtuse, sometimes ascending to the base of the awn
Awn: generally reddish or orange throughout, sometimes hyaline at the top, spinulose, (sometimes spiny per Mishler (1994), 0.5-1.2 mm long.
Marginal recurvature: plane to weakly recurved near mid-leaf, or recurved in basal 2/3.
Marginal border? none
Basal to leaf length %: 25-33%
Medial cell width: (12.5)15-22.5 μm
Medial cell papillae: 4-8, bifurcate, ca 2.5 μm tall (up to 5-8 μm tall fide Mishler (1994)
Hydroids present? no
Dorsal stereid band: 2-4 layers, not reaching the apex, causing the distal third of the costa to appear the same as the lamina, or with stereids reaching the apex: see notes
Upper dorsal costal ornamentation: dorsal costal surface with cells equal to the laminal cells
Laminal stratosity: 1
Propagules: none
Sexuality: Dioicous
Peristome: teeth 0.9-1.1 mm tall; basal membrane of 8-10(12) layers of cells, 0.25-0.35 μm tall
Habitat: higher elevation soil and rocks
Range: North America, Mexico, Europe

Most of the latest authors agree that the character most often cited for this species—the awn reddish throughout—is not diagnostic (Mishler 1985) The best characters seem to be the large cell size, the lack of hydroids in the costa, and margins plane in at least the distal ¼. Gallego (2002) believes that the dorsal stereid band that dies out before the apex (so that the upper third of the costa has dorsal cells equal to the laminal cells) is diagnostic. This character is apparently variable. Mishler (1994) describes the costa as “papillose at back and sometimes serrulate near the apex because of projecting cell ends”, a character usually describing stereid cells in surface view. However, Mishler (1985) states that the “costa is weak or lacking near the apex of many mature leaves.” Kramer describes two states: on plants with substereids in the costa (the most common form per Kramer), the dorsal costa has papillae similar to the laminal cells; on plants with stereids, the dorsal costa has low, simple or bifurcate or branched papillae. Flowers (1973) did describe the loss of stereids in some plants: “Among these variable forms is a curious condition where the costa is interrupted near the leaf apex by a mass of thin-walled chlorophyllous tissue, three to eight cells thick beyond which the costa resumes its form at the apex and continues as a long or short hair point”.

Mishler (1985) states that another character often used for this taxon, the smooth or spinulose awn, is quite plastic in culture, and therefore unreliable.

Gallego (2002) and Noguchi (1988) describe the marginal recurvature as weakly recurved near midleaf, or sometimes plane, or recurved up to the upper third of the leaf. Apparently, this character is variable as Mishler (1994) describes marginal recurvature as “tightly revolute in the lower ¼”, and Flowers (1973) states “margins revolute below, plane in the upper 1/3”. Steere (1940) describes the
margin as “narrowly revolute from the base to or slightly above the middle”, and Kramer (1980) indicates marginal recurvature in the basal ¾ of the leaf. All agree that this species has marginal recurvature shorter than *S. ruralis* which has margins recurved from the base to near the apex.

Flowers’ concept of the species is somewhat suspect, as he relied a great deal on the red awn. He described the typical medial cell as 10-14 μm wide; numbers near or below the minimums cited by other authors. He also described forms that could scarcely be told from *Tortula ruraliformis* “except for the red hair points”. His concept was at least somewhat supported by Steere (1940) who described the “upper leaf cells as in *T. ruralis*” which he delineated as 12-16 μm.

**var. calva** (Amann) Ochyra 1992  
*Tortula norvegica* var. *calva* (Amann) Kramer 1980

Habitat: on rock and soil
Range: Europe
Illustrations: Kramer (1980)

This variety differs only from the typical variety by the lack of a hairpoint. It is not clear where this variety fits in with descriptions by Flowers (1973) of plants from Utah in which most of the leaves are muticous, but others have long, green, smooth awns, and others have “a thick, blunt, green point”

**Syntrichia obtusissima** (C. Müller Hal.) Zander 1993  
*Tortula obtusissima* (Müll. Hal.) Mitt. 1869  
*Tortula connectens* Card. 1909  
*Tortula obtusissima* var. *connectens* (Card.) Thér. 1931

Moist leaf stance: wide spreading to squarrose
Leaf Dimensions: 3-4 x 1-1.5 mm
Leaf shape: oblong or obovate [Steere 1940] or lingulate to spatulate, keeled
Constricted at midleaf? yes
Shape of apex: emarginate to retuse, occasionally truncate or acute; somewhat cucullate [Steere 1940]
Awn: toothed, hyaline, usually longer than the leaf.
Marginal recurvature: revolute in the lower 3/4-7/8, entire, often laxly undulate
Marginal border? none
Basal to leaf length %: not described
Medial cell width: 15-23(24) μm
Medial cell papillae: 4-7, bifurcate
Hydroids present? yes
Dorsal stereid band: massive
Upper dorsal costal ornamentation: minutely papillose, but not serrate
Laminal stratosity: 1
Propagules: none
Sexuality: autoicous, sometimes dioicous
Peristome: ca 1.5 mm long; teeth twisted nearly twice; the basal membrane 1/3 the total length
Habitat: on dry or moist rock or soil, rarely at the base of trees
Range: North America, Mexico
Illustrations: Steere (1939), Mishler (1994)
Both Steere (1940) and Mishler (1994) describe dry plants with a characteristic twisting of the leaves around the stem. The plant is further defined by the following combination of characters: presence of hydroids in the costa, the large upper and medial laminal cells, the usually emarginate apex with a long spiny awn, and the leaves constricted at midleaf. The upper costa is not smooth, as keyed in Norris & Shevock (2004), but rather covered with low, apparently verrucose papillae.

**Syntrichia papillosa** (Wilson in Spruce) Juratzka 1882


*Pottia russellii* Sull. 1848


**Moist leaf stance:** spreading or patent
**Leaf Dimensions:** 1.6-3.1 x 0.8-1.3 mm
**Leaf shape:** spatulate or lingulate-spatulate
**Constricted at midleaf?** yes
**Shape of apex:** rounded or obtuse, not ascending to the awn
**Awn:** smooth or very weakly toothed, hyaline, 0.2-0.6 mm long
**Marginal recurvature:** plane or weakly incurved throughout the leaf
**Marginal border?** none
**Basal to leaf length %:** 14-23 %
**Medial cell width:** (12.5)15-22.5
**Medial cell papillae:** smooth on ventral surface; 1-2 simple, rarely bifurcate papillae on the dorsal side.
**Hydroids present?** yes
**Dorsal stereid band:** 3-5 layers
**Upper dorsal costal ornamentation:** pedicellate or simple or bifurcate or branched papillae
**Laminal stratosity:** 1
**Propagules:** 2-many-celled, spherical or ovoid, sessile, 50-75 x 30-50 μm; borne on the ventral costal surface
**Sexuality:** dioicous
**Peristome:** teeth 0.7-1.8 mm long; basal membrane of 10-15 rows of cells, 0.2-0.5 mm tall
**Habitat:** on tree bark, also on concrete
**Range:** North America, Mexico, Europe


The plant is known by the leaves incurved when dry, the papillae only on the dorsal surface, and the abundant gemmae borne on the ventral costa. The upper cells are collenchymatous which in combination with the simple papillae and the rounded gemmae cement this specie’s inclusion in section *Collo TORTULA*. Zander (1993) describes this plant as having interior laminal cells with occasional, large, round central pores. This might be seen by staining transverse sections of the leaf.

**Syntrichia papillosissima** (Coppey) Loeske 1910


*Barbula ruralis* var. *hirsuta* Vent. 1890

*Tortula ruralis* var. *hirsuta* (Vent.) Par. 1906

*Tortula papillosissima* (Copp.) Broth. 1909

*Syntrichia ruralis* var. *hirsuta* (Vent.) Podp. 1954
**Tortula hirsuta** (Vent.) Laz. 1971
**Tortula ruralis** ssp. **hirsuta** (Vent.) var. **hirsuta** Kramer 1980

Moist leaf stance: generally recurved-squarrose, sometimes patent

Leaf Dimensions: 3.0-4.5 x 0.8-1.5 mm

Leaf shape: ovate, ovate-elliptic, or ovate-lingulate

Constricted at midleaf? no

Shape of apex: rounded, acute or obtuse, ascending to the base of the awn, rarely serrate or hyaline

Awn: strongly spinose, 0.5-4.0 mm long, hyaline, sometimes red at the base

Marginal recurvature: recurved from the base to near the apex, sometimes only in basal 2/3

Marginal border? none

Basal to leaf length %: 29-45%

Medial cell width: 10-12.5 μm

Medial cell papillae: a single, pedicellate, bifurcate or branched papillae per cell, on both surfaces of the lamina

Hydroids present? no

Dorsal stereid band: (2)3-5 layers

Upper dorsal costal ornamentation: bifurcate or branched papillae, 2.5-7.5 μm tall

Laminal stratosity: 1

Propagules: none

Sexuality: dioicus

Peristome: teeth 0.5-1.0 mm long; basal membrane of 20-29 rows of cells, 0.5-0.8 mm tall

Habitat: on rock

Range: North America, Europe


This is a well defined species, marked by the single, pedicellate, branched papilla, the absence of hydroids, the strong stereid band, and the large leaf size. It is separated from *S. echinata* by the lack of hydroids, and from *S. minor* by the larger size of the leaves and the stronger stereid band.

**Syntrichia percarnosa** (C. Müller) Zander 1993


*Tortula percarnosa* (Müll. Hal.) Broth. 1902

*Tortula kingii* Robins. 1967

*Tortula nigra* Zand 1986

Moist leaf stance: spreading

Leaf Dimensions: 2-2.5 mm

Leaf shape: ligulate-spatulate

Constricted at midleaf? not described

Shape of apex: obtuse, cucullate

Awn: costa subpercurrent

Marginal recurvature: weakly recurved at base, plane above

Marginal border? none

Basal to leaf length %: not described

Medial cell width: 6-15 μm
Medial cell papillae: densely pluripapillose; c-shaped or branched
Hydroids present? not discussed directly, but implied by a weakly defined stem central strand.
Not drawn with hydroids in Eckel’s drawings in Zander (1993) or in Mishler (1994)
Dorsal stereid band: sometimes ventral substereids present, dorsal substereids present
Upper dorsal costal ornamentation: not described
Laminal stratosity: usually one, but sometimes margins or laminal streaks are bistratose
Propagules: none
Sexuality: dioicous
Peristome: not described
Habitat: on limestone rock
Range: Mexico, Central America, South America

This species is known by the following combination of characters: the cucullate apex with no hint of an awn, the relatively small cells with collenchymatous walls, the presence of substereids in the costa, and the patchy bistratosity of some leaves. It is included in section Collotortula by Zander (1993).

Mishler (1994) discussed an “Andean complex of cucullate-leaved species, including T. kingii, T. percarnosa, and T. nigra Zand.” Both of the other species mentioned with T. percarnosa were synonymized with T. percarnosa and inserted into Syntrichia by Zander (1993).

**Syntrichia princeps** (De Notaris) Mitten 1859

*Barbula muelleri* B.S.G. nom. illeg. 1842
*Tortula muelleri* Hook. f. & Wilson nom. illeg. 1847
*Barbula princeps* (De Not.) Müll. Hal. 1849
*Barbula lato-excisa* Müll. Hal. & Kindb. 1892
*Barbula megalocarpa* Kindb. 1889
*Barbula pulvinata* Jur. ssp. lato-excisa (Müll. Hal. & Kindb.) Par. 1900
*Tortula megalocarpa* (Kindb.) Broth. 1902

Moist leaf stance: patent or spreading
Leaf Dimensions: 2.6–5.0 x 1.0–1.9 mm
Leaf shape: lingulate or lingulate-spatulate
Constricted at midleaf? yes
Shape of apex: rounded or obtuse, sometimes ascending to the awn
Awn: hyaline; spinose (sometimes strongly so); 0.2–2.7 mm long
Marginal recurvature: in the basal 2/3 of the lamina
Marginal border? none
Basal to leaf length %: 23–40%
Medial cell width: 12.5–15(17.5) μm
Medial cell papillae: (4)6-8(12), bifurcate, ca 2.5 μm tall
Hydroids present? yes
Dorsal stereid band: 3–7 rows
Upper dorsal costal ornamentation: simple or bifurcate, not pedicellate, ca. 2.5 μm tall
Laminal stratosity: 1
Propagules: none
Sexuality: synoicous or dioicous
Peristome: teeth 0.6-1.4 mm tall; basal membrane of 12-42 rows of cells, 0.4-1.4 mm tall
Habitat: on rock or soil or on tree bark
Range: Cosmopolitan

*S. princeps* is known by the presence of hydroids in the costa, the large leaf size, cells 12-15 µm wide with non-pedicellate papillae, the spiny awn, and the margins recurved ca 2/3 of the leaf. It was once thought of as exclusively synoicous, (see also notes under var. *parnassica* below) but Lightowlers (1985) showed that it’s sexuality varies.

In Western North America it is sometimes confused with *S. ruralis*, but the latter species is recurved to near the apex, has no hydroids in the costa, and is not constricted at mideleaf. *S. obtusissima* has larger median cells, and the upper dorsal costa is smoother than *S. princeps*.

**var. parnassica** (Schiffn.) Podp. 1954
*Tortula princeps* var. *parnassica* (Schiffn.) Wijk *Marg. 1961
*Tortula princeps* sspp. *parnassica* (Schiffn.) Kramer 1980

Habitat: on rock or soil or on tree bark
Range: Europe, Middle East
Illustrations: Kramer (1980)

Differs from the typical variety by a sometimes shorter hyaline leaf base, and dioicous sexuality. Kramer (1980) maintained that the typical variety (subspecies) is purely synoicous.

**Syntrichia pseudohandelii** (Fröhlich) Agnew & Vondracek 1975
*Syntrichia handelii* (Schiffn.) Agnew & Vondr. var. *pseudodesertorum* Vondr. 1965
*Syntrichia caninervis* var. *pseudodesertorum* (Vondr.) Gallego 2002

Moist leaf stance: mostly recurved, rarely spreading
Leaf Dimensions: 3.2-4 x 0.9-1.1 mm
Leaf shape: ovate-lingulate or ovate-lanceolate
Constricted at mideleaf? no
Shape of apex: rounded, obtuse, sometimes cucullate
Awn: not described
Marginal recurvature: from base to near the apex
Marginal border? none
Basal to leaf length %: 29-35%
Medial cell width: (5)7.5-10 µm
Medial cell papillae: 6-8, bifurcate, non-pedicellate, ca. 2.5 µm tall
Hydroids present? yes
Dorsal stereid band: 2-5 rows; substereids sometimes present
Upper dorsal costal ornamentation: long, pedicellate, variously branched papillae covering the entire abaxial costa; (15)17.5-25 µm tall
Laminal stratosity: regularly bistratose above mideleaf
Propagules: none
Sexuality: dioicous
Peristome: unknown
Habitat: on limestone rock
Range: Middle East, Europe
Illustrations: Kramer (1980). As S. caninervis var. pseudodesertorum: Gallego et al. (2002a)
Heyn & Herrnstadt (2004)

Kramer (1980) recognized Tortula pseudohandelii Frölich at the species level, citing no intermediate forms between it and T. caninervis. Gallego et al (2002a) found many intermediate forms and therefore, felt that the taxon should be a variety of S. caninervis (var. pseudodesertorum (Vondr.) M.T. Gallego). Without viewing specimens, and with no serious consequence if I am wrong, I accept Kramer’s interpretation. The Pottiaceae have several such continuously varied species complexes that have extreme forms designated as species (Didymodon vinealis (Brid.) Zand., D. nicholsonii Culm., D. brachyphyllus (Sull.) Zand. for example). In general, if a taxon is worth designating as a variety, my tendency is to accept it as a species. Beyond that, however, I have no opinion on the correct taxonomic level for this taxon.

It is known by its bistratose upper lamina, the pedicellate, often stellate-branched papillae on the distal adaxial costa, and its large leaves which are squarrose when moist. The latter two characters separate it from S. caninervis, which usually has erect or spreading, much shorter leaves. The stratosity of the upper lamina and the dorsal costal ornamentation easily distinguish S. pseudohandelii from S. ruralis, which is unistratose, and has low papillae on the upper dorsal costa.

**Syntrichia rigescens** (Brotherus & Geheeb)Ochyra 1992

*Tortula rigescens* Broth. & Geh. Allg. Bot. Z. Syst. 9:188. 1903

**Moist leaf stance:** patent, spreading or recurved
**Leaf Dimensions:** 1.6-2.8 x 0.5-0.9 mm
**Leaf shape:** ovate-lingulate, lingulate
**Constricted at midleaf?** somewhat
**Shape of apex:** rounded or obtuse or sometimes emarginate
**Awn:** not described
**Marginal recurvature:** recurved in basal 2/3 of leaf
**Marginal border?** none
**Basal to leaf length %:** 26-33%
**Medial cell width:** 7.5-10(12.5) μm
**Medial cell papillae:** 6-10, bifurcate, non-pedicellate, ca. 2.5 μm tall
**Hyroids present?** yes
**Dorsal stereid band:** 3-5 rows, sometimes with substereids
**Upper dorsal costal ornamentation:** pedicellate, stellate-branched papillae, 10-17.5(35) μm tall
**Laminal stratosity:** bistratose irregularly in the upper third and at midleaf
**Propagules:** multicellular, elliptical, brownish, smooth gemmae borne on the adaxial costa in the upper third of the leaf; 25-45 x 27.5-37.5 μm
**Sexuality:** dioicus
**Peristome:** sporophyte unknown
**Habitat:** on rock or cedar stumps
**Range:** Europe, Middle East, Northern Africa
S. rigescens is relatively easy to differentiate due to the abundant gemmae on the distal ventral costal surface, and the patchy bistratosity of the leaves. S. caninervis var. astrakhanica is bistratose, but bears gemmae on branched stalks at the apex of the stem. The other gemmiferous plants are all unistratose.

Syntrichia rupicola Allen

Moist leaf stance: erect spreading
Leaf Dimensions: 2-4 mm
Leaf shape: oblong-spatulate
Constricted at midleaf? not described, but Allen’s illustration shows one leaf with constriction
Shape of apex: obtuse to emarginate
Awn: long, hyaline, serrate
Marginal recurrvature: widely revolute at the base, plane above. Allen’s illustration shows recurrvature in approximately 2/3 the basal portion of the leaf.
Marginal border? none
Basal to leaf length %: not discussed
Medial cell width: 9-10 μm.
Medial cell papillae: not discussed, but Allen’s illustration shows 4-6 c-shaped papillae per cell.
Hydroids present? not addressed directly, but no hydroids in Allen’s illustration
Dorsal stereid band: not specifically noted. Steere (1939) states that the stereid band is “thick”
Upper dorsal costal ornamentation: rough on the back
Laminal stratosity: 1
Propagules: none
Sexuality: dioicous
Peristome: tube pale and equal in length to the teeth
Habitat: on calcareous rock or soil
Range: Northern North America
Illustrations: Allen (2005)

This taxon is a source of great confusion in the literature. Steere (1939) apparently started the problem by calling this plant Tortula intermedia Brid. (treated in this work as S. montana). However, that plant has hydroids in the costa, and this plant apparently does not. Thus, when Mishler (1994) and Crum and Anderson (1981) synonymized T. intermedia with T. ruralis they were referring to this plant, and not the European plant.

It can be separated from S. ruralis by the following characters: moist leaves erect-spreading with margins recurved to approximately 2/3. Cell size is inconclusive (see notes under S. ruralis). The lack of hydroids needs to be confirmed, otherwise, this plant sounds very much like S. montana.
If this plant lacks hydroids, then comparison will have to be made with the European Tortula densa which Gallego has synonymized with S. calcicola and Kramer has synonymized with S. ruralis.

When Allen (2005) described this plant, he discussed its separation from S. ruralis, but referred to Steere (1939) for a more complete description.

Syntrichia ruralis (Hedwig) Weber & D. Mohr 1803
Barbula ruralis Hedw. Spec. Musc. 121.1801
Bryum ruralis (Hedw.) With. 1801
Tortula ruralis (Hedw.) Gaertn., Meyer et Scherb. 1802
Tortula ruralis var. vulgaris Hook. et Grev. nom. illeg. 1824
Barbula ruralis var. gigantea Lesq. 1868

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Barbula laeviuscula Kindb. 1892
Barbula ruralis var. subintermedia Ren. & Card. 1892
Barbula ruralis ssp. alaskana Kindb. 1897
Tortula ruralis var. densa Velen. 1897 fide Kramer (1980). [See notes under S. calcicola]
Tortula laeviuscula (Kindb.) Broth 1902
Tortula ruralis ssp. alaskana (Kindb.) Par. 1906
Tortula ruralis var. californica Par. 1906
Tortula ruralis var. fulva Gyoerffy 1906
Tortula subintermedia (Ren. & Card.) Card. 1910
Syntrichia ruralis var. glacialis J.J. Amann 1920
Tortula reflexa Li hom. illeg. 1981
Syntrichia reflexa Zander 1993

Moist leaf stance: generally recurved to squarrose
Leaf Dimensions: 2.2-3.8(5.4) x 0.5-1.5 mm
Leaf shape: ovate-lingulate,
Constricted at midleaf? no
Shape of apex: rounded, obtuse, rarely acute or acuminate
Awn: hyaline, spinose, rarely spinulose, 0.4-2.8 mm long
Marginal recurvature: from base to near the apex
Marginal border? none
Basal to leaf length %: 27-45%
Medial cell width: (5)7.5-10(12.5)(16) μm. See notes.
Medial cell papillae: 4-6(8), bifurcate, non-pedicellate, ca. 2.5 μm tall
Hydroids present? no
Dorsal stereid band: (2)4-5 rows
Upper dorsal costal ornamentation: simple or bifurcate papillae, ca. 2.5 μm tall
Laminal stratosity: 1
Propagules: none
Sexuality: dioicous
Peristome: teeth 0.6-1.75 mm tall; basal membrane of 22-34 rows of cells, 0.4-1.1 mm long
Habitat: on rock or soil, sometimes at the base of trees
Range: North America, Europe

The typical variety is easily recognized by the squarrose leaves, the lack of hydroids, no midleaf constriction, margins recurved from the base to near the apex, and the spinose awn. The first four characters separate S. ruralis from S. montana which has leaves patent or spreading, hydroids in the costa, midleaf constriction, and margins recurved in the basal 2/3 of the leaf. See notes under S. princeps for differentiation from that species.

There is some disagreement in cell size between Gallego (2002), Gallego et al. (2002a) versus Steere (1940), Allen (2005) and Smith (2004). Gallego limits the median cell width to an occasional 12.5 μm, while Steere, Allen and Smith describe the plant with median cells between 12-16μm wide.

var. ruraliformis (Besch.) Delogne 1885
Barbula ruralis var. ruraliformis (Besch.) Husn. 1873
Habitat: on calcareous soil, sand dunes

Range: Europe, Asia, Middle East, Africa, North America, Macaronesia


This variety differs from the typical variety in the apex of the leaf, which is hyaline and ascends to the awn. The margin is sometimes toothed below the awn.

Mishler (1985) showed with controlled growth experiments that the decurrent awn of *T. ruraliformis* (Besch.) Mans. is a character that is environmental, and not heritable. This casts doubt on the validity of *S. ruraliformis* as a species. Apparently, plants fitting the description of *S. ruraliformis* are common in Europe and parts of Western North America. (Steere 1940, Willis 1964) Therefore, I have included this taxon as *S. ruralis* (Hedwig) Weber & D. Mohr var. *ruraliformis* (Besch.) Delogne It might be more appropriately be called a form of *S. ruralis* rather than a variety, but I leave that debate to others.
Hydroids present? yes
Dorsal stereid band: 3-5 layers of stereids
Upper dorsal costal ornamentation: simple, non pedicellate, sometimes smooth
Laminal stratosity: 1
Propagules: none
Sexuality: autoicous
Peristome: teeth 0.8-1.1 mm long; basal membrane of 3-6 rows of cells, 0.09-0.16 mm tall.
(Gallego 2002). Basal membrane “high, 1/3 the length of the teeth.
Habitat: on protected rocks or soil
Range: Europe, Asia

There is very little agreement about the characteristics of S. sinensis. Kramer (1980) and Gallego (2002) agree that the awn is short and weakly toothed. However, Kramer states that the awn is usually brown, while Gallego calls it hyaline. They also disagree on the length of recurvature in the leaf margin, with Kramer describing the recurvature extending to ½-2/3 the leaf length, and Gallego describing weak recurvature in the middle of the leaf or in the proximal 1/3 of the leaf. The key in Li et al (2001) leads to S. sinensis through couplets including plane margins or with weak recurvature, but the description states “margins often recurved”. She describes the awn as rather long, smooth and reddish brown. Noguchi (1988) describes the awn as long, yellowish-brown, and indistinctly toothed, with the margins recurved near the middle, and plane above and below. Moreover, Gallego (2002) describes S. sinensis with a low peristome basal tube, but Li et al. (2001) describes the basal tube as 1/3 the length of the teeth.

If plants with long awns are included in the concept of S. sinensis, then it is quite difficult to separate from forms of S. laevipila without gemmae or modified leaf borders…the dominant form in California (personal observation). It is interesting that none of the Asian authors include S. laevipila in their floras. Clearly, this is a matter for further investigation.

Due to the inconsistency of descriptions, it also might be difficult to tell S. sinensis from elimbate forms of S. longimucronata. For now, I have chosen to key out S. sinensis with both a long and a short awn, and use the peristome and the medial cell papillae (cited in Gallego 2002) to separate them, however much study needs to be done.

Syntrichia subaristata (C. Müller Hal) Zander 1993
Barbula subaristata Müll. Hal. Syn 1:644. 1849
Tortula subaristata (Müll. Hal.) 1902

Moist leaf stance: erect-somewhat spreading, slightly recurved
Leaf Dimensions: not described
Leaf shape: broadly oblong-lanceolate, concave
Constricted at midleaf? not described
Shape of apex: not described, but drawn as acute in Townsend (1984)
Awn: short, recurved (reflexed?) dentate, hyaline
Marginal recurvature: revolute
Marginal border? not described
Basal to leaf length %: not described
Medial cell width: not described
Medial cell papillae: lightly papillose, somewhat opaque
Hydroids present? not described, but Townsend’s drawing shows none.
Dorsal stereid band: not described, but Townsend’s drawing shows 3, with the dorsal layer somewhat enlarged.

Upper dorsal costal ornamentation: not described

Laminal stratosity: not described

Propagules: not described

Sexuality: dioicous

Peristome: long-tubulose, whitish

Habitat: on trees in mountains

Range: Central Africa

Illustrations: Townsend (1984)

Translation from the original latin description by Eckel.

The original description by Müller includes two features that distinguish the plant. First, the capsule is elliptical on a short seta. Second, although the perichaetial leaves are similar to the cauline leaves, the perigonial leaves are differentiated as follows: broadly ovate, shortly acute, and with an excurrent costa. The inner perigonial leaves are obtuse with the costa disappearing before the apex.

Townsend (1984) illustrated the plant essentially without further discussion.

**Syntrichia submontana** (Brotherus) Ochyra 1992


*Syntrichia mongolica* Boros 1970

Moist leaf stance: ± erect

Leaf Dimensions: scaled drawing of 2 leaves shows 1.6-2.3 x 0.6-1.0 mm [Kramer 1980]

Leaf shape: ± lingulate

Constricted at midleaf? not described

Shape of apex: rounded

Awn: hyaline, not or weakly toothed (warty), more or less short; scaled drawing shows ca. 0.3 mm

Marginal recurvature: recurved from the base to near the apex

Marginal border? none

Basal to leaf length %: not described

Medial cell width: large; scaled drawing shows 14-15 μm

Medial cell papillae: several smallish c-shaped papillae per cell

Hydroids present? yes

Dorsal stereid band: 4 rows (from drawing)

Upper dorsal costal ornamentation: verrucose papillae

Laminal stratosity: 1

Propagules: none

Sexuality: dioicous

Peristome: not described

Habitat: on soil

Range: Mongolia

Illustrations: Kramer (1980)

Related to *S. princeps* by the shape of the leaf, the median leaf cell size and papillosity, and the presence of hydroids in the costa, *S. submontana* differs from that species by the shorter and smooth or warty awn, and the smaller size of the leaves that are recurved from the base to near the apex.
**Syntrichia subpapillosissima** (Bizot & Pierrot ex W. Kramer) M. Gallego & Guerra 2002


*Tortula ruralis* var. *subpapillosissima* Bizot & Pierrot nom. inval. 1973

*Tortula ruralis var. submamillosa* W. Kramer 1980

*Syntrichia ruralis* var. *subpapillosissima* (Bizot & Pierrot ex W. Kramer) Zander 1993

*Syntrichia ruralis* var. *submamillosa* (W. Kramer) Zander 1993

Moist leaf stance: generally recurved-squarrose or spreading, sometimes patent

Leaf Dimensions: 2.5-5.8 x 0.9-2.2 mm

Leaf shape: ovate, lingulate, ovate-lingulate

Constricted at midleaf? no

Shape of apex: rounded, obtuse, acute, acuminate, ascending to the base of the awn, sometimes marginally toothed below the awn

Awn: strongly spinose, hyaline, 1-4 mm long

Marginal recurvature: usually recurved from base to the apex, sometimes just to 2/3

Marginal border? none

Basal to leaf length %: 28-33%

Medial cell width: (7.5)10-12.5 μm

Medial cell papillae: (2)3-4(6), bifurcate or rarely branched, pedicellate, (5) 7.5-10 μm tall

Hydroids present? no

Dorsal stereid band: 3-6 layers of stereids

Upper dorsal costal ornamentation: simple or bifurcate, 2.5-5 μm tall

Laminal stratosity: 1

Propagules: none

Sexuality: dioicous

Peristome: teeth 0.4-0.8 mm long; basal membrane of 28-35 rows of cells, 0.7-1 mm tall

Habitat: on soil or rock, rarely epiphytic

Range: Europe, Southwestern Asia, North Africa

Illustrations: Gallego et al. (2002), Gallego (2002)

The primary debate over this taxon revolves around its taxonomic rank. Gallego (2002) and Gallego et al. (2002) believe that it deserves specific status, while Kramer (1980) believes that it is only a variety of *Tortula ruraliformis*. Zander (1993) and Frey & Kürschner (1991) make it a variety of *S. ruralis*. Its hallmark character is the medial cell papillosity--multiple pedicellate papillae per cell. This immediately separates it from *S. papillosissima* and *S. minor*, the other plants without hydroids and with pedicellate papillae. Those two species have only one papilla per cell. *S. subpapillosissima* can be separated from *S. echinata* by the lack of hydroids, and the single pedicellate papilla per cell in the latter.

**Syntrichia sucrosa** Kellman *The Bryologist* 111: 2007

Moist leaf stance: spreading or patent

Leaf Dimensions: 1.5-2.6 x 0.6-1.3 mm

Leaf shape: lingulate, lingulate-spatulate, ovate-lingulate

Constricted at midleaf? Weak to none

Shape of apex: obtuse or rounded

Awn: hyaline, spinose or spinulose, 1/3 to equal leaf length

Marginal recurvature: recurved in basal 2/3 of leaf

Marginal border? no

Basal to leaf length %: 25-35(50)%
Medial cell width: (8)10-12(15) μm
Medial cell papillae: 1-4, variously branched or forked, pedicellate, 8μm or taller
Hydroids present? yes
Dorsal stereid band: 2-4
Upper dorsal costal ornamentation: verrucose to prorate
Laminal stratosity: 1
Propagules: none
Sexuality: dioicous
Peristome: spirally twisted teeth from a tessellated base, base 120-400μm tall; teeth 250 -600 μm long
Habitat: on rock in dryer habitats
Range: Western U.S.
Illustrations: Kellman (2007)

*Syntrichia virescens* (De Notaris) Ochyra 1992
*Barbula ruralis* (Hedw.) var. *virescens* (De Not.) Bert. 1858
*Barbula pulvinata* Jur. 1863
*Barbula virescens* (De Not.) *Lor. hom. illeg.* 1865
*Barbula danica* Lang. 1869
*Tortula ruralis* ssp. *danica* (Lang.) C. Hartm. 1871
*Barbula ruralis* var. *pulvinata* (Jur.) Limpr. 1876
*Syntrichia pulvinata* (Jur.) Jur. 1882
*Barbula ruralis* ssp. *pulvinata* (Jur.) Boul. 1884
*Tortula ruralis* var. *danica* (Lang.) Lang. 1887
*Tortula danica* (Lang.) C. Hartm. 1888
*Tortula pulvinata* (Jur.) Limpr. 1888
*Tortula ruralis* ssp. *ruralis* var. *substereidosa* Kramer. 1980

Moist leaf stance: patent or erect-patent
Leaf Dimensions: 1.3-2.8 x 0.5-1.0 mm
Leaf shape: ovate-lingulate, spatulate, spatulate-lingulate
Constricted at midleaf? yes
Shape of apex: rounded or emarginate, not ascending to the awn
Awn: spinulose, 0.25-1.2 mm long, hyaline, sometimes red at base
Marginal recurvature: plane to weakly recurved near midleaf. See discussion below
Marginal border? none
Basal to leaf length %: 20-45%
Medial cell width: 12.5-15(17.5) μm
Medial cell papillae: 4-6(8), bifurcate
Hydroids present? no See notes below
Dorsal stereid band: 1-2(3) See notes below
Upper dorsal costal ornamentation: simple or bifurcate ca 2.5 μm tall
Laminal stratosity: 1
Propagules: occasional, multicellular, smooth, brown or green, 50-70 x 30-40 μm, spherical or ovoid, borne on the ventral costa
Sexuality: dioicous
Peristome: teeth 0.3-0.4 mm, basal membrane 170-300 μm with 8-13 rows of cells
Habitat: usually on bark of trees, occasionally on rock
**Range**: Europe, Middle East, North Africa, North America


*S. virescens* is known by the following suite of characters: plane or weakly recurved margins, costa with 1-2 rows of stereids and without hydroids, leaf constricted at midleaf, and a spinulose awn.

Kramer (1980) describes his *Tortula virescens* ssp. *virescens* var. *virescens* as usually with 2-3 layers of substereids, but occasionally with 3-4 layers of stereids. He also states that this taxon can occasionally have hydroids in the costa.

Kramer (1980) named *Tortula ruralis* var. *substereidosa* defining it as a plant with costal substereids, margins recurved in the basal ¾ or almost to the apex, laminal cells 10-13 μm, and leaves somewhat squarrose when moist. He contrasts that taxon with *T. virescens* var. *iranica* with the description of the latter as follows: Costa with substereids, leaf margin weakly recurved, laminal cells 12-15 μm, leaves erect when moist. After examination of the type material, Gallego et al. (2002a) synonymize *T. ruralis* var. *substereidosa* with *S. virescens*, stating that *S. virescens* sometimes have substereids. Apparently they found the marginal recurvature differing from Kramer’s description. These authors did not review *T. virescens* var. *iranica* as it was beyond the scope of their study, but Gallego (2002) allows for bifurcate dorsal costal ornamentation in typical *S. virescens*.

Smith (1978) claims that *S. virescens* can be separated from *S. laevipila* by shorter basal cells in the leaf, but Gallego’s measurements (2002) show this to be unreliable. However, the lack of hydroids, and the fewer rows of stereids in *S. virescens* make separation a relatively easy matter.

Frahm (1994) in his key to species claims that *S. virescens* (and *S. calcilcola* in Frahm & Sabovlievic 2006) has a central strand in the stem. This conflicts with the general correlation between presence of hydroids and the presence of a stem central strand.

**var. iranica** Kramer (Zand.) 1993


Kramer separates this variety from the typical variety by the presence of substereids in the costa and the upper dorsal costal ornamentation similar to the laminal cells (as opposed to verrucose papillae on the dorsal costa in the typical variety). Otherwise it is the same as the typical variety. Given the acceptance by Gallego et al. (2002a) of costal substereids in typical *S. virescens*, and the presence of either simple or bifurcate papillae on the dorsal costa (Gallego 2000), this is apparently a weak segregate.

**Habitat**: on rock

**Range**: Iran

**Illustrations**: Kramer (1980)

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**EXCLUDED TAXA**

*Syntrichia mucronifolia* (Schwägrichen) Bridel

*Tortula mucronifolia* Schwägrichen has sometimes (Brown 1824, Chen 1941) been included in *Syntrichia* but most present authors who accept *Syntrichia*, keep it in *Tortula* (Norris & Shevock, 2004; Zander 1993; Ignatov & Ignatova 2003; Cano, 2004). The shape of the costal stereid band is certainly more like *Tortula* than *Syntrichia*. I have therefore excluded *S. mucronifolia*

*Syntrichia bolanderi* (Lesq. & James) Zander

*Syntrichia glabra* Frahm & Gallego

Frahm and Sabovlievic (2006) explain that *S. glabra* is a juvenile form of *Syntrichia densa*.

*Syntrichia inermis* (Brid.) Bruch
Syntrichia subulata (Hedwig) Weber & Mohr
Gallego (2002) and Cano & Gallego (2003), after a morphological study which included the study of the type material, showed that Tortula bolanderi and T. inermis were placed in the genus Tortula on the basis of the differentiated dorsal epidermis of the costa and a semicircular transverse section of the dorsal stereid band. Subsequently Werner et al. (2002, 2003) supported the position of these species in Tortula together with T. subulata by molecular studies. Other authors (Mönkemeyer 1927; Zander 1993; Kürschner 2000; and Cortini Pedrotti 2001) have included these taxa in Syntrichia.

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APPENDIX I

Synonymies

Please note that this list of synonymies is not exhaustive. It is only meant as a convenient way to track confusing or non-intuitive name changes. Therefore, listed synonymy are included only when the specific and/or varietal epithet of the synonymized taxa is different than the specific or varietal epithet of the accepted name. (For example: *Tortula virescens* (De Not.) De Not. = *Syntrichia virescens* is not included in this list.) Where the taxon was known with the same epithets in *Barbula* and *Tortula*, or *Tortula* and *Syntrichia*, only the *Tortula* is included.

The taxa are listed alphabetically primarily by the specific epithet and secondarily by the varietal epithet of the old name. The earliest reference (I have found) noting the synonymy in either *Tortula* or *Syntrichia* is given at the end of the synonymy. The second reference (in brackets) is the earliest reference synonymizing the taxon in *Syntrichia* with the accepted epithet.

*Tortula aciphylla* B.S.G. = *S. norvegica* fide Steere(1940) Kramer (1980)
*Tortula alpina* B.S.G. = *S. sinensis* fide Kramer (1980) [Ochyra (1992)]
Tortula alpina (B.S.G.) Bruch = S. sinensis fide Kramer (1980) [Ochyra (1992)]
Tortula alpina var. propagulifera = S. laevipila fide Gallego et al. (2004)
Tortula bistratosa Flow. = S. caninervis var. caninervis fide Kramer (1980)
Tortula bizotti Laz. = S. minor fide Gallego et al. (2000)
Tortula bornmuelleri Schiffn. = S. caninervis var. caninervis fide (Kramer 1980)
Tortula brachypila (Müll Hal.) Broth. = S. sinensis fide Kramer (1980) [Ochyra (1992)]
Tortula caroliniana Andr. = S. amphidacea fide Zander (1993)
Tortula chiapensis Broth. ex Card. = S. fragilis fide Steere (1940) [Ochyra (1992)]
Tortula connectens Card. = S. obtusissima fide Mishler (1994)
Tortula danica (Lang.) C. Hartm. = S. virescens fide Kramer (1980) [Ochyra (1992)]
Tortula desertorum Broth. = S. caninervis var. caninervis fide Kramer (1978)
Tortula erythrotricha (Müll Hal.) Broth. = S. sinensis fide Kramer (1980)
Tortula ferganensis Lazar. = S. handelli var. ferganensis fide [Ochyra (1992)]
Tortula fragilifolia Bartram = S. fragilis fide Steere (1940) [Ochyra (1992)]
Syntrichia glabra Frahm & Gallego = S. densa fide Frahm & Sabovljević (2006)
Syntrichia hadacii Vondr. = S. caninervis var. gypsophila fide Kramer (1980) [Ochyra (1992)]
Tortula hirsuta (Vent.) Laz. = S. papillosissima fide Kramer (1980)
Tortula intermedia (Brid.) De Not. = S. montana fide Steere (1940)
Tortula kingii Robins. = S. percarnosa fide Zander (1993)
Tortula laevipiliformis De Not. = S. laevipila fide Gallego (2002)
Tortula laeviuscula (Kindb.) Broth. = S. ruralis fide Steere (1940)
Tortula lemniscata Zand. = S. andicola fide Mishler (1994)
Barbula leptotricha Müll. Hal. & Kindb. = S. montana fide Steere (1940)
Tortula megalocarpa (Kindb.) Broth. = S. princeps fide Steere (1940)
Syntrichia mongolica Boros = S. submontana fide Kramer (1980) [Ochyra (1992)]
Tortula muelleri (Bruch.) Wilson = S. princeps fide Steere (1940)
Tortula mutica Lindb. = S. latifolia fide Steere (1940) [Kramer (1980)]
Tortula nigra Zand. = S. percarnosa fide Zander (1993)
Tortula novoguinensis Bartr. = S. amphidacea fide Eddy (1991)
Tortula pagorum (Milde) De Not. = S. laevipila fide Gallego et al. (2004)
Tortula parva Card. = S. fragilis fide Mishler (1994)
Tortula pilosa Vent. = S. laevipila fide Gallego et al. (2004)
Tortula pringlei Card. = S. fragilis fide Steere (1940) [Ochyra (1992)]
Tortula pseudodesertorum Froehl = S. caninervis var. caninervis fide Kramer (1980)
Tortula pulvinata (Jur.) Limpr. = S. virescens fide Kramer (1980)
Tortula reflexa Li nom. illeg. = S. ruralis fide Li et al. (2001)
Tortula remotifolia Tak. = S. norvegica fide Kramer (1980)
Tortula rubripila Dix. = S. norvegica fide Kramer (1980)
Tortula rufipilis Broth. = S. norvegica fide Steere (1940) [Kramer (1980)]
Tortula ruralis var. alpina Wahlenb. = S. norvegica fide Kramer (1980)
Tortula ruralis var. fulva Gyöerffy = S. ruralis fide Kramer (1980)
Tortula ruralis var. hirsuta (Vent.) Podp. = S. papillosissima fide Kramer (1980)
Syntrichia ruralis (Hedw.) Web. & Mohr var. pseudoaciphylla (Wint.) Podp. = S. norvegica fide Kramer (1980)
Syntrichia ruralis var. pseudodesertorum Podp. = S. caninervis var. gypsophila fide Kramer (1980) [Ochyra (1992)]
Tortula ruralis var. submamillosa Kramer = S. subpapillosissima fide Gallego et al. (2002a)
Tortula ruralis var. substereidosa = S. virescens fide Gallego et al. (2002a)
Pottia russellii Sull. = S. papillosa fide Steere (1940)
Tortula subintermedia Card. = S. ruralis fide Steere (1940)
Tortula submuralis Müll. Hal. = S. sinensis fide Wijk. et al. 1959
Tortula saccardoana De Not. = S. laevipila fide Gallego et al. (2004)
Tortula saharae Trab. = S. caninervis var. caninervis fide Kramer (1978)
Tortula satoi Sakurai = S. sinensis fide Li & Iwatsnot (1993)
Tortula solomensis (Broth.) Zand. = S. sinensis fide Li et al. (2001)
Tortula spuria Amann = S. caninervis var. gypsophila fide Kramer (1978) [Ochyra (1992)]
Tortula tanganyikae Dix. = S. amphidacea fide Zander (1993)
Tortula trianae Hampe = S. fragilis fide Steere (1940) [Ochyra (1992)]