A taxonomic study of Syntrichia laevipila (Pottiaceae, Musci) complex

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A taxonomic study of Syntrichia laevipila and S. pagorum has been carried out. A morphological description and distribution data of S. laevipila are provided. Three lectotypes for Syntrichia laevipila, Barbula laevipila var. meridionalis and Tortula laevipilaformis are proposed. After studying the type material of the S. laevipila and S. pagorum complex and samples from numerous localities throughout the world, we conclude that S. laevipila and S. pagorum are the same taxon and that the typical forms in which it is found are simply the extremes of its wide morphological range. In this way, the different varieties described for S. laevipila are really different transitional states between both taxa. For this reason, Barbula laevipila var. meridionalis, Barbula pagorum, Tortula laevipila var. notarisii and Tortula laevipila var. wachteri are included in the synonymy of Syntrichia laevipila.

ADDITIONAL KEYWORDS: bryophyte – morphological characters – nomenclature – taxonomy.

INTRODUCTION

Many authors have remarked on the taxonomic proximity of Syntrichia laevipila Brid. and S. pagorum (Milde) J.J. Amann. Barkman (1963) made a broad study of the laevipila-pagorum complex, in which he described new varieties of S. laevipila, whereas Kramer (1980) did not treat this complex in any depth in his monograph of Tortula Hedw. section Rurales De Not. owing to the limited availability of material and the absence of type material of some taxa. However, he did insist on the need for a detailed study of this group, neither confirming nor rebutting Barkman (1963).

Barkman (1963) recognized seven varieties for Tortula laevipila: var. laevipila, var. meridionalis (Schimp.) Wijk & Margad., var. wachteri Barkman, var. notarisii Barkman, var. saccardoana (De Not.) Barkman, var. propagulifera Lindb. and var. gemmifera Squivet, basing his argument exclusively on gametophytic characteristics, principally on the presence or absence of differentiated leaf margins and the morphology of the propagules. His defence of the validity of these taxa, despite reiterated observations of the degree of intergradation between the samples studied, seems surprising, especially when he concluded that the only differentiating character is the form of the propagule apex.

Ever since 1862, when Milde described Barbula pagorum, controversy has existed concerning the taxonomic status of this moss because it has not always been recognized as a species. Lindberg (1864) considered it a variety of T. laevipila – T. laevipila var. propagulifera, whereas De Notaris (1869) placed it in the genus Tortula at species level, T. pagorum, and Husnot (1886) considered it once again a Barbula Hedw., but at the varietal level, B. laevipila var. pagorum. It kept this status in Limpricht (1885–1889) but again under T. laevipila – T. laevipila var. laevipilaformis. Kindberg (1898) placed it in Barbula, B. alpina var. pagorum, Amann, Culman & Meylan (1912) raised it to species level, Syntrichia pagorum, and Mönkemeyer (1927) maintained it in the genus Syntrichia Brid., but as a variety, S. laevipila var. pagorum.

Some American and Australian authors consider S. pagorum to be different from S. laevipila by the
presence of propagules (S. laevipila does not possess these asexual reproduction structures, sensu Steere, 1937; Catcheside, 1967; Zander, 1993) and by its sexuality (S. pagorum is dioecious, whereas S. laevipila is autoecious). Furthermore, the discovery of S. pagorum with sporophytes (Stone, 1971) provided further information.

Zander (1993) described the section Aesiotortula R.H. Zander, within the genus Syntrichia, whose type is Syntrichia pagorum (Milde) J.J. Amann, for small plants with leaf-shaped propagules, plane leaf margins and semicircular nerve cross section. This author did not include S. laevipila in the section Aesiotortula because he did not consider it as a propaguliferous species, including it instead in the typical section of the genus Syntrichia.

Crum & Anderson (1981) accepted reports of propagules in varieties of T. laevipila (var. propagulifera as they understand T. pagorum and var. wachteri). They noted intermediates forms within smooth and papillose apiculate varieties in both North America and Europe, so they did not follow Barkman’s concept.

In Europe a slightly different concept of S. laevipila is maintained and it is recognized as containing some propaguliferous varieties (Potier de la Varde, 1954; Demaret & Castagne, 1959; Barkman, 1963; Dixon, 1970; Smith, 1978; Ségrio, 1981; Nieuwkoop & Arts, 1995) as valid taxa. Lawton (1971) shared this European view and recognized a propagulose variety of S. laevipila, S. laevipila var. meridionalis, mentioning that it is distinguished from S. pagorum only by the presence of a nerve in the propagules.

For our study, we have analysed many samples of both S. pagorum and S. laevipila and their varieties, together with the corresponding type material. The conclusions reached are detailed below.

MATERIAL AND METHODS

All available types and numerous collections from throughout the world have been studied. Samples deposited in the following institutional and personal herbaria were revised: B, BCB, BCC, BM, BR, CANM, DUKE, E, GE, GZU, FH, FI, I, LISU, L, M, MA-Musci, MEL, MICH, MGC, MUB, O, PAD, PRE, RO, SALA-Bryo, TFC, UNLV, VAL, herbarium T.L. Blockeel, herbarium J.-P. Frahm, herbarium C.C. Townsend and herbarium B.O. van Zanten.

For the study of the morphological characters an Olympus-BH2 light microscope was used. The photomicrographs were obtained with an Olympus PM-10AK camera on this microscope.

RESULTS

SYNTRICHA LAEVIPILA AND ITS PROPAGULIFEROUS FORMS

After studying numerous samples of S. laevipila, the enormous variation in the morphology of the propagules and the great number of intermediate forms was apparent (Figs 1–10). Some authors (Limpricht, 1885–1889; Correns, 1899; Mönkemeyer, 1927; Lawton, 1971) defend the existence of two types of propagule, (i) without a nerve and with a short and papillose hyaline apical cell (typical of S. pagorum) (Fig. 1), or (ii) longer, with a nerve, and with a mucro-like (even hair-like), smooth, elongated, hyaline apical cell (typical of S. laevipila) (Fig. 6).

Barkman (1963) distinguished the varieties of S. laevipila on the basis of the presence or absence of propagules, their morphology and distribution, and by the presence or not of a differentiated leaf margin. For this author the typical variety had no propagules and no differentiated margins; var. meridionalis had no propagules either but did have differentiated margins; var. wachteri had no differentiated leaf margins but had propagules on the stem apex, with a pointed, smooth apical cell; var. saccardoana possessed the same type of propagule but had a differentiated leaf margin; var. propagulifera had propagules on the stem apex, with a different morphology (the apical cell was stunted and papillose), and no differentiated margin; var. notarissi had the same type of propagules but the leaves had differentiated margins; finally, var. gemifera was distinct because the propagules were on the leaf edges.

In the material studied we found propagules 150–600 μm in length, with or without a nerve (sometimes in the same plant), and smooth and papillose apical cells, 30–100 μm in length. For this reason, all the forms with propagules of S. laevipila could be simply different transitional stages of the normal development of the propagules (van Zanten & During, 1974). Furthermore, the evidence suggests that the propaguliferous forms of S. laevipila are a response to environmental stress as a result of atmospheric pollution (Ségrio, 1981), nitrification of the substrate or influ-

Figures 1–12. Syntrichia laevipila. Figs 1–10. Variation in the morphology of the propagules (Figs 1, 8 from Tan 95-1687-FH; Figs 2, 5 from Streimann 5246-FH; Fig. 3 from Correll 8997-FH; Figs 4, 6, 9 from Bicchi s.n.-FI; Fig. 7 from Correll 8704-FH; Fig. 10 from Stark NV-95-UNLV). Fig. 11. Leaf margin differentiated formed by 2–3 columns of thicker walls and less papillose cells. Fig. 12. Spores of two different sizes (Figs 11, 12 from TFC 738). Scale bars: Figs 1, 5, 11, 12 = 35 μm; Figs 2–4, 6–10 = 120 μm.

ence of climatic conditions. These forms, then, simply represent a stage in their survival strategy, in which the taxon reproduces asexually. Hence, *Barbula laevipila* var. *meridionalis*, *Tortula laevipila* var. *notarisii*, *Tortula laevipila* var. *wachteri* and *Tortula laevipila* var. *propagulifera* (= *Barbula pagorum*) swell the list of synonyms of *S. laevipila*.

*Tortula laevipila* var. *gemmifera* might also be added to the list of synonyms of *S. laevipila* because, according to Squivet de Carondelet (1962), it only differs from the typical variety in the distribution of its propagules (on the leaf edges in var. *gemmifera*; and on the stem apex or at the base of the upper leaves in var. *laevipila*). For our study we were unable to analyse the type material of the Squivet variety, *Tortula laevipila* var. *gemmifera*, despite requests to the herbaria where it might be.

*Tortula alpina* f. *propagulifera* Squivet is a name not validly published because Squivet de Carondelet (1962) did not provide a direct and specific reference to a previously and effectively published description or diagnosis, as this name was published after 1 January 1953 (articles 32.3 and 33.3, Greuter et al., 2000). However van der Wijk, Margadant & Florschütz (1969) accepted *Tortula alpina* f. *propagulifera* and considered *T. laevipila* var. *propagulifera* and *T. pagorum* as synonymous of this taxon.

*Barbula pilosa* Bruch ex Venturi is a name not validly published because Venturi (1890) cited it merely as synonymous of *B. laevipila* (Brid.) Garov. (article 34.1(c), Greuter et al., 2000).

**SYNTRICHIA LAEVIPILA VAR. MERIDIONALIS**

*Syntrichia laevipila* var. *meridionalis* has been subject to several taxonomic changes since Schimper described it in 1860. Most authors have considered it at variety level, probably because its differentiating characters seemed insufficient to merit species status. To date, it has been separated from the typical variety by the existence of a clearly differentiated leaf margin (Fig. 11) and because of the presence of propagules very similar to those of *S. pagorum* (Steere, 1940; Potier de la Varde, 1954; Demaret & Castagne, 1959; Lawton, 1971; Smith, 1978), or simply owing to the differentiated leaf margin (Barkman, 1963; Bilewsky, 1965), as indicated in the original description because Schimper (1860) made no mention of the presence of such propagules.

Dixon (1970) commented on the strong possibility of finding modified leaf margins in the highly variable *S. laevipila* var. *meridionalis* and noted the frequency with which samples with no propagules could be found, preferring to treat this taxon at variety level.

Barkman (1963) could not find the type material of this taxon (despite searching the herbaria of Paris, Kew, Edinburgh, Vienna and Toulouse) and so decided to select a lectotype with Schwägrichen's sample, *Tortula laevipila* var. *meridionalis*, from Ermenonville (France), deposited in L. However, this lectotype is inappropriate because material was not selected from the geographical areas and collectors mentioned in the original description of *T. laevipila* var. *meridionalis* ['In Europae partibus meridionalibus; in Italia (De Notaris), in Hispania meridionali ad Oleas sat copiose legi']. Instead, what Barkman (1963) really did was to establish a neotype. For our study, we looked for suitable material for designating a lectotype in BM, FH and H herbaria and found in Schimper's herbarium at BM a sample under *Tortula laevipila* var. *meridionalis* from Italy, Genova, the label for which seems to have been handwritten by De Notaris (the handwriting is the same as that appearing on another envelope on the same sheet and which is signed by him). In addition, this sample displays the morphological characteristics described for the taxon and that can be used as lectotype, instead of the sample designated by Barkman (1963). We have designed this sample from BM as lectotype (article 9.17(a), Greuter et al., 2000).

Both the material chosen as type by Barkman (1963) and that found in BM of *S. laevipila* var. *meridionalis* lack propagules and have leaves with differentiated margins, as with the typical variety. Furthermore, in the type material of *S. laevipila* var. *laevipila* we found plants with clearly differentiated margins, a character that (as we have seen) may vary enormously in this taxon. After studying the type material of *S. laevipila* var. *laevipila* and *S. laevipila* var. *meridionalis*, we conclude that they are the same taxon because no morphological, gametophytic or sporophytic differences were found to justify their belonging to two taxa.

**BARBULA PAGORUM**

Stone (1971) described in detail the sporophyte of *S. pagorum* and, in comparison with that of *S. laevipila*, pointed to several characteristics that have until now been accepted as differentiating both taxa. However, we have observed many samples showing mixed sporophytic characteristics. Below, we enumerate and discuss the differential sporophytic characteristics mentioned by Stone (1971) for *S. pagorum* and *S. laevipila*.

(1) The seta of *S. pagorum* (5–9 mm) is shorter than that of *S. laevipila* (8–15 mm). In the material studied we found samples with the typical characteristics of *S. laevipila* (autoecious, differentiated margin, no propagules, lingulate leaves) and setae of 4.5–15 mm.

(2) The capsule of *S. pagorum* (1.5–2.4 × 0.8 mm) is shorter and broader than that of *S. laevipila* (2.5–4 × 0.75 mm). However, this character varied.

enormously in the material studied, some capsules of *S. laevipila* measuring 1.8–4.7 × 0.3–0.85 mm (Figs 13, 14).

(3) The operculum of *S. pagorum* is two-thirds or more than the capsule length, whereas that of *S. laevipila* is less than two-thirds. However, again this character has been seen to vary, and *S. laevipila* opercula measuring two-thirds of capsule length have been observed (Figs 13, 14).

(4) The operculum of *S. pagorum* is formed of cells distributed in straight lines along a quarter of its length, which are then oblique, whereas in *S. laevipila* they are in spiral form from near to the base. In the material studied we have observed opercula in *S. laevipila* with cells orientated the same way as Stone (1971) ascribed to *S. pagorum*.

(5) The cells making up the capsule length of the *S. pagorum* peristome are in almost straight lines, as opposed to an obliquely spiralled disposition in *S. laevipila*. This character has no weight taxonomically because most sporophytes of *S. laevipila* show a peristome membrane made up of practically straight cells (Figs 15, 16).

(6) Both the exothecial and the opercular cells of *S. pagorum* have thickened walls, whereas those of *S. laevipila* are thin. Such a difference was not evident in the material studied because we found many sporo-

**Figures 13–16.** *Syntrichia laevipila*. Figs 13, 14. Sporophyte, operculum and capsule (Fig. 13 from TFC 10082; Fig. 14 from Størmer s.n.-OSLO). Figs 15, 16. Basal membrane of the peristome (Fig. 15 from TFC 738; Fig. 16 from TFC 10082). Scale bars: Figs 13, 14 = 1.3 cm; Figs 15, 16 = 35 μm.
phytes of *S. laevipila* with thickened exothelial cell walls (Figs 17–20, 24, 25).

(7) The ornamentation of peristome teeth in *S. pagorum* has papillose formations that are coarser and shorter than is found in *S. laevipila*. In the samples we studied, this character varies with the length of the peristome, the projections becoming thinner as the teeth are longer (Figs 21–23).

(8) The spores of *S. pagorum* (8–10 µm) are smaller than those of *S. laevipila* (10–18 µm). Again, this difference was not evident in the material studied because the spores of *S. laevipila* varied greatly in size: (10)12.5–17.5(25) µm in diameter (Fig. 12). Some capsules contain spores of two clearly different sizes (10–12.5 µm and 15–25 µm in diameter), although to understand the origin for this, a deeper study of the spore morphology and functionality in *S. laevipila* would be needed.

Moreover, Stone (1971) also emphasized the difference in sexuality of the two taxa, *S. pagorum* being dioecious and *S. laevipila* autoecious. However, in the Pottiaceae it is not unusual to find heteroeccious taxa, as in the case of *Aloina brevirostris* (Hook. & Grev.) Kindb., *Aloina catillum* (Mull. Hal.) Broth. or *Cossidium crassinerve* (De Not.) Jur. (Delgadillo, 1975). Furthermore, other authors such as Smith (1978) or Touw & Rubers (1989) considered *Tortula laevipila* as autoecious or dioecious species. The principal distinguishing characteristics at the morphological level between *S. laevipila* and *S. pagorum* are the presence or absence of propagules, plant size and sexuality. A wide range of variation in the morphological characteristics proposed as differential characters for these two taxa have been observed, as well as a multiplicity of combinations between them. This variability is also reflected in the sporophyte.

Based on our findings, we conclude that *S. pagorum* and *S. laevipila* are the same taxon and that the forms in which they frequently present themselves are merely the variation’s extremes of a wide morphological range. The varieties of *S. laevipila* therefore are different stages in the transition from *S. laevipila* to *S. pagorum*.

**TAXONOMIC CONCLUSIONS**


TYPE: ITALY, Tirol, Meran, Villa Maurer, Gratfch, 2.xi.1861, *Milde* [lectotype: H!, designated by Barkman (1963); isolectotype BM!, H!, M!, RO!].


Figures 17–20. *Syntrichia laevipila*. Figs 17, 19. Opercular cells. Fig. 18. Detail of Fig. 17. Fig. 20. Detail of Fig. 19 (Figs 17, 18 from TFC 738; Figs 19, 20 from TFC 10082). Scale bars: Figs 17, 19 = 120 µm, Figs 18, 20 = 35 µm.

Figures 21–25. Syntrichia laevipila. Figs 21–23. Ornamentation of peristome teeth (Fig. 21 from TFC 738; Fig. 22 from Herbarium Gray-FH; Fig. 23 from TFC 10082). Figs 24, 25. Exothecial cells (Fig. 24 from TFC 10082; Fig. 25 from TFC 738). Scale bars = 35 μm.
Tortula laevipila

PLANTS (0.15)0.4–1(2) cm high, growing in olive-green dense, sometimes open turfs. STEM erect, branched. LEAVES spirally twisted when dry, spreading or patent, sometimes weakly recurved when moist, 1.0–3.8 × 0.3–1.3 mm, lingulate to spathulate, constricted in mid leaf, sometimes weakly, unistratose, bordered or not, when is bordered, it is formed by 2–5 columns of thicker walls from base to 2/3 of the leaf, papillose-crenulate or plane or slightly recurved at middle of leaf, rarely with 4–6(8) bifurcate, not pedicellate papillae per cell, 2.5 µm high; juxtapostal basal cells quadratce or rectangular, 25–92.5 × 15–32.5 µm, hyaline or chlorophyllose, with thin walls, sometimes collechymatous, forming a clearly differentiated hyaline area up to 20–38% of leaf length, sometimes hardly distinguished; marginal basal cells chlorophyllose, in 4–9 columns, generally smooth. PROPAGULES multicellular, generally present, on the stem apex or in the base of upper leaves, often forming a rosette in the upper leaves, lanceolate, elliptical or ovate, with form of leaves, 150–400(600) × 35–280 µm, apical hyaline cell with or without papillae, 30–100 µm long, with or without nerve, green, papillose. Dioecious or autoecous. SETA erect, 0.45–1.5 cm long, spirally twisted to right above, to left below or to right above and below, reddish brown. CAPSULE erect, cylindrical, 1.8–4.7 × 0.3–0.8 mm, brownish. PERISTOME of 32 papillose, spirally twisted teeth, 0.4–1.3 mm long; basal membrane of 11–20 rows of cells, 0.2–0.6 mm high. OPERCULUM long conical, 1.0–2.1 mm long; SPORES spherical (10)12.5–17.5(25) µm in diameter, papillose.

Habitat: This is a corticolous, rarely saxicolous species, found from 30 to 4000 m, frequently in localities where the environment has been influenced by man (Anderson, 1943; Stone, 1971; Magill, 1981; Studlar, Caponetti & Sharp, 1984), probably only rupestral when conditions are exceedingly favourable for its growth (Anderson, 1943).

Distribution: Europe; Asia; Africa; North and Central America; south of South America; Australia; New Zealand.

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