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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 laevipilaeformis* 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*. © 2004 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2004, **145**, 219–230.

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. *laevipilaeformis*. 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

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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 because it is recognized as containing some propaguliferous varieties (Potier de la Varde, 1954; Demaret & Castagne, 1959; Barkman, 1963; Dixon, 1970; Smith, 1978; Sérgio, 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, H, L, LISU, LU, 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

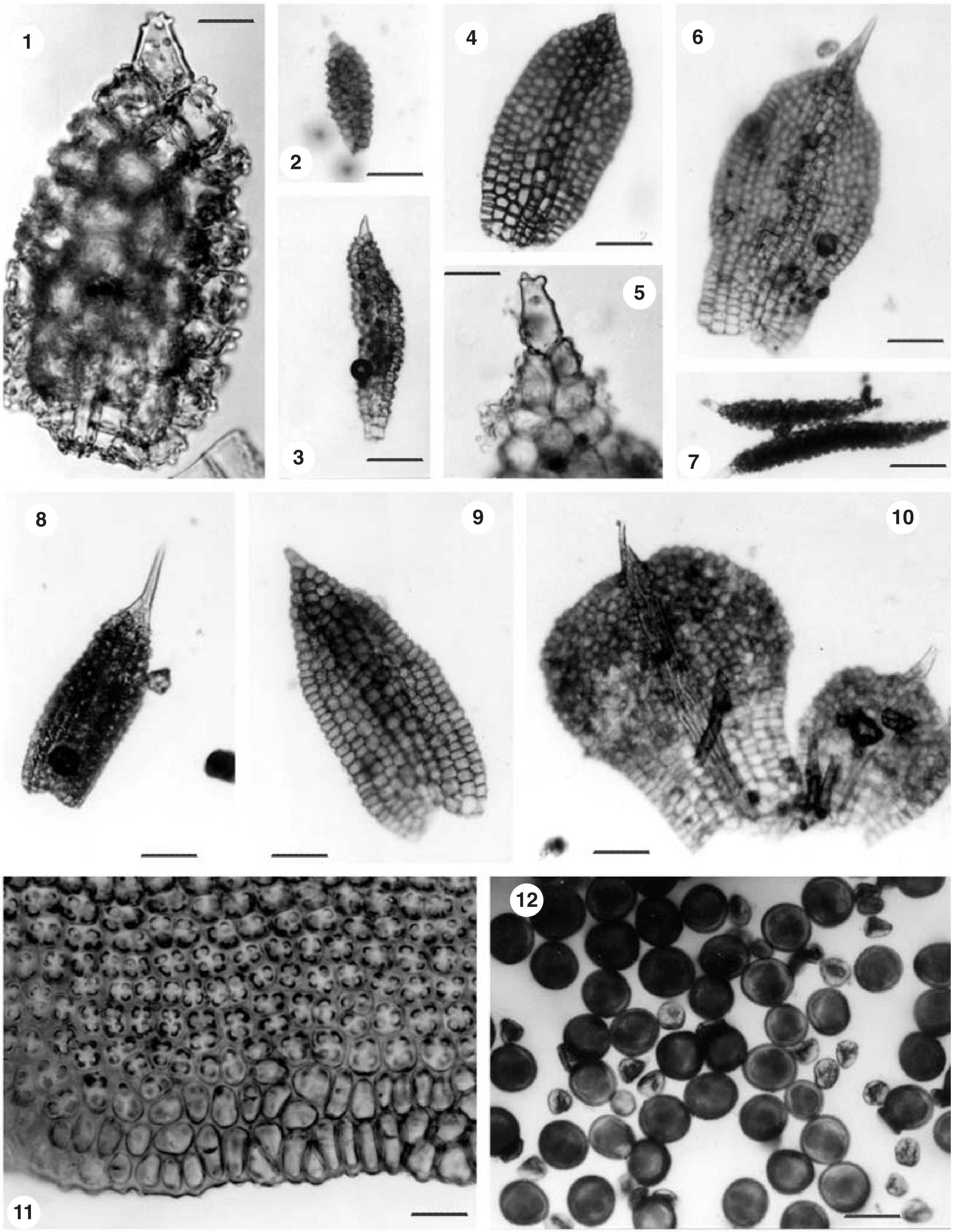
SYNTRICHIA LAEVIPILA AND ITS PROPAGULIFEROUS FORMS

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. *notarisii* had the same type of propagules but the leaves had differentiated margins; finally, var. *gemmifera* 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 (Sérgio, 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.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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, Gombo, 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* ($1.5–2.4 \times 0.8$ mm) is shorter and broader than that of *S. laevipila* ($2.5–4 \times 0.75$ mm). However, this character varied

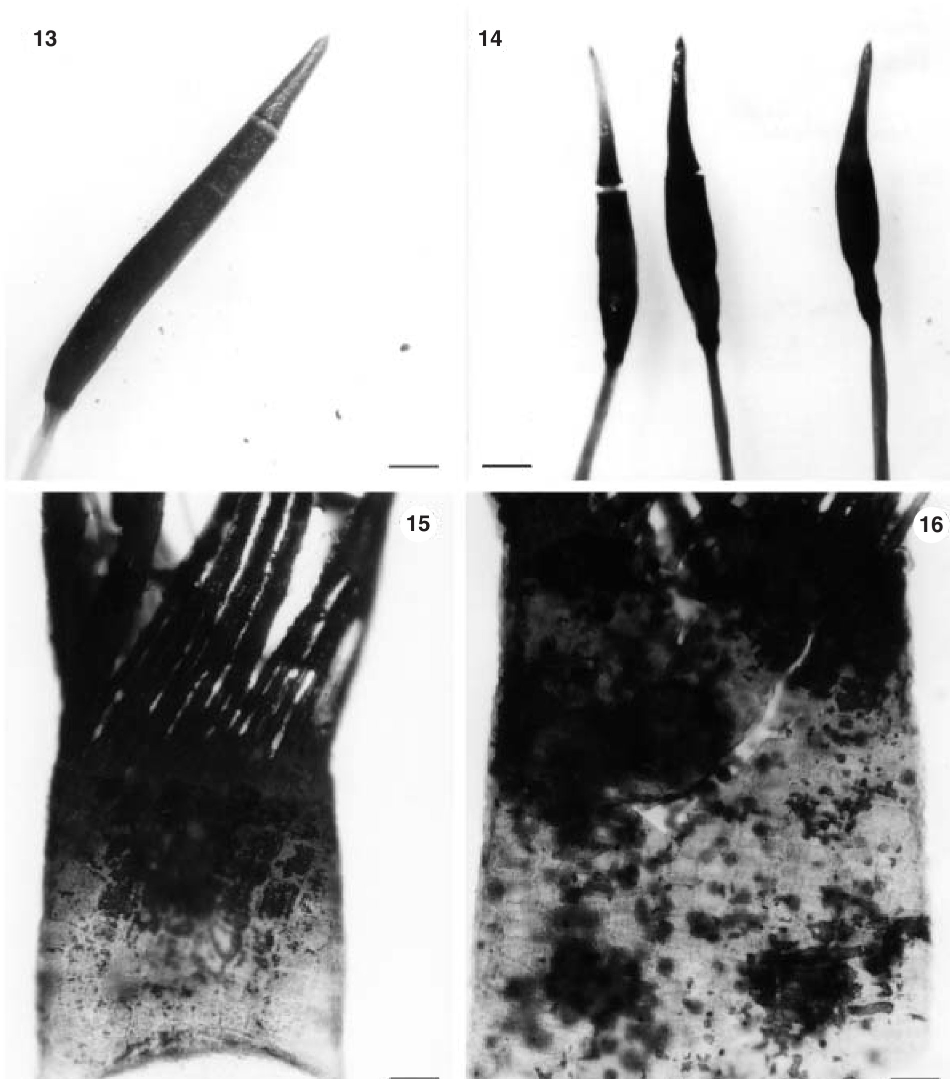
enormously in the material studied, some capsules of *S. laevipila* measuring 1.8–4.7 × 0.3–0.85 mm (Figs 13, 14).

(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 basal membrane 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 exothecial 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 heteroecious taxa, as in the case of *Aloina brevirostris* (Hook. & Grev.) Kindb., *Aloina catillum* (Müll. Hal.) Broth. or *Crossidium 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

Syntrichia laevipila Brid., Muscol. Recent. Suppl. 4: 98. 1818 [1819]. *Tortula laevipila* (Brid.) Schwägr., Sp. Musc. Frond., Suppl. 2: 66. 1823, *Tortula ruralis* var. *laevipila* (Brid.) Hook. & Grev., Edinburgh J. Sci. 1: 293. 1824, *Syntrichia ruralis* var. *laevipila* (Brid.) Spreng., Syst. Veg. 4: 177. 1827, *Barbula laevipila* (Brid.) Garov., Bryol. Austr. Excurs. 37. 1840. TYPE: ITALY, Around Rome & Naples, 1803 [lectotype: B!, designated here].

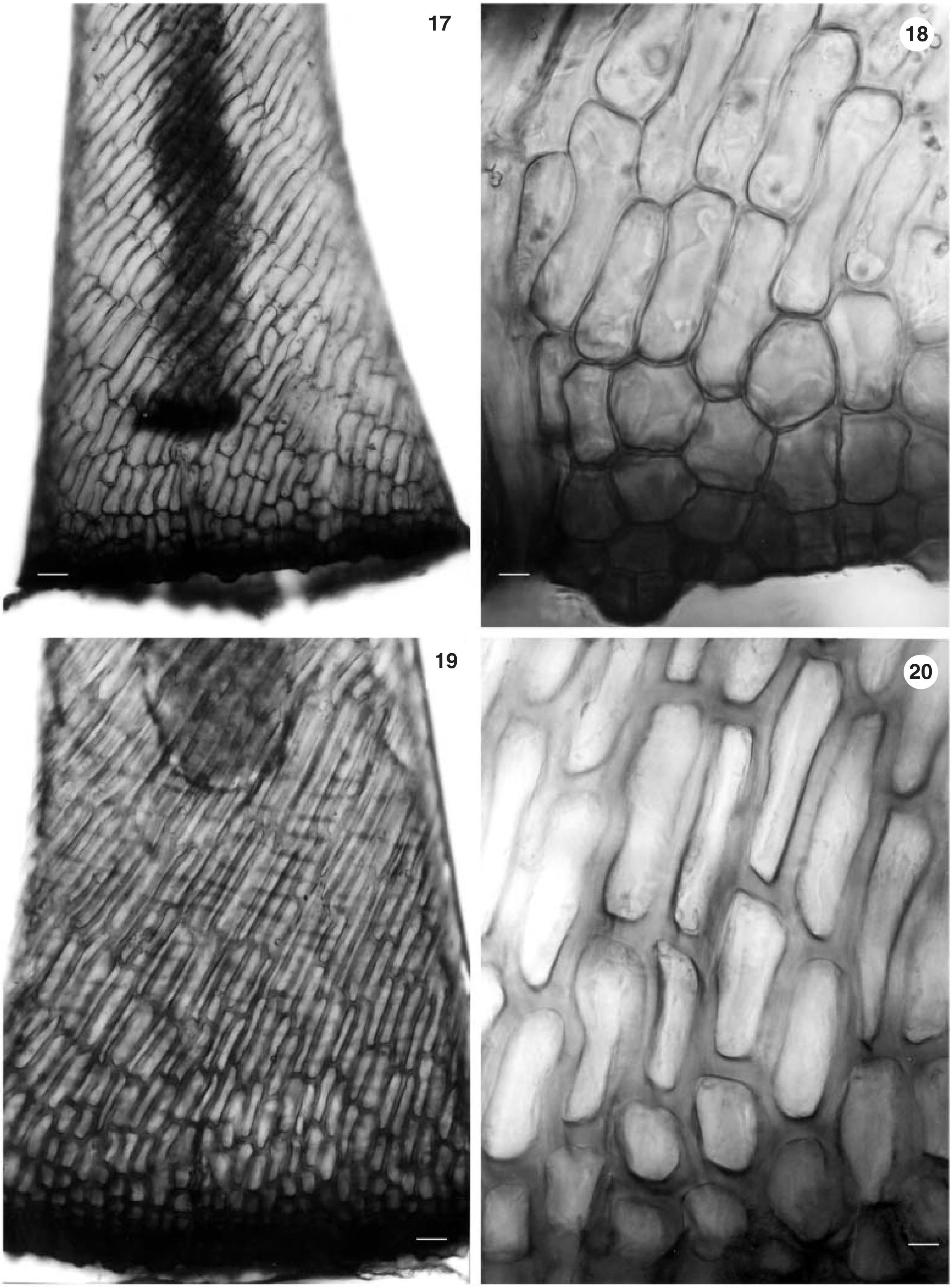
Barbula laevipila var. *meridionalis* Schimp., Syn. Musc. Eur. 699. 1860, *syn. nov*., *Syntrichia laevipila* var. *meridionalis* (Schimp.) Jur., Laubm.-Fl. Oesterr.-Ung. 141. 1882, *Tortula laevipila* var. *meridionalis* (Schimp.) Wijk & Margad., Taxon 8: 75. 1959. TYPE: ITALY, Gombo, *De Notaris* [lectotype: BM!, designated here].

Tortula laevipilaeformis De Not., Musci Ital. 1: 7. 1862, *Tortula laevipila* var. *marginata* Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 21: 245. 1864, *Syntrichia laevipilaeformis* (De Not.) Cardot, Bull. Soc. Roy. Bot. Belgique 22: 162. 1883, *Barbula laevipila* var. *laevipilaeformis* (De Not.) Husn., Muscol. Gall. 114. 1886, *nom. illeg.* [article 52.1, Greuter *et al*., 2000], *Tortula laevipila* var. *laevipilaeformis* (De Not.) Limpr., Laubm. Deutsch. 1: 680., 1888, *nom. illeg.* [article 52.1, Greuter *et al*., 2000], *Barbula laevipila* var. *marginata* (Lindb.) Baroni, Nuovo Giorn. Bot. Ital. 23: 313. 1891, *Syntrichia laevipila* var. *laevipilaeformis* (De Not.) J.J. Amann, Fl. Mouss. Suisse 2: 117. 1918, *nom. illeg.* [article 52.1, Greuter *et al*., 2000], *Tortula laevipila* ssp. *laevipilaeformis* (De Not.) Giacom., Atti Ist. Bot. University Pavia ser. 5, 4: 216. 1947. TYPE: ITALY, Sardinia, 1835, *De Notaris* [lectotype: RO!, designated here].

Barbula pagorum Milde, Bot. Zeitung (Berlin) 20: 459. 1862, *syn. nov.*, *Tortula laevipila* var. *propagulifera* Lindb., Oefvers. Förh. Finska Vetensk.-Soc. 21: 245. 1864, *Tortula pagorum* (Milde) De Not., Atti Reale University Genova 1: 542. 1869, *Syntrichia laevipila* var. *propagulifera* (Lindb.) Jur., Laubm.-Fl. Oesterr.-Ung. 141. 1882, *Barbula laevipila* var. *pagorum* (Milde) Husn., Muscol. Gall. 115. 1886, *nom. illeg.* [article 52.1, Greuter *et al*., 2000], *Barbula alpina* var. *pagorum* (Milde) Kindb., Eur. N. Amer. Bryin. 2: 247. 1898, *nom. illeg.* [article 52.1, Greuter *et al*., 2000], *Syntrichia pagorum* (Milde) J.J. Amann, Fl. Mouss. Suisse 2: 117. 1918, *Tortula alpina* var. *propagulifera* (Lindb.) E.B. Bartram, Bull. Torrey Bot. Club 51: 337. 1924, *Syntrichia laevipila* var. *pagorum* (Milde) Mönk., Laubm. Eur. 309. 1927, *nom. illeg.* [article 52.1, Greuter *et al*., 2000]. TYPE: ITALY, Tirol, Meran, Villa Maurer, Gratfch, 2.xi.1861, *Milde* [lectotype: H!, designated by Barkman (1963); isolectotypes BM!, H!, M!, RO!].

Tortula saccardoana De Not., Atti Reale Univ. Genova 1: 752. 1869, *Barbula saccardoana* (De Not.) Grav., Rev. Bryol. 10: 23. 1883, *Tortula laevipila* var.

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.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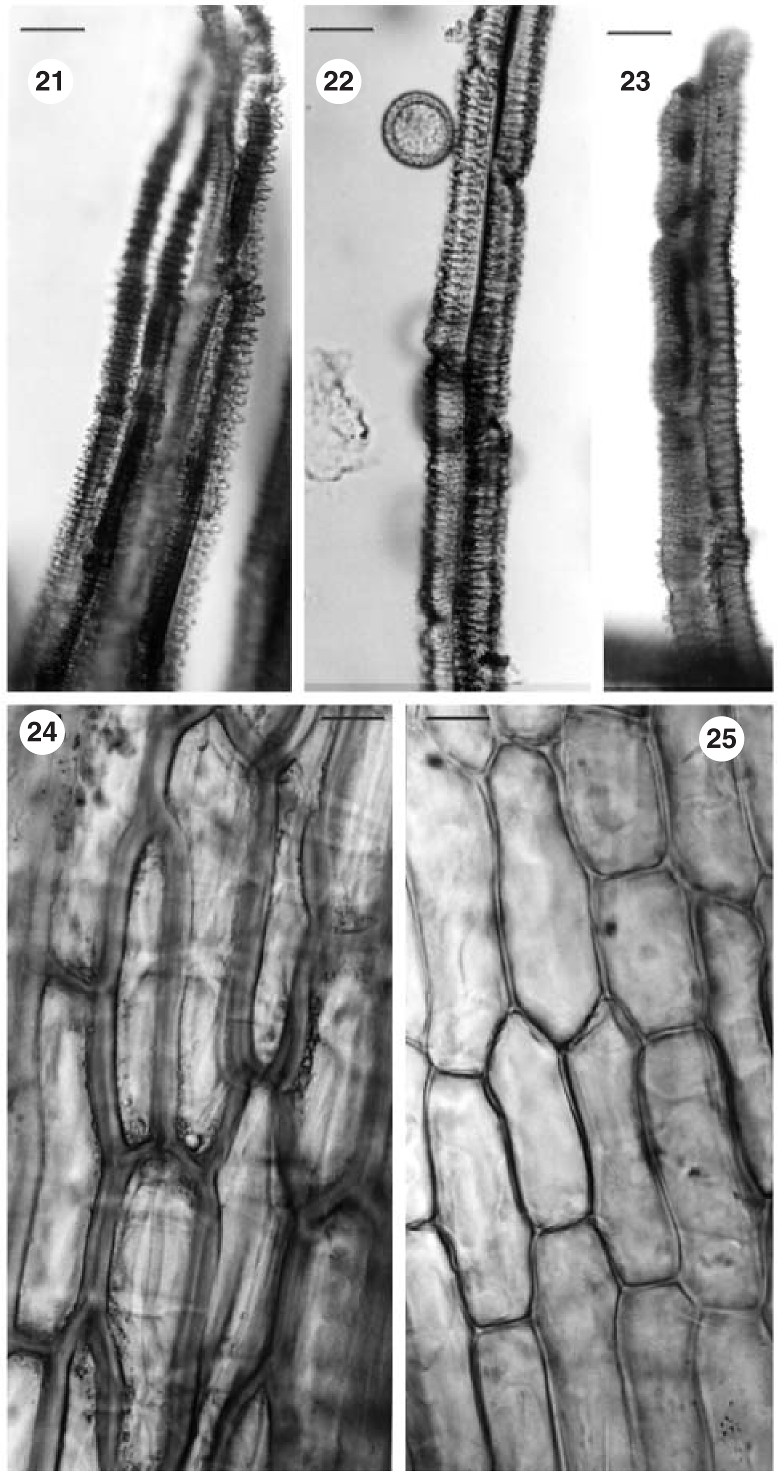

Figures 21–25. *Syntrichia laevipila.* Figs 21–23. Ornamentation of peristome teeth (Fig. 21 from TFC 738; Fig. 22 from Herbarium Gray-FH; Fig. 23 from TFC 10082). Figs 24, 25. Exothecial cells (Fig. 24 from TFC 10082; Fig. 25 from TFC 738). Scale bars = 35 μm.

saccardoana (De Not.) Barkman, Phytosociol. & Ecol. Cryptog. Epiph. 531. 1958. [lectotype: PAD!, designated by Barkman (1963)].

Tortula pilosa Venturi, Musc. Trentino: 37. 1899, *nom. illeg.* (article 53.1, Greuter *et al*., 2000).

Tortula propagulata Laz., Bot. urn. (Kiev) 3: 61. 1946. TYPE: USSR, Northern Tian-Shian Dala-Ashyk (Kazakhstania) Ak-Kija, 1940, *Lazarenko s.n.* [type: not located, not at LE, LWS?, KW?].

Tortula laevipila var. *notarisii* Barkman, Phytosociol. & Ecol. Cryptog. Epiph. 531. 1958, *syn. nov.* TYPE: Italy, Lucca 1858, *Bicchi 173* [lectotype: L!, designated by Barkman (1963); isolectotypes FI!, L!].

Tortula laevipila var. *wachteri* Barkman, Phytosociol. & Ecol. Cryptog. Epiph. 531. 1958, *syn. nov.* TYPE: HOLLAND, Zuid Holland, Goeree Island, Goederede, 15.iv.1952, *Barkman* [lectotype: L!, designated by Barkman (1963)].

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; apex rounded, obtuse, emarginate; margins plane or slightly recurved at middle of leaf, rarely from base to 2/3 of the leaf, papillose-crenulate or smooth, unistratose, bordered or not, when is bordered, it is formed by 2–5 columns of thicker walls and less papillose cells, sometimes smooth, brown or yellowish; hyaline hair point smooth, sometimes weakly spinulose and brown at base (0.2)0.4–0.9(1.6) mm; nerve 65–125 μm wide, in transverse section with 1–2 guide cell rows and 3–5(7) dorsal stereid rows, with hydroids; on the abaxial side without papillae; upper and middle laminal cells quadrate, rectangular or rounded, thin walls (10)12.5–15(25) × (7.5)10–15(17.5) μm, with 4–6(8) bifurcate, not pedicellate papillae per cell, 2.5 μm high; juxtacostal basal cells quadrate or rectangular, 25–92.5 × 15–32.5 μm, hyaline or chlorophyllose, with thin walls, sometimes collenchymatous, 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 autoecious. 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.

Selected specimens examined: ALGERIA: Argel, Boujareal, iii.1869, *Reuter* (GE). Tizi Ouzou, 28.x.1894, *Graef* (O). Mt. Tilimsen, *c*. 1050 m, 22.i.1950, *Jelenc* (O). Blida near Algiers, *Rojkowski 456* (CANM 267486). AUSTRALIA: WESTERN AUSTRALIA, Darling, Kings Park, Perth, 31°57′S, 115°51′E, *Stone 4880* (MEL 2103873A). NEW SOUTH WALES, Cowra, 33°50′S, 148°41′E, *Streimann 5246* (FH). CHINA: QINGHAI PROVINCE, Yushu Tibetan Autonomous Prefecture, Nangqian co., 31°55′05″N, 96°27′39″E, *Tan 95-1687* (FH). XINJIANG PROVINCE, Altai Prefecture, Qinghe co., 46°41′N, 90°23′W, *Tan 93-882* (FH). CROATIA: ISTRIA, Rovinj, Niederung gegen S. Felice an der Mündung des Lemekanales, 26.iii.1924, *Baumgartner* (MA-MUSCI s.n.). RAB, Cap Fronte, *Frahm 10075* (GZU). CYPRUS: Paphos Forest, a few km east of Pano Panayia, *Blockeel 26-189* (HERB. T.L. BLOCKEEL). DENMARK: Fünen, Dorf Lunde, vi.1906, *Hesselbe* (MA-MUSCI 4936). FRANCE: ALPES-MARITIMES, Nice, iv.1886, *Noday* (E). BOUCHES-DU-RHÔNE, Valdonne, à 3 km de Peynier en venant d'Aúberge, 3.vi.1984, *Ros & Jiménez* (MUB 1041). BRITTANY, dept. Morbihan, Carnac, *Long 23484* (E); CENTRE, Indre-et-Loire, Amboise, 47°24′50″N, 00°59′13″E, 70 m, 13.viii.2002, *Cano 945* (MUB 13597). CORSICA, Porto Vecchio, 20.v.1976, *Hübschmann* (HERB. J.-P. FRAHM). GARD, Pont du Gard, 10.vi.1965, *Størmer* (O). HAUTE-GARONNE, Toulouse (FH). HAUTS-DE-SEINE, Versailles, 22.iv.1913, *Bryhn* (O). HÉRAULT, Lodève, 11.vi.1965, *Størmer* (O); MANCHE, Cherbourg, 13.iii.1890, *Corbiere* (FH). MAINE-ET-LOIRE, St. Lambert SO for Chalonnes, 29.vi.1954, *Størmer* (O). MORBIHAN, Carnac SV for Auray, 25.vi.1954, *Størmer* (O). NORD, Dunkerque, Trones de Saline, 4.iv.1896 (E). NORMANDY, Sarthe, St. Remy du Val, SE of Alencon, *Long 23491* (E). PYRÉNÉES ORIENTALES, Consolation Heremitage près Collioure, 18.vi.1965, *Størmer* (O). VAL-D'OISE, Coteau de Chennevières, vi.1903, *S. et O.* (FH). VAR, Fayence, 43°40′N, 0°14′E, 14.iv.2001, *Gallego* (MUB 11392). VENDÉE, St. Hilaire-de-Talmont, ved Les Sables d'Olonne, 27.vi.1954, *Størmer* (O). GERMANY: RENANIA-PALATINADO, Trier, an Pyramidenpappeln der Bitburger, Landstrasse über Pallien, 20.iii.1917, *Freiberg* (MA-MUSCI 5569). Unweit Loppersum, MB Loppersum, Ostfriesland, 6.vii.1968, *Hübschmann* (GZU). GREECE: ATTIKI, 7.xi.1871 (GE). CRETA, Chanià, Katsimatádos, S. of Topólia, 16.iv.1967, *Gradstein & Smittenberg* (BR 276763-22); Psikhro, above the Lasithi Plain, 14.ii.1979, *Blockeel* (HERB. T.L. BLOCKEEL). DRAMA, 41°08′42″N, 24°08′20″E, 3.viii.1999, *Cano* (MUB 11396). DODECANESO, Ins. Rhodos, Mount Profitas Elias, *Townsend 70/162* (HERB. C.C. TOWNSEND). EPIRUS, Ioannina, Louros Gorge, south of Perdika, *Blockeel 19-167* (HERB. T.L. BLOCKEEL). FTHÍOTIS, Carretera de Lamía a Karpenissi, río Sperhios, 38°56′28″N, 22°13′15′E, 28.vii.1999, *Cano* (MUB 11395). CORINTIA, Óasis, 38°07′47″N, 22°20′43″E, 21.iii.1999, *Cano et al*. (MUB 11371). MAGNISÍA, Káto Gatzéa, 39°18′46″N, 23°05′40″E, 23.iii.1999, *Cano et al*. (MUB 11370). PELLA, Edessa, x.1980, *Blockeel* (HERB. T.L. BLOCKEEL). PELOPONESO, Arkadia, by the coast road south of Sapounakeika, NE of Leonidi, *Blockeel 24-186* (HERB. T.L. BLOCKEEL). SÁMOS, Ewoia, in the valley of the Alepotria River, near Pagóndas, *Blockeel 29-2695* (HERB. T.L. BLOCKEEL). ITALY: CAMPANIA, Pompeii, the ruins, 17.x.1975, *Størmer* (O). SARDINIA, Cagliari, Tal des Rio Giutturu Mannu, N-exponierte Quarzit-Wand 5 km W der Kreuzung Ciri Foddi, 18.vii.1985, *Nimis & Poelt* (GZU). LAZIO, Villa d'Este in Tivoli, 12.x.1975, *Størmer* (O). LIGURIA, Hanbury Garten in La Mortola bei Ventimiglia, 25.x.1992, *Poelt* (GZU). LOMBARDIA, Como, 10.xii.1897, *Artaria* (CANM 132699). PIAMONTE, Novara, Lago Maggiore, 10.ii.1914, *Corti* (FH). ROMA, Forum Romanum, 10.x.1975, *Størmer* (O). TOSCANA, Lucca, 1858, *Bicchi* (FI); Florencia, Colli, 21.6. 1918, *Leroy* (BR 181424). VALLE D'AOSTA, Meran, 1861, *Milde* (FI). JAPAN: HONSHU, Yamanashi-ken, Higashi-Yamato-Gun, Yamato-mura, en route between Hajikano and Sasado, 15.v.1978, *Osada & Osada* (HERB. J.-P. FRAHM). Ibidem (GZU). MOROCCO: A 4 km de Azrou a Marrackech, 22.iv.1984, *Ros* (MUB 12821). Ifrane, 22.iv.1984, *Ros* (MUB 12822). Atlas Medio, Refugio de Taffert, 33°39′N, 4°09′W, 1890 m, 15.vi.1998, *Cano et al*. (MUB 12799). Atlas Medio, carretera del Jbel Bou Iblane a Talzemt, 33°36′N, 4°11′W, 1800–1900 m, 17.vi.1998, *Cano et al*. (MUB 12800). MÉXICO: SAN LUIS POTOSÍ, Charcas, *Lundell 64* (FH). CHIHUAHUA, Texcoco, *Patrick 205* (FH). NETHERLANDS: FRIESLAND, N. of town Leeuwarden, near village Minnertsga, *Sollman 80-6* (GZU). NOORD-BRABANT, Krabbendijke, *Nannenga 82* (FH). NEW ZEALAND: NORTH ISLANDS, Wanganui, in city park, *Otto & Deneger 31-832* (GZU). POLAND: MASUREN, Eók lake District, in the village of Sajzy, 12 km N of Eók, *Bednarek-Ochyra & Ochyra 499/90* (GZU). PORTUGAL: ALGARVE, SE facing slope immediately above the village, Caldas de Monchique, *Townsend 89/168* (HERB. C.C. TOWNSEND). ALTO ALENTEJO, estrada de Mora para Montagril, a 9 km de Montagril, *Sim-Sim & Sérgio M41* (LISU 161378). BAIXO ALENTEJO, Sierra de Arrabida, 4.i.1999, *Cano* (MUB 11467). BEIRA LITORAL, Souse Degracias, 13.xii.1984, *Sérgio et al*. (BCB 19348). DOURO LITORAL, Covelo, Minas do Montalto, junto ao rio Sousa, *Sim-Sim & Sérgio M42* (LISU 161380). ESTREMADURA, Pero Pinheiro, Pedra Furada, 14.i.1977, *Correia* (BR 276764–23). MINHO, Esposende, Apulia, Fonte Boa, *Sim-Sim & Sérgio M73* (LISU 161394). RIBATEJO, Santarém, Abrantes, Jardim do Castelo, *Sérgio & Sim-Sim 3* (LISU 157847). TRÁS-OS-MONTES E ALTO DOURO, Vinhais, Quinta da Ria Sos, *Sim-Sim & Sérgio M88* (LISU 161396). SPAIN: ALBACETE. Cancarix, 17.iii.1996, *Guerra & Ros* (MUB 6045). ALICANTE, carretera Alcolecha-Penáguila, km 2 (Penáguila), iii.1994, *Cano* (MUB 5744). ALMERÍA, Tabernas, Sierra de Alhamilla, cercanías a El Puntal, 17.v.1991, *García-Zamora & Ros* (MUB 8170). BADAJOZ, Parque de la Legión, 18.xii.1982, *Muñoz & Viera* (LU 64). BARCELONA, Tibidabo, *Cuesta* (TFC 738). CÁCERES, entre el Puerto de la Berzocana y Navezuelas, 15.vi.1984, *Chamorro et al*. (MA-MUSCI 5154). CASTELLÓN, Peñagolosa, Barranco del Espino, 9.ii.1980, *Puche* (VAL 98). GERONA, La Bajol, 27.v.1974, *Brugués* (BCB 6075). GRANADA, Sierra de Lujar, 10.iii.1985, *Kuc* (CANM 312337). HUELVA, Coto de Doñana, alcornocal del Ajonjolí, 7.iv.1984, *Guerra* (MGC 684). ISLAS BALEARES, Mallorca, Ses Tres Creus, 39°45′N, 2°43′E, 14.iv.1999, *Cano et al*. (MUB 11490). LUGO, La Puebla de San Julián (MA-MUSCI 11163). MADRID, El Escorial, La Herrería, *Pinar et al*. (MA-MUSCI 9481). MÁLAGA, parque de Antequera, 25.iii.1978, *Guerra* (MGC 39). MURCIA, Alhama de Murcia, Sierra de Carrascoy, Rambla de Roy, 2.iv.1996, *Cano & Ros* (MUB 6041). LAS PALMAS, Lanzarote, Caldera del Corazoncillo, *Malme 725* (O); Fuerteventura, Mt. Muda, *Malme 1847* (O); Gran Canaria, Santa Brigida, 25.iv.1908, *Bryhn* (O). SANTA CRUZ DE TENERIFE, La Palma, Cumbre Nueva, above Brena Alta, Lomo Grande, 13.iv.1957, *Lid* (O); El Hierro, Trayecto Cruz de los Reyes, Montaña Mercader, 16.vii.1981, *Hernández-Padrón & Pérez de Paz* (TFC 9866); Tenerife, Sierra de Anaga, Monte de Las Mercedes, north to north-west facing slope, 30.i.1975, *Redfearn et al*. (HERB. J.-P. FRAHM). SALAMANCA, Valle de las Batuecas, 17.iii.1985, *Elías* (SALA 366).

SEVILLA, Cabecera del río Guadiamar, Finca La Sauceda, 26.i.2001, *Gallego et al*. (MUB 11472). VALENCIA, Benalí, 12.i.1998, *Segarra* (VAL 4284). ZAMORA, Arribes del Duero, proximidades a Cozcurrita, 41°26′N, 6°16′W, 15.iv.2001, *Cano* (MUB 11402). TUNISIA: Bei Ain Draham, nördlich des Ortes, 11.iv.1968, *Poelt* (GZU). TURKEY: ANTALYA, 3 km north-east of Yavi, *c*. 30 km east of Kas, *Nyholm & Crundwell 1412* (e). ISTANBUL, in the grounds of the Seraglio, 24.v.1963, *Townsend* (HERB. C.C. TOWNSEND). UNITED KINGDOM: ENGLAND, Dalston, 18.iv.1919, *Murray* (FH); S Devon, Kingsbridge, Stapton, an Bäumen am Nordrand von Stapton Ley, wenig über Meereshöhe, *Poelt 11769* (GZU). SCOTLAND. *Collins 3996* (FH). USA: ARIZONA, Catalina Foot Hills, Pinal, *Bartram 11693* (FH). GEORGIA, Augusta, 1.vii.1895, *Small* (FH). INDIANA, Hanover, Jefferson County, Presbyterian Church lawn, *Welch 7361* (FH). KANSAS, Barber County, 38 km SW of Medicine Lodge, 37°10′N, 98°56′W, Red Hills, *Churchill 9434* (FH). NEVADA, Clark County, Lake Mead National Recreation Area, Newberry Mountains, Grapevine canyon, 2 mi N on Christmas Tree Pass Road from hwy 77E, beyond petroglyphs to the E, *Stark NV-38A* (UNLV); Clark County, Lake Mead National Recreation Area, Newberry Mountains, 'Needles Eye', *c*. 4.5 mi N on Christmas Tree Pass Road from Hwy 77e, *Stark NV-78A* (UNLV). OHIO, Pickaway, 11.iii.1938, *Bartley* (FH). NORTH CAROLINA, Durham, Woman's Campus, Duke University, *Blomquist 8731* (FH); SOUTH CAROLINA, Darlington, in Society Hill, *Correll & Correll 8705* (FH). SOUTH DAKOTA, Custer, Black Hills, Sylvan Lake, SW of Custer, Sec. 30, T2S, R5E, *Churchill 8613* (FH). TENNESSEE, Knoxville, Knox County, *Sharp 34176* (FH); Knoxville, iii.1934, *Sharp* (FH). TEXAS, Sulphur Spring, Hopkins County, *Sharp 423* (FH). WASHINGTON. Westport, 12.i.1908, *Foster* (FH).

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REFERENCES

Amann JJ, Culman P, Meylan C. 1912. [1918]. *Flore des Mousses de la Suisse 2*. Lausanne: Publication de L'Herbier Boissier.

Anderson LE. 1943. The distribution of *Tortula pagorum* (Milde) De Not. in North America. *Bryologist* **46:** 47–66.

Barkman JJ. 1963. A contribution to the taxonomy of the *Tortula laevipila–T. pagorum* complex. *Revue Bryologique et Lichénologique* **32:** 183–192.

Bilewsky F. 1965. Moss-Flora of Israel. *Nova Hedwigia* **9:** 335–434.

Catcheside DG. 1967. *Tortula pagorum* in Australia. *Muelleria* **1:** 227–230.

Correns C. 1899. *Untersuchungen über die Vermehrung der Laubmoose*. Jena: Gustav Fischer.

Crum HA, Anderson LE. 1981. *Mosses of eastern North America*. New York: Columbia University Press.

De Notaris G. 1869. Epilogo della briologia italiana. *Atti della R. Università Genova* **1:** 1–781.

Delgadillo C. 1975. Taxonomic revision of *Aloina, Aloinella* and *Crossidium* (Musci). *Bryologist* **78:** 245–303.

Demaret F, Castagne E. 1959. *Flore Générale de Belgique. Bryophytes*, Vol. II. Fasc. I. Bruxelles: Ministère de l'Agriculture, Jardin Botanique de L'État.

Dixon HN. 1970. *The student's handbook of British mosses*, 3rd edn. Eastbourne: V. Sumfield.

Greuter W, McNeill J, Barrie FR, Burdet HM, Demoulin V, Filgueiras TS, Nicolson DH, Silvia PC, Skog JE, Trehane P, Turland NJ, Hawksworth DL. 2000. International Code of Botanical Nomenclature (Saint Louis Code). *Regnum Vegetabile* **138**.

Husnot T. 1886. *Muscologia gallica*, Part. I. Paris: Cahan.

Kindberg. 1898. *European and N. American Bryineae*, Part II. Sweden.

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

Lawton E. 1971. *Moss flora of the Pacific Northwest*. Nichinan: The Hattori Botanical Laboratory.

Limpricht KG. 1885–1889. *Die Laubmoose Deutschlands, Österreichs und der Schweiz. Abth 1: Sphagnaceae, Andreaceae, Archidiaceae, Bryineae.* Leipzig: Eduard Kummer.

Lindberg SO. 1864. Om de Europeiske Trichostomeae – Öfversigt af förhandlingar: Kongl. *Svenska Vetenskaps-Akademien.* **21:** 213–254.

Magill RE. 1981. *Flora of Southern Africa*, Part. I, Fascicle I. Pretoria: Department of Agriculture and Fisheries.

Mönkemeyer W. 1927. *Die Laubmoose Europas. Andreales-Bryales*. Leipzig: Akademische Verlagsgesellschaft.

Nieuwkoop J, Arts T. 1995. Additions to the bryophyte flora of Madeira. *Lindbergia* **20:** 35–39.

Potier de la Varde R. 1954. Sur la présence de *Tortula laevipilaeformis* De Not. dans la Manche. *Mémoires de la Société des Sciences Naturelles et Mathématiques de Cherbourg* **46:** 75–80.

Schimper WP. 1860. *Synopsis Muscorum Europaeorum*. Stuttgart: Schweizerbart.

Sérgio C. 1981. Alterações da Flora Briológica epifítica na área urbana de Lisboa, nos últimos 140 anos. *Boletim da Sociedade Broteriana* **54:** 313–331.

Smith AJE. 1978. *The moss flora of Britain and Ireland*. Cambridge: Cambridge University Press.

Squivet de Carondelet J. 1962. *Tortula laevipila* forma *propagulifera* ratio nova et *Tortula gemmifera* var. nova (adhuc innominata). *Revue Bryologique et Lichénologique* **30:** 213–215.

Steere WC. 1937. Tortula. In: Grout AJ, ed. *Moss flora of North America*, Vol. 1. Newfrane: Privately published, 228–246.

Steere WC. 1940. *Tortula* in North America north of Mexico. *Bryologist* **43:** 12–109.

Stone IG. 1971. The sporophyte of *Tortula pagorum* (Milde) De Not. *Transactions of the British Bryological Society* **6:** 270–277.

Studlar SM, Caponetti JD, Sharp AJ. 1984. Morphology of the urban moss, *Tortula pagorum* in sterile culture. *Journal of the Hattori Botanical Laboratory* **56:** 351–368.

Touw A, Rubers WV. 1989. *De Nederlandse bladmossen: flora en verspreidingsatlas van de Nederlandse Musci (sphagnum uitgezonderd)*. Utrecht: Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging.

Venturi G. 1890. Barbulae rurales. *Revue Bryologique* **17:** 49–53.

van der Wijk R, Margadant WD, Florschütz PA. 1969. Index Muscorum V. *Regnum Vegetabile* **65**.

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

van Zanten BO, During HJ. 1974. Contribution to the moss-flora of the départements Pyrénées-Orientales and Aide. *Revue Bryologique et Lichénologique* **40:** 203–217.