

## New Taxonomic Data on a Circum-Tethyan Group of *Syntrichia* (Pottiaceae, Bryophyta): the *S. caninervis* Complex

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**ABSTRACT.** New taxonomic data are presented from a revision of the *Syntrichia caninervis* complex. Seven taxa have been recognized, based on morphological characters of about 180 samples. An identification key is presented. Lectotypes for *Syntrichia handelii* and *Tortula bornmuelleri* are proposed. *Syntrichia pseudodesertorum* is included as a synonym of *S. caninervis* var. *caninervis*. *Syntrichia pseudohandelii* is reduced to the rank of variety as *S. caninervis* var. *pseudodesertorum*. Two taxa are cited for first time for N. Africa, *S. rigescens* and *S. caninervis* var. *gypsophila*, and one for Morocco, *S. caninervis* var. *caninervis*.

The *Syntrichia caninervis* Mitt. complex comprises a group of taxa that share numerous morphological characteristics, the most obvious of which (and therefore not the least discussed) is the bistratose leaf lamina between the margins from midleaf to apex. Many authors emphasize the importance of this character, which they use as diagnostic in order to differentiate taxa (Magill et al. 1983; Werner and Hébrard 1986; El-Oqlah et al. 1988; Martínez-Sánchez et al. 1991; Boudier 1992; Hébrard and Pierrot 1994; Hébrard 1995). However, others such as Kramer (1978) maintain that a bistratose lamina is not a good taxonomic character because it is probably an adaptation to arid climates. For an investigation into this problem and related research on *Syntrichia* Brid., we have studied a large number of taxa and samples collected in arid and semiarid areas, and in so doing confirmed that the stratification of the lamina is a stable character within the *Syntrichia caninervis* group.

This complex, which is known from S. Europe, N. Africa, N. America, and Asia, comprises seven taxa: *Syntrichia caninervis* Mitt. var. *caninervis*, *S. caninervis* var. *gypsophila* (J.J. Amann ex G. Roth) Ochyra, *S. caninervis* var. *abranchesii* (Luisier) R. H. Zander, *S. handelii* (Schiffner) S. Agnew & Vondr. var. *handelii*, *S. handelii* var. *ferganensis* (Laz.) Ochyra, *S. pseudohandelii* (J. Froehl.) S. Agnew & Vondr., and *S. rigescens* (Broth. & Geh.) Ochyra (taxonomic status *sensu* Zander 1993). All these taxa share the following combination of characters: leaves ovate, ovate-lingulate or lanceolate, patent or spreading when moist (except *S. pseudohandelii* and *S. handelii*, in which they are sometimes recurved), not constricted in midleaf (except *S. handelii* and *S. rigescens*, which sometimes shows such constriction), costa in transverse section showing 1–3(4) rows of stereids, with hydroids, usually with pseudostereids, hyaline hair-point strongly spinose (except *S. caninervis* var. *abranchesii*, which has no hair-point and *S. rigescens* which has a spinulose hair-point), and a bistratose lamina.

A further species with a bistratose lamina occurs in N. America, Mexico, and S. Africa: *Syntrichia chisosa* (Magill, Delgad. & L.R. Stark) R.H. Zander. However, the shape of the leaves and the anatomy of the costa exclude it from the group of species being described. Furthermore, the presence of leaf-shaped gemmae brings it close to the *Tortula pagorum* (Milde) De Not.-*T. laevipila* (Brid.) Schwägr. complex (Magill et al. 1983) or section *Aesiotortula* (Zander 1993).

All taxa of this complex are dioicous. The perichaetia are terminal and the perigonia lateral. Perichaetial leaves are undifferentiated and somewhat narrower than the vegetative leaves. Perigonial leaves are smaller than vegetative leaves and usually without or with shorter hair-point.

### MATERIAL AND METHODS

All available types and numerous collections from Mediterranean countries, North America and Asia have been studied. Samples deposited in the following institutional and personal herbaria were examined: B, BCB, BCC, BM, BR, E, EGR, H, HBG, JE, LE, LISU, LU, M, MA-Musci, MGC, MUB, NY, OXF, SALA, TR, U, UNLV, VAB, W, ZT, herbarium T.L. Blockeel (Sheffield), herbarium J.-P. Frahm (Bonn), herbarium C.C. Townsend (Twickenham, London), herbarium B.O. van Zanten (Noordlaren).

Leaf surface was studied using a Jeol JSM-6100 SEM. The material was fixed in 3% glutaraldehyde with 0.1M cacodylate buffer at 4°C, washed in cacodylate and saccharose buffer, dehydrated in an increasing acetone gradient (30%-50%-70%-90% and 100%), critical-point dried and sputtered with a gold layer 200–300 Å thick.

The nomenclature used for the taxa recognized in the present paper will be used from this point onwards.

## KEY TO TAXA

1. Leaves with gemmae on the adaxial side of the costa . . . . . 1. *S. rigescens*
1. Leaves without gemmae on the adaxial side of the costa . . . . . 2
2. Leaves unistratose at midleaf . . . . . 3
3. Leaves without hair-point. Abaxial side of the costa in the upper third of the leaf with bifurcate or branched papillae, 5–12.5  $\mu\text{m}$  tall, in the lower part smooth . . . . . 3. *S. caninervis* var. *abranchesii*
3. Leaves with hair-point. Abaxial side of the costa in the upper third of the leaf with branched papillae, 12.5–37.5  $\mu\text{m}$  tall, in the lower part smooth or with bifurcate papillae, 2.5–5  $\mu\text{m}$  tall . . . . . 4. *S. caninervis* var. *gypsophila*
2. Leaves regularly or irregularly bistratose at midleaf . . . . . 4
4. Abaxial side of the costa strongly papillose, with simple, bi to trifurcate or pedicellate and branched papillae. Leaves not constricted at the middle, margins recurved to near the apex . . . . . 5
5. Plants 0.4–1.1 cm high. Costa 75–115  $\mu\text{m}$  wide at midleaf, with simple bifurcate or pedicellate and branched papillae, 2.5–30  $\mu\text{m}$  tall, along the whole of the abaxial side . . . . . 2. *S. caninervis* var. *caninervis*
5. Plants 2.5–7 cm high. Costa 120–135  $\mu\text{m}$  wide at midleaf, with pedicellate and branched papillae, (15)17.5–25  $\mu\text{m}$  tall, along the whole of the abaxial side . . . . . 5. *S. caninervis* var. *pseudodesertorum*
4. Abaxial side of the costa weakly papillose, with simple, verrucose papillae. Leaves sometimes constricted at the middle, margins recurved to 2/3 of the leaf . . . . . 6
6. Leaves with hair-point. Costa mostly without substereids . . . . . 6. *S. handelii* var. *handelii*
6. Leaves without hair-point. Costa mostly with substereids . . . . . 7. *S. handelii* var. *ferganensis*

1. SYNTRICHIA RIGESCENS (Broth. & Geh.) Ochyra, *Frags. Florist. Geobot.* 37: 212. 1992. (Figs. 1–6). *Tortula rigescens* Broth. & Geh., *Allg. Bot. Z. Syst.* 9: 188. 1903.—TYPE: EGYPT. Sinai Peninsula, Dschebel Kathrin, 5.4.1902, *Kneucker s.n.* (lectotype: H, designated by Kramer (1980); isolectotypes: JE!, M!).

Plants 1–2 cm high, growing in olive-green dense turfs. Stems erect, weakly branched. Leaves lightly spirally twisted when dry, mostly patent, spreading or recurved when moist, ovate-lingulate, lingulate, sometimes constricted in midleaf, 1.6–2.8  $\times$  0.5–0.9 mm, bistratose irregularly in the upper third and at midleaf; apex rounded, obtuse, sometimes emarginate; margins recurved to 2/3 of the leaf, papillose-crenulate, unistratose, without a differentiated border; hair-point hyaline, sometimes brownish at base, spinulose, 1.2–2.6 mm long; costa 100–137.5  $\mu\text{m}$  wide at middle, in transverse section with 2–3 rows of guide cells and 3–5 rows of dorsal stereids, sometimes with substereids, with hydroids, on the abaxial side with pedicellate, bifurcate, stellately branched papillae, 10–17.5(35)  $\mu\text{m}$  tall; upper and middle laminal cells quadrate, rectangular, thin-walled, 7.5–10(12.5)  $\times$  7.5–10(12.5)  $\mu\text{m}$ , with 6–10 bifurcate, non-pedicellate papillae per cell, 2.5  $\mu\text{m}$  tall; juxtacostal basal cells rectangular, 30–125  $\times$  10–25  $\mu\text{m}$ , hyaline, thin-walled, forming a differentiated hyaline area to 26–33% of leaf length; marginal basal cells chlorophyllose, in 10–24 columns, generally smooth. Gemmae multicellular, elliptical, brownish and smooth, 25–45  $\times$  27.5–37.5  $\mu\text{m}$ , on the adaxial side of the costa in the upper third of the leaf. Dioicous. Sporophyte unknown.

**Habitat.** On granite and calcareous rocks; also on *Juniperus oxycedrus* L. stumps; 1200–1900 m.

**Distribution.** Europe, S.W. Asia, N. Africa. Cited for the first time in N. Africa (Morocco).

**Selected Specimens Examined:** JORDAN. Karak, Taf-

ilah, Dhana, Umm el-Sarab, 23 Apr 1987, *El-Oqlah s.n.* (ex Nr. 771 Yarmouk Univ. Herb. in MUB 3082).

MOROCCO. Jbel Touchka, 8 km al N. de las Cascadas Imaouzzar-Ida-Outanen, 30°43' N, 9°26' W, 12 Mar 2001, *Cano & Muñoz s.n.* (MUB 11378).

This species is characterized by its leaves with margins recurved to 2/3, sometimes constricted, the lamina partially bistratose, the hair-point spinulose and hyaline, the abaxial side of the costa strongly papillose throughout, and the presence of multicellular elliptical brown gemmae situated on the adaxial side of the costa in the upper third of the leaves.

According to Kramer (1980) this species is close to *S. caninervis* var. *pseudodesertorum* and *S. handelii*, although it can be distinguished from the first by the constriction, stratification and recurved leaf margin and from the second by the papillosity of the abaxial surface of the costa.

2. SYNTRICHIA CANINERVIS Mitt. var. CANINERVIS, J. Proc. Linn. Soc. Bot. Suppl. 1: 39. 1859. (Figs. 8–11) *Barbula caninervis* (Mitt.) A. Jaeger, *Ber. Thätigk. St. Gallischen Naturwiss. Ges.* 1871–72: 453. 1873. *Tortula caninervis* (Mitt.) Broth., *Nat. Pfl.* 1(3): 435. 1902.—TYPE: PAQUISTAN. Tibet, Rondu, Thomson 174 (lectotype: BM!, designated by Kramer (1980); isolectotype: NY!).

*Tortula desertorum* Broth., *Bot. Centralbl.* 34: 24. 1888. *Barbula desertorum* (Broth.) Paris, *Ind. Bryol.* 71. 1894. *Syntrichia desertorum* (Broth.) J.J. Amann, *Fl. Mouss. Suisse* 3: 39. 1933; synonymized by Kramer (1978).

*Tortula desertorum* Podp., *Sborn. Klub. Prirod. Brno* 5: 123. 1923, *hom. illeg.*, (article 53.1 [Greuter et al. 2000]).

*Tortula bornmuelleri* Schiffner, *Oesterr. Bot. Zeitschr.* 47: 128. 1897. *Barbula bornmuelleri* (Schiffner) Paris, *Ind. Bryol. Suppl.* 21. 1900.—TYPE: IRAN. Persia

borealis. Teheran, 8 Feb 1892, *Bornmüller 4456* (lectotype: BM!, designated here).

*Tortula saharæ* Trab., Bull. Soc. Hist. Nat. Afr. Nord 18: 12–13. 1927; synonymized by Kramer (1978).

*Tortula bistratosa* Flowers, Bryologist 54: 278. 1–10. 1951.—TYPE: USA. Utah, Salt Lake County, about 12 miles west of Salt Lake City, 1 Apr 1950, *Flowers 7412* (isotype: FH!).

*Tortula pseudodesertorum* J. Froehl., Ann. Naturhist. Mus. Wien 67: 155. 1964. *Syntrichia pseudodesertorum* (J. Froehl.) S. Agnew & Vondr., Feddes Rept. 86: 402. 1975.—TYPE: AFGANISTAN. Prov. Mazar-i Sharif, Balkh, Aq Kupruk, 36°05' N, 66°52' E, 7–8 Jun 1962, *Rechinger 19675* (holotype: W!, isotype: W!).

Plants 0.4–1.1 cm high, growing in olive-green, whitish dense turfs. Stems erect, branched. Leaves lightly spirally twisted or appressed when dry, mostly patent or spreading, rarely recurved when moist, ovate, ovate-lingulate, not constricted in midleaf, 1.5–2.6 × 0.6–1.2 mm, bistratose regularly in the upper third and at midleaf; apex rounded, acuminate, cucullate, sometimes hyaline and tapering to the base of the hair-point; margins recurved from base to near the apex, papillose-crenulate, unistratose, without a differentiated border; hair-point hyaline, sometimes brownish at base, strongly spinose, 0.6–2.3 mm long; costa 75–115 µm wide at the middle, in transverse section with (1)2–3 rows of guide cells and (1)2–4(5) rows of dorsal stereids, sometimes with substereids, with hydroids, on the abaxial side with simple, bifurcate or pedicellate and branched papillae, 2.5–30 µm tall; upper and middle laminal cells quadrate, rectangular or rounded, thick-walled, 7.5–10 × 7.5–10 µm, with 4–6 bifurcate, non-pedicellate papillae per cell, 2.5 µm tall; juxtacostal basal cells rectangular, 50–75 × 10–17.5 µm, hyaline, thin-walled, sometimes collenchymatous, forming a differentiated hyaline area to 28–38% of leaf length; marginal basal cells chlorophyllose, in 10–14 columns, generally smooth. Dioicous. Seta erect, 0.6–1.4 cm long, spirally twisted to right above, to left below, reddish brown. Capsule erect, ovoid-cylindrical, 2.5–2.6 × 0.6–0.7 mm, reddish brown. Peristome of 32 papillose, spirally twisted teeth, 0.7–0.8 mm long; basal membrane of 10–12 rows of cells, 0.3–0.4 mm high. Operculum long conical, 1.5 mm long. Spores spherical, 7.5 µm in diameter, papillose.

**Habitat.** Usually on gypsum-rich soils; also on bare basic soils and rocks but rarely on acid strata, not collected as an epiphyte; 650–1300 m.

**Distribution.** Europe, N. Africa, Asia, N. America.

**Selected Specimens Examined:** AFGHANISTAN. Prov. Ghorat, infra Parjuman (Partcheman), 33°10' N, 63°52' E, 30 Jul 1962, *Rechinger 19792* (GZU).

CHINA. Xinjiang Prov., Bo-le Co., Salimu Lake, 44°33' N, 81°21' E, 4 Aug 1993, *Tan 93-944* (FH).

JORDAN. Dana Reserve, 24 Mar 2000, *Hooper* (Herb. C.C. Townsend).

LEBANON. Below columns of the Temple of Jupiter and facing the Temple of Bacchus, Baalbek, 24 Apr 1967, *Townsend* (Herb. C.C. Townsend). Hillside above Baalbek, 5 May 1974, *Townsend* (Herb. C.C. Townsend).

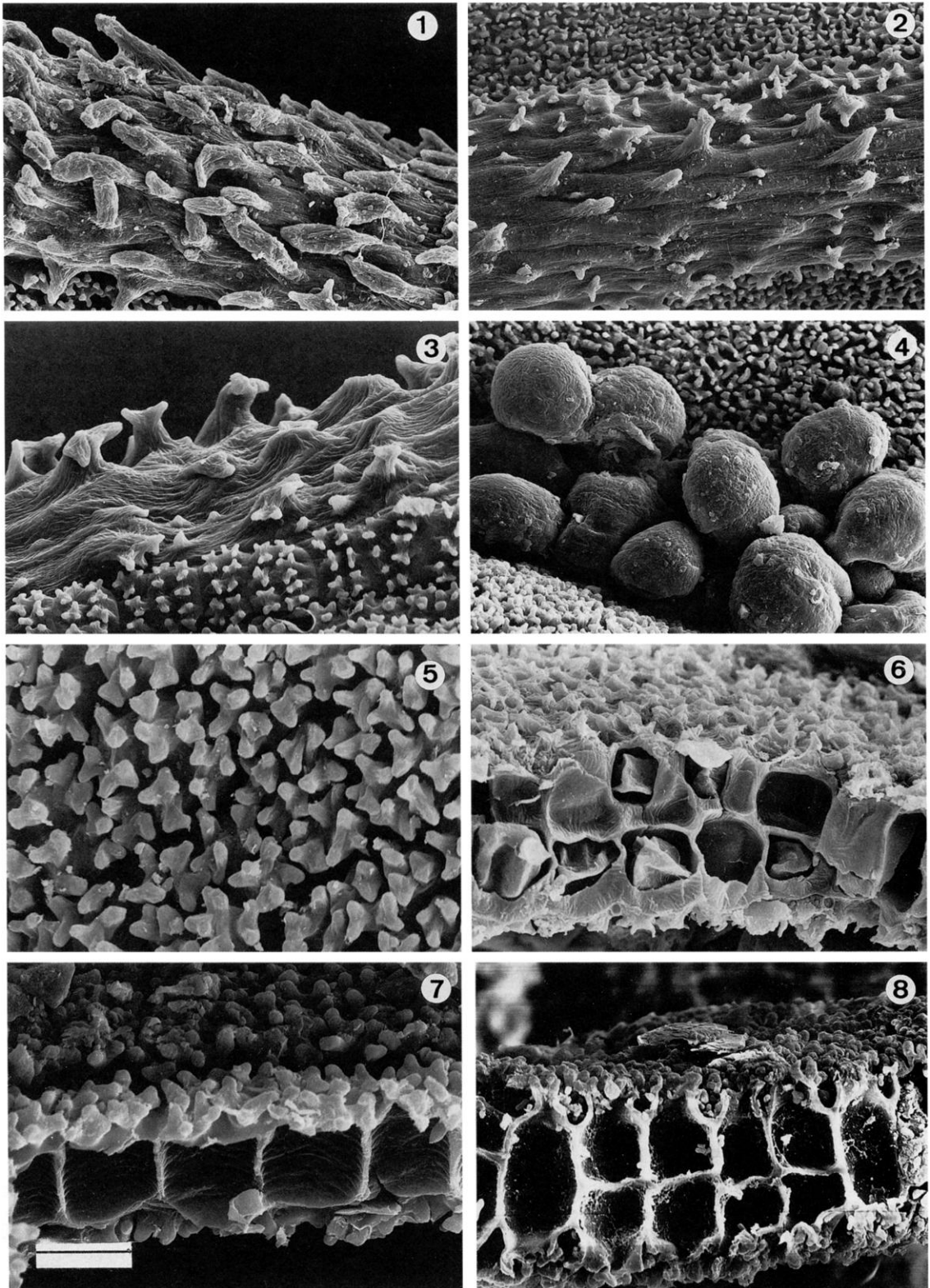
MOROCCO. Ifrane, 8 Apr 1969, *Davis & Davis 49306e* (BM).

SPAIN. Albacete, Los Yesares, XJ0932, Mar 1991, *Guerra & Ros s.n.* (MUB 4536). Alicante, sierra de Aitana, 13 Apr 1982, *Casas s.n.* (BCB 6818). Almería, c. 16 Km W of Sorbas, Los Yesos, near gypsum mine S of N340 road, 37°5' N, 2°18' W, 28 Apr 1990, *Jury & Maun-der s.n.* (BCB 30034). Cuenca, Mota del Cuervo, 17 Apr 1973, *Casas s.n.* (BCB 5945). Ciudad Real, Ruidera, 25 Mar 1972, *Casas & Brugués s.n.* (BCB 3060). Guadalajara, Saelices de la Sal, 19 Nov 2000, *Cano s.n.* (MUB 10977). Madrid, Chinchón, 5 Jan 1980, *Fuertes-Lasala & Galán s.n.* (MA-Musci 4371). Murcia, Caravaca, Royos de Abajo, 8 Jun 1983, *Ros s.n.* (MUB 1199). Navarra, Los Arcos, 23 Feb 1975, *Fuertes & García s.n.* (MA-Musci 1598). Palencia, Villaviudas, vertiente sur, 28 Apr 1983, *Fuertes s.n.* (MA-Musci 1599). Tarragona, Baix Camp, Prades, muntanyes de Els Rancs, 21 Feb 1989, *Casals s.n.* (BCB 46722). Teruel, Libros, 8 Dec 1975, *Casas s.n.* (BCB 5922). Toledo, Quero, Mar 1913, *Beltrán s.n.* (MA-Musci 11181). Zaragoza, Bujaraloz, Torcal del Ciervo, 24 Apr 1977, *Casas s.n.* (BCB 5923).

TURKEY. Prov. Ankara, shore of Tuz Gölü 25 km north of Kochisar, 28 Jul 1956, *McNeill 305* (E). Prov. Ankara, above Tuz Gölü 25 km north of Kochisar, 29 Jul 1956, *McNeill 341* (E). Prov. Corum, at the Hittite site of Alcahyuh, 16 May 2000, *Townsend* (Herb. C.C. Townsend). Prov. Malatya, Kangal-Hekimhan, 7 Jun 1960, *Staiton & Henderson 5392* (E). Prov. Malatya, 8 Jun 1960, *Stainton & Henderson 5415A* (E). Prov. Sivas, Pinarbasi, 25 Jun 1960, *Staiton & Henderson 5161* (E). Prov. Van, old town of Van, 1 Sep 1956, *McNeill 722* (E).

USA. Colorado. Mesa Co., north end of Colorado, National Monument, ca. 3 mi. South of fruita, 12 May 1955, *Shushan & Weber 9080* (FH). Nevada. Clark County, Eldorado Mountains, Keyhole Canyon Archeological Site, 8 Apr 1994, *Stark NV-209B* (UNLV). Nevada. Clark County, Lake Mead National Recreation Area, foothills of Black Mountains, 8 Oct 1997, *Stark NV-1870* (UNLV).

*Syntrichia caninervis* var. *caninervis* is a variable taxon characterized by the following combination of characters: position of the leaves when moist (usually patent or spreading), plant size (0.4–1.1 cm high), leaf shape (usually ovate), length of hair-point (the longest in the group in relation to the lamina), the stratification of the lamina (bistratose throughout) and the papillosity of the abaxial face of the costa (generally with longly pedicellate and branched papillae in the upper part of the costa and non-pedicellate and bifurcate papillae in



FIGS. 1-8. Scanning electron photomicrographs of surface and transverse section of leaves. 1-6. *Syntrichia rigescens* (Cano & Muñoz s.n., MUB 11378). 1, 2. Abaxial side of the costa in the upper third. 3. Abaxial side of the costa in the middle part. 4.

the lower part). Sometimes the leaf apex is hyaline and tapering to the hair-point, occasionally finely toothed.

Apart from var. *caninervis*, three other taxa can be recognized: *S. caninervis* var. *abranchesii* (Luisier) R.H. Zander, *S. caninervis* var. *gypsophila* (J.J. Amann ex G. Roth) Ochyra and *S. caninervis* var. *pseudodesertorum* (Vondr.) M.T. Gallego.

The papillosity on the abaxial side of the costa is a very variable character in *S. caninervis*. In some samples, the dorsal surface of the costa is covered with bifurcate non-pedicellate papillae; others have largely pedicellate, branched papillae or intermediate forms. Samples of *S. caninervis* var. *caninervis* which show the same type of papillosity as var. *pseudodesertorum* can be distinguished because the latter is larger in size and its leaves are recurved when moist (while those of var. *caninervis* are patent or spreading).

3. *SYNTRICHIA CANINERVIS* var. *ABRANCHESII* (Luisier) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 267. 1993. *Tortula abranchesii* Luisier, Broteria ser. Bot. 14: 115. 3. 1916. *Syntrichia montana* subsp. *abranchesii* (Luisier) Podp., Consp. 259. 1954. *Tortula caninervis* var. *abranchesii* (Luisier) W.A. Kramer, Bryophyt. Biblioth. 21: 108. 1980. *Syntrichia abranchesii* (Luisier) Ochyra, Fragm. Florist. Geobot. 37: 212. 1992.—TYPE: SPAIN. Salamanca, La Flecha, Mar 1915, Luisier s.n. (lectotype: BM, designated by Kramer (1980); isoclectotype: LISU!).

Plants 0.5–1.2 cm high, growing in olive-green or brownish loose turfs. Stems erect, branched. Leaves appressed when dry, mostly spreading when moist, ovate, ovate-lanceolate, not constricted in midleaf, 1.9–2.3 × 0.8–1.0 mm, bistratose irregularly in the upper third, unistratose at midleaf; apex rounded, obtuse, sometimes cucullate, apiculate or mucronate, up to 25–38 μm tall; margins recurved from base to near the apex, papillose-crenulate, unistratose, without a differentiated border; costa 65–90 μm wide at midleaf, in transverse section with 1 row of guide cells and 1–2(3) rows of dorsal stereids, sometimes with substereids, with hydroids, on the abaxial side with bifurcate or branched papillae, 5–12.5 μm all, in the upper third, smooth in the lower part; upper and middle laminal cells quadrate, rectangular or rounded, thick-walled, 10–12.5 × (7.5)10(12.5) μm, with 2–4 simple, bifurcate, non-pedicellate papillae per cell, 2.5 μm tall; juxtacostal basal cells rectangular, 60–85 × 10–20 μm, hyaline, thick-walled, forming a differentiated hyaline area to 22–33% of leaf length; marginal basal cells chloro-

phyllous, in 8–12 columns, generally smooth. Dioicous. Sporophyte unknown.

**Habitat.** Terricolous.

**Distribution.** Europe (Spain).

This taxon is characterized by the papillosity of the abaxial side of the costa and by the absence of a hyaline hair-point, which distinguishes it from the rest of the taxa in the *Caninervis* group. *Syntrichia caninervis* var. *abranchesii* shares with *Syntrichia intermedia* var. *calva* (Durieu & Sagot) Delogne the absence of hyaline hair-points, the presence of hydroids in the costa and cell size, but differs in the stratification of the lamina, the constriction of the leaf, the recurved margins and the papillosity of the costa.

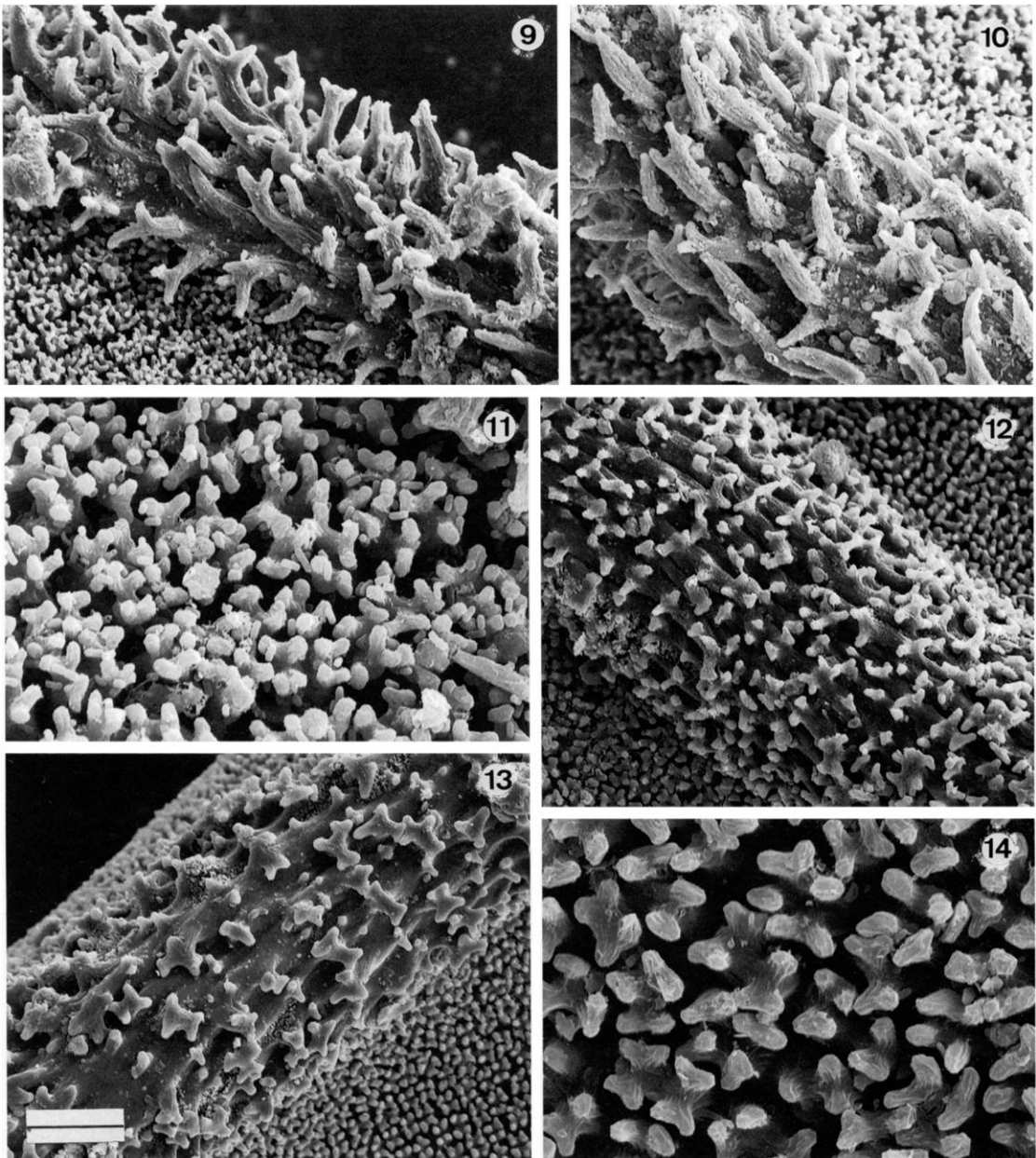
It should be noted that this description was prepared from the type material because it is the only known sample.

4. *SYNTRICHIA CANINERVIS* var. *GYPHOPHILA* (J.J. Amann ex G. Roth) Ochyra, Fragm. Florist. Geobot. 37: 212. 1992. (Figs. 12–14). *Tortula ruralis* var. *gypsophila* J.J. Amann ex G. Roth, Hedwigia 57: 135. 1915. *Tortula gypsophila* J.J. Amann ex G. Roth, Hedwigia 57: 135. 1915, *nom. inval.* (article 34.1(c), [Greuter et al. 2000]). *Syntrichia ruralis* var. *gypsophila* (J.J. Amann ex G. Roth) J.J. Amann, Fl. Mouss. Suisse 2: 118. 1918. *Tortula caninervis* subsp. *spuria* var. *gypsophila* (J.J. Amann ex G. Roth) W.A. Kramer, Bryoph. Biblioth. 21: 106. 1980. *Tortula spuria* J.J. Amann, Bull. Murith., Soc. Valais. Sci. Nat. 39: 351. 1916. *Syntrichia spuria* (J.J. Amann) J.J. Amann, Fl. Mouss. Suisse 2: 119, 384. 1918. *Tortula ruralis* subsp. *spuria* (J.J. Amann) Giacom., Atti Ist. Bot. Univ. Lab. Crit. Pavia ser. 5, 4: 217. 1947. *Syntrichia ruralis* var. *spuria* (J.J. Amann) Podp., Consp. 257, 1954, *nom. illeg.* *Syntrichia caninervis* var. *spuria* (J.J. Amann) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 267. 1993, *nom. illeg.*—TYPE: SWITZERLAND. Valais, Sion-Montorge, 8.12.1912, Amann s.n. [lectotype: ZT!, designated by Kramer (1980)].

*Syntrichia hadacii* Vondr., Bull. Soc. Amis Sci. Lett. Poznan, Sér. D, Sci. Biol. 6: 121. f. 3. 1965 [1966]; synonymized by Kramer (1980).

Plants 0.3–1.6 cm high, growing in olive-green, whitish dense turfs. Stems erect, branched. Leaves lightly spirally twisted or appressed when dry, mostly patent or spreading, sometimes recurved when moist, ovate, ovate-lanceolate, not constricted in midleaf, 0.9–2.4 × 0.6–1.1 mm, irregularly bistratose in the upper

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FIGS. 9–14. Scanning electron photomicrographs of leaf surface. 9–11. *Syntrichia caninervis* var. *caninervis* (Staiton & Henderson 5161A, E). 9. Abaxial side of the costa in the upper third. 10. Abaxial side of the costa in the middle part. 11. Middle laminal cells. 12–14. *Syntrichia caninervis* var. *gypsophila* (Davis & Davis 49306c, BM). 12, 13. Abaxial side of the costa in the middle part. 14. Middle laminal cells. Scale bar: 9 = 25  $\mu\text{m}$ ; 10, 12, 13 = 25  $\mu\text{m}$ ; 11 = 8  $\mu\text{m}$ ; 14 = 6  $\mu\text{m}$ .

third, unistratose at midleaf; apex rounded, obtuse, sometimes cucullate or hyaline; margins recurved from base to near the apex, sometimes to 2/3 of the leaf, papillose-crenulate, unistratose, without a differentiated border; hair-point hyaline, strongly spinose, 0.3–1.8(2.6) mm long; costa 60–112  $\mu\text{m}$  wide at midleaf, in transverse section with 1–2 rows of guide cells and (1)3–4 rows of dorsal stereids, sometimes with substereids, with hydroids, on the abaxial side with

branched papillae, 12.5–37.5  $\mu\text{m}$  tall, in the upper third, and with simple or bifurcate papillae, 2.5–5  $\mu\text{m}$  tall, in the lower part; upper and middle laminal cells quadrate, hexagonal or rounded, thick-walled, 7.5–10(12.5)  $\times$  (5)7.5–10(12.5)  $\mu\text{m}$ , with (2)4–5 bifurcate, non-pedicellate papillae per cell, 2.5–5  $\mu\text{m}$  tall; juxtacostal basal cells rectangular, 25–75  $\times$  10–20  $\mu\text{m}$ , hyaline, thick-walled, forming a differentiated hyaline area to 28–48% of leaf length; marginal basal cells chlo-

rophyllous, in 8–15 columns, generally smooth. Dioicous. Seta erect, 1.3–1.8 cm long, spirally twisted to right above, to left below, reddish brown. Capsule erect, cylindrical,  $2.8\text{--}3.2 \times 0.6\text{--}0.8$  mm, brownish. Operculum long conical, 1.5 mm long. Spores spherical,  $7.5 \mu\text{m}$  in diameter, papillose.

**Habitat.** A characteristic taxon of gypsiferous soils, although it may also be found on bare calcareous, clayey or sandy soils, on limestone and walls; more rarely as comophyte, not found as an epiphyte; 550–1500 m.

**Distribution.** Europe, S.W. Asia, N. Africa. First record in N. Africa.

**Selected Specimens Examined:** FRANCE. Département des Hautes-Alpes, Saint-Crépin, friche au-dessus du cimetière, 27 Jun 1991, *Pierrot & Pierrot s.n.* (MUB 4772).

ITALY. Südtirol, Vinschgau, Sonnenberg zw. Eysr und Spondinig, 28 Oct 1989, *Köckinger s.n.* (GZU).

MOROCCO. Ifrane, 8 Mar 1969, *Davis & Davis 49306* (E). Anti-Atlas, Sebti-Boumaamane,  $29^{\circ}28'N$ ,  $9^{\circ}50'W$ , 4 Mar 2001, *Cano & Muñoz* (MUB 11625).

SPAIN. Albacete, Yesos de Montealegre del Castillo, carretera a Bonete, 20 Apr 1991, *Martínez-Sánchez & Ros s.n.* (MUB 4533). Alicante, El Maigmo, 19 Mar 1991, *Ros & Moya s.n.* (MUB 4365). Almería, Tabernas, Venta de los Yesos, 20 Nov 1988, *Martínez-Sánchez et al. s.n.* (MUB 3077). Ciudad Real, castillo de Peñarroya, 17 Apr 1973, *Casas s.n.* (BCB 5944). Cuenca, Mota del Cuervo,  $39^{\circ}30'N$ ,  $2^{\circ}52'E$ , 14 Oct 2000, *Cano s.n.* (MUB 10976). Granada, entre Cúllar y Baza, 1 Feb 1990, *Gueerra & Ros s.n.* (MUB 3825). Huesca, Albero Alto, 15 Feb 1973, *Casas s.n.* (BCB 5943). Murcia, Archivel, Puntal la Vieja, WH81, 10 Mar 1985, *Ros s.n.* (MUB 3522). Teruel, Arcos de Salinas, 1 Apr 1974, *Casas s.n.* (BCB 5935). Valencia, Jarafuel, *Puche & Gimeno s.n.* (VAB 2720).

*Syntrichia caninervis* var. *gypsophila* is similar in appearance to *S. caninervis* var. *caninervis*, but with shorter, less stout hyaline hair-points, thinner cell walls and an irregularly stratose lamina (since it is only irregularly bistratose in the upper third). No samples were found with the peristome in good condition so that this character could not be described.

5. *SYNTRICHIA CANINERVIS* var. *PSEUDODESERTORUM* (Vondr.) M.T. Gallego *comb. nov.* (Figs. 7, 15–17). *Syntrichia handelii* var. *pseudodesertorum* Vondr., Bull. Soc. Amis Sci. Lett. Poznan, Sér. D, Sci. Biol. 6: 121. f. 6. 1965 [1966].—TYPE: IRAQ. Pira Magrun, distr. Sulaimania, 21 Oct 1960, *Hadač* (holotype: not located, not at PL; isotype: BUH?).

*Tortula pseudohandelii* J. Froehl., Ann. Naturhistor. Mus. Wien 67: 155. 1964. *Syntrichia pseudohandelii* (J. Froehl.) S. Agnew & Vondr., Feddes Repert. 86: 401. 1975.—TYPE: AFGANISTAN. Prov. Mazar-i

Sharif, Balkh, Aq Kupruk, 7–8 Jun 1962, *Rechinger 19673* (holotype: W!; isotype: GZU!).

Plants 2.5–7 cm high, growing in olive-green, dense turfs. Stems erect, branched. Leaves lightly spirally twisted or appressed when dry, mostly recurved, rarely spreading when moist, ovate-lingulate, ovate-lanceolate, not constricted in midleaf,  $3.2\text{--}4 \times 0.9\text{--}1.1$  mm, regularly bistratose in the upper third and at midleaf; apex rounded, obtuse, sometimes cucullate; margins recurved from base to near the apex, papillose-crenulate, unistratose, without a differentiated border; hair-point hyaline, sometimes brownish at base, strongly spinose, 1.4–2.1 mm long; costa 120–135  $\mu\text{m}$  wide at midleaf, in transverse section with 2–3 rows of guide cells and 2–5 rows of dorsal stereids, sometimes with substereids, with hydroids, on the abaxial side with bi-trifurcate, pedicellate and stellately branched papillae, (15)17.5–25  $\mu\text{m}$  tall; upper and middle laminal cells quadrate or hexagonal, thin-walled,  $7.5\text{--}10 \times (5)7.5\text{--}10 \mu\text{m}$ , with 6–8 bifurcate, non-pedicellate papillae per cell, 2.5  $\mu\text{m}$  tall; juxtacostal basal cells rectangular,  $47.5\text{--}100 \times 7.5\text{--}12.5 \mu\text{m}$ , hyaline, thin-walled, forming a differentiated hyaline area to 29–35% of leaf length; marginal basal cells chlorophyllous, in 10–15 columns, generally smooth. Dioicous. Sporophyte unknown.

**Habitat.** On limestone rocks; 700–1900 m.

**Distribution.** S.W. Asia.

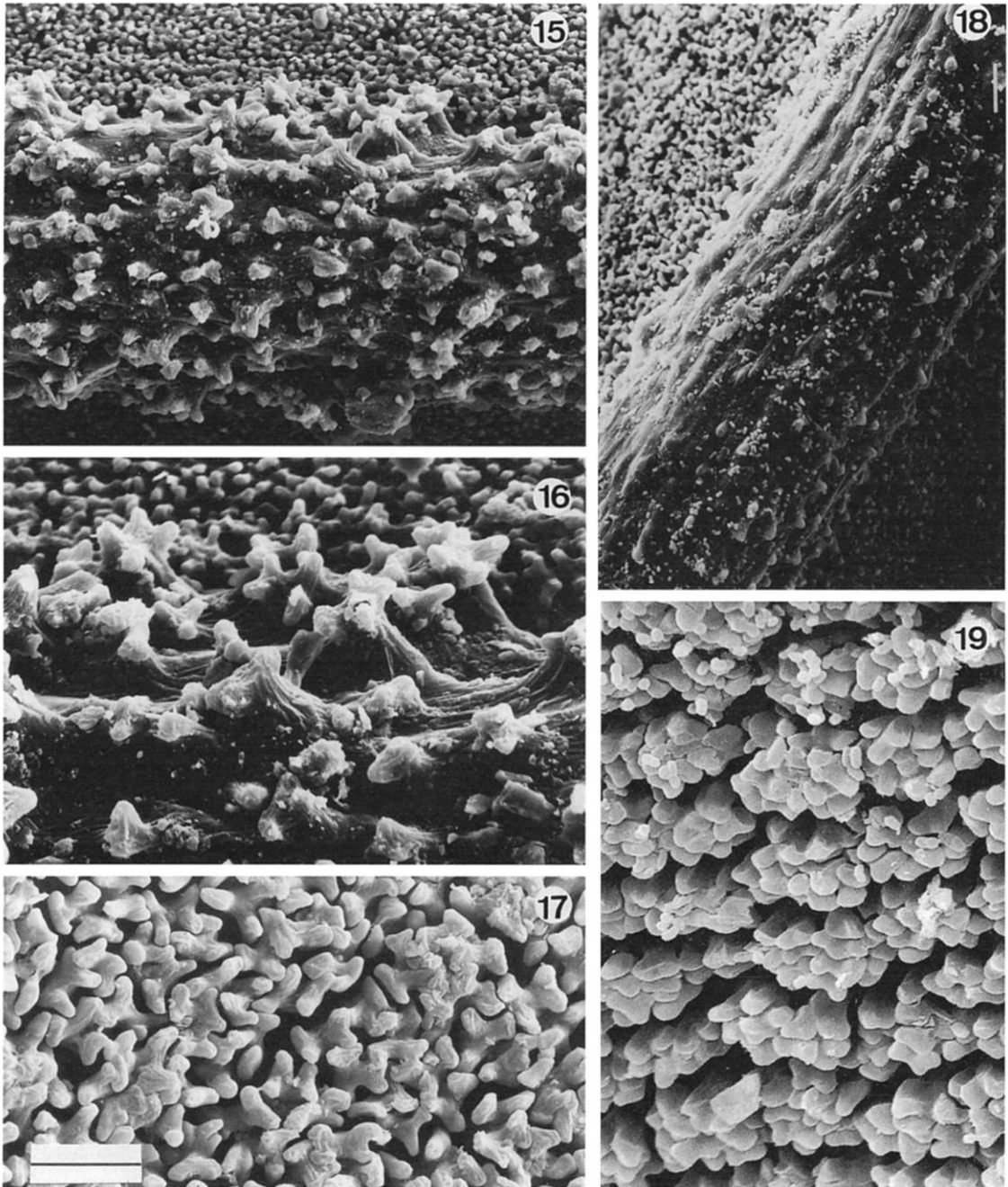
**Selected Specimens Studied.** AFGHANISTAN. Prov. Kabul, Kabul, in declivibus borealibus montis Scher Darwasa,  $34^{\circ}30'N$ ,  $69^{\circ}10'E$ , 19 Jun 1962, *Rechinger 19698* (GZU).

IRAN. Gilán, 10 Mar 1958, *Merton* (E). N.W. Chavan bata, E. of lake Urmia in Kuh-i-Sahand, 10 Aug 1966, *Warren 33* (BM).

TURKEY. Prov. Ankara, Gerede-Ankara nr. Kizilcahamam, 22 Jul 1956, *McNeill 286* (E).

This variety is characterized by its long pedicellate, bi-trifurcate stellately branched papillae covering the whole of the abaxial surface of the costa, and the leaves recurved when moist and relatively large compared with the other varieties of *S. caninervis*. In the W. Mediterranean region this taxon has been cited from only one locality in the Iberian Peninsula as *S. pseudohandelii* (Casas 1993), although a careful study of the samples shows that the material corresponds to *Syntrichia caninervis* var. *caninervis* and not *Syntrichia caninervis* var. *pseudodesertorum*.

This taxon combines characters of *S. caninervis* and *S. ruralis* (Hedw.) F. Weber & D. Mohr, particularly the latter in regard to habit. It also shares with *S. ruralis* the recurved margins, the shape and position of the leaves when moist and cell size, but it is easily distinguished by the stratification of the lamina (unistratose in *S. ruralis*; bistratose in *S. c.* var. *pseudodesertorum*),



FIGS. 15–19. Scanning electron photomicrographs of leaf surface. 15–17. *Syntrichia caninervis* var. *pseudodesertorum* (McNeill 286, E). 15, 16. Abaxial side of the costa in the upper third. 17. Middle laminal cells. 18–19. *Syntrichia handelii* (Coode & Jones 2934, E). 18. Abaxial side of the costa in the upper third. 19. Middle laminal cells. Scale bar: 15, 18 = 20  $\mu\text{m}$ ; 16 = 10  $\mu\text{m}$ ; 17, 19 = 8  $\mu\text{m}$ .

the papillosity of the dorsal side of the costa (simple or bifurcate papillae, 2.5  $\mu\text{m}$  tall, in *S. ruralis*; pedicellate, bi-trifurcate, stellately branched papillae, (15)17.5–25  $\mu\text{m}$  tall, in *S. c.* var. *pseudodesertorum*) and the anatomy of the costa (without hydroids and substereids in

*S. ruralis*; with hydroids and substereids in *S. c.* var. *pseudodesertorum*).

We have not been able to study the type material of *Syntrichia handelii* var. *pseudodesertorum* (not in PL, BUH?). However, in a later paper, Vondráček synonymy-



mized this taxon with *S. pseudohandelii* (Agnew and Vondráček 1975).

6. *SYNTRICHIA HANDELI* (Schiffner) S. Agnew & Vondr. var. *HANDELI*, Feddes Repert. 86: 401. 1975. (Figs. 18,19). *Tortula handelii* Schiffner, Ann. Naturh. Hofmus. Wien 27: 485. f. 34–39. 1913. *Syntrichia montana* subsp. *handelii* (Schiffner) Podp., Consp. 258. 1954. *Tortula intermedia* subsp. *handelii* (Schiffner) Wijk & Margad., Taxon 14: 198. 1965.—TYPE: TURKEY. Mt. Tauro, dist. Mamuraê, 10 Jul 1910, *Handel-Mazzetti* 1978 (lectotype: W!, designated here; isolectotype: FH!).

Plants 1.3–3 cm high, growing in olive-green, dense turfs. Stems erect, branched. Leaves lightly spirally twisted or appressed when dry, mostly patent, sometime recurved when moist, lingulate, lingulate-lanceolate, sometimes constricted in midleaf, 2.4–2.8 × 0.4–0.8 mm, regularly bistratose or sometimes tristratose in the upper third, irregularly bistratose at midleaf; apex rounded, acute, obtuse, sometimes emarginate; margins recurved to 2/3 of the leaf, sometimes to near the apex, papillose-crenulate, unistratose, sometimes bistratose in the upper part of the leaf, without a differentiated border; hair-point hyaline, sometimes brownish at base, strongly spinose, 0.5–1.5 mm long; costa 75–105 µm wide at midleaf, in transverse section with 1–2 rows of guide cells and (2)3–4 rows of dorsal stereids, generally without substereids, with hydroids, on the abaxial side with simple, verrucose papillae, 2.5 µm tall; upper and middle laminal cells quadrate, hexagonal or rounded, thin-walled, 5–7.5(10) × 5–7.5(10) µm, with 4–6 bifurcate, non-pedicellate papillae per cell, 2.5 µm tall; juxtacostal basal cells rectangular, 35–87 × (7.5)15–17.5 µm, hyaline, thick-walled, sometimes collenchymatous, forming a differentiated hyaline area to 26–36% of leaf length; marginal basal cells chlorophyllose, in 6–17 columns, generally smooth. Dioicous. Seta erect, 1–1.5 cm long, spirally twisted to right throughout, reddish brown. Capsule erect, cylindrical, 2.8–4.1 × 0.6–0.8 mm, reddish brown. Peristome of 32 papillose, spirally twisted teeth, 0.6–0.8 mm long; basal membrane of 12–17 rows of cells, 0.3–0.6 mm high. Operculum long conical, 1.5–1.9 mm long. Spores spherical, (10)12.5–7.5(17.5) µm in diameter, papillose.

**Habitat.** On limestone rocks; 800–1800 m.

**Distribution.** Europe, N. Africa; S.W. Asia.

**Selected Specimens Examined.** CYPRUS. Between Pano Platres and Troodos village, 24 Mar 1997, *Blockeel* (Herb. T.L. Blockeel 26–78).

IRAQ. Mosul Liwa, Jul 1961, *Agnew s.n.* (BCB 5967).

ITALY. Sicilia, Bosco di Ficuzza, 10 km south of Marineo, 9 Apr 1999, *Blockeel* (Herb. T.L. Blockeel 28–86).

GREECE. Creta, Iraklion, slopes above the Nida Plain, Mt. Ida, Oct 1992, *Blockeel* (Herb. T.L. Blockeel 21–382). Creta, Pr. Rethimnon, 8.3 km südlich oberh.

Anogia bei d.kl. Kirche Hochmont, 3 Apr 1972, *Düll 108* (Herb. J.-P. Frahm). Sterea Ellada, Viotia, Mt. Parnassos, below the Kellaria Ski Centre, Apr 1990, *Blockeel* (Herb. T.L. Blockeel 19–94). Peloponnese, Arkadia, Mt. Parnon, 5 km north-east of Kosmas, 11 Mar 1995, *Blockeel* (Herb. T.L. Blockeel 24–101). Peloponnese, Ahaia, Mt. Helmos on the approach to Xirokambos, SE of Kalavrita, 18 Apr 1995, *Blockeel* (Herb. T.L. Blockeel 24–224).

MOROCCO. Jbel Bouhalla, cordillera del Rif, 35°07'31" N, 5°08'10" W, 15 Jun 1997, *Cano & Ros s.n.* (MUB 11352). Jbel Bouhalla, cordillera del Rif, 35°08'17" N, 5°08'20" W, 16 Jun 1997, *Cano & Ros s.n.* (MUB 10876).

SYRIA. Mesopotamia, Dschebel Abd el Asis, Gharra, 22 Jun 1910, *Handel-Mazzetti* 1796 (W).

SPAIN. Málaga, puerto del Viento, entre Ronda y El Burgo, 5°03'22", 36°45'56", 13 Apr 1988, *Hébrard s.n.* (BCB 31835). Málaga, serranía de Ronda, puerto del Viento, 13 Aug 2000, *Guerra s.n.* (MUB 11341).

TURKEY. Prov. Antalya, dist. Akseki, Gorge below Erenkaya between Manavgat and Akseki, 10 Apr 1956, *Davis & Polunin* 25802 (E). Prov. Gaziantep, 25 km W. of Gaziantep, 13 Sep 1956, *McNeill* 834 (E). Prov. Hakkari, Cilo Dag in Diz deresi, 6 Aug 1954, *Davis & Polunin* 23874, 24011 (E). Prov. Maras, Elbistan, 6 May 1957, *Davis & Hedge* 27658 (E). Prov. Mersin, Findikpinari above Mersin, 7 Apr 1956, *Davis & Hedge* 26480 (E). Prov. Urfa, 5 km west of Urfa, 7 May 1957, *Davis & Hedge* 28176 (E). Kütahya, Simav, Simav Dag, 18 Jun 1965, *Coode & Jones* 2934 (E). 6 km from Timar (Canik) to Van, 3 Jun 1966, *Davis* 44189 (E).

This species is characterized by the presence of simple, non-pedicellate papillae on the abaxial side of the costa, the leaves sometimes constricted in midleaf and patent when moist, and the margins recurved to the upper third of the leaves. *Syntrichia handelii* has been considered a subspecies of *Syntrichia intermedia*—*Syntrichia montana* subsp. *handelii* (Podpera 1954), *Tortula intermedia* subsp. *handelii* (Wijk & Margadant 1965). It shares with *Syntrichia intermedia* Brid. a similar cell size, leaf constriction, the presence of hydroids, and the position of the leaves when moist. However it differs in the stratification of the lamina (unistratose in *S. intermedia*), the recurvature of the leaf margins (sometimes reaching the apex in *S. handelii*, but never exceeding ¾ of length in *S. intermedia*) and the position of the leaves when moist (sometimes recurved in *S. handelii* but never in *S. intermedia*). When *S. handelii* shows the last two characteristics, it has the same habit as *Syntrichia ruralis* var. *ruralis*, but *S. handelii* has a bistratose lamina and hydroids.

7. *SYNTRICHIA HANDELI* var. *FERGANENSIS* (Laz.) Ochyra, Fragm. Florist. Geobot. 37: 212. 1992. *Tortula ferganensis* Laz., Ukrayinsk. Bot. Zhurn. 4: 64. 1–

3. 1928. *Syntrichia ferganensis* (Laz.) Laz., Zhurn. Inst. Bot. Vseukrainsk. Akad. Nauk. 26–27: 203. 1938. *Tortula handelii* var. *ferganensis* (Laz.) W.A. Kramer, Bryologist 81: 385. 1978.—TYPE: UZBEKISTAN. Fergana, near Kishlak Gava, 19 Jun 1928, Lazarenko s.n. (lectotype: HBG!, designated by Kramer (1978); isolectotype: LE!).

Plants 0.7–1.8 cm high, growing in olive-green, dense turfs. Stems erect, branched. Leaves lightly spirally twisted or appressed when dry, mostly patent, sometimes recurved at the apex when moist, lingulate, ovate-lingulate, sometimes lightly constricted in midleaf, 2.1–3.3 × 0.7–1.0 mm, regularly bistratose in the upper third and at midleaf; apex rounded, obtuse, mucronate, the mucro up to 300 μm long, formed by the costa and part of the adjacent lamina; margins recurved to 2/3 of the leaf, papillose-crenulate, unistratose, without a differentiated border; costa 112.5–125 μm wide at midleaf, in transverse section with 1–2 rows of guide cells and 3–4(6) rows of dorsal stereids, generally with substereids and hydroids, on the abaxial side with simple, verrucose papillae, 2.5 μm tall; upper and middle laminal cells quadrate or rounded, thin-walled, 7.5–10 × 7.5–10 μm, with 4–6 bifurcate, non-pedicellate papillae per cell, 2.5 μm tall; juxtacostal basal cells rectangular, 12.5–30 × 10–12.5 μm, hyaline, thick-walled, forming a differentiated hyaline area to 28–37% of leaf length; marginal basal cells chlorophyllose, in 10–14 columns, generally smooth. Dioicous. Seta erect, 0.8–1.0 cm long, spirally twisted to right throughout, reddish brown. Capsule erect, cylindrical or ovoid-cylindrical, 2.0–2.7 × 0.6–0.8 mm, reddish brown. Peristome of 32 papillose, spirally twisted teeth, 0.6–0.8 mm long; basal membrane of 12–20 rows of cells, 0.5–0.7 mm high. Operculum long conical, 1.4–1.6 mm long. Spores spherical, 12.5–15 μm in diameter, papillose.

**Habitat.** On limestone rocks.

**Distribution.** Central Asia.

*Syntrichia handelii* var. *ferganensis* is characterized by its mucronate leaves, the abaxial side of the costa with verrucose papillae, and the margins recurved to the upper third. This taxon shares with *Syntrichia caninervis* var. *abranchesii* the absence of a hair-point. However the two taxa can be distinguished by the size and shape of the leaves (ovate-lingulate or lingulate in *S. handelii* var. *ferganensis*; sometimes ovate, not constricted in the middle part in *S. c.* var. *abranchesii*), the papillosity of the dorsal side of the costa (verrucose papillae in *S. handelii* var. *ferganensis*; bifurcate or branched papillae in *S. c.* var. *abranchesii*), the stratification of the lamina (regularly bistratose throughout in *S. handelii* var. *ferganensis*; irregularly bistratose in the upper third and unistratose at midleaf in *S. c.* var. *abranchesii*), the transverse section of the costa (3–6

rows of dorsal stereids in *S. handelii* var. *ferganensis*; 1–3 rows of dorsal stereids in *S. c.* var. *abranchesii*) and by the leaf apex (longly mucronate, formed by the costa and part of the adjacent lamina in *S. handelii* var. *ferganensis*; formed only by the costa in *S. c.* var. *abranchesii*).

The description has been prepared from the type material, the only known specimen.

#### DISCUSSION

As can be seen from the characters used to distinguish the taxa and the numerous taxonomic observations made for each taxon, this is an extraordinarily complex group whose taxa are not always easy to distinguish. It may be considered to be a group of Iranian-Turanic origin, spreading out to the western Mediterranean (Iberian Peninsula, N Africa) with a disjunction in America (Lawton 1971; Stark and Catter 1982), whose taxa colonize gypsiferous, loamy-gypsiferous, or limestone substrates, generally in relatively arid or semiarid areas. Therefore, this group can be considered Circum-Tethyan.

The most easily recognizable taxon is *Syntrichia rigescens* because of its gemmae, which are widely used as diagnostic characters (Kramer 1980; El-Oqlah et al. 1988; Boudier 1992); however, this is not the most important or valid taxonomic feature since propagule formation may be due to environmental stress, as occurs in other taxa of *Syntrichia*, such as *S. laevipila* Brid. and its varieties (Sérgio 1981). According to El-Oqlah et al. (1988), *S. rigescens* may be derived from an ancestral *T. pseudohandelii* J. Froehl. (= *Syntrichia caninervis* var. *pseudodesertorum*) from SW Asia, thus representing an evolutionary line separate from the remaining *Syntrichia* taxa which produce gemmae.

According to Agnew and Vondráček (1975), *Syntrichia caninervis* var. *pseudodesertorum* may be a hybrid between *S. caninervis* and *S. handelii*; this claim is based on another "intermediate form" between these two taxa described as *S. pseudodesertorum*. Kramer (1978) regarded this last species as a synonym of *S. caninervis* and rejects the above conjecture, claiming that *S. handelii* is never associated with *S. caninervis* or *Syntrichia caninervis* var. *pseudodesertorum*. Furthermore, he denied the existence of intermediate states between the typical forms of *S. caninervis* and *Syntrichia caninervis* var. *pseudodesertorum*.

After studying the type material of *S. pseudodesertorum*, we agree with Kramer (1978) that this species is synonymous with *S. caninervis*. However, we disagree with regard to the absence of intermediate forms between *S. caninervis* and *Syntrichia caninervis* var. *pseudodesertorum* because we have identified forms with the diagnostic characteristics of both taxa. This lends weight to the idea that *Syntrichia caninervis* var. *pseudodesertorum* is merely an extreme variation of *S. cani-*

*nervis* or even a hybrid between some taxa of *Syntrichia*. Hence, in this paper we consider that its correct taxonomic status should be *S. c.* var. *pseudodesertorum* and we do not accept specific status (*S. pseudohandelii*).

*Syntrichia caninervis* var. *caninervis*, *S. c.* var. *abranchesii* and *S. c.* var. *gypsophila* are usually found on gypsiferous substrates, rarely on limestone. This homogeneity in habitat and the variability in morphological characters suggest extremes of variation within a species rather than any taxonomic significance.

*Syntrichia handelii* can be recognized by the presence of simple papillae on the abaxial side of the costa. It appears to be a species adapted to growing on rocky, limestone substrates at relatively high altitude, generally above 1000 m, such isolation probably being the cause for its speciation.

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