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An overview of *Syntrichia ruralis* complex (Pottiaceae: Musci) in the Mediterranean region and neighbouring areas

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The *Syntrichia ruralis* complex is revised in the Mediterranean region and neighbouring areas. A critical study of six quantitative and eight qualitative gametophytic characters from a total of 232 samples has been carried out. On the basis of this survey five taxa have been recognized. An identification key is provided. *S. ruralis* var. *subpapillosissima* is elevated to the rank of species as *S. subpapillosissima*. A lectotype for *S. calcicola* is proposed. *S. ruralis* var. *submamillosa* and *S. ruralis* var. *glacialis* are regarded as synonymous with *S. subpapillosissima* and *S. ruralis*, respectively. Also, *Tortula densa* is included in the variability shown by *S. calcicola*. *Syntrichia ruralis* var. *substereidosa* (*Tortula ruralis* var. *substereidosa*) is excluded from the *Syntrichia ruralis* complex and is included in the synonymy of *S. virescens*. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, **138**, 209–224.

ADDITIONAL KEYWORDS: bryophyte – gametophytic character analysis – nomenclature – taxonomy.

INTRODUCTION

Generic boundaries in the Pottieae, notably in the series *Pottia–Desmatodon–Tortula–Syntrichia,* are particularly difficult to delimit (Blockeel, 1990), and for this reason many authors have considered the genus *Syntrichia* Brid. to be not distinct from *Tortula* Hedw. (cf. Lawton, 1971; Smith, 1978; Catcheside, 1980; Crum & Anderson, 1981; Magill, 1981; Noguchi, 1988; Mishler, 1994). Others, such as Brotherus (1924), Bilewsky (1965), Augier (1966) and Dixon (1970), considered it as a section (section Rurales) of the genus *Tortula*. Kramer (1980) and Corley *et al*. (1981) group the species of the genus *Syntrichia* in the section Rurales, although they did not agree on the taxa that should be included. Finally Zander (1989, 1993) considered this section to be synonymous with the genus *Syntrichia* and provided convincing characters to recognize this genus (*S. ruralis* (Hedw.) F. Weber & D. Mohr, *typus*) as a segregate of *Tortula.* We agree with Zander (1989, 1993), Ochyra (1992) and Anderson (1997) that this combination of characters defining *Syntrichia* is sufficient to justify its segregation as a separate genus. Also, analyses of ribosomal DNA sequences support the segregation of *Syntrichia* from *Tortula* (Spagnuolo *et al*., 1999).

In this work we have focused our attention on the taxonomic problems of the taxa included in the *Syntrichia ruralis* group. This is represented in Europe by seven taxa that are quite similar (cf. Kramer, 1980) and whose morphological boundaries and taxonomic categories have been treated in different ways. This has probably been because the major diagnostic characters have usually been neglected, whereas other characters that were believed up to now to be of great taxonomic value we interpret as simple morphological variants. The sporophytic features do not have taxonomic value, due to their homogeneity.

Without doubt, *Syntrichia ruralis* var. *ruralis* is a rather polymorphic variety, due to modifications in response to different ecological conditions, but it seems also that the variety consists of several genotypes (Geissler & Frahm, 1995). For this reason, it has been considered as a problematic taxon. The other six taxa that constitute the Ruralis complex in the

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Mediterranean Region are: *Syntrichia ruralis* var. *hirsuta* (Venturi) Podp., *S. ruralis* var. *subpapillosissima* (Bizot & R.B. Pierrot) R.H. Zander, *S. ruralis* var. *arenicola* J.J. Amann, *S. ruralis* var. *submamillosa* (W.A. Kramer) R.H. Zander, *S. ruralis* var. *substereidosa* (W.A. Kramer) R.H. Zander and *S. calcicola* J.J. Amann (taxonomic status according to Zander, 1993). This assemblage of taxa does not currently have any taxonomic status, but it shares a combination of morphological characters that differentiate it from the rest of taxa of the genus *Syntrichia*. These include leaves ovate or ovate-lingulate, recurved to squarrose when moist (except *S. calcicola* with spreading or patent leaves), not constricted in mid-leaf; margins strongly recurved almost to the apex (except *S. calcicola* with margin recurved to 2/3 of the lamina); costa without hydroids. Some authors (for example, Mishler, 1985), included *Tortula princeps* (De Not.) Mitt. and *Tortula intermedia* Brid. within the Ruralis complex. Others (for example Frahm, 1994) included in addition *Tortula virescens* (De Not.) Ochyra and *Tortula densa* (Velen.) J.-P. Frahm. We do not accept these species in this complex. Hydroids are present in the costa of *T. princeps* and *T. intermedia,* and these species and *T. virescens* have leaves constricted in the middle. Although *T. virescens* does not have hydroids, the transverse section of the costa, with only 1–2 layers of stereids, is different from that in the Ruralis complex. In addition the recurved margins in this species only reach the lower third of the lamina or the leaves are plane.

MATERIAL AND METHODS

All available types and numerous collections from Mediterranean countries and bordering areas have been studied. Moreover, material from many countries of north and central Europe have been examined. Samples deposited in the following institutional and personal herbaria were revised: B (Berlin), BCB (Barcelona), BCC (Barcelona), BM (London), BR (Brussels), C (Copenhagen), CANM (Ottawa), E (Edinburgh), EGR (Eger), GZU (Graz), H (Helsinki), JE (Jena), K (Kew), LISU (Lisboa), LU (Lugo), MA-Musci (Madrid), MGC (Málaga), MUB (Murcia), NY (New York), OXF (Oxford), PRC (Prague), SALA-Bryo (Salamanca), TR (Trento), U (Utrecht), VAB (Valencia), ZT (Zurich), herbarium J.-P. Frahm (Bonn), herbarium T.L. Blockeel (Sheffield), herbarium B.O. van Zanten (Noordlaren).

For the study of the morphological characters an Olympus-BH2 light microscope was used. Photomicrographs were obtained using an Olympus PM-10AK camera attached to this microscope. The leaf surfaces were studied using a Jeol JSM-6100 scanning electron microscope. Material was fixed in glutaraldehyde 3% with 0.1 M cacodylate buffer at 4 °C, washed in cacodylate and sacarosa buffer, dehydrated in an increasing acetone gradient (30%, 50%, 70%, 90% and 100%), critical-point dried and gold-sputtered with a gold layer 200–300 Å thick.

The nomenclature used for the taxa recognized in the present paper will be employed from now on.

A total of 232 samples have been studied using morphological characters, as follows: *Syntrichia calcicola* N = 50, *S. papillosissima* (*S. ruralis* var. *hirsuta*) N = 21, *S. subpapillosissima* (*S. ruralis* var. *subpapillosissima*) $N = 31$, *S. ruralis* var. *ruralis* $N = 65$ and *S. ruralis* var. *ruraliformis* (*S. ruralis* var. *arenicola*) N = 65. We have selected 14 variables to determine the relationship and degree of association between the five recognized taxa of the Ruralis complex. Characters which have been traditionally considered important in the literature for distinguishing between species and those which have shown certain variability in our study have been selected. The following characters were studied: (1) revolution of the leaf margins; (2) number of papillae per cell at mid-leaf; (3) papilla length on cells at mid-leaf; (4) papilla shape on cells at mid-leaf; (5) colour of the hair-point; (6) length of the hair-point; (7) ornamentation of the hair-point; (8) size of the middle laminal cells; (9) shape of the leaf apex; (10) colour of the leaf apex; (11) papilla shape on the abaxial side of the costa; (12) papilla length on the abaxial side of the costa (13) length of the hyaline basal area in the leaf lamina, and (14) orientation of leaves when moist.

Qualitative variables were assessed using Chi-Square contingency tables to determine the independence and significance of the characters, while the Cramer (V_{Cramer}) coefficient was used to determine the association between the variables. For quantitative variables, we used analysis of variance (ANOVA). All statistical analyses were carried out with the SPSS program 9.0 version (SPSS Base 9.0 for Windows User's Guide, 1999).

RESULTS

(1). *Revolute leaf margins.* All taxa included have revolute leaf margins, but the principal variation is in the length of this revolute margin. The relationship between the species and the length of the revolute margin is significant (χ^2, $P < 0.05$; $V_{Cramer} = 0.569$, $P < 0.05$). This character is useful to separate *S. calcicola,* where the revolute margin only extends to two thirds of the leaf length, from the rest of the species of this group, where the revolute margin reaches to the apex (Fig. 1A).

(2) (3) and (4). *Number, length and shape of papillae on cells at mid-leaf*. This important assemblage of

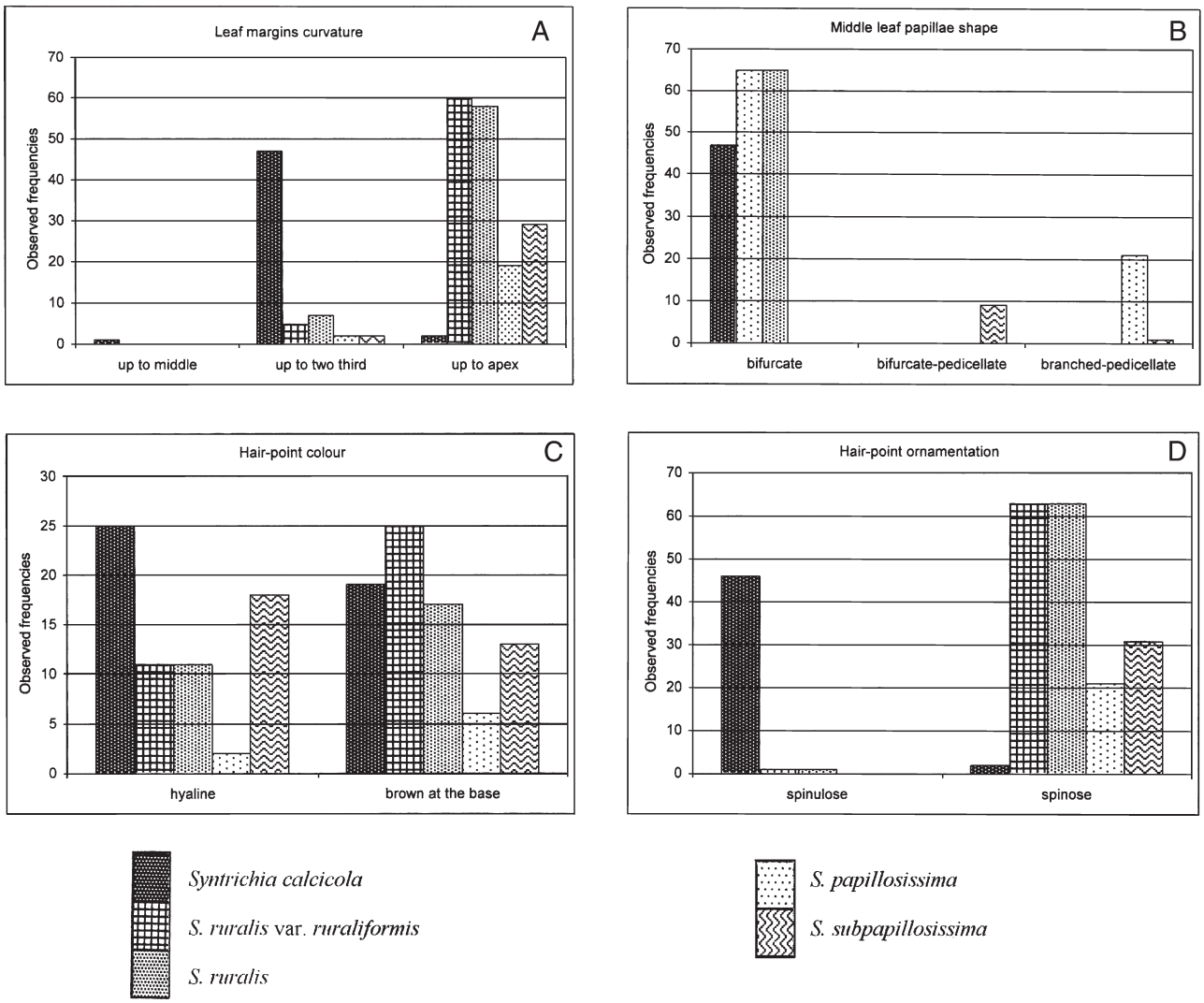


Figure 1. Observed frequencies (absolute values) in *Syntrichia* species for: A. Recurvature of the leaf margins; B. Shape of papillae on cells at mid-leaf; C. Hair-point colour; D. Hair-point ornamentation.

characters has been poorly understood for many years. Leaf papillosity is of importance not only for species determination in the Ruralis group, but also in all members of the genus *Syntrichia*. Thus, *S. virescens* (De Not.) Ochyra and *S. minor* (Bizot) M.T. Gallego *et al*. are two related species which can be easily distinguished by the type and number of papillae per cell (Gallego *et al*., 2000). This is also the case for *S. princeps* (De Not.) Mitt. and *S. echinata* (Schiffn.) Herrnst. & Ben-Sasson (Herrnstadt *et al*., 1982) and for *S. papillosa* (Wilson) Jur. and *S. subpapillosa* (Cardot & Broth.) Matteri (Matteri, 1994). In recent years many authors have considered leaf papillosity to be very useful and not only in Pottiaceae (cf. Hedenäs, 1994).

The number of papillae per cell ranges from one (*S. papillosissima*) to eight (*S. ruralis*), on both the abaxial and adaxial side of the leaf. This character is strongly associated with the species (ANOVA, $P < 0.05$) (Table 1, Fig. 3A).

The papillae length varies from 2.5 µm (*S. ruralis* var. *ruraliformis*) to 15 µm (*S. papillosissima*) and is also strongly associated with the species (ANOVA, $P < 0.05$) (Table 1, Fig. 3B).

The papillae shape ranges from bifurcate and not pedicellate (*S. calcicola*, Fig. 6) to pedicellate and branched (*S. subpapillosissima*, Fig. 19), sometimes star-shaped (*S. papillosissima*, Fig. 15). A strong association between this variable and the species is observed ($\chi^2, P < 0.05; V_{Cramer} = 0.850, P < 0.05$) (Fig. 1B).

(5) (6), and (7). *Colour, length and ornamentation of the hair point*. Hair-point colour does not have

diagnostic value, since all taxa have hyaline hair-points that are sometimes brown at the base. Frahm (1994) used the colour of the hair-point at the base as a taxonomic character in order to differentiate *Tortula densa* (often reddish to 1/2 of its length) from *T. calcicolens* W.A. Kramer (hair-point hyaline throughout). Nevertheless, in the studied samples this character has not been shown to have any taxonomic value, due to its variability within populations. There is no association between this character and the species (χ^2, $P > 0.05$) (Fig. 1C).

The hair-point length varies from 0.2 to 4 mm. This character is useful for distinguishing *S. calcicola*, which has the shortest hair-points (0.2–1.7 mm) (Table 1, Fig. 3C). In *S. subpapillosissima* the hair-point can reach as long as 4 mm. There is a strong

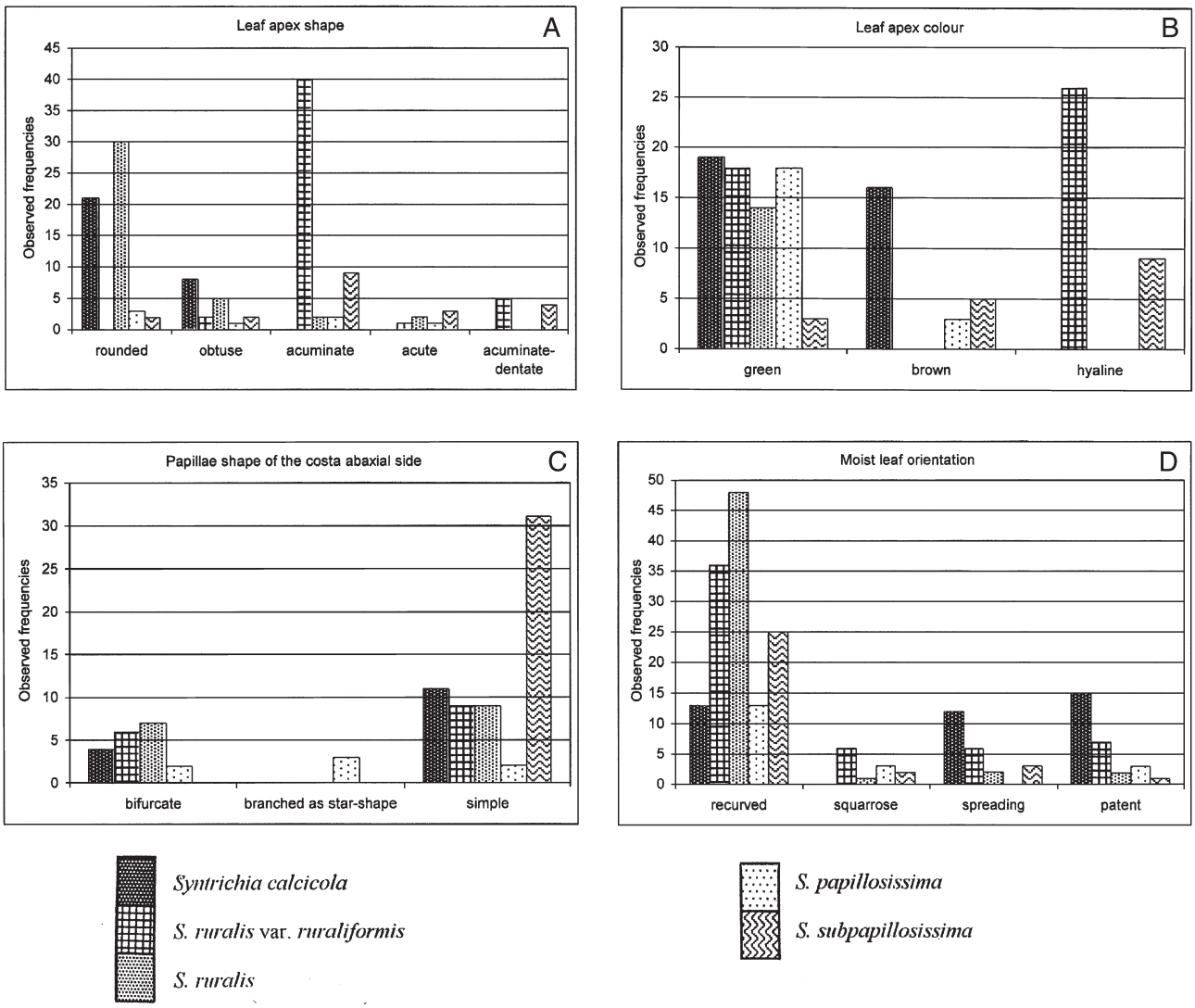


Figure 2. Observed frequencies (absolute values) in *Syntrichia* species for: A. Leaf apex shape; B. Leaf apex colour; C. Shape of papillae on the abaxial side of the costa; D. Orientation of the distal leaves when moist.

Figure 3. Average values of the different quantitative variables of *Syntrichia* species used in the analysis (mean and 95% C.L. for samples of six or more specimens). A. Number of papillae per cell in the middle part of the leaf; B. Length of the papillae in the middle part of the leaf; C. Length of the hair-point; D. Width of the cells in the middle part of the leaf; E. Length of papillae on the abaxial side of the costa; F. Length of the basal hyaline area in the leaf lamina.

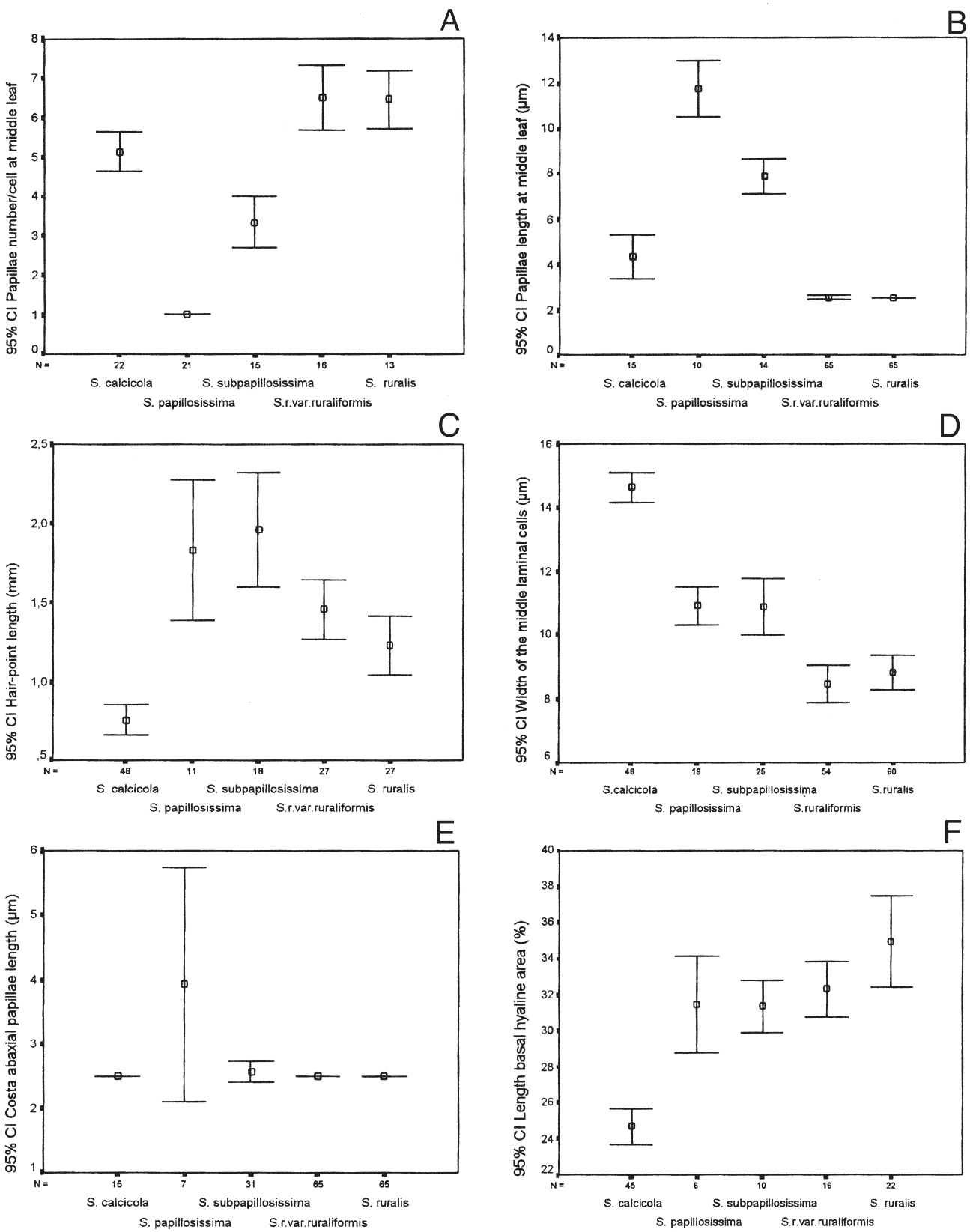

A
95% CI Papillae number/cell at middle leaf
N = 22 21 15 16 13
S. calcicola S. subpapillosissima S. ruralis
S. papillosissima S.r.var.ruraliformis
B
95% CI Papillae length at middle leaf (µm)
N = 15 10 14 65 65
S. calcicola S. subpapillosissima S. ruralis
S. papillosissima S.r.var.ruraliformis
C
95% CI Hair-point length (mm)
N = 48 11 18 27 27
S. calcicola S. subpapillosissima S. ruralis
S. papillosissima S.r.var.ruraliformis
D
95% CI Width of the middle laminal cells (µm)
N = 48 19 25 54 60
S.calcicola S. subpapillosissima S.ruralis
S. papillosissima S.ruraliformis
E
95% CI Costa abaxial papillae length (µm)
N = 15 7 31 65 65
S. calcicola S. subpapillosissima S. ruralis
S. papillosissima S.r.var.ruraliformis
F
95% CI Length basal hyaline area (%)
N = 45 6 10 16 22
S. calcicola S. subpapillosissima S. ruralis
S. papillosissima S.r.var.ruraliformis

Table 1. Quantitative morphological variables in *Syntrichia* species. (*N* = number of samples studied; Mean and 95% Confidence Limits (C.L.) for samples)

Variables	Taxa	*N*	Mean
Length of revolute leaf margin	*S. calcicola*	50	0.61 ± 0.022
	S. papillosissima	21	0.96 ± 0.051
	S. subpapillosissima	31	0.97 ± 0.035
	S. ruralis var. *ruraliformis*	65	0.96 ± 0.026
	S. ruralis	65	0.95 ± 0.030
Number of papillae per cell at the middle of the leaf	*S. calcicola*	22	5.13 ± 0.487
	S. papillosissima	21	1 ± 0
	S. subpapillosissima	15	3.3 ± 0.594
	S. ruralis var. *ruraliformis*	16	6.5 ± 0.759
	S. ruralis	13	6.46 ± 0.651
Hair point length (mm)	*S. calcicola*	48	0.75 ± 0.097
	S. papillosissima	11	1.83 ± 0.393
	S. subpapillosissima	18	1.96 ± 0.338
	S. ruralis var. *ruraliformis*	27	1.45 ± 0.181
	S. ruralis	27	1.22 ± 0.175
Papilla length at the middle of the leaf (μm)	*S. calcicola*	15	4.33 ± 0.890
	S. papillosissima	10	11.75 ± 1.045
	S. subpapillosissima	14	7.89 ± 0.698
	S. ruralis var. *ruraliformis*	65	2.53 ± 0.075
	S. ruralis	65	2.50 ± 0
Middle laminal cell width (μm)	*S. calcicola*	48	14.63 ± 0.461
	S. papillosissima	19	10.92 ± 0.557
	S. subpapillosissima	25	10.90 ± 0.843
	S. ruralis var. *ruraliformis*	54	8.47 ± 0.555
	S. ruralis	60	8.83 ± 0.526
Papilla length on the abaxial side of the costa (μm)	*S. calcicola*	15	2.5 ± 0
	S. papillosissima	7	3.92 ± 1.457
	S. subpapillosissima	31	2.58 ± 0.158
	S. ruralis var. *ruraliformis*	65	2.5 ± 0
	S. ruralis	65	2.5 ± 0
Length of the hyaline area formed by the basal cells (% with regard to total leaf length)	*S. calcicola*	45	24.68 ± 0.960
	S. papillosissima	6	31.50 ± 2.045
	S. subpapillosissima	10	31.37 ± 1.261
	S. ruralis var. *ruraliformis*	16	32.33 ± 1.416
	S. ruralis	22	34.93 ± 2.370

association between the hair point length and the species (ANOVA, $P < 0.05$).

The hair-point ornamentation also separates *S. calcicola* (spinulose) from the remaining taxa in the Ruralis complex (strongly spinose). Similarly, there is a strong association between this character and the species (χ^2, $P < 0.05$; $V_{Cramer} = 0.947$, $P < 0.05$) (Fig. 1D).

(8). *Size of the mid-lamina cells.* The width of the mid-lamina cells varies from 5 μm (*S. ruralis*) to 17.5 μm (*S. calcicola*) and was used to indicate the cell size, since the length is more or less constant in all the species. A strong association between the species and the width of mid-lamina cells has been observed (ANOVA, $P < 0.05$) (Table 1, Fig. 3D).

(9) and (10). *Shape and colour of the leaf apex*. There is a strong association between the taxon and the leaf apex shape (χ^2, $P < 0.05$; $V_{Cramer} = 0.463$, $P < 0.05$). The leaf apex ranges from rounded in *S. ruralis* var. *ruralis* and *S. calcicola* to acuminate, sometimes dentate in *S. ruralis* var. *ruraliformis* and *S. subpapillosissima* (Fig. 2A).

The colour of the leaf apex is generally the same as that of the lamina, although it is sometimes hyaline. This is also strongly associated with the species (χ^2, $P < 0.05$; $V_{Cramer} = 0.557$, $P < 0.05$). When present, this character is useful to separate the only two species that develop a hyaline apex (*S. ruralis* var. *ruraliformis* and *S. subpapillosissima*) from the rest (Fig. 2B).

(11) and (12). *Papilla shape and length on the abaxial side of the costa*. The papilla shape is strongly associated with the species (χ^2, $P < 0.05$; $V_{Cramer} = 0.557$, $P < 0.05$) and ranges from simple (*S. subpapillosissima*) to bifurcate, sometimes branched-pedicellate (*S. papillosissima*) (Fig. 2C). The papilla length ranges from 2.5 µm (*S. ruralis*, *S. calcicola*) to 7.5 µm (*S. papillosissima*). There is also a strong association between papilla length and the species (ANOVA, $P < 0.05$) (Table 1, Fig. 3E).

(13). *Length of the hyaline basal area in the leaf lamina*. This character varies from a minimum of 19% of the total leaf length in *S. calcicola* to 45% in *S. ruralis*. In *S. calcicola,* the hyaline basal area usually reaches to no more than 25% of the leaf length, but we have observed some samples in which the hyaline basal area reaches 33% of the total leaf length. Despite this, there is a strong association between the length of the hyaline basal area and the species (ANOVA, $P < 0.05$). This character is useful for separating *S. calcicola* from the rest of the species, in which the hyaline basal area clearly and consistently exceeds 25% of the total leaf length (Table 1, Fig. 3F). This character was also used by Kramer (1980) to separate *S. calcicola* (short hyaline basal area) from *S. ruralis* (long hyaline basal area).

(14). *Orientation of leaves when moist*. The oldest leaves are usually spreading or even patent in the basal part of the stem in all species, whereas the orientation of the leaves in the upper part of the stem has frequently been used to differentiate species. Frahm (1994) separates *S. ruralis* s.str., with leaves squarrose when moist, from the rest of the taxa of this complex, with leaves erect when moist. However, in all the material of these species studied by us the leaves vary from recurved to squarrose when moist. *S. calcicola* is the only species which shows slight differences in this character, with spreading or patent leaves that are very atypical for the rest of the species. There is a strong association between this character and the species (χ^2, $P < 0.05$; $V_{Cramer} = 0.318$, $P < 0.05$). However, the V of Cramer coefficient is very low and consequently the degree of association between the variables 'species' and 'orientation of the leaves when moist' is small (Fig. 2D).

A synopsis of the main morphological gametophytic characters is shown in Table 2.

TAXONOMY

(1) *Syntrichia calcicola* J.J. Amann, Fl. Mousses Suisse 2: 119. 1918. (Figs 4–7)

Type. Germany, Essen, Hofgeismar, 15.v. 1905, *Grebe* (lectotype JE!, selected here).

Tortula calcicola Grebe, Hedwigia 49: 1910 [1909], *illegitimate, later homonym* (article 53.1, St. Louis Code) [*Tortula calcicola* (Hampe) Mitt., Trans. Roy. Soc. Victoria, 19: 60. 1882; basionym: *Trichostomum calcicola* Hampe, Icon. Mus. Nov: 29. 1884 = *Didymodon australasiae* (Hook. & Grev.) R.H. Zander, cf. Sollman (1995)].

Syntrichia ruralis var. *calcicola* Mönk., Laubm. Eur. 312. 1927.

Tortula ruralis ssp. *calcicola* Giacom., Atti Ist. Bot. Laboratory Crittog. University Pavia ser. 5, 4: 217. 1947.

Tortula ruralis var. *calcicola* Barkman, Phyt. Ecol. Cryp. Epiphyte: 625. 1958.

Tortula calcicolens W.A. Kramer, Bryophyt. Biblioth. 21: 90. 1980.

Tortula ruralis var. *calcicolens* (W.A. Kramer) Düll, Bryol. Beitr. 4: 83. 1984.

Syntrichia ruralis ssp. *calcicolens* (W.A. Kramer) Düll, Bryol. Beitr. 8/9: 56. 1992.

Tortula ruralis var. *densa* Velen., Rozpr. České Akad. Císaře Františka Josefa Vědy, Tř. 2, Vědy Math. Přír. 2,6: 166. 1897. Type: Czech Republic, Bohemia, Revnice, ix. 1893, *Velenovsky (*lectotype PRC!, selected by Frahm, 1994), **syn. nov.**

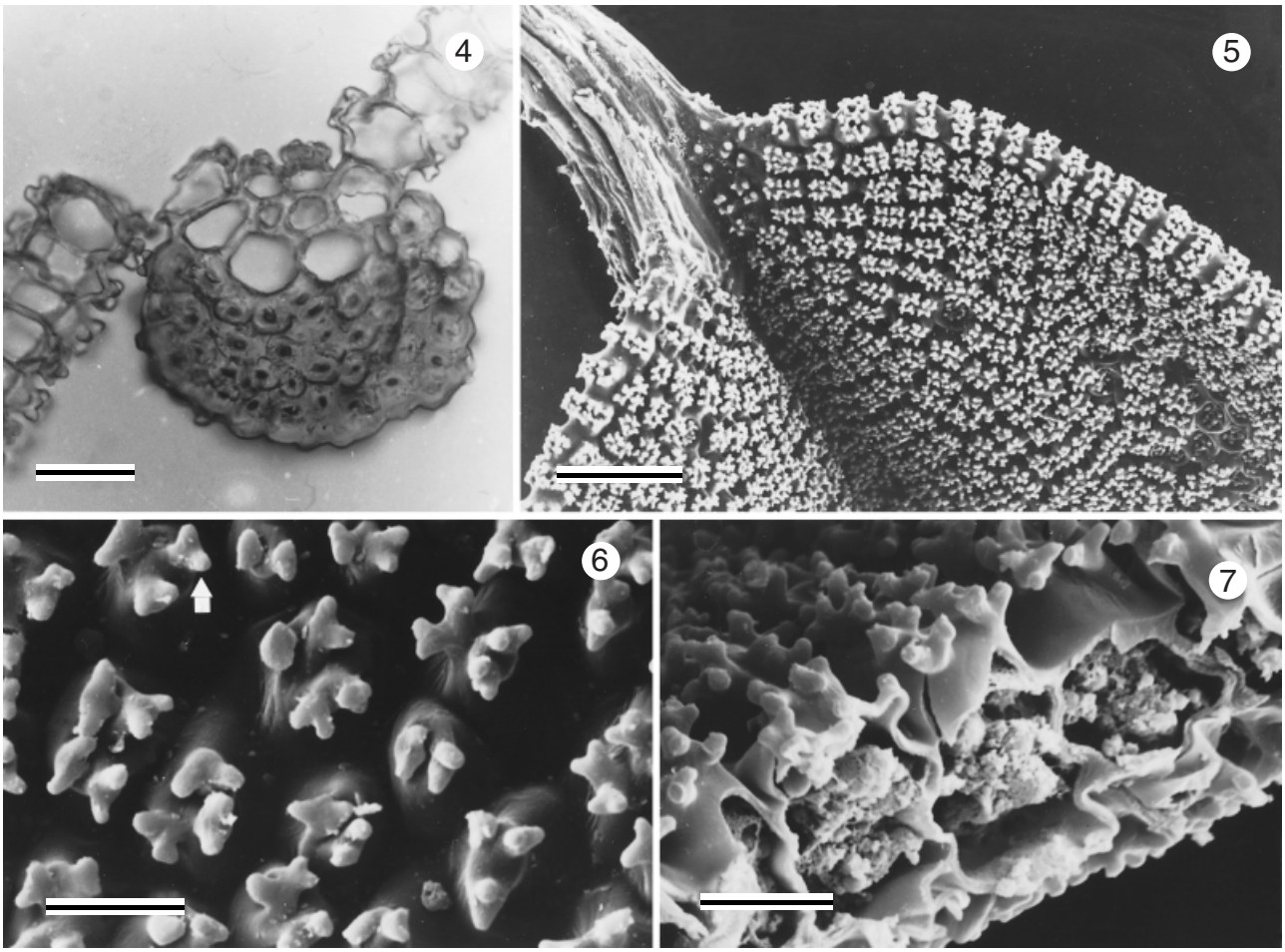
Tortula densa (Velen.) J.-P. Frahm, Fragm. Florist. Geobot. 39(2): 393. 1994.

PLANTS 0.4–2.3 cm high. LEAVES spirally twisted when dry, spreading or patent when moist, 1.7–3.8 × 0.6–1.6 mm, ovate-lingulate, lingulate, or elliptical-lingulate; apex generally rounded, sometimes obtuse, not tapering into hair point, not hyaline; margins revolute from base to 2/3 of the leaf, rarely to the middle; hyaline hair point spinulose, sometimes brown at base, 0.2–1.7 mm long; costa 70–112.5 µm wide in transverse section, with (1)2–3 guide cell rows (2)3–5 dorsal stereid rows, without hydroids, on the abaxial side with simple or bifurcate papillae, 2.5 µm high; upper and middle laminal cells quadrate, rectangular or hexagonal, thick walls, 12.5–15(17.5) × 12.5–15(17.5) µm, with 4–6(8) bifurcate, not pedicellate papillae per cell, 2.5–7.5 µm high; basal cells hyaline, rectangular, 62.5–92.5 × 12.5–25 µm, forming a clearly differentiated hyaline area up to 19–25(33)% of leaf length; marginal basal cells chlorophyllose, in 8–14 columns.

Distribution. Europe, south-western Asia and Macaronesia (Düll, 1984, 1992), North Africa (Ros *et al*., 2000).

Table 2. A synopsis of the main morphological gametophytic characters of the taxa of *Syntrichia ruralis* complex recognized in the studied area

	S. calcicola	*S. ruralis*	*S. papillosissima*	*S. subpapillosissima*
Revolute leaf margins	to 2/3	Near the apex	Near the apex	Near the apex
Papillosity on cells at mid-leaf				
Number per cell	4–6 (8)	(4) 6–8	1	(2) 4–6
Length	2.5–7.5 µm	2.5 µm	(7.5) 10–12.5 (15) µm	(5) 7.5–10 µm
Shape	Bifurcate, not pedicellate	Bifurcate, not pedicellate	Star-shaped, pedicellate	Bifurcate, pedicellate
Hair-point				
Length	0.2–1.7 mm	0.4–2.8 mm	0.5–4 mm	1–4 mm
Ornamentation	Spinulose	Strongly spinose	Strongly spinose	Strongly spinose
Width mid-laminal cells	12.5–15 (17.5) µm	(5) 7.5–10 (12.5) µm	10–12.5 µm	(7.5) 10–12.5 µm
Leaf apex	Rounded, no hyaline	Rounded, not hyaline (var. *ruralis*); acuminate, tapering into hair-point, generally hyaline (var. *ruraliformis*)	Rounded or acuminate, not hyaline	Acuminate, tapering into hair-point, usually hyaline
Papillae on the abaxial side of the costa				
Shape	Simple or bifurcate	Simple or bifurcate	Bifurcate	Simple
Length	2.5 µm	2.5 µm	2.5–7.5 µm	2.5–5 µm
Length of the hyaline basal area formed by the paracostal cells in the leaf lamina	19–25 (33)% of the laminal length	27–45% of the laminal length	29–45% of the laminal length	28–33% of the laminal length
Orientation of leaves when moist	Spreading or patent	Recurved or squarrose	Recurved or squarrose	Recurved



Figures 4–7. *Syntrichia calcicola* MUB 10382. Fig. 4. Transverse section (TS) of the leaf. Scale bar = 30 μm. Fig. 5. Leaf apex. Scale bar = 50 μm. Fig. 6. Lamina cells. Scale bar = 10 μm. Fig. 7. TS of the lamina cells. Scale bar = 10 μm.

Selected material studied. FRANCE: Dep. Haute-Saône, Faucogney Felsen und Brücken mauern an der Strasse nach Esmouliéres, *c*. 450 m, 23.iii. 1993, *Frahm* (*sub T. densa*, *in* Herb. J.P. Frahm). GREECE: Oros Parnitha, 750 m, 14.iii. 1999, *Cano et al*. (MUB 11360). Carretera de Epidauros a Methana, prox. a Fanari, 400 m, 15.iii. 1999, *Cano et al*. (MUB 11363). ITALY: Reg. Marche, prov. Macerata, monti Sibillini, *c*. 4 km SE of Visso on road to Castelsantago, 17.vii. 1985, *Jury et al*. (BCB 29993). Emilia-Romagna, prov. Ravenna, Apennino Tosco-Emiliano, Zattaglia, Mt. Mauro, 500–520 m, 12.v. 1995, *Nimis & Poelt* (GZU). MOROCCO: Ifrane,*c*. 1700 m, 8.iv. 1969, *Davis & Davis* (BM). Alto Atlas, Toubkal, subida desde Armt hacia el refugio de Nelthner, 2000 m, 19.vi. 1998, *Cano et al*. (MUB 8394). SPAIN: Albacete, Paterna del Madera, 1100 m, 22.ii. 1991, *Martínez-Sánchez & Heras* (MUB 4579). Granada, Puerto de la Mora, 15.xii. 1989, *Varo* (BCC 1382). Islas Baleares, Mallorca, El Nudo de la Corbata, 725 m, 15.iv. 1999, *Cano et al*. (MUB 10382). Murcia, Cehegín, Sierra de la Lavia, 950–1110 m, 5.ii. 1983, *Ros* (MUB 3339). TURKEY: Prov. Denizli, Cukurköy, 1200 m, 4.iv. 1956, *Davis & Polunin* (E).

(2) *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr, Ind. Mus. Pl. Crypt. 2., 1803. (Figs 8–10)

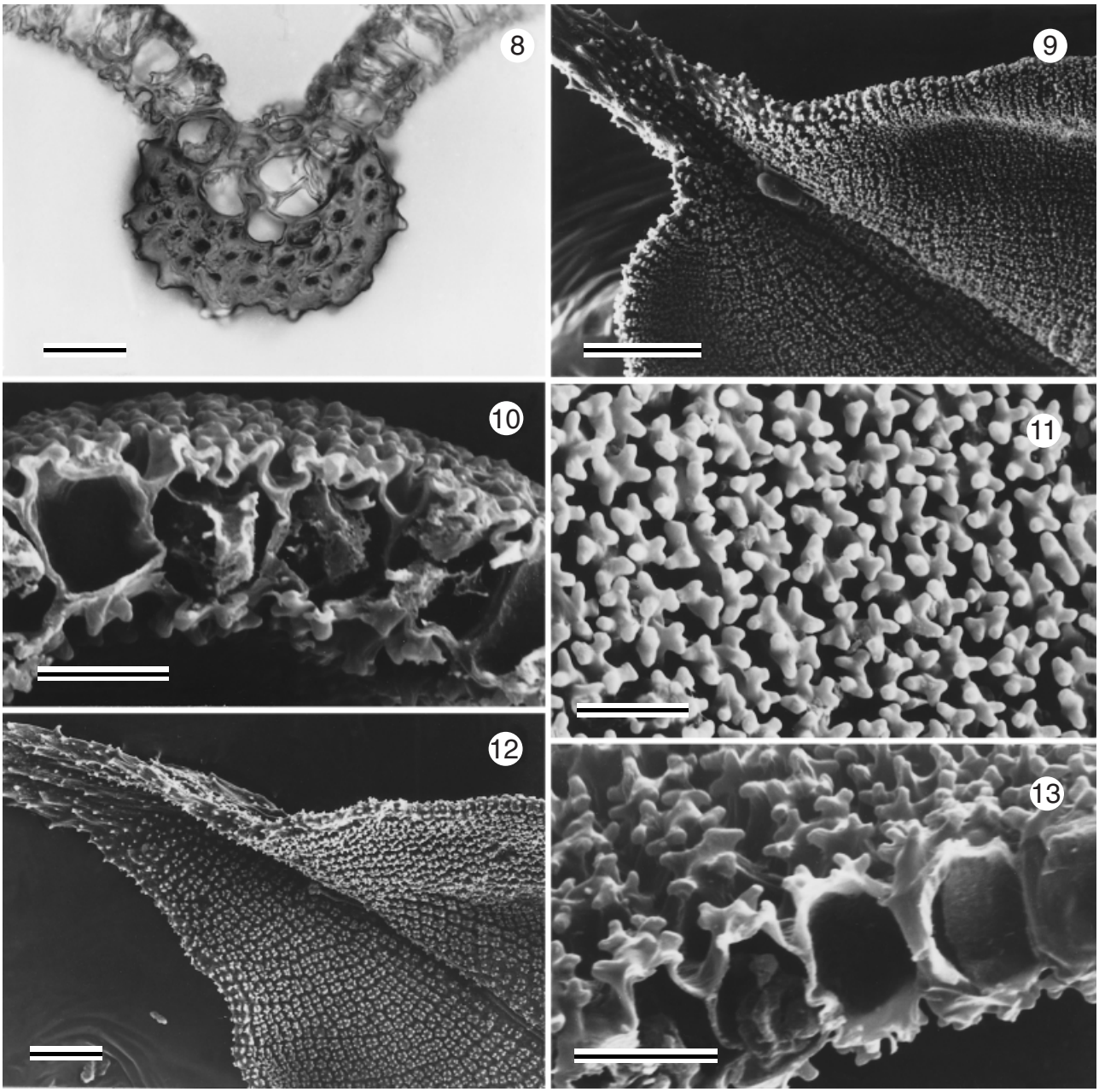
Type. *Bryum rurale* specimen marked 1c (lectotype G, selected by Geissler & Frahm, 1995).

Basionym. *Barbula ruralis* Hedw., Spec. Musc. 121. 1801.

Bryum ruralis (Hedw.) With., Syst. Arr. Brit. Pl., ed. 4, 3: 819. 1801.

Tortula ruralis (Hedw.) P. Gaertn., B. Mey. & Schreb., Oek. Techn. Fl. Wetterau 3(2): 91. 1802.

Tortula ruralis var. *vulgaris* Hook. & Grev., Edinburgh J. Sci. 1: 293. 1824, *nom. illeg. incl. typ. spec.*



Figures 8–13. *Syntrichia ruralis* MUB 2717. Fig. 8. Transverse section (TS) of the leaf. Scale bar = 30 µm. Fig. 9. Leaf apex. Scale bar = 100 µm. Fig. 10. TS lamina cells. Scale bar = 10 µm. *Syntrichia ruralis* var. *ruraliformis* MUB 1139. Fig. 11. Lamina cells. Scale bar = 10 µm. Fig. 12. Leaf apex. Scale bar = 50 µm. Fig. 13. TS lamina cells. Scale bar = 10 µm.

Barbula ruralis var. *subintermedia* Renauld & Cardot, Rev. Bryol. 19: 84. 1892.

Tortula ruralis ssp. *alaskana* (Kindb.) Paris, Ind. Bryol., ed. 2, 5: 56. 1906.

Tortula ruralis var. *fulva* Györffy, Magyar Bot. Lapok. 5: 342. 1906.

Tortula ruralis var. *subintermedia* (Renauld & Cardot) Parl., Ind. Bryol., ed. 2, 5: 57. 1906.

Tortula subintermedia (Renauld & Cardot) Cardot, Bryologist 13: 54. 1910.

Syntrichia ruralis var. *glacialis* J.J. Amann, Bull. Soc. Vaudoise Sc. Nat. 53: 90. 1920. Type: Switzerland, prés la Cabane Britannia, *Amann* (holotype ZT!), **syn. nov.**

PLANTS (0.6)1–5(8) cm high. LEAVES spirally twisted when dry, generally recurved to squarrose when

moist, sometimes spreading or patent in lower part of the stem, 2.2–3.8(5.4) × 0.5–1.5 mm, ovate-lingulate; apex rounded, obtuse, rarely acute or acuminate, not tapering into hair point, not hyaline; margins revolute from base to near the apex, sometimes to 2/3 of the leaf; hyaline hair point strongly spinose, rarely spinulose, sometimes brown at base, 0.4–2.8 mm long; costa 70–125 µm wide, in transverse section with (1)2–3 guide cell rows (2)4–5 dorsal stereid rows, without hydroids, on the abaxial side with simple or bifurcate papillae, 2.5 µm long; upper and middle laminal cells quadrate, rectangular or rounded, walls thin (5)7.5–10(15) × (5)7.5–10(12.5) µm, with (4)-6(8) bifurcate, not pedicellate papillae per cell, 2.5 µm long; basal cells hyaline, rectangular, 37–128 × 12.5–20 µm, forming a clearly differentiated hyaline area up to 27–45% of leaf length; marginal basal cells chlorophyllose, in (9)13–20 columns.

Distribution. Europe; north-east, east, south-western and Central Asia; North, Central and South Africa; Macaronesia; north-western and southern South America; North and Central America; Australia, Oceania (Düll, 1984, 1992); New Zealand (Beever *et al.,* 1992).

Selected material studied. ANDORRA: Riu Madriu-Tal bei Escaldes, *c*. 1300 m, 28.vii. 1966, *Pócs* (BM). BOSNIA HERZEGOVINA: Motajica, bei Davor, Rijeka-Graben, 20.vii. 1904, *Glowacki* (GZU). Mt. Vranica, in valle torrentis Borovnica, 1080 m, 9.vi. 1979, *Rusinska* (CANM 284888). BULGARIA: Montes de Rila, cima del monte Mussala, 270 m, 25.vii. 1993, *Ros & Düll* (MUB 4732). FRANCE: Savoie, Massif de la Vanoise, Pralognan, Vallée de Chaviéres, 1500 m, 18.viii. 1961, *Bonnot* (BCB 6114). Corse, Vizzavone, iv. 1938, *Mosseray* (BR 182256). GREECE: West-Mazedonien, Distr. Kozani, Pieria-Gebirge, 1600–1800 m, 11.vii. 1959, *Rechinger* (BM). Creta, near S. Nicolaos, Mt. Psycros, ix. 1971, *Holmen* (C). IRAN: Prov. Gorgan, Asterabad, prope Hadjilang, *c*. 2400–2600 m, 27.vii. 1948, *Rechinger & Rechinger* (BM). ITALY: Reg. Marche, prov. Macerata, Monti Sibillini, *c*. 4 km SE of Visso on road to Castelsantango, 740 m, 17.vii. 1985, *Jury et al*. (BM). Sicily, Mt. Etna, Portella Mandrazzi, south of Novara di Sicilia, *c*. 1100 m, iv. 1993, *Blockeel* (Herb. T.L. Blockeel 22/166). MOROCCO: Ifrane, 1760 m, 19.i. 1993, *Brugués* (BCB 31736). Bab Taza, ascensión al Jbel Bouhalla, 1700 m, 17.iii. 1997, *Cano et al*. (MUB 10884). PORTUGAL: Beira Alta, Serra da Estrella, Covão da Ametade, 1450 m, 9.iii. 1927, *Melo* (LISU 155029). Beira Litoral, Coimbra, Benfeita, Mata da Margaraça, 400–900 m, 8.v. 1985, *Sérgio & Santos e Silva* (LISU 155817). SPAIN: Albacete, sierra del Relumbrar, cerro de la Calva, 9.iii. 1986, *Heras & Ros* (MUB 2717). Málaga, Torcal de Antequera, 18.i. 1976, *Guerra & Varo* (MGC 40). Santa Cruz de Tenerife, La Palma, Caldera de Taburiente, Roque de los Muchachos, 2435 m, 26.vii. 2000, *Cano* (MUB 10383). Zaragoza, Bujaraloz, La Playa, 31.iii. 1977, *Casas* (BCB 26810). TURKEY: Prov. Hatay, dist. Belen (Amanus), Karlik tepe above Boguk Oluk, 1000–1200 m, 24.iv. 1957, *Davis & Hedge* (BM). Prov. Trabzon, 2 miles S. of Trabzon, 100 m, 16.v. 1960, *Henderson & Staiton* (E). YUGOSLAVIA: Montenegro, Crna Gora, Paß zw. Andrijevica und Babljak, 15.vii. 1974, *Mayrhofer* (GZU).

(3) *Syntrichia ruralis* var. *ruraliformis* (Besch.) Delogne, Ann. Soc. Belg. Microscop. 9: 177. 1885. (Figs 11–13)

Type. France, Dép. Nord, prope Dunkerque, 1.vi. 1864, *Bescherelle*. Dép. Maine et Loire, Angers, *de la Perraudière*. Barré, *de la Perraudière (*syntypes BM?, not seen).

Basionym. *Barbula ruraliformis* Besch., Bull. Soc. Bot. France 11: 335. 1864.

Barbula ruralis var. *ruraliformis* (Besch.) Husn., Fl. Mousses Nord-Ouest: 87. 1873.

Barbula ruralis ssp. *ruraliformis* (Besch.) Boulay, Musc. France: 404. 1884.

Tortula ruralis ssp. *ruraliformis* (Besch.) Dixon, Stud. Handb. Brit. Mosses: 188. 1896.

Tortula ruralis var. *ruraliformis* (Besch.) De Wild., Prodr. Fl. Belg. 2: 442. 1899.

Tortula ruraliformis (Besch.) Ingham, J. Bot. 41: 119. 1903.

Syntrichia ruraliformis (Besch.) Mans., Bull. Soc. Roy. Bot. Belgique 41(2): 184. 1904.

Tortula ruraliformis (Besch.) Grout, Moss. Hand-lens Microsc. 167. 1906.

Tortula ruralis var. arenicola Braithw., Brit. Moss Fl. 1: 226. 1885, *illegitimate, incl. typ. var*.

Syntrichia ruralis var. *arenicola* J.J. Amann, Fl. Mousses Suisse 2: 118. 1918, *illegitimate, incl. typ. var*.

Tortula ruralis var. *aciphylloides* Podp., Sborn. Klub. Prírod. Brno 5: 13. 1923.

Syntrichia ruralis var. *aciphylloides* (Podp.) Podp., Consp. 257. 1954.

Tortula ruralis var. *maritima* Rigaux, Cat. Pl. Vasc. Mouss. env. de Boulogne-sur-Mer: 36. 1877, *nom. nud.*

LEAVES ovate-lanceolate, lanceolate, sometimes ovate-lingulate; apex acuminate, rarely obtuse or acute, tapering into hair point, dentate or not, hyaline, sometimes with the same colour as the rest of the lamina. Other characters as *S. ruralis*.

Distribution. Europe; north-east, south-western and Central Asia; North America; East Africa (O'Shea, 1999); North Africa and Macaronesia (Düll, 1984).

Observations. This taxon can be primarily distinguished from *S. ruralis* by the shape and colour of the leaf apex, although Mishler (1994) does not consider these characters of taxonomic value. *S. ruralis* var. *ruraliformis* grows in soils rich in gypsum and very often in coastal dunes. Some authors assign this taxon to the rank of species (Steere, 1937; Dixon, 1970; Lawton, 1971; Nyholm, 1989; Frey *et al*., 1995) and others (Zander, 1993; Smith, 1978) to the rank of variety. In our study we have observed intermediate forms between *S. ruralis* and *S. ruraliformis* and for this reason consider the rank of variety more appropriate.

Selected material studied. BOSNIA HERZEGOVINA: Plivatal, oberhalb von Jezero, 28.vii. 1904, *Glowacki* (GZU). Südlich von Sarajevo, Podstok, 7.viii. 1904, *Glowacki* (GZU). CYPRUS: High on Papousa, 4000 ft., 10.v. 1962, *Meikle* (K). Kannoures Springs, 2.iv. 1974, *Meikle* (K). FRANCE: Vauclause, crêite du Pett Lubéron a l'entrée de la forêt en venant de Bonnieux, 700 m, 10.vi. 1984, *Hébrard* (MUB 1139). Nemours (Seine et Marne), v, *Bescherelle* (BM). GREECE: Prov. Voiotia, above the monastery Osios Loukas, 9.v. 1962, *Townsend* (K). Ráhes (dirección a Volos), 0 m, 22.iii. 1999, *Cano et al*. (MUB 11367). IRAN: Gilan, Persia borealis, Enseli, 24.iv. 1902, *Bornmüller & Bornmüller* (BM). Nr. Ardabil, 10 km E of Arpa Tappech, NW Iran, 1500 m, 14.viii. 1966, *Crisp* (BM). ITALY: Völlan S von Meran, an Glimmerschiefer, 10.v. 1884, *Glowacki* (GZU). MOROCCO: Ifrane, 1700 m, 8.iv. 1969, *Davis & Davis* (E). PORTUGAL: Aveiro, Vagueira, 16.viii. 1968, *Sérgio* (BCB 26922). Beira Litoral, Reserva Natural das Dunas de São Jacinto, 0 m, 13.iv. 2001, *Cano* (MUB 11404). SPAIN: Asturias, dunas de Luanco, 7.vii. 1977, *Casas* (BCB 6154). Badajoz, Sierra de Tentudia, Cabeza de Vaca, 24.iv. 1992, *Casas & Cros* (BCB 31225). Santa Cruz de Tenerife, La Palma, Caldera de Taburiente, Degollada de Hoyo Verde, 26.vii. 2000, *Cano* (MUB 10384). Teruel, Palomita, La Loma Gorda, 1600 m, 27.viii. 1978, *Puche* (VAB 1252). TURKEY: Prov. Adana, dist. Pozanti, Bürücek, 1300 m, 3.IV. 1957, *Davis & Hedge* (E). Prov. Hatay, dist. Belen (Amanus), 1400 m, 24.iv. 1957, Davis & Hedge (E). SLOVENIA: Bachergebire nahe Maribor, Frauhein, 28.x. 1901, *Glowacki* (GZU).

(4) *Syntrichia papillosissima* (Copp.) Loeske, Hedwigia 49: 44. 1910. (Figs 14–16)

Type. Greece, Aroania, Mt. Kelmos, 2100–2300 m, 12.viii. 1906, *Maire & Petitmengin 3403* (holotype NCY?, not seen).

Basionym. *Barbula papillosissima* Copp., Bull. Séances Soc. Sci. Nancy, sér. 3, vol. 8, fasc. 3: 314. 1907.

Tortula papillosissima (Copp.) Broth., Nat. Pfl. 1(3): 1196. 1909.

Barbula ruralis var. *hirsuta* Venturi, Rev. Bryol. 17: 52. 1890. Type: Italy, Sardegna, montis Genargentu, G. *Venturi*. (lectotype TR!, selected here).

Tortula ruralis var. *hirsuta* (Venturi) Paris, Ind. Bryol., ed.2, 5: 57. 1906.

Tortula hirsuta (Venturi) Laz. in Laz., Bjull. Moskovsk. Obsc. Isp. Prir. Otd. Biol. 73(2): 146. 1968.

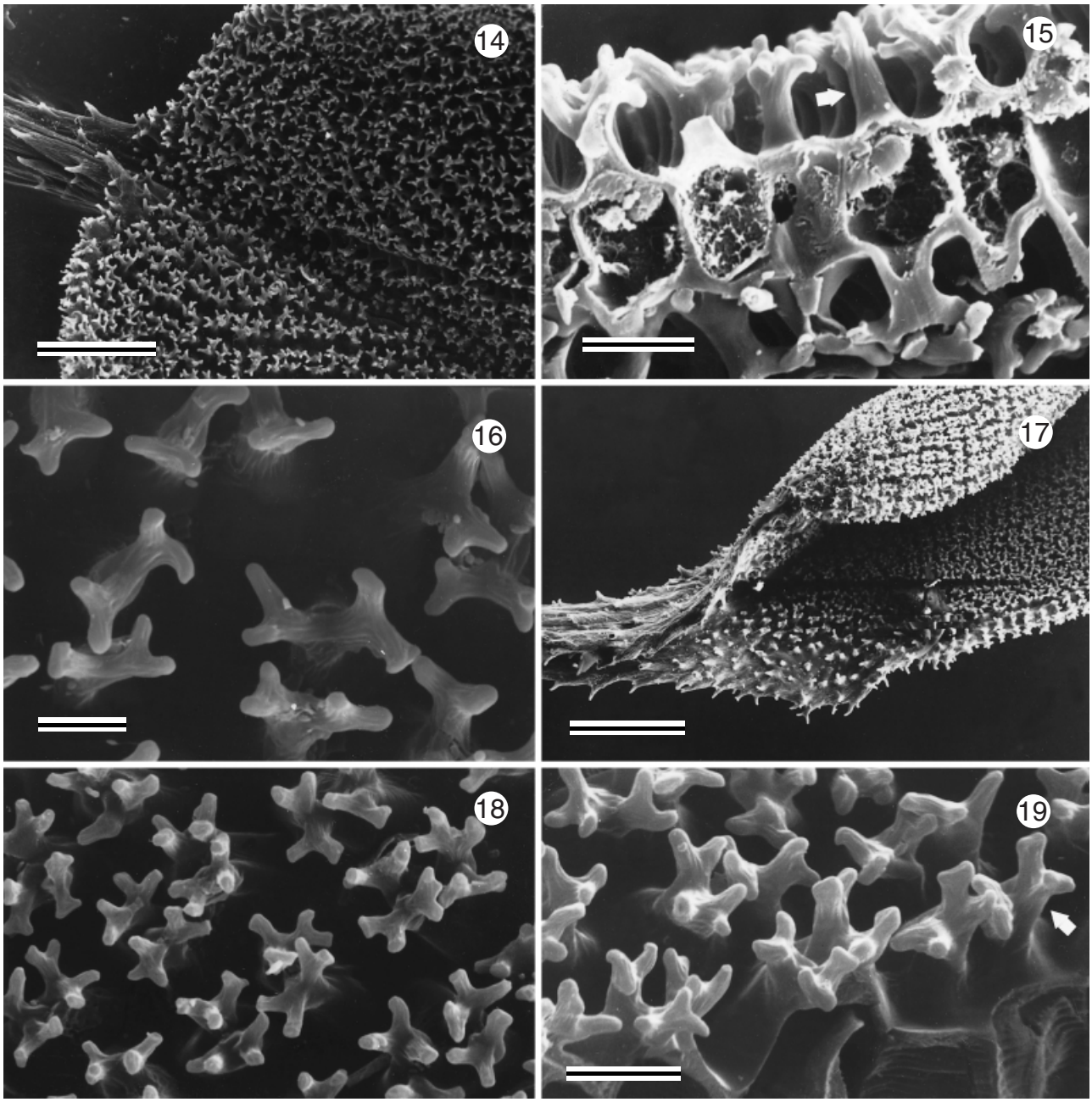
Tortula ruralis ssp. *hirsuta* (Venturi) W.A. Kramer, Bryophyt. Biblioth. 21: 126. 1980.

Syntrichia ruralis var. *hirsuta* (Venturi) Podp., Consp. 256. 1954.

PLANTS (1)2–5(8) cm high. LEAVES lightly spirally twisted when dry, usually recurved or squarrose, sometimes patent in lower part of the stem when moist, 3–4.5 × 0.8–1.5 mm, ovate, ovate-lingulate or ovate-elliptical; apex usually rounded or acuminate, rarely obtuse or acute, not tapering into hair point, not hyaline; margins revolute from base to near the apex, sometimes to 2/3 of the leaf; hyaline hair point strongly spinose, brown at base, 0.5–4 mm long; costa 92–138 µm wide, in transverse section with (1)2–3(4) guide cell rows, (2)3–5 dorsal stereid rows, without hydroids, on the abaxial side papillae pedicellate and branching as a star-shape, or bifurcate, rarely simple, 2.5–7.5 µm long; upper and middle laminal cells quadrate, rectangular or hexagonal, thin walls, 10–12.5 × 10–12.5 µm, with 1 pedicellate, branched, star-shaped papilla per cell (7.5)10–12.5(15) µm long; basal cells hyaline, rectangular, sometimes sinuose, 75–100 × 12.5–17.5 µm, forming a clearly differentiated hyaline area up to 29–45% of leaf length; marginal basal cells chlorophyllose, in 10–24 columns.

Distribution. Europe; north-east, central and south-western Asia; North America and North Africa (Düll, 1984, 1992).

Selected studied material. CYPRUS: Eastern Troodos, northern slopes of Mt. Kionia, 1100–1500 m, 28.iii. 1997, *Blockeel* (Herb. T.L. Blockeel 26/105). MOROCCO: Tizi-n′-Test pass., 2100 m, 31.iii. 1969, *Davis & Davis* (BM). Grand Atlas, Ravin de Tarfleht, 15.iv. 1952, *Pazenat* (E). PORTUGAL: Miranda do Douro, 400 m, 15.iv. 2001, *Cano* (MUB 11405). SPAIN: Madrid, Ciempozuelos, 550 m, 31.iii. 1984, *Cros et al*. (BCB 30552). Murcia, sierra de Moratalla, barranco Las Conchas, 1400–1500 m, 16.iv. 1992, *Ros* (MUB 3357). Soria, Tiesmes, 8.viii. 1995, *Casas* (BCB 43841). Málaga, Ronda, Puerto del Viento, 13.viii. 2000, *Guerra* (MUB 10410). SYRIA: Feesen (Dist. Hermel), 3000 ft., 24.iv. 1943, *Davis* (BM). TURKEY: Prov. Adana, dist. Bahce (N Amanus) between Haruhiye and Fevzipass, 1150 m, 18.iv. 1975, *Davis & Hedge* (BM). Alpes Alexandri, in valle fl. Schamsi, 29.v. 1896, *Brotherus* (BM).



Figures 14–19. *Syntrichia papillosissima* MUB 3357. Fig. 14. Leaf apex. Scale bar = 50 μm. Figure 15. TS lamina cells (arrow shows a star-shaped papilla). Scale bar = 10 μm. Fig. 16. Detail of the leaf papillosity. Scale bar = 5 μm. *Syntrichia subpapillosissima* MGC 885. Fig. 17. Leaf apex. Scale bar = 50 μm. Figs 18 and 19. Detail of the leaf papillosity (arrow shows a bifurcate and pedicellate papilla). Scale bars = 10 μm.

(5) ***Syntrichia subpapillosissima*** (Bizot & R.B. Pierrot ex W.A. Kramer) M.T. Gallego & J. Guerra, **stat. nov.** (Figs 17–19)

Type. Algeria, djebel Belezma, 15 km W Batna, 1950–2000 m, 27.ii. 1967, *Balázs (*lectotype herb. M. Bizot, selected by Kramer (1980); isolectotype EGR!).

Basionym. *Tortula ruraliformis* var. *subpapillosissima* Bizot & R.B. Pierrot ex W.A. Kramer, Bryophyt. Biblioth. 21: 120. 1980.

Tortula ruralis var. *subpapillosissima* Bizot & R.B. Pierrot, Acta Bot. Acad. Sci. Hung. 18: 11. 1973, *nom. inval.* (art. 37.3, St. Louis Code)

Table 3. Key to the taxa of the *Syntrichia ruralis* complex

1. Margins revolute to 2/3 of the leaf, rarely to the middle. Middle laminal cells 12.5–17.5 µm wide	**1.** *S. calcicola*
1. Margins revolute to near the leaf apex, sometimes to 2/3. Middle laminal cells (5)7.5–12.5 µm wide	**2.**
2. Papillae on mid-lamina cells not pedicellate, 2.5 µm high	**3.**
2. Papillae on mid-lamina cells pedicellate, 5–12.5(15) µm high	**4.**
3. Leaf apex not hyaline, generally rounded, not tapering into hair-point	**2.** *Syntrichia ruralis* var. *ruralis*
3. Leaf apex generally hyaline and acuminate, tapering into hair point	**3.** *Syntrichia ruralis* var. *ruraliformis*
4. Middle laminal cells with only 1 papilla, with stellate branching at the apex. Papillae on the abaxial side of the costa with stellate branching or bifurcate, rarely simple, 2.5–7.5 µm high	**4.** *S. papillosissima*
4. Middle laminal cells with more than 1 papilla, bifurcate, rarely with stellate branching at the apex. Papillae on the abaxial side of the costa simple, 2.5–5 µm high	**5.** *S. subpapillosissima*

Syntrichia ruraliformis var. *subpapillosissima* (Bizot & R.B. Pierrot [ex W.A. Kramer]) Ochyra, Fragm. Florist. Geobot. 37: 212. 1992.

Syntrichia ruralis var. *subpapillosissima* (Bizot & R.B. Pierrot [ex W.A. Kramer]) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 270. 1993.

Tortula ruralis var. *submamillosa* W.A. Kramer, Bryophyt. Biblioth. 21: 127. 1980. Type: Turkey, Vil. Yozgat, 90 km E of Yozgat, W of Ologozu, 1240 m, *Uotila 15603* (holotype H!, isotype herb. Kramer), **syn. nov.**

Syntrichia ruralis var. *submamillosa* (W.A. Kramer) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 270. 1993.

PLANTS (1)1.8–5(9) cm high. LEAVES lightly spirally twisted when dry, usually recurved, sometimes squarrose, spreading or patent when moist, 2.5–5.8 × 0.9–2.2 mm, lingulate to ovate-lingulate; apex acuminate, rarely rounded, obtuse or acute, sometimes dentate and hyaline, tapering into hair point; margins revolute from base to near the apex, sometimes to 2/3 of the leaf; hyaline hair-point strongly spinose, brown at base, 1–4 mm long; costa 95–150 µm wide, in transverse section with (1)2–3 guide cell rows, 3–6 dorsal stereid rows, without hydroids, on the abaxial side with simple papillae, 2.5–5 µm long; upper and middle laminal cells quadrate, rectangular or hexagonal, thin walls, 10–12.5 × (7.5)10–12.5 µm, with (2)4–6 bifurcate, sometimes pedicellate, rarely branched star-shaped papillae per cell (5)7.5–10 µm long; basal cells hyaline, rectangular, thin walls, sometimes sinuous and collenchymatous, 75–112.5 × (10) 12.5–25 µm, forming a clearly differentiated hyaline area up to 28–33% of leaf length; marginal basal cells chlorophyllose, in 10–24 columns.

Distribution. Europe; south-western Asia; North Africa (Düll 1984).

Observations. This species can be easily separated from *S. ruralis* var. *ruraliformis* by the papillosity of the lamina cells. Traditionally the taxon has been considered as a variety of *S. ruralis* (Zander 1993) or *S. ruraliformis* (Kramer 1980; Frey & Kürschner 1991). In our opinion, the type of papillosity in this taxon is constant and a sufficiently stable character to support its status as a species.

Selected material studied. GREECE: Crète, route Kerá-Lagoú, 800 m, 3.iv. 1980, *Lawalree* (BR 182311). IRAQ: Arbil Luira, lower slopes of mountain west of Shaglawa, 22.iii. 1958, *Agnew* (BM). MOROCCO: Ifrane, *c*. 1700 m, 8.iv. 1969, *Davis & Davis* (E). Anti-Atlas, prox. Askaoun, 1840 m, 10.iii. 2001, *Cano & Muñoz* (MUB 11374). PORTUGAL: Tras os Montes, Miranda do Douro, 400 m, 15.iv. 2001, *Cano* (MUB 11405). SPAIN: Alicante, Font Roja, 1200 m, 7.ii. 1983, *Sérgio et al*. (BCB 10201). Murcia, Jumilla, Sierra del Carche, pico El Carche, 1370 m, 3.iii. 1985, *Ros* (MGC 885). Teruel, Orihuela del Tremedal, 1600 m, 21.ix. 1977, *Casas* (BCB 6067). Toledo, río Algodor, finca del Quemadillo, 26.xi. 1977, *Casas* (BCB 6115). TURKEY: Prov. Bitlis, Suphan Dag, above Adilcevaz, 4300 m, 27.viii. 1954, *Davis & Polunin* (BM). Prov. Maras, Elbistan, 1100 m, 6.v. 1957, *Davis & Hedge* (BM).

Some of the above information is summarized in the key in Table 3.

EXCLUDED TAXA

Tortula densa (Velen.) J.-P. Frahm

Velenovský (1897) described *Tortula ruralis* var. *densa* Velen. on the basis of its peculiar leaf papillosity. Later Frahm (1994) recognized it at the species level as *T. densa*, an opinion shared by Sollman (1997). Frahm (1994) separated *T. densa* from *T. calcicolens* by the following characters: the former is a larger plant, with leaves plane when moist and up to 4 mm in length, having a hyaline hair-point reddish at the base, and dense verrucose papillae in the upper laminal cells, whereas the latter is a smaller plant, with leaves keeled when moist and 2.5–3 mm in length, having a hyaline hair-point and plain horseshoe-shaped papillae in the upper laminal cells. After the study of the type and much material of this taxon, we think it belongs to the *Syntrichia ruralis* complex, but we do not agree on its taxonomic status. Thus, we have observed samples of *Syntrichia calcicola* (*T. calcicolens*) with leaves up to 3.8 mm length, dense verrucose papillae mixed with others that are bifurcate (which show the horseshoe-like shape), with hair-points that are hyaline with a reddish base (a character without any taxonomic value, as we have demonstrated above) and young plants with distal leaves plane and basal leaves keeled when moist. Other authors such as Kramer (1980) and Zander (1993) consider *T. densa* to be synonymous with *S. ruralis*. In summary, we think that these characters are not sufficient to distinguish and separate *T. densa* from *S. calcicola*.

Tortula ruralis var. *substereidosa* W.A. Kramer

Kramer (1980) described this variety on the basis of the costa anatomy, considering this taxon very similar to tiny forms of *Tortula ruralis* ssp. *ruralis* var. *ruralis* (*sic*), but with substereids reaching the leaf apex. After the study of the type material, we conclude that this taxon is morphologically identical to *Syntrichia virescens* (De Not.) Ochyra. Thus, both taxa share the following characters: leaves constricted at middle, margins plane or slightly recurved in the lower third, cross-section of the costa without hydroids, but with 1–2 rows of stereids and sometimes, substereids. Therefore, *Tortula ruralis* var. *substereidosa* W.A. Kramer can be included in the synonymy of *S. virescens*, and should be excluded from the *Syntrichia ruralis* complex.

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