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 Pottiaceae, 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 Br. 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
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. *substeroidosa* (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 (Zürich), 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 glutaralde-hyde 3% with 0.1M cacodylate buffer at 4°C, washed in cacodylate and sacarose buffer, dehydrated in an increasing acetone gradient (30%, 50%, 70%, 90% and 100%), critical-point dried and gold-sputtered with a gold layer 200–300Å 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. *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 ($\chi^2$, $P < 0.05$; $V_{Cramer} = 0.569$, $P < 0.05$). 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
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.) Herrnstadt & 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 ($\chi^2, P<0.05; V_{\text{Cramer}} = 0.850, P<0.05$) (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 ($\chi^2, P > 0.05$) (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.
OVERVIEW OF SYNTRICHIA RURALIS COMPLEX

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

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

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 ($\chi^2$, *P* < 0.05; $V_{\text{Cramer}} = 0.947$, *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 17.5µm (*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 taxa and the leaf apex shape ($\chi^2$, *P* < 0.05; $V_{\text{Cramer}} = 0.463$, *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 ($\chi^2$, $P < 0.05$; $V_{\text{Cramer}} = 0.557$, $P < 0.05$). 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 ($\chi^2$, $P < 0.05$; $V_{\text{Cramer}} = 0.557$, $P < 0.05$) and ranges from simple (S. subpapillosissima) to bifurcate, sometimes branched-pedicellate (S. papillosissima) (Fig. 2C). The papilla length ranges from 2.5 $\mu$m (S. ruralis, S. calcicola) to 7.5 $\mu$m (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 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 ($\chi^2$, $P < 0.05$; $V_{\text{Cramer}} = 0.318$, $P < 0.05$). 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).


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 to 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 chlorophylllose, 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

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

(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).


Barbula ruralis var. subintermedia Renauld & Cardot, Rev. Bryol. 19: 84. 1892.
Tortula ruralis var. fulva Győrffy, Magyar Bot. Lapok. 5: 342. 1906.
Tortula ruralis var. subintermedia (Renauld & Cardot) Parl., Ind. Bryol., ed. 2, 5: 57. 1906.


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

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

Europe; north-east, east, south-western and Central Asia; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; North, Central and South Africa; Macaronesia; north-western and southern South America; 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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.


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!).


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


**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 sinusuous 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 chlorophylllose, 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.


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

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**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* |
| 2. Papillae on mid-lamina cells not pedicellate, 2.5 μm high | 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 one 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* |
| 5. Middle laminal cells with more than one 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* |

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**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. calciocolens* 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 material, we conclude that *Syntrichia densa* (De Not.) Ochyra. Thus, both taxa share the virescens, and should be excluded from the *Syntrichia ruralis* complex.

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**REFERENCES**


