Micromorphology of Scirpus (Cyperaceae) and related genera in south-west Europe

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Glume surface, fruit surface, perianth bristles and pollen morphology in Scirpus L. and related genera from south-west Europe have been investigated by light and scanning electron microscopy. The results of this analysis confirm the heterogeneity of the group and provide further support to the current recognition of the genera Scirpus L., Bolboschoenus (Rchb.) Palla, Scirpoides Ség., Schoenoplectus (Rchb.) Palla, Isolepis R.Br., Trichophorum Pers. and Blysmus Panz. as well as to a re-appraisal of subg. Actaeogeton (Rchb.) Oteng-Yeb. of Schoenoplectus. © 2004 The Linnean Society of London, Botanical Journal of the Linnean Society, 2004, 145, 45–58.


INTRODUCTION

The genus Scirpus L. has long proved problematic in the Cyperaceae. Until recently, some authors still treated it as a single, highly variable genus (Koyama, 1958; Schultze-Motel & Hegi, 1967; De Filippis, 1980). Today, most authors split it into segregate genera (Blysmus Panz., Scirpus L., Bolboschoenus (Rchb.) Palla, Schoenoplectus (Rchb.) Palla, Scirpoides Ség., Isolepis R.Br. and Trichophorum Pers.), with Scirpus s.s. being recognized as a small genus of about nine species (Wilson, 1981; Haines & Lye, 1983; Goetghebeur, 1998; Kukkonen, 1998). This interpretation is based on evidence from embryology (Van der Veken, 1965), micromorphology (Schuyler, 1971) and molecular biology (Muasya et al., 1998, 2000b; Muasya, Simpson & Chase, 2001; Young, Molvray & Kores, 2002).

Recent cladistic analyses of the subfamily Cyperoideae, based on a wide range of morphological, anatomical, embryological, phytochemical and physiological characters, identified heterogeneity even at tribal level among several of the mentioned genera (Bruhl, 1995; Goetghebeur, 1998). Bruhl (1995) included Scirpus, Blysmus, Bolboschoenus, Schoenoplectus, Scirpoides, Isolepis and Trichophorum in the single tribe Scirpeae, stating at the same time its polyphyletic nature and defining it as ‘the most poorly supported’ of the tribes he recognized in Cyperaceae. In Goetghebeur’s (1998) analysis, the genera at issue were concluded to belong to four different tribes: Scirpeae (Scirpus, Trichophorum), Fuireneae (Bolboschoenus, Schoenoplectus), Cypereae (Isolepis, Scirpoides) and Dulichieae (Blysmus). Muasya et al. (2000a), in a combined DNA and morphological analysis, resolved the tribe Scirpeae s.l. into five clades, which did not agree with either of the two above mentioned classifications. The instability of tribal limits in Scirpeae s.l. was highlighted by Muasya et al. (2000a).

Micromorphological characters, mainly those concerning the reproductive structures, are considered an important parameter in systematic studies on Cyperaceae.

With regard to investigations by light microscopy (LM), a morphological survey was performed on fruits and perigone bristles of European species of Cyperaceae, including Scirpus s.l., by Kowal (1958), who pointed out a similarity between the fruits of Eriophorum and Schoenoplectus and the heterogeneity of Isolepis. The anatomy of the fruits of some European genera was studied by Marek (1958), with particular regard to the pericarp and epidermis. His paper offers...
a useful tool for the correct interpretation of the micromorphology of the fruit surface.

Scanning electron microscopy (SEM) investigation of fruits of *Scirpus s.l.* was performed by Schuyler (1971), who studied the structure of achene epidermal cells by removing their outer walls, thus choosing a microstructural rather than a micromorphological approach. Schuyler's work exhibited the heterogeneity of the assemblage. Leu & Lin (1980) included species of *Schoenoplectus* within an SEM survey on seed morphology of some weed species in Compositae, Cyperaceae and Poaceae.

This paper provides the first SEM analysis of the morphology of glumes and perianth bristles in *Scirpus s.l.* An analogous analysis was performed by Toivonen & Timonen (1976) on the perigynium ('utricle' after Kukkonen, 1994) epidermis in species of *Carex* L. subg. *Vignea* (P. Beauv. ex T. Lestib.) Nees.

Pollen morphology of Cyperaceae has been investigated by several authors, who tried to assess its systematic value within the family. Two (Erdtman, 1966; Padhye & Makde, 1980; Haines & Lye, 1983; Bruhl, 1995), three (Koyama, 1961) and up to six (Fernandez, 1987) different morphological types have been distinguished within the family, based on shape, size and sporoderm apertures of the grains. More recently, van Wichelen *et al.* (1999), using LM and SEM analysis of representatives from the four subfamilies of the Cyperaceae (classification after Goetghebeur, 1986), singled out the groups of Mapanioideae (anaulcerate, frequently spheroidal, ± thick-walled pollen grains), Sclerioideae–Caricoideae (anaulcerate with three lateral pores, broadly obovoid, thin-walled pollen grains) and Cyperoideae (anaulcerate with several lateral pores or colpi, mostly broadly obovoid and thin-walled pollen grains). The last of these groups appeared heterogeneous, perhaps distinguishable in species with lateral colpi and species with lateral pores.

Ontogeny of pollen grains in Cyperaceae is nearly unique among angiosperms (van Wichelen *et al.*, 1999); microsporogenesis is simultaneous (Furness & Rudall, 1999) and only one meiotic nucleus of a tetrad survives to form a pseudomonad (Selling, 1947), but these characteristics seem independent of the nature of the pollen grain wall (van Wichelen *et al.*, 1999) and of aperture type (Furness & Rudall, 1999), respectively.

In the present paper, the micromorphology of the glume surface, fruit surface, perianth bristles and pollen of the plants traditionally included in *Scirpus s.l.* from south-west Europe are investigated, in order to provide further data toward the systematic definition of the group in this area. In particular, the group referable to *Scirpus sensu* Schultze-Motel (1967) has been chosen, including *Blysmus*, *Scirpus*, *Bolboschoenus*, *Schoenoplectus*, *Scirpoides*, *Isolepis* and *Trichophorum*. The same analysis was performed on two species of *Eriophorum* L. (namely *Eriophorum angustifolium* Honck. and *E. latifolium* Hoppe), in order to make a comparison with *Trichophorum* Pers., with particular reference to *T. alpinum*. Since Linnaeus (1753), *Eriophorum* has been traditionally appraised as a segregate genus, but *T. alpinum*, described by Linnaeus under *Eriophorum*, has a certain resemblance to members of this genus. The results of the microanalysis conducted on *Eriophorum* are described along with those of the other genera.

Data on pollen comparative morphology by LM and SEM, as well as perianth bristles and glume surface morphology by SEM, are new for the examined taxa.

The results of the present analysis have been taken into account in a study that has been performed by one of the authors on the systematics of *Scirpus* L. and related genera in Italy (Pignotti, 2003).

**MATERIAL AND METHODS**

The morphology of glumes, fruits, perianth bristles and pollen of 21 taxa was investigated, using living plants and herbarium specimens. The voucher specimens and their localities are listed in Table 1.

With regard to glumes, fruits and bristle morphology, either samples from herbarium specimens or from living plants have been examined under SEM after gold coating: owing to the scarious and dry nature of mature glumes, fruits (nutlet) and bristles, no appreciable difference was noticed in SEM analysis between samples from living plants (fixed in FAA, dehydrated with acetone, critical point dried and gold coated) and from herbarium specimens. A Philips 515 electron microscope was used.

Attention was given to the following portions of the mentioned organs, which were observed to vary more significantly in accordance with the macromorphology of the groups: the abaxial surface of the glume cells, particularly the medio-distal and lateral, but not strictly marginal cells; the latero-abaxial surface of mature fruits; the medio-distal portion of bristles. Descriptive macromorphological terms are those adopted by Kukkonen (1994) for Cyperaceae.

With regard to pollen morphology, SEM analysis was conducted on specimens treated following Halbritter (1997) for living, fragile pollen grains. This technique, slightly modified by presinking anthers in a watery mixture of glycerine and lactic acid (1 : 2 : 1) for 10 min, was also adopted for pollen grains from herbarium specimens. Pollen preparation for LM was slightly modified from Fernandez (1987): pollen was treated with 5% NaOH for 30 min and was directly
sunk in a solution of 50% water and glycerine for observation. The following parameters, characteristic of roughly conical to broadly obovoid pollen grains, have been taken into account in the observations made by LM (Fig. 1):
1. Longitudinal, main axis of the grain = P
2. Diameter, or shorter axis = D
3. Distance between the cone apex (proximal pole) and the projection on the longitudinal axis of the surface circle of maximum curving = \( p' \); \( p' \) was calculated as \( (P - p') \)
4. When clearly distinguishable, diameter of the roughly circular polar aperture (distal ulcus) and length of 1–2 of the 3–5, roughly elliptical (colpi) to cir-

Table 1. Taxa and specimens examined

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Collector(s)</th>
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<tbody>
<tr>
<td>Blysmus compressus (L.) Panz.</td>
<td>Passo del Pura (Ud), ix.1996</td>
<td>L. Pignotti (Botanical Garden, University of Florence)</td>
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<tr>
<td>Bolboschoenus maritimus (L.) Palla</td>
<td>Vione della Bigattiera (Pi), vi.1995</td>
<td>L. Pignotti, G. Fiorini et S. Turrini (FI)</td>
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<tr>
<td>Bolboschoenus maritimus (L.) Palla</td>
<td>Osmannoro at Casa Bianca (Fi), 6.vi.1999</td>
<td>L. Pignotti et A. Arcara (FI)</td>
</tr>
<tr>
<td>Isolepis cernua (Vahl) R. Br.</td>
<td>S. Brigida (Fi), ix.1995, N. et L. Pignotti (Botanical Garden, University of Florence)</td>
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<tr>
<td>Isolepis fluitans (L.) R. Br.</td>
<td>South Harris, Outer Hebrides, 23.viii.1999</td>
<td>L. Pignotti and A. Arcara (Botanical Garden, University of Florence)</td>
</tr>
<tr>
<td>Isolepis pseudosetacea (Daveau) Láinz</td>
<td>Between Capalbio and Lago Acquato (Gr), 28.v.1895</td>
<td>S. Sommier (FI)</td>
</tr>
<tr>
<td>Isolepis pseudosetacea (Daveau) Láinz</td>
<td>Saltino (Fi), A. Arcara et L. Pignotti (Botanical Garden, University of Florence)</td>
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<tr>
<td>Isolepis setacea (L.) R. Br.</td>
<td>Rabat, Marocco, 9.iv.1996 (FI)</td>
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<td>Schoenoplectus junoides (Roxb.) Krecz.</td>
<td>Vercelli 1891, M. Desfayes (FI)</td>
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<td>Schoenoplectus lacustris (L.) Palla</td>
<td>Padul di Fucechio (Fi), 4.vi.1999</td>
<td>L. Pignotti et N. Vestri (Botanical Garden, University of Florence)</td>
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<tr>
<td>Schoenoplectus lacustris (L.) Palla</td>
<td>Lake of Chiusi (Si), vi.1996</td>
<td>L. Pignotti et S. Turrini (Botanical Garden, University of Florence)</td>
</tr>
<tr>
<td>Schoenoplectus litoralis Schrad.</td>
<td>Mouth of river Imera Settentrionale (Pa), vii.1995</td>
<td>S. Pasta, E. Nardi et L. Pignotti (FI)</td>
</tr>
<tr>
<td>Schoenoplectus litoralis Schrad.</td>
<td>Mouth of river Simeto (Ct), vii.1995</td>
<td>E. Nardi et L. Pignotti (FI)</td>
</tr>
<tr>
<td>Schoenoplectus litoralis Schrad.</td>
<td>Pantelleria, Specchio di Venere (Tp), 18.iv.1996</td>
<td>S. Pasta et A. Troia (FI)</td>
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<td>Schoenoplectus mucronatus (L.) Palla</td>
<td>Crevalcore (Bo), VII. 1997, L. Pignotti (Botanical Garden, University of Florence)</td>
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<td>Schoenoplectus pungens (Vahl) Palla</td>
<td>Bosco della Mesola (Fe), ix.1997, N. et L. Pignotti (Botanical Garden, University of Florence)</td>
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<td>Schoenoplectus supinus (L.) Palla</td>
<td>Peschiera Colomboaro, Ceresole d’Alba (Cn), 23.ix.1996</td>
<td>G. Abbà, A. Arcara et L. Pignotti (FI)</td>
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<td>Schoenoplectus tabernaemontani (C.C. Gmel.) Syme</td>
<td>Barcaggio, Cap Corse, v.1999, L. Pignotti et A. Arcara (FI)</td>
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<tr>
<td>Schoenoplectus triqueter (L.) Palla</td>
<td>Ditches along Dora (To), 12.ix.1904</td>
<td>L. Pignotti et G. Fiorini (FI)</td>
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<td>Scirpoides holoschoenus (L.) Sójak</td>
<td>S. Rossore (Fi), 15.vi.1999, L. Pignotti et G. Fiorini (FI)</td>
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<td>Scirpoides holoschoenus (L.) Sójak</td>
<td>Between Stagno e Guasticce (Li), vi.1995, L. Pignotti et S. Turrini (FI)</td>
<td></td>
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<tr>
<td>Scirpoides holoschoenus (L.) Sójak</td>
<td>Between S. Lucia and Pruneccio (Fi), vii.1996, L. et N. Pignotti (FI)</td>
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<tr>
<td>Scirpus atrovirens Willd.</td>
<td>Parco La Mandria, Venaria Reale (To), vii.1999, L. Pignotti et M. Tardelli (FI)</td>
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<td>Scirpus radicans Schkuhr</td>
<td>Ossola Inferiore (Vb), 23.v.1912, O. Boggiani (FI)</td>
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<td>Scirpus radicans Schkuhr</td>
<td>Vercelli 1863, Cesati (FI)</td>
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<td>Scirpus sylvaticus L.</td>
<td>Prati di Logarzhen (Ms), 8.vii.1999, L. Pignotti et S. Turrini (FI)</td>
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<tr>
<td>Trichophorum alpinum (L.) Pers.</td>
<td>S. Caterina Valfurva (So), 1870, E. Levier (FI)</td>
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<tr>
<td>Trichophorum ceposum (L.) Hartman</td>
<td>Valle del Brocan (Cn), vii.1999, L. Pignotti et M. Tardelli (FI)</td>
<td></td>
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<tr>
<td>Trichophorum pumilum (Vahl) Schinz et Thell.</td>
<td>Valfredda (To), 23.vii.1999, L. Pignotti et M. Tardelli (FI)</td>
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<td>Erriophorum angustifolium Honck.</td>
<td>Monte Bondone (Tn), 18.vi.1962, Moggi et Ricceri (FI)</td>
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<tr>
<td>Erriophorum latifolium Hoppe</td>
<td>Fontana Vaccaia (Pt), 20.vi.1915, A. Fiori (FI)</td>
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</table>

cular (pores) lateral apertures (respectively da and la in Fig. 1).

Palynological terminology is after Punt et al. (1999).

LM measurements were carried out on at least 100 pollen grains from each locality.

The nomenclature here adopted is after Goetghebeur (1998). Author abbreviations are according to Brummitt & Powell (1992).

RESULTS

On the basis of the micromorphological features, several groups have been identified relative to the abaxial surface of glumes (G), fruit surface (F), perianth bristles (B) and pollen (P). The groups are described in the following synopsis.

GLUME SURFACE.

Note that wherever barbed or haired cells are present, some of them are strictly marginal, so that the margin of barbed-cell-bearing species is ciliolate or ciliate, respectively.

Four main groups have been identified:

G1. This group shows one kind of oblong, smooth cells, 30–85 μm long, with deeply wavy margins. The periclinal cell walls are invariably not collapsed, resulting in a pillowed appearance. This morphology is present in *Trichophorum* (*T. alpinum* (L.) Pers., *T. pumilum* (Vahl) Schinz & Thell. and *T. cespitosum* (L.) Hartman) (Fig. 2).

G2. This group shows two kinds of oblong, roughly rectangular cells, 35–100 μm long, with almost linear margins:

1. Cells bearing a longitudinal, simple row of (1–) 7–12 prominent bodies.
2. Smooth cells.

It can be subdivided in three subgroups on the basis of the different pattern of distribution of the two kinds of cells.

In the first subgroup, the cells of the first kind are the most numerous and are homogeneously scattered over the surface. The cells of the second kind are mostly situated at the margins. This distribution gives a smooth appearance to the glumes. This pattern is present in *Schoenoplectus* p.p. (*S. litoralis* (Schrad.) Palla, *S. pungens* (Vahl) Palla and *S. triqueter* (L.) Palla) (Fig. 3).

In the second subgroup, the cells of the first kind are mostly concentrated in rough stripes in the perimedian region, making the glumes appear roughly ribbed. This pattern is present in *Scirpus* s.s. (*S. sylvaticus* L., *S. atrovirens* Willd. and *S. radicans* Schkuhr) (Fig. 4).

In the third subgroup, the cells of the first kind are arranged in regularly spaced, often protruding, longitudinal stripes of 3–6 rows of cells. These stripes are separated by the cells of the second kind. This pattern is present in *Schoenoplectus* p.p. (*S. mucronatus* (L.) Palla, *S. juncoideus* (Roxb.) V.I.Krecz. and *S. supinus* (L.) Palla), in *Isolepis* (*I. cernua* (Vahl) R.Br., *I. setacea* (L.) R.Br., *I. pseudosetacea* (Daveau) Laínz and *I. fluitans* (L.) R.Br.) and *Blysmus compressus* (L.) Panz.; the stripes are more widely spaced in *B. compressus* than in the others. They converge towards the apex in *Schoenoplectus* p.p. and *Blysmus*, and diverge in *Isolepis* (Fig. 5).

This kind of glume (first subgroup) has been noticed in *Eriophorum* (*E. latifolium*), but the cells of the first kind are shorter (10–25 μm long) and bear only 1–2(3) prominent bodies.

G3. This group has three kinds of cells:

1. Quadrangular, generally oblong cells (30–130 μm long) bearing a longitudinal, simple row of 1–9 main prominent bodies; smaller satellites may surround the main bodies.
2. Shorter cells (25–70 μm long) bearing an antrorse barb 25–100 μm long.
3. Oblong, smooth cells (45–170 μm long).

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**Figures 2–9.** Glume surface. Fig. 2. *Trichophorum cespitosum*, group G1. Fig. 3. *Schoenoplectus litoralis*, group G2, first subgroup. Fig. 4. *Scirpus radicans*, group G2, second subgroup. Fig. 5. *Isolepis pseuderatae*, group G2, third subgroup. Fig. 6. *Bolboschoenus maritimus*, group G3, first subgroup. Fig. 7. *Scirpoïdes holoschoenus*, group G3, second subgroup. Figs 8, 9. *Schoenoplectus lacustris*, group G3. Scale bars = 50 μm in Figs 2–5, 8 and 100 μm in Figs 6, 7, 9.
It can be subdivided in two subgroups on the basis of the different pattern of distribution of the three kinds of cells.

In the first subgroup, the barbs are acuminate and widespread (Fig. 6); smooth cells occur mostly next to the margins and on the midvein. This pattern is present in Bolboschoenus maritimus (L.) Palla.

In the second subgroup, the barbs are inflated to broadly acuminate, mostly concentrated in the distal part of the glume; smooth cells are gathered in longitudinal stripes of various widths alternating with stripes of cells of the first kind (Fig. 7). This pattern is present in Scirpoides holoschoenus (L.) Sojak.

This group has four kinds of cells:
1. Oblong cells (37–65 µm long) bearing a longitudinal, simple row of 2–7 main prominent bodies, which are generally surrounded by smaller sized satellites; these cells are arranged in evenly spaced, longitudinal stripes of 1–3 rows of cells.
2. Oblong cells (15–60 µm long) bearing a papilla, perhaps a rudimentary barb, at the distal end. These cells are organized in large, longitudinal stripes of 5–6 rows of cells alternating with those previously described.
3. Oblong cells (30–50 µm long) bearing a barb 37–110 µm long, at the distal end. These cells are scattered over the surface. Occasionally, they bear a hair up to 185 µm long.
4. Smooth cells, mostly in submarginal and marginal position.

This pattern is present in Schoenoplectus lacustris (L.) Palla and S. tabernaemontani (C.C.Gmel.) Palla. The cells of the second kind are much more numerous in S. lacustris (Fig. 8) than in S. tabernaemontani. The cells of the third kind bear mostly inflated barbs and are distributed in the distal area and along the margin, which appears ciliate, in S. tabernaemontani; they are bound to the midvein and the barbs are mostly tapering in S. lacustris (Fig. 9).

**Fruit surface**

Four main groups have been identified:

F1. The cells of the pericarp are roughly hexagonal and isodiamictrical, smooth. The anticlinal cell walls can be more or less evident. This pattern is present in Bolboschoenus, Blysmus, Scirpoides holoschoenus, Schoenoplectus p.p. (S. lacustris, S. tabernaemontani, S. triqueter, S. pungens and S. litoralis), Isolepis p.p. (I. fluitans), Trichophorum p.p. (T. pumilum). In Schoenoplectus litoralis, 1–2 small prominent bodies per cell are occasionally present. Depending on the prominence of the anticlinal walls, the fruit surface appears reticulate (in Scirpoides holoschoenus, Schoenoplectus p.p., Isolepis; Fig. 10) or smooth (in Bolboschoenus maritimus, Blysmus compressus, Schoenoplectus p.p. and Trichophorum p.p. and Trichophorum pumilum; Fig. 11).

F2. The cells of the pericarp are hexagonal and isodiamicetrical; all of the cells always bear a central, prominent body. This pattern characterizes Scirpus s.s., Isolepis p.p. (I. cernua, I. pseudotacea) and Trichophorum p.p. (T. cespitosum and T. alpinum) (Fig. 12). It is present also in Eriophorum (E. latifolium).

F3. The cells of the pericarp are extremely narrow, longitudinally oblong, arranged in transverse, wavy rows bearing furrows and prominent ridges. This pattern is present in Schoenoplectus p.p. (S. mucronatus, S. juncoideus and S. supinus). Ridges are sharper in S. supinus than in S. mucronatus and S. juncoideus (Fig. 13).

F4. The cells of the pericarp are longitudinally short (<10 µm) and transversely wide (80 µm), and are arranged in longitudinal rows. Transverse borders between the cells of the same row are not as evident, and the sharply prominent, longitudinal margins give a ridged appearance to the fruit. This pattern is present in Isolepis setacea (Fig. 14).

**Perianth bristles**

Seven groups have been described on the basis of the micromorphological characters of the perianth bristles.

B0. Perianth bristles absent. This pattern is present in Isolepis and Holoschoenus.

B1. Perianth bristles lacking or 1–3 rudimentary, smooth (up to 0.5 mm long). This pattern is present in Trichophorum p.p. (T. pumilum) and Schoenoplectus p.p. (S. supinus).

B2. Perianth bristles 3–6 shorter to much longer than the nutlet, with retrorse, spirally arranged to roughly distichous unicellular barbs. This pattern is present in Blysmus compressus, where they are particularly long, Bolboschoenus maritimus, Schoenoplectus p.p. (S. lacustris, S. tabernaemontani, S. pungens, S. triqueter, S. mucronatus, S. juncoideus) and Scirpus p.p. (S. sylvaticus and S. atrovirens) (Figs 15, 16). In S. pungens, where the bristles are shorter than the nutlet, the barbs may be confined to the distal end of the bristles.

B3. Perianth bristles 6, generally somewhat longer than the nutlet, smooth or with small, rudimentary hairs near the apex. This pattern is present in Trichophorum cespitosum (Fig. 17).

B4. Perianth bristles 6, c. 5 mm long, thin, irregularly volute beyond the glume, smooth or with scattered hairs 20–70 µm long near the apex; sometimes one bristle ribbon-shaped, bifid in the last 2 mm. This pattern is present in Scirpus radicans (Fig. 18).
B5. Perianth bristles 6, ribbon shaped, 20–30 mm long and 0.1–0.2 mm wide, white, soft, protruding from the spiklet. This pattern is present in *Trichophorum alpinum* (Fig. 19). Bristles of *Eriophorum* (*E. latifolium* and *E. angustifolium*) are similar, but always more than 6 in number and much longer.

B6. Perianth bristles 6, as long as the nutlet (up to 1.3 mm long), with numerous, adaxially crowded multicellular hairs of 1–5 cells, <0.5 mm in length. This pattern is present in *Schoenoplectus litoralis* (Fig. 20).

**POLLEN**

Pollen morphology of the examined species follows a general pattern. Pollen grains are obovoid (roughly conical) to subspheroidal, small to large in size, with scabrate-perforate surface. The apertures are 3–6. One of them is an ulcus, i.e. polar, situated on the distal pole (corresponding to the thick end of the cone, so that it is geometrically basal), and it is always circular. For this character, the pollen grains can be defined as ‘anaulcerate’. The other apertures are lateral (not strictly equatorial), circular (Fig. 21) in the small-sized grains (average length of the main axis less than 40 μm), elongated (Fig. 22) in the large-sized grains (average length of the main axis more than 40 μm). Table 2 summarizes the values of the parameters measured under the light microscope. A statistically sufficient number of pollen grains could not be obtained from *Trichophorum alpinum* and *Isolepis pseudosetacea*, so that only an indicative value of mean length is given for all the parameters of *Trichophorum alpinum* and for the apertures of *Isolepis pseudosetacea*. The former seems to bear scarcely fertile anthers, so that a large number of both living and herbarium specimens only yielded a small number of grains. As regards *Isolepis pseudosetacea*, the lack of a sufficient number of grains is mainly due to the few, generally rather old, herbarium specimens available of a species with small anthers and a very small amount of pollen.

The main axis ranges from 23.5 μm in *Isolepis pseudosetacea* to 54.6 μm in *Schoenoplectus tabernaemontani*.

Two dimensional groups are clearly recognizable on the basis of the P length, with mean values higher or
lower than 40 μm, although the peripheral values of the variation intervals of some species do overlap (see Fig. 27):
P1. The first group (pollen grains longer than 40 μm) includes *Bolboschoenus maritimus* and *Schoenoplectus* p.p. (*S. lacustris, S. tabernaemontani, S. triguer, S. pungens, S. litoralis*) (Fig. 23).
P2. The second group (pollen grains shorter than 40 μm) includes *Scirpus s.s., Scirpoides holoschoenus, Schoenoplectus* p.p., *Isolepis, Trichophorum* and *Blysmus compressus* (Figs 24, 25). *Eriophorum* (*E. angustifolium*) also belongs to this group. *Blysmus compressus* and *Schoenoplectus mucronatus, S. juncoideus and S. supinus* are placed in this group (mean values lower than 40 μm), although their upper values largely overlap those of the first group. Thus, they appear as a dimensionally transitional subgroup (Fig. 26).

D is on average less variable than P within the examined species, ranging from 20.3 μm in *Isolepis pseudosetacea*, to 32.5 μm in *Schoenoplectus litoralis*, even though the extreme values are variable. The obovoid shape is thus apparently less clear in the smaller grains, which often approach a spherical shape.

By contrast, the p’/p” ratio does not change appreciably, being low (0.01–0.50) and varying similarly within and between the dimensional groups, indicating that the heteropolarity is substantially preserved.

As previously mentioned, the length of the main axis also affects the kind of lateral apertures (pores/colpi). This is shown in Figure 28, in which the ratio

---

**Figures 15–20.** Perianth bristles. Fig. 15. *Bolboschoenus maritimus*, group B2. Fig. 16. *Schoenoplectus tabernaemontani*, group B2. Fig. 17. *Trichophorum cespitosum*, group B3. Fig. 18. *Scirpus radicans*, group B4. Fig. 19. *Trichophorum alpinum*, group B5. Fig. 20. *Schoenoplectus litoralis*, group B6. Scale bars = 50 μm except in Fig. 16 (100 μm).
lateral/basal aperture increases with increasing main axis. In this regard, the subdivision adopted here agrees with that suggested by van Wichelen et al. (1999) for Cyperoideae, between species with lateral pores and species with lateral colpi, although their distinction is not always precise.

The surface follows a constant pattern throughout the examined taxa. It is scabrate because of prominent

Figures 21–26. Pollen morphology. Fig. 21. Isolepis setacea, small size grain (P₂) with circular lateral aperture. Fig. 22. Schoenoplectus lacustris, large size grain (P₁) with oblong lateral aperture. Fig. 23. Schoenoplectus lacustris, group P₁. Fig. 24. Scirpoides holoschoenus, group P₂. Fig. 25. Isolepis setacea, group P₂. Fig. 26. Blysmus compressus, group P₂. Scale bars = 2 µm in Figs 21, 22 and 10 µm in Figs 23–26.
Table 2. Pollen morphology. Values of the parameters in μm surveyed at LM

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<th>p''</th>
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granules of about 0.1 μm, and perforate because of puncta of 0.1–0.3 μm. The apertures show a poorly defined outline. The aperture membrane has islands whose surface follows the same pattern as the rest of the surface.

**DISCUSSION**

The examined microcharacters highlight similarity and dissimilarity within and among the studied groups. A synopsis of the examined microcharacters is given in Table 3.

Some groups have essentially homogeneous microcharacters. In particular, in *Scirpus*, *S. atrovirens* and *S. sylvaticus* share all of the examined features. Embryological data support this resemblance (Van der Veken, 1965). In *Isolepis*, *I. cernua* and *I. pseudosetacea* share all of the examined features; *I. setacea* and *I. fluitans* differ from each other and from the previous species in the fruit surface, which is costate and smooth, respectively. From a macroscopic point of view, *I. setacea* is very similar to *I. cernua* and *I. pseudosetacea*, whereas *I. fluitans* differs morphologically from the other species. For this reason, some authors kept *I. fluitans* separated from *Isolepis* and attributed it to the genus *Eleogiton* Link (Nees, 1836; Goetghebeur, 1986; Stace, 1997). Only a minor embryological difference was pointed out between *Eleogiton* and *Isolepis* (Van der Veken, 1965).

A high variability of the examined characters is present in *Schoenoplectus*. It is possible to identify two
groups, recognizable on the basis of fruit surface, glume surface (belonging to two different subgroups) and pollen size. The first group comprises five taxa (*S. lacustris*, *S. tabernaemontani*, *S. triqueter*, *S. pungens*, *S. litoralis*). The first four share all of the evaluated features, but *S. litoralis* has peculiar bristles. In this regard, this group was divided into two series by Koyama (1958), *Lacustres* (C.B. Clarke) Beetle and *Littorales* (C.B. Clarke) T. Koyama, on the basis of needle-like and plumose bristles, respectively. An analogous segregation (groups *Schoenoplectus* and *Pterolepis*) was proposed by Raynal (1976a). In a later paper, Koyama (1963) united them again, based on occurrence of a species [namely *Scirpus californicus* (C.A. Meyer) Steud., an American vicariant of *S. litoralis*] with intermediate plumose–needle-like bristles, that diminished the taxonomic value of his previous distinction. Embryological features also lead to this conclusion (Van der Veken, 1965).

The second group appears to be very homogeneous, although *Schoenoplectus supinus* differs in its lacking or having only rudimentary bristles. Segregation on micromorphological basis of *Schoenoplectus mucronatus*, *S. juncoideus* and *S. supinus* from the other representatives of *Schoenoplectus* is also supported by other morphological characters (Beetle, 1942) and by embryological characters (Van der Veken, 1965), which have already led to their inclusion in the section *Actaeoge-

ton* Rchb. (Beetle, 1942). Molecular data (Young et al., 2002) have recently given further support to this distinction. On the basis of the kind of bristles and occurrence of amphicarpy, *S. supinus* and related species are segregated by several authors in section *Supini* (Cherm.) Raynal (Raynal, 1976b; Smith & Hayasaka, 2002), as yet supported neither by embryological characters (Van der Veken, 1965) nor by molecular data (but see Young et al., 2002).

*Scirpoides holoschoenus* and *Bolboschoenus maritimus* have a similar kind of glume and fruit, but greatly differ in all of the other characters. *Blysmus compressus* appears isolated from the other genera, as is evident in the literature (Van der Veken, 1965; Goetghebeur, 1998).

*Trichophorum* is distinguished by a peculiar glume morphology. Within the genus, the species differ from each other in bristles and in fruit surface.

The affinity reported in the literature (Koyama, 1958; Goetghebeur, 1998) between *Trichophorum* and *Eriophorum* is confirmed here by fruit surface and pollen morphology. Perianth bristles of *Eriophorum*, although similar to those of *T. alpinum*, have peculiarities that easily distinguish them, whereas glume surface differs from that of *Trichophorum* and is similar to that of *Schoenoplectus* p.p. The placing of *T. alpinum* in *Trichophorum* rather than in *Eriophorum* is confirmed.

Table 3. Synopsis of the microcharacters surveyed in *Scirpus s.l.* Abbreviations refer to the groups described in the Results section

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<th>Fruits (F)</th>
<th>Bristles (B)</th>
<th>Pollen (P)</th>
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CONCLUSIONS

Most of the examined microcharacters occur across the genera, several of the identified types occurring in more than one genus. In contrast, some characters have proved to be uniform within each group at generic or at least infrageneric level, e.g. glume surface (with an exception occurring within Schoenoplectus s.s.) and pollen morphology. Fruit surface is more variable than the previous features within the same genus, more than one type of fruit surface being represented in Isolepis and Trichophorum. Perianth bristles are the most variable character, three of the examined genera (Scirpus, Schoenoplectus, Trichophorum) bearing more than one type of bristles.

The distribution of the surveyed characters within and among the groups examined does not permit us to choose any of them in a key to identify all of the taxa. However, this distribution confirms heterogeneity among the groups and affinities among the species within each group, which are supported by morphological, embryological and molecular data from the literature (Van der Veken, 1965; Bruhl, 1995; Goetghebeur, 1998; Muasya et al., 2000a). Thus the results support the current splitting of Scirpus s.l. into different genera, confirming that an interpretation at genus level of the segregates is most suitable. Heterogeneity among several of these genera has now been recognized at even a tribal level (Goetghebeur, 1998; Muasya et al., 2000a). Our results give contrasting information in the current splitting of Scirpus s.l.

The recognition of the genera Bolboschoenus, Scirpoidea, Scirpus, Schoenoplectus, Isolepis, Trichophorum and Blysmus as well as the segregation of subgenus Actaeogeton (Rchb.) Oteng-Yeb. within Schoenoplectus here find further support.

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REFERENCES


