



A SYNOPSIS OF THE GENERA *SKYTTEA*, *LLIMONIELLA* AND *RHYMBOCARPUS* (LICHENICOLOUS ASCOMYCOTA, LEOTIALES)

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Abstract: The genus *Skyttea* is characterized by urceolate ascomata, with a narrow pore when young, a greenish or brownish, rarely reddish exciple of conglutinate hyphae with subglobose to \pm cylindrical lumina, bordered near the margin by hyaline to greenish or brownish, usually smooth, straight hairs, the absence of periphyses, rarely branched and apically hardly thickened paraphyses, asci and a hymenium that are entirely I – and KI – , a thin lateral and a very thick apical ascus wall with a small ocular chamber, and normally aseptate ascospores. It is considered to belong to the Leotiales and not to the Ostropales. It comprises at least 17 species, including *S. caesii* sp. nov., *S. carboneae* sp. nov., *S. lecanorae* sp. nov., *S. mayrhoferi* sp. nov., *S. pyrenulae* sp. nov., *S. radiatilis* comb. nov., *S. tavaresae* sp. nov. and *S. thelotrematis* sp. nov. *Rhymbocarpus* is shown to be a distinct leotialean genus, distinguished from *Llimoniella* by a different excipular structure, different pigments and the presence of excipular hairs, which, in some species, are embedded in the excipular gel and thus not visible macroscopically. In addition to the type species, *R. geographicus*, of which a neotype is designated, it includes *R. boomii* sp. nov., *R. cruciatus* comb. nov., *R. fuscoatrae* comb. nov., *R. makarovae* sp. nov., *R. neglectus* comb. nov., *R. pertusariae* sp. nov., *R. pubescens* comb. nov. and *R. stereocaulorum* comb. nov. *Llimoniella* s. str. comprises at least 6 species, including the type, *L. scabridula*, *L. adnata*, *L. pertusariae* sp. nov., *L. pyrenulae* sp. nov., *L. ramalinae* comb. nov. and *L. vinosa* comb. nov. Several species formerly assigned to *Skyttea* or *Llimoniella* are now included in the leotialean genus *Unguiculariopsis*, and the following new combinations are proposed: *Unguiculariopsis acrocordiae* comb. nov., *U. groenlandiae* comb. nov. and *U. lesdaimii* comb. nov. A lectotype is chosen for *Lichen stictoceros*, which is shown to be a synonym of *Evernia prunastri*. Keys are given for the species of *Skyttea*, *Llimoniella* and *Rhymbocarpus*, and for the lichenicolous genera of Leotiales and Ostropales. © 2000 The British Lichen Society

Introduction

The generic name *Skyttea* was introduced by Sherwood *et al.* (1981) for a number of minuscule lichenicolous ostropalean discomycetes with urceolate apothecia, a hairy margin and generally non-septate, hyaline ascospores. In the original account, seven species were accepted. In subsequent papers (Hawksworth 1982; Diederich 1986; Kalb *Lichenes Neotropici* 449 [1988]; Zhuang & Korf 1989; Rambold & Triebel 1992; Etayo & Diederich 1998) more species were added, but at the same time the genus, which since the

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beginning was heterogeneous (as already noted by Sherwood *et al.* 1981), became more and more an assemblage of non-related species.

Zhuang (1988: 62) was the first to recognize that *Skyttea* included a leotialean species, and she consequently transferred *S. thallophila* to *Unguiculariopsis*, a genus with mainly fungicolous (incl. lichenicolous) taxa. Later Coppins (in Rambold & Triebel 1990: 386–387) combined two other species, *S. lettaui* and *S. refractiva* into *Unguiculariopsis*, a genus which we know to comprise at least 10 lichenicolous species.

The genus *Skyttea* was originally said to be related to *Odontotrema* (Sherwood *et al.* 1981), a genus with lignicolous species. Later, Hawksworth & Sherwood (1982) described the new family *Odontotremataceae* (Ostropales) to include *Odontotrema*, *Skyttea* and five other genera. A more general overview of the *Odontotremataceae*, together with keys and descriptions of the accepted genera, is provided by Sherwood-Pike (1987).

Triebel (1989: 142–147) proposed to treat *Skyttea* in a broad sense as a recent synonym of *Rhymbocarpus*, and combined three known species of *Skyttea* into that genus. Coppins *et al.* (1991: 51) showed, however, that the type species of *Rhymbocarpus* has a very different ascus type and a different excipular structure, and suggested that the monotypic genus *Rhymbocarpus* should be best considered as ‘*incertae sedis* pending the availability of fresh material’.

The aim of this paper, initially, is to give a new circumscription of a homogeneous genus *Skyttea*, to discuss its systematic position, to transfer all excluded species to other genera, to study and solve some taxonomic problems concerning those genera, and to describe several new taxa. We did not plan a complete revision of the genus, and some well-known species presenting no taxonomic problems, and of which a modern published treatment is available, were not studied in detail. While preparing this synopsis, we examined a large number of other leotialean lichenicolous fungi, and we realised that a completely new arrangement of the taxa previously included in *Llimoniella* should be proposed, including the recognition of an enlarged genus *Rhymbocarpus*. As a consequence, we also prepared synopses of *Llimoniella* and *Rhymbocarpus*. Some species formerly included in *Skyttea* or *Llimoniella* are excluded and are treated as species of the genus *Unguiculariopsis*.

Materials and Methods

The specimens examined are located in the institutional herbaria ASU, BG, BM, CBG, E, FH, G, GZU, H, HBG, IMI, LE, LG, LUX, M, MA, MARSSJ, NY, TRH, UC, UPS and VAB, or in the personal collections of J. Alvarez, A. Aptroot, P. van den Boom, P. Diederich, J. Etayo, K. Kalb, V. Kummer and H. T. Lumbsch. In the enumeration of specimens, the abbreviation (h) means the private herbarium of the collector. In the case of several collectors, only the first, or the owner of the specimen is cited.

The morphological characters (dimensions, colour, fissures, etc.) of dry herbarium specimens have been studied and illustrated with a dissecting microscope at a magnification of $\times 40$ or $\times 80$. Microscopical examinations (including all microscopical measurements) were carried out using hand-cut sections in water; semi-permanent preparations of some species have been prepared in lactophenol cotton blue (LCB). As almost all the herbarium specimens are at least five years old, descriptions and measurements are normally based on dead cells. The excipular pigments have been studied in water, in 5–10% KOH (K) and in concentrated nitric acid (N); the dark red

TABLE 1. *Excipular pigments present in Skyttea species*

Colour of pigment	K-reaction	N-reaction	Occurrence in species
Greenish	Dull to olive-green	—	In all species except <i>S. nitschkei</i> and <i>S. tavaresae</i>
Dark reddish black (or dark greyish)	Bright aeruginose green	Dark brown (reddish brown)	<i>S. carboneae</i> , <i>S. nitschkei</i> , <i>S. tavaresae</i>
Brownish (orange brown)	Purple to violet	—	<i>S. nitschkei</i> (strong K-reaction), <i>S. mayrhoferi</i> , <i>S. radiatilis</i> and <i>S. tavaresae</i> (weak K-reaction, sometimes difficult to observe)
Brownish	—	—	E.g. in the basal exciple of <i>S. radiatilis</i> , often indistinct, as intermixed with the green pigment, and appearing olivaceous

pigment present in some *Skyttea* species, when very concentrated and appearing as dark greyish or blackish, is best seen as reddish in commercial bleach ('Eau de Javel') (C) after *c.* 1 min; the excipular structure in species of *Rhymbocarpus* and *Llimoniella* has been studied in C, which eliminates the obscuring effect of the dark pigments. The iodine reaction has been tested in Lugol's reagent, with (KI) or without (I) pre-treatment with KOH. The ascus base, and the presence of croziers, has been studied in KOH, with or without Congo red. Spore guttules have been studied in the few recent specimens (in water), in which living ascospores were present; guttules in dead ascospores have been examined in KOH, but this information rarely proved to be useful due to the possible coalescence of several lipid drops.

Results

Skyttea Sherwood, D. Hawksw. & Coppins

Trans. Br. mycol. Soc. 75: 482 (1981 [1980]); type: *Skyttea nitschkei* (Körb). Sherwood, D. Hawksw. & Coppins.

Ascomata apothecioid, lichenicolous, commensalistic, immersed or erumpent, dark-coloured, *c.* 100–300 µm diam., initially almost completely closed, except for a pore-like opening, remaining deeply urceolate when old (dry ascomata); margin in some species with fissures. *Exciple* greenish, brownish, dark reddish or greyish, with one or several characteristic pigments (see Table 1), mostly of conglutinate hyphae with subglobose to ± cylindrical lumina (especially in the upper part), bordered near the margin by hyaline to greenish or brownish, straight, cylindrical, obtuse, smooth, thin-walled or apically refractive, 0–1-septate hairs (Fig. 1D), with rarely a distinct annellate ornamentation (pigments covering the wall). *Subhymenium* thin, hyaline. *Hymenium* I– and KI–. *Epihymenium* hyaline or pale. *Paraphyses* filiform, simple or rarely branched below, equidistantly septate, *c.* 1.5 µm thick, apically not or poorly enlarged, not separating easily in KOH. *Asci* cylindrical to elongate clavate, unitunicate, wall laterally thin,

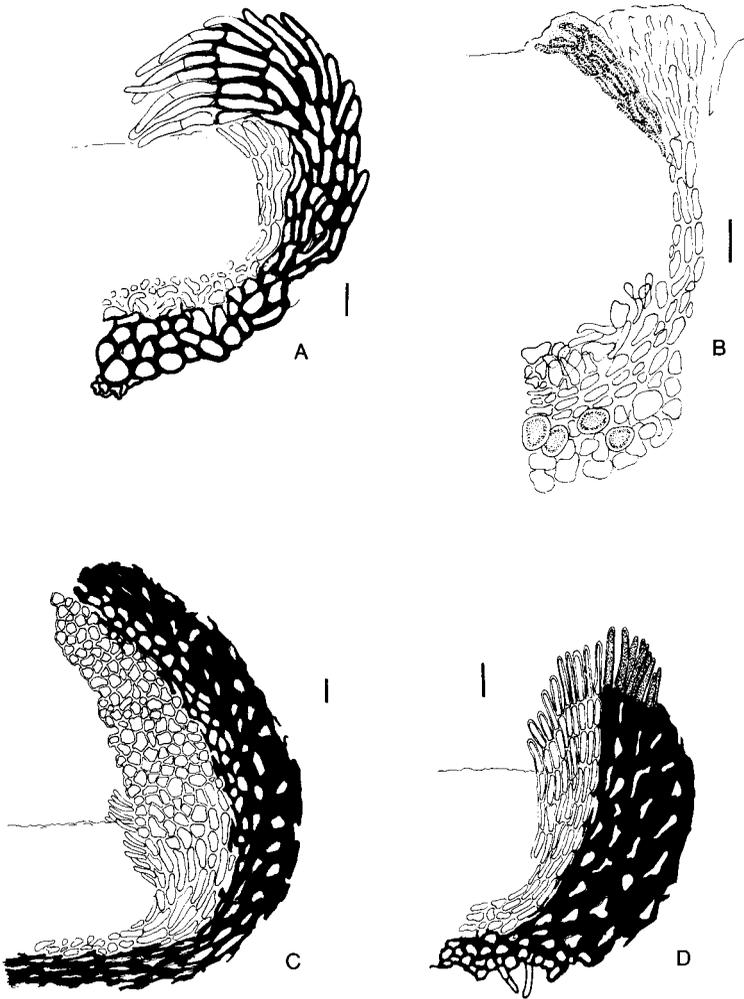


FIG. 1. Exeiple of different genera (in H₂O). A, *Rhymbocarpus cruciatus* (Santesson 16182); B, *R. geographici* (Arnold *Lichenes exsiccati* 1772, UPS); C, *Lethariicola* sp. nov. [Russia, Franz Josef Land, Hooker Island, on *Thamnolia vermicularis* (Sw.) Schaer. var. *subuliformis* (Ehrh.) Schaer., 1930, Demme (UPS)]; D, *Skyttea elachistophora* (Santesson 13277i). Scales: A–D=10 μ m.

apically strongly thickened, with a small, but distinct ocular chamber, without any amyloid reactions (I – and KI –), generally 8-spored; ascogenous hyphae with croziers have been observed in some species. *Ascospores* hyaline, ellipsoid, more rarely fusiform, in some species slightly curved or sigmoid to helicoid, smooth, 0(–3)-septate (true septa!), biguttulate. *Conidiomata* unknown.

Observations. For the species delimitation within *Skyttea*, a number of characters rarely used in the past proved to be of a high taxonomic value, such

as the excipular pigments, the diameter of the ascomata, the thickness of the ascomatal margin, the diameter of the opening pore in mature ascomata, the colour and morphological structure of the margin, the presence or absence of fissures, and the number of fissures per ascomatal margin and their depth. The form and size of the ascospores, often used to distinguish species in other genera of lichenicolous fungi, are here of limited use, as most are ellipsoid and similar in size, with the exception of a few species, in which the ascospores are elongate fusiform, sigmoid or helicoid.

With our current knowledge, and without any cladistic analysis, it is not possible to recognize any groups of closely related taxa within the whole genus. All species are very similar, and any tentative division of the genus, based on the characters available (e.g. pigments, form and size of ascospores and ascomata), may result in an artificial subdivision. We believe that a cladistic study could be useful and informative, but we prefer to wait at least until the possibly related genus *Spirographa* has been revised.

Contrary to what was proposed by Sherwood *et al.* (1981), Hawksworth & Sherwood (1982) and Sherwood-Pike (1987), we believe that the genus *Skyttea* is not a typical member of the *Odontotremataceae*, nor of the Ostropales. In the type genus *Odontotrema*, and also in several other related genera, the ascomata are cleistohymenial, i.e. the immature hymenium is completely covered by the exciple, which later opens by a circular pore or radial fissures to expose the deeply urceolate disc (Sherwood-Pike 1987). The exciple is generally devoid of hairs (except in *Phragmiticola*). The inner excipular layer is typically covered by periphysoids. The ascus wall and the hymenium are normally hemi-amyloid [in *Phragmiticola rhopalospermum* (Kirschst.) Sherwood, only an I+ blue apical ring is present], although this is rarely mentioned in the literature, as mycologists often used Melzer's reagent without pre-treatment with KOH (Baral, *in litt.*). Ascospores are always septate.

In *Skyttea*, the ascomata are urceolate, with a narrow pore when young, but they are not cleistohymenial; the margin of the exciple is covered by hairs; periphyses are absent; the asci and the hymenium are entirely I- and KI-; the ascospores are normally aseptate, but septate spores can occasionally be observed. Although the ascus apex and some additional characters are not the same, many of these characters are shared by the genus *Unguiculariopsis* (Leotiales), and we propose therefore to include the genus *Skyttea* in the same order (in agreement with Baral, *in litt.*). The lichenicolous genus *Spirographa* [syn. *Pleospilis*, *Spilomela*], which was also included in the *Odontotremataceae* by Hawksworth & Sherwood (1982), lacks cleistohymenial ascomata as well as positive iodine reactions, and might therefore also be a member of the Leotiales.

A few specimens of *Skyttea* could not be included in a convincing way in any of the accepted taxa, and some of them might represent additional, undescribed species (e.g., see specimens discussed under *S. buelliae*, *S. caesii*, *S. fusispora* and *S. megalosporae*). One specimen which is too scanty for a complete description has been collected on the cephalodia of *Placopsis gelida* in Norway (Santesson 31620, UPS).

It is interesting to note that most *Skyttea* species are highly specialized taxa. All, with the possible exception of *S. elachistophora*, are known only from one

lichen genus, and several well-documented species (e.g. *S. nitschkei* and *S. gregaria*) might even be restricted to a single lichen species. Some species are known from related, congeneric or even the same lichens (e.g. *S. carboneae*, *S. lecanorae*, *S. elachistophora* and *S. tavaresae* on members of the *Lecanoraceae*; *S. caesii* on *Mycoblastus caesius* and other sorediate *Mycoblastus* spp. and *S. gregaria* on *M. fucatus*; *S. nitschkei* and *S. thelotrematis* both on *Thelotrema lepadinum*), but in none of these cases (except perhaps *S. carboneae* and *S. tavaresae*) are there indications of a closer relationship between the corresponding species of *Skyttea*.

Curiously, all species (except a specimen of *S. aff. fusispora* on *Physcia*) grow on crustose lichens, whilst members of the Peltigerales, which are known to be especially rich in lichenicolous fungi (e.g. Hawksworth 1980*b*; Etayo & Diederich 1996; Hawksworth & Miądlikowska 1997; Wedin & Hafellner 1998), are devoid of them. There are more species known on corticolous lichens than on saxicolous ones, but two (*S. elachistophora* and *S. mayrhoferi*) have been collected on both substrata. Most known species seem to be commensalistic, causing no visible damage to their hosts. *Skyttea nitschkei* has been said to be 'most frequent in forests with an exceptionally long history of ecological continuity' (Sherwood *et al.* 1981), and Diederich (1991) even used this species as an indicator for ancient forests with a long historical continuity in Luxembourg. The widespread *S. gregaria* is far from being a ubiquitous species: in the Benelux countries, where the host *Mycoblastus fucatus* is very common and has been carefully screened for lichenicolous fungi in the field, not one single specimen has been found; this species is definitely absent in large areas of the distribution range of the host and is possibly restricted to regions with an oceanic climate. Several other species have rarely or never been recorded in Europe although their hosts are widespread and common (e.g. *S. mayrhoferi* on *Pertusaria* or *S. tavaresae* on *Pyrrhospora querneae*); these species may well be restricted to areas with special ecological conditions. Two species, *S. megalosporae* and *S. thelotrematis*, which we initially knew only from the Atlantic Pyrenees, have recently been collected by the second author in high altitude forests in Columbia.

Key to the species of *Skyttea*

For the identification of *Skyttea* species, a good quality dissecting microscope with a micrometer scale and a magnification of up to $\times 40$ or $\times 80$ is necessary for an accurate measurement of the ascomatal diameter, the thickness of the ascomatal margin and the diameter of the pore. Excipular pigments, which are important diagnostic characters, have to be studied in water, in K and in N. The length of excipular hairs is indicated for many species, but the diagnostic value of this character should not be overestimated (except for species with very long hairs). In some species (e.g. *S. mayrhoferi*, *S. nitschkei*) 1-septate ascospores have been observed, but this character is not considered here to be of any taxonomic value.

- 1 Exciple in large parts dark reddish to greyish purplish, sometimes almost black (red pigment best seen as purplish in C), K+ bright aeruginose green, often with additional pigments reacting K+

- olivaceous or reddish violet; ascomata dark brown, dark green or black, never covered with a whitish layer or pruina 2
- Exciple greenish, K+ olivaceous, never reacting K+ bright aeruginose green (but basal exciple sometimes with an additional brown, K+ weakly violet pigment); ascomata dark green or black, never dark brown, sometimes appearing whitish due to a whitish layer or pruina 4
- 2(1) Exciple with two main pigments (one of them often being dominant): a dark reddish pigment, most abundant in the upper exciple just below the hairs, reacting K+ bright aeruginose green, and a brownish pigment, occasionally also present in the epihyemium and subhyemium, reacting K+ purplish violet (a strong reaction!) [if the second pigment is dominant, the aeruginose reaction is best visible *c.* 1 min after adding the KOH solution]; ascomata dark brown to black, 130–250 μm , often in a poor condition; hairs up to 30 μm long, but often much shorter; ascospores narrowly ellipsoid, 8–13 $\mu\text{m} \times 2\text{--}3 \mu\text{m}$; on *Thelotrema lepadinum* **S. nitschkei**
 The brown, K+ purplish reacting pigment either absent, or if present, then reduced to the area under the subhyemium (a weak reaction with K!); the red, K+ aeruginose-reacting pigment in the exciple is obscured by a possibly additional dark greyish pigment or by a too high concentration and appears as dark grey to blackish (only in smaller areas appearing as dark red); ascomata black (not dark brown), over 200 μm 3
- 3(2) Ascospores narrowly ellipsoid, 9–12 \times 2.5–3 μm , typically biguttulate; asci *c.* 43–50 \times 5–8 μm ; exciple and excipular hairs dark greyish brown (only in smaller areas dark red), K+ bright aeruginose green; brownish pigment under subhyemium weakly K+ reddish violet; hairs 30–48 μm long; ascomata 200–300 μm ; on the thallus of *Pyrrhospora cf. querneae* **S. tavaresae**
 Ascospores broadly ellipsoid, 6–7.5 \times 2.5–3 μm ; asci 28–33 \times 4.5–7 μm ; exciple dark reddish to blackish, K+ bright aeruginose green, with an additional greenish pigment (difficult to observe), often located in the outer excipular layer, reacting K+ olivaceous; hairs up to 40 μm long; ascomata 200–275 μm ; on the thallus of *Carbonea montevidensis* **S. carboneae**
- 4(1) Ascospores 18–46 \times 2.5–3.5 μm 5
 Ascospores mostly less than 12 μm long 7
- 5(4) Ascospores sigmoid to helicoid, with \pm pointed ends, 22–46 μm long; ascomata 70–120 μm ; excipular hairs up to 20 μm long; on *Megalospora tuberculosa* **S. megalosporae**
 Ascospores straight or curved, with \pm rounded ends, 18–28(–42) μm long; ascomata mostly larger 6
- 6(5) Ascomatal margin thin, 40–60 μm ; ascomatal opening (pore) up to 50% of the ascomatal diameter, when mature; ascomata

- 100–150(–170) μm , superficial; asci 35–45 μm long; excipular hairs 7.5–10 μm long; on *Mycoblastus* spp. **S. caesii**
 Ascumatal margin thicker, 65–85 μm ; pore 10–20% of the ascumatal diameter, when mature; ascumata 110–190 μm , immersed; asci 60–70 μm long; excipular hairs 10–15 μm long; on *Ochrolechia rosella* **S. fusispora**
- 7(4) Ascospores 1–2(–2.5) μm wide; if ascospores up to 2.5 μm , then excipular hairs 30–60 μm long, with a thick-walled and therefore refractive apex (cf. *S. hawksworthii*) 8
 Ascospores (2–)2.5–5 μm wide; if excipular hairs longer than 30 μm , then apex not refractive 10
- 8(7) Ascumata 120–340 μm ; wall of excipular hairs apically not thickened, not appearing refractive; hairs 20–38 μm long; ascospores 5–7 \times 1.5–2 μm ; on the thallus of cf. *Micarea denigrata* **S. viridis**
 Ascumata 75–175 μm ; wall of excipular hairs apically thickened, appearing refractive 9
- 9(8) Excipular hairs 20–35 μm long, not visible with a dissecting microscope; ascospores 6–7(–7.5) \times 1.5–2 μm ; ascumata almost superficial when mature; on sterile thalli of *Verrucaria nigrescens* **S. spinosa**
 Excipular hairs 30–60(–80) μm long, easily visible with a dissecting microscope, and almost hiding the apothecia; ascospores 6–8(–10) \times 2–2.5 μm ; mature ascumata immersed; on *Verrucaria* sp. **S. hawksworthii**
- 10(7) Ascospores 4–7 \times 2.5–3.5(–4.5) μm ; ascumata black, 100–225 μm ; margin 50–60 μm ; on *Buellia punctata* **S. buelliae**
 Ascospores (6–)7–12 μm long; if most ascospores 6–7 μm long, then ascumatal margin thicker 11
- 11(10) Ascumata mostly 90–160 μm ; ascumatal margin 30–50(–55) μm thick. 12
 Ascumata (125–)150–225(–350) μm ; ascumatal margin 45–125 μm thick. 14
- 12(11) Ascospores 9–12(–16) \times 3.5–5 μm ; ascumata 100–140 μm , margin 40–50 μm thick; excipular hairs 10–20 μm long; exciple partly with a brown, K+ violet pigment (reaction sometimes weak and difficult to observe); on *Loxospora pustulata* **S. radiatilis**
 Ascospores mostly 2.5–3.5 μm wide 13
- 13(12) Ascumatal opening (pore) c. 20% of the ascumatal diameter in mature ascumata; ascumata (75–)90–125(–150) μm ; margin striate, often appearing whitish, mainly when young; lateral exciple 10–25 μm thick; excipular hairs 8–13 μm long; hymenium 45–55 μm ; asci 35–50 μm ; ascospores 7–9(–13) \times (2–)3–3.5(–4.5) μm ; on *Lecanora* spp. **S. lecanorae**

- Ascomatal opening up to 50% of the ascomatal diameter; ascomata 125–160 µm (in elongate ascomata up to 200 µm); margin not striate, not whitish (except the inner border of the margin); lateral exciple up to 55 µm thick; excipular hairs 4–7 µm long; hymenium 50–65 µm; asci 45–60 µm; ascospores 8–12 × 2.5–3 µm; on *Pyrenula* **S. pyrenulae**
- 14(11) Ascomata often appearing cruciate, with 3–5 deep marginal fissures, blackish; margin 60–125 µm thick; pore in mature ascomata 25–50(–75) µm; excipular hairs 20–50 µm long; exciple of ± globose cells of 5–10 µm; ascospores 6.5–8 × 3–3.5(–4) µm; on *Tephromela atra* s. lat., *T. tropica* and an unidentified, crustose, saxicolous lichen (*Tylothallia biformigera?*) [rare specimens with ascomata not appearing cruciate may be identified using the other characters mentioned in this key] **S. elachistophora**
 Ascomatal margin entire, poorly or distinctly striate; fissures, if present, not deep, and more numerous (c. 5–10 per margin); excipular hairs 5–30 µm long; exciple of smaller cells or of elongate interwoven hyphae 15
- 15(14) Ascospores narrowly ellipsoid, (7.5–)9–10(–11) × (1.7–)2.3–3 µm; ascomata blackish, but around the pore generally whitish; margin 45–60 µm, striate, with numerous fissures, partly whitish; pore in mature ascomata 40–60% of the ascomatal diameter; excipular hairs up to 16 µm long; exciple of globose to elongate cells of 4–8 µm, without a brownish, K+ violet pigment; on *Thelotrema lepadinum*. **S. thelotrematis**
 Ascospores at least 3 µm wide; ascomatal margin never whitish; pore often smaller 16
- 16(15) Ascomatal margin 70–105 µm thick; pore in mature ascomata 10–30 µm; basal exciple partly with a brown, K+ violet pigment (reaction sometimes weak and difficult to observe); ascomata black, in outline irregular due to numerous small marginal fissures; exciple of ± globose cells of 3.5–7 µm; excipular hairs 15–30 µm long; ascospores 6–12 × 3–4 µm; on *Pertusaria* . . **S. mayrhoferi**
 Ascomatal margin 55–85 µm thick; pore in mature ascomata 25–50 µm; basal exciple without a brown, K+ violet pigment; ascomata dark greyish, not black, in outline ± regularly circular; exciple of elongate, ± interwoven hyphae, 4–5 µm thick and over 10 µm long in microscopical section; excipular hairs 5–20 µm long; ascospores 7–8.5 × 3–3.5 µm; on *Mycoblastus fucatus* (= *M. sterilis*) **S. gregaria**

Skyttea buelliae Sherwood, D. Hawksw. & Coppins

Trans. Br. mycol. Soc. 75: 483, (1981 [‘1980’]); type: Great Britain, V.C. 54, North Lincolnshire, near Wold Newton, on *Ulmus*, on *Buellia punctata*, vii 1976, *Seaward* (E—holotypus, non vid.).

For a description and illustrations, see Sherwood *et al.* (1991).

Host. Buellia punctata (thallus).

Distribution. Belgium, Germany (Spier 1998), Great Britain, Italy and the Netherlands.

Observations. *Skyttea buelliae* is well characterized by its broad but short biguttulate ascospores. In addition to the material enumerated below, we studied a specimen on *Lecanora* which is almost identical to *S. buelliae* [Norway, Nord-Trøndelag, Mt Røythaugfjellet, on *Betula*, xi 1983, Tønsberg (BG)]; as the single specimen is quite reduced and the host in a poor condition, we prefer to await the discovery of more material before we decide if it really belongs to *S. buelliae* or if an undescribed species is involved. In this context it is interesting to note that the species has also been reported from The Netherlands on *Lecanora* sp. (Brand *et al.* 1988). Furthermore, we examined several specimens on thalli of *Ochrolechia* on branches of *Picea abies*, which were difficult to separate from *S. buelliae* [Norway, S-Trøndelag: Skaun, Råbygda, SW of Syrstadsetra, vi 1993, *Holien* 5693 (TRH); Overhalla, W of Foss, iii 1997, *Holien* 7102 (TRH); Meldal, Urdvatnet, vii 1993, *Holien* 5806 (TRH); Meldal, NE of Storliåsen, vii 1993, *Holien* 5801 (TRH); Meldal, S of Lomtjørna, viii 1993, *Holien* 5900 b (TRH)]. As almost all species of *Skyttea* are host-specific, we hesitate to include them in *S. buelliae*, and we prefer to leave them unnamed until more material of these short-spored species is available.

Specimens examined (all on *Buellia punctata*). **Belgium:** Annevoie-Rouillon, Jardins d'Annevoie, on *Tilia*, 1999, *Diederich* 13843 (h); Zwalm, Roborst, on *Tilia* near church, 1999, *Diederich* 13925 (h).—**Italy:** S of Rome, near the catacombs of Saint-Calixte, on *Cupressus*, 1997, *Diederich* 12560 (h).—**The Netherlands:** Utrecht, Polsbroek, 120 m, on *Populus* along a road, iii 1996, *van Herk* (hb. Aptroot); Noord Holland, Overveen, Cios-Noord, 1977, *Aptroot* 2120 (h); Zuid-Holland, Goudriaan, Protestant church, on *Tilia*, 1999, *Aptroot* 45989 (h, hb. *Diederich*).

***Skyttea caesii* Diederich & Etayo sp. nov.**

Skyttea insignis ascomatibus 100–150(–170) μm diam., margine 40–60 μm crasso, non striato, poro magno, excipulo viridibrunneo, K+ olivaceo, pilis 7.5–10 μm longis, ascis 35–45(–50) \times 6–9 μm , ascosporis 18–28(–42) \times 3–3.5 μm .

Typus: Great Britain, Scotland, V.C. 104, North Ebudes, Isle of Skye, SW of Broadford, Drinan (NG.55.15), on *Mycoblastus caesius* growing on *Betula*, 25 May 1987, *Diederich* 8211 (E—holotypus; hb. *Diederich*—isotypus).

Ascomata initially immersed, later erumpent, dark greyish to blackish, 100–150(–170) μm diam., margin in opened ascomata 40–60 μm thick, not striate (surface view, \times 80); pore reaching half of the ascomatal diameter in mature ascomata. *Exciple* laterally greenish brown, K+ olivaceous, more brownish in the outer parts, 20–35 μm thick; basal exciple greenish brown, 13–18 μm thick; excipular hairs hyaline to greenish, not distinctly curved, 7.5–10 \times 3–4 μm . *Subhymenium* hyaline, 6–10 μm thick. *Hymenium* c. 50 μm thick. *Epihymenium* hyaline to pale greenish. *Paraphyses* filiform, simple or rarely branched, 1–1.5 μm thick. *Asci* cylindrical to clavate, wall apically thicker, 8-spored, 35–45(–50) \times 6–9 μm . *Ascospores* hyaline, narrowly ellipsoid, slightly curved, not sigmoid, 0(–3)-septate, 18–28(–42) \times 3–3.5 μm .

Hosts. *Mycoblastus caesius* (syn. *Haematomma caesium*), *Mycoblastus* sp. (a sorediate species with a whitish thallus, 0.4–0.7 mm convex soralia, blackish apothecia of 0.3–0.4 mm, a bluish violet, K+ aeruginose green epihymenium and ascospores of 33–46 × 21–35 µm, which are 2 per ascus from Réunion) and two unidentified sterile corticolous lichens, one from the Canary Islands, which has a whitish sorediate thallus, and one from Guinea, which looks similar to *M. caesius*, with a grey, sorediate thallus and a black hypothallus, but is UV –.

Distribution. We have examined material from Great Britain (Scotland), Canary Islands, Guinea, Réunion and USA, but some of these specimens are included here only provisionally (see below).

Observations. Two specimens of this species on *M. caesius*, which were ‘too scanty to investigate critically’ were included provisionally in *S. fusispora* by Sherwood *et al.* (1981). These authors observed that the ascospores may become 3-septate, and up to 38 µm long. Our recent Scottish collections prove that the two species *S. caesii* and *S. fusispora* are very close, but nevertheless clearly distinct. The ascomata in *S. caesii* have a thin margin, which is 40–60 µm thick when mature; in *S. fusispora*, the margin is 65–85 µm thick. In young ascomata of *S. caesii*, which are 100–120 µm diam., the ascomatal opening (pore) is still small (c. 25–35% of the ascomatal diameter), but in older ascomata (c. 150 µm), the opening reaches 50% of the ascomatal diameter; in *S. fusispora*, the much thicker margin covers almost completely the hymenium, and the opening in mature ascomata is just 10–20% of the ascomatal diameter. There are several other differences: *S. caesii* has shorter asci (35–45 µm long), and shorter excipular hairs (7.5–10 µm long) than *S. fusispora*, which has 60–70 µm long asci and 10–15 µm long excipular hairs. The ascomata of *S. fusispora* also tend to be slightly larger, 110–190 µm diameter, and ± completely immersed in the thick thallus or the apothecia of the host, whilst those of *S. caesii* are superficial on the very thin thallus or prothallus of *M. caesius*.

Three additional specimens are provisionally attributed here to the same species on account of similar morphological and anatomical characters: one from the Canary Islands (Etayo 3459) has erumpent apothecia, 120–150 µm diam., margin 50 µm, ascomatal opening 20–50 µm, lateral exciple 50–60 µm, basal exciple 30 µm, excipular hairs 8–12 × 3 µm, asci 47–53 × 9–10 µm, ascospores non-septate, 24–32 × 2.5 µm; one from Réunion on an unidentified species of *Mycoblastus* (Kalb 26331), which differs by longer ascospores, 39–42 × 3 µm, and one from Guinea (Santesson 10548) with ascomata superficial, 100–170 µm, margin 40–70 µm, ascomatal opening 25–40 µm, excipular hairs 10–15 × 3 µm long, ascospores non-septate, 26–30 × 2–4 µm, asci 55–60 × 8–11 µm. The Guinea specimen differs from typical *S. caesii* by larger asci, slightly longer and narrower ascospores and a slightly smaller ascomatal opening, and might prove later to represent another species.

Additional specimens examined. **Great Britain** (all on *M. caesius*): **Scotland:** V.C. 104, North Ebuades: Isle of Skye, Tokavaig Wood, 1987, Diederich 8025 (h); SSE Broadford, Ardnamurchan, 1987; Diederich 8306 (h); Isle of Raasay, South Fearn, 1987, Diederich 8769 (h).—**Canary**

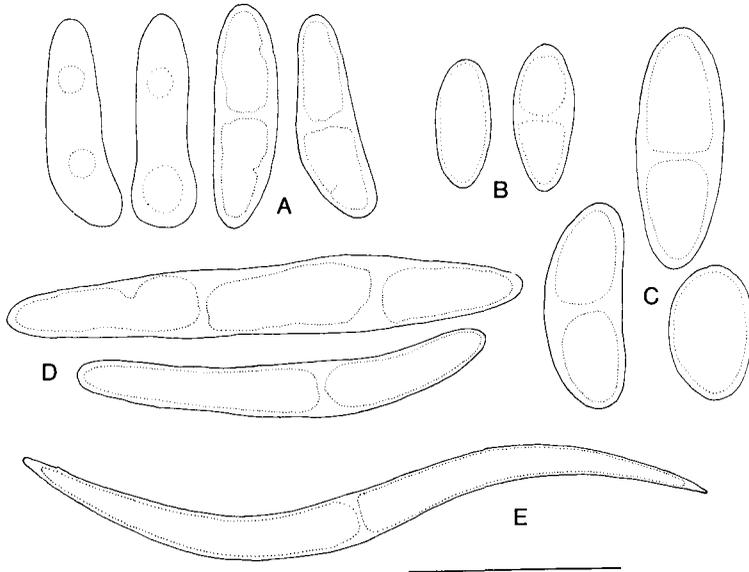


FIG. 2. Ascospores of *Skyttea* species (in H_2O). A, *S. tavaresae* (holotypus), note two living biguttulate ascospores on the left; B, *S. carboneae* (holotypus); C, *S. mayrhoferi* (van den Boom 18483); D, *S. cf. fusispora* (UPS L-83900); E, *S. megalosporae* (holotypus). Scale = 10 μm .

Islands: *Tenerife:* Between Pico del Inglés and La Cruz del Carmen, 900 m, on a crustose lichen in Laurisilva, 1991, *Etayo* 3459 (h); Monte Aguirre, on *M. caesius*, on *Erica arborea*, 1990, *Becker* (hb. Diederich).—**Guinea:** Cercle of N'Zérékoré, Mts Nimba, c. 6 km SE of Zouépo (Zigueta), just below the camp, 1.5 km SSW of the top '1611', c. 1550 m, on a corticolous sterile sorediate crust on a tree in the outskirts of a mountain forest, 1954, *Santesson* 10548 (UPS).—**Réunion** (Mascarene Is.): Cirque de Cilaos, Aufstieg von der Straße zwischen Cilaos und Ilet à Cordes auf den Col du Taïbit, 1500–2000 m, on *Mycoblastus* sp., 1991, *Kalb* 26331 (h).—**USA** (all on *M. caesius*): *Washington:* Clallam Co., 3 km NNE of Forks village centre, N of River Calawah, along Rough Ridge Road (FR29), 1998, *Tønsberg* 25795 (BG L-36193); Clallam Co., between Forks and La Push, E of Quillayute, S of Quillayute Rd just E of Soleduck River Bridge, 1994, *Tønsberg* 21552 (BG L-34885); Jefferson Co., along Upper Hoh Rd, 1.4 km along the road W of Alder Creek, 1994, *Tønsberg* 21622 (BG L-34909).

Skyttea carboneae Diederich & Etayo sp. nov.

Skyttea insignis ascomatibus 200–275 μm diam., margine 90–100 μm crasso, poro 0–60 μm , excipulo duobus pigmentis, uno atrorubro, K+ verdigri, altero viridi, K+ olivaceo, pilis ad 40 μm longis, ascis 28–33 \times 4.5–7 μm , ascosporis 6–7.5 \times 2.5–3 μm .

Typus: Bolivia, Depto. La Paz, Prov. Murillo, etwas unterhalb des Ortes Ñuñumayuni im Tal des Rio de La Paz oberhalb Mecapaca, linke Talseite, 3400 m, Sandstein, auf *Carbonea montevidensis*, 29 March 1981, *Feuerer* 12432d, *Höhne & Gerstmeier* (HBG—holotypus).

(Fig. 2B)

Ascomata dispersed on the host thallus, superficial, black, 200–275 μm diam.; margin in opened *ascomata* 90–100 μm thick (surface view), with numerous fissures; pore 0–60 μm diam. *Exciple* laterally dark reddish to

blackish, K+ bright aeruginose green, N+ dark reddish brown, 25–45 µm thick, with an additional greenish pigment, often located in the outer excipular layer, reacting K+ olivaceous; basal exciple the same colour and reactions, 25–45 µm thick; excipular hairs greyish brown, K+ brownish or green, straight, wall apically not thickened, up to 40 × 2.5–3.5 µm. *Subhymenium* hyaline to yellowish, c. 10 µm thick. *Hymenium* c. 50 µm thick. *Epihymenium* ± hyaline. *Paraphyses* filiform, simple, septate, 1.5–2 µm thick, apically slightly thicker. *Asci* subcylindrical, wall apically thicker, 8-spored, c. 28–33 × 4.5–7 µm. *Ascospores* hyaline, ellipsoid, non-septate, 6–7.5 × 2.5–3 µm.

Host. On the thallus of *Carbonea montevidensis*.

Distribution. Known only from the type locality in Bolivia.

Observations. The single known specimen of this species was included in the concept of *S. elachistophora* by Triebel (1989). Both taxa are nevertheless very distinct: in *S. elachistophora* the reddish, K+ green pigment is missing, whilst the green, K+ olivaceous pigment is dominant, the asci are distinctly longer, the ascospores are slightly longer, and the ascomal margin (× 80) has a smaller number of fissures (c. 3–6 per ascoma, versus 5–10 in *S. carboneae*), which are generally deeper, the ascomata often appearing cruciate.

Skyttea carboneae is distinguished from most *Skyttea* species by the dark reddish, K+ aeruginose green pigment. The differences with *S. nitschkei* and *S. tavaresae*, two other species with the same pigment, are given in the identification key.

***Skyttea elachistophora* (Nyl.) Sherwood & D. Hawksw.**

In Sherwood *et al.*, *Trans. Br. mycol. Soc.* 75: 484 (1981 [‘1980’]).—*Verrucaria elachistophora* Nyl., *Flora* 61: 246 (1878).—*Rhymbocarpus elachistophorus* (Nyl.) Triebel, *Bibl. Lichenol.* 35: 145 (1989); type: Ireland, Co. Galway, Kylemore, ‘in a stream’, on an unidentified sterile lichen (see discussion below), 1876, C. du Bois Larbalestier 88 (H-NYL 452—lectotypus, vid.).

?*Skyttea tephromelarum* Kalb & Hafellner, in Kalb *Lichenes Neotropici Exs.* Fasc. 10, 449: 15 (1988); type: Kenya, Central Prov., Nanyuki Distr., between Naro Moru and Nanyuki, between Bantu Lodge and Mao Mao caves, 2050 m, on *Tephromela tropica*, 18 vii 1985, Kalb & Schrögl (Kalb *Lichenes Neotropici Exs.* 449) (hb. Kalb—holotypus, vid.).

(Fig. 1D)

For a description and additional illustrations, see Sherwood *et al.* (1981), Kalb *Lichenes Neotropici Exs.* 449 and Triebel (1989).

Hosts. *Tephromela atra* (incl. the corticolous var. *torulosa*) and *T. tropica*, and a sterile, crustose, saxicolous lichen containing atranorin and confluent acid, which has been assigned to *Lecidea* s. lat. by Sherwood *et al.* (1981) and to cf. *Tylothallia biformigera* by Rambold in Triebel (1989) (see discussion below).

Distribution. Austria, France (Corsica), Great Britain, Ireland, Italy, Norway, Russia, Spain, Canary Islands, Madeira, Kenya, USA, Argentina, Subantarctic Islands (Prince Edward Island, Marion Island) (Santesson 1960, 1993; Triebel 1989; Hafellner & Türk 1995; Hofmann *et al.* 1991; Triebel *et al.* 1991; Kalb & Hafellner 1992; Hafellner 1993, 1994a, b, 1996b).

Observations. As the type specimen of *S. elachistophora* comprises a relatively small number of ascomata in a good condition, we did not make a complete study of this fungus, of which a modern description is available in Sherwood *et al.* (1981). The lateral exciple is, however, not 'brown, without any greenish tint' as stated by these authors, but distinctly greenish in large parts, and brownish only in the uppermost region. In KOH, the greenish pigment becomes olivaceous, whilst the brown region remains (reddish) brown. We confirm the presence of unusually large outer excipular cells, a character stressed by Sherwood *et al.* (1981).

In the protologue of *S. tephromelarum*, that species was said to differ from *S. elachistophora* by an olivaceous exciple and shorter excipular hairs (12–20 µm long, versus 40–50 µm). However, the excipular pigments are exactly the same in the material studied by us, and the excipular hairs in the material growing on *Tephromela* appear to be quite variable, with hairs over 40 µm long dominant in some specimens (e.g. Hafellner 32807).

The host of the type specimen of *S. elachistophora* is sterile and in a poor condition. It has been examined by Sherwood *et al.* (1981: 484) who stated that it contains atranorin and confluent acid (examined by TLC by P. W. James) and who proposed that it might be a *Lecidea* s. lat. Rambold (in Triebel 1989) noticed a morphological and chemical resemblance with *Tylothallia biformigera*. As all other known *Skyttea* species are highly specialized fungi growing on one single host genus or species, it seems unlikely that *S. elachistophora* is confined to two non-related host genera, *Tephromela* (*Bacidiaceae*) and *Tylothallia* (*Lecanoraceae*). It is also unlikely that *Tylothallia biformigera* is a misunderstood species of *Tephromela*. As long as the identity of the host is not correctly understood, and no recent collections of a *Skyttea* on *Tylothallia* are made, we believe that it is best to consider both taxa *S. elachistophora* and *S. tephromelarum* as conspecific, growing on *Tephromela* and an unidentified crustose lichen.

Triebel (1989) mentioned an additional specimen of *S. elachistophora* on *Carbonea montevidensis* from Bolivia. We re-examined the Bolivian material (Feuerer 12432d) and found that this specimen represents a distinct species, *S. carboneae* (for differences, see under that species).

Additional specimens examined (all on *T. atra*; unless otherwise mentioned, all saxicolous). **Austria:** Kärnten: Nationalpark Hohe Tauern, Tauerntal NW von Mallnitz, 1989, Hafellner 24252, 28432 (GZU). Steiermark: Gurktaler Alpen, Frauenalm S von Murau, v 1981, Poelt (GZU); *ibid.*, 1983, Poelt (2 spec.) & Hafellner 10364 (GZU). Tirol: Ötztaler Alpen, in der Klamm E ober Pfunds, 1991, Hafellner 30223 (GZU).—**France:** Haute-Corse: Monte d'Oro-Massiv, Kuppe N ober dem Col de Vizzavona, 1993, Hafellner 31576 (GZU).—**Great Britain:** Scotland: V.C. 102, South Ebuades: Islay, 3–4 km S of Port Askaig, Baleachdrach, 1992, Coppins 15118 (E).—**Norway:** Hordaland, Odda, 1984, Hafellner 12025 (GZU); Hordaland, Voss, 1984, Hafellner 14502 (GZU).—**Russia:** Karelia, Karelia ladogensis, Sortavala, Valamo, Bajonnoi, vii 1938, Pankakoski (H, hb. Diederich).—**Spain:** Alava, near Murua, c. 15 km NNW of Vitoria, on

Quercus, 1959, *Santesson* 132771 (UPS); Teruel, cerca de Tormón, 1997, *Calatayud* (VAB-lich. 7917); Tarragona, Sierra de Prades, an der Straße vom Monasteria de Poblet nach Prades, 1983, *Hafellner* 17451 (GZU).—**Sweden**: Bohuslän, Koster-Archipel SW von Strömstad, Insel Sör-Koster, 1990, *Poelt* (GZU).—**Canary Islands**: *Gran Canaria*: Degollada de Tasartico SE ober San Nicolás, 1994, *Hafellner* 32928 (GZU); zw. Ayacata und Las Lagunetas, 1994, *Hafellner* 32900 (GZU). *La Gomera*: Zw. Chipude und El Cercado, auf *Ficus carica*, 1991, *Hafellner* 32807 (GZU). *Tenerife*: Macizo de Anaga, c. 3 km E von San Andres, 1989, *Hafellner* 24316 (GZU).—**Madeira**: Penha de Aguiá, 1990, *Hafellner* 27863 (GZU); Pico Escalvado, c. 1 km S vom Pico do Areiro, 1990, *Hafellner* 27347 (GZU); Pico dos Estanquinhos am NE-Rand des Hochplateaux Paul da Serra, 1990, *Hafellner* 27463 (GZU).

***Skyttea fusispora* Sherwood, D. Hawksw. & Coppins**

Trans. Br. mycol. Soc. 75: 484 (1981 [‘1980’]); type: India, Assam, Bashahr State, Muniapur, Sechi-Sirpara Forest I. Pandrabis, 8000 ft, on *Ochrolechia rosella*, 3 v 1891, *Watt* (E—holotypus, vid.).

For illustrations of the type specimen, see Sherwood *et al.* (1981: figs 1D, 5).

Ascomata immersed, blackish, 110–190 µm diam., pore reaching 10–20% of the ascomatal diameter in mature ascomata; margin in opened ascomata 65–85 µm thick (surface view, × 80). *Exciple* greenish brown, K+ olivaceous; excipular hairs greenish to brownish, 10–15 × 2.5–3 µm. *Subhymenium*, *hymenium* and *epihymenium* hyaline. *Paraphyses* filiform, septate, simple or rarely branched, 1.5–2 µm thick. *Asci* cylindrical to clavate, wall apically thicker, 8-spored, 60–70 × 6–8 µm. *Ascospores* hyaline, narrowly ellipsoid, not or slightly curved, not sigmoid, non-septate, 20–28 × 2.5–3.5 µm.

Host. *Ochrolechia rosella*.

Distribution. India, known only from the type locality.

Observations. This species is very close to *S. caesii*, and in the original description, material of *S. caesii* was even provisionally included in *S. fusispora* (Sherwood *et al.* 1981). Both species are, however, clearly distinct. For the differences, see under *S. caesii*. Without a microscopical examination, *S. fusispora* might be confused with a possibly undescribed species with short ascospores occurring on *Ochrolechia* in Scandinavia (see under *S. buelliae*).

One additional specimen should be compared with *S. fusispora*: **Australia**: Victoria, Suggan Buggan, along the road in the SW slope just NE of the river, 37°57'S, 148°20'E, 100 m, on epiphytic *Physcia*, 1992, *Moberg* A57:5 (UPS L-83900). *Ascomata* growing on the thallus, or rarely the ascomatal disc of the host, first immersed, later superficial, 150–200 µm diam., margin 50–70 µm, ascomatal opening 50–120 µm, exciple green, excipular hairs 15–20 µm, asci 50–55 µm long, ascospores (Fig. 2D) non-septate (but appearing 1–3-septate due to the disposition of guttules), 19–26 × 2.5–3 µm. This specimen is distinguished from the type of *S. fusispora* by the much narrower ascomatal margin and the larger ascomatal opening, the green exciple (it is olivaceous brown in *S. fusispora*), and the different host, and might represent an

additional, distinct species. More material on *Physciaceae* is needed to ascertain if such specimens should be excluded from *S. fusispora*.

Skyttea gregaria Sherwood, D. Hawksw. & Coppins

Trans. Br. mycol. Soc. 75: 486 (1981 [‘1980’]).—*Rhymocarpus gregarius* (Sherwood, D. Hawksw. & Coppins) *Triebel, Bibl. Lichenol.* 35: 144 (1989); type: Great Britain, NW Yorkshire (V.C. 65), Swaledale, Downholm Park, on *Mycoblastus fucatus*, 20 viii 1969, *Coppins* (E—holotypus, non vid.).

For a description and illustrations, see Sherwood *et al.* (1981).

Host. This species seems to be restricted to *Mycoblastus fucatus* (syn. *M. sterilis*). The literature records on *Lecanora farinaria* (Tønsberg 1992) and on an unidentified lichen crust (Santesson 1993) almost surely refer to other species, such as *S. lecanorae*.

Distribution. Austria, Finland, Germany, Great Britain, Norway, Slovenia, Spain, Sweden and USA (Muhr 1987; Santesson 1993; Hafellner 1994a; Wirth 1994; Berger 1996).

Observations. *Skyttea gregaria* is very similar to *S. elachistophora* and *S. thelotrematis*, and also to specimens of *S. mayrhoferi* in which the brown, K+ violet pigment is indistinct (for differences, see the identification key). Specimens on unusual or unidentified hosts resembling *S. gregaria* can be identified by careful study of the ascomatal characters with a good quality dissecting microscope.

Additional specimens examined. **Austria:** *Kärnten:* Karawanken, im Obojnikbach Graben WSW von Eisenkappel, kurz S von Unter-Bistritschnig, 720 m, 1990, *Hafellner* 26706 (GZU). *Steiermark:* Gesäuse, an der Einmündung des Haindlkars c. 2 km W von Gstatterboden, 610 m, 1988, *Hafellner* 20320, 20368 (GZU); Hochschwab-Gruppe, Hinterseeau Graben E des Leopoldsteiner Sees, N von Eisenerz, nahe Einmündung des Geharts Baches, 700 m, 1990, *Hafellner* 25098 (GZU); Hochschwab-Gruppe, Seetal W von Seewiesen, c. 10 km NE von Aflenz, 930 m, 1993, *Hafellner* 30802 (GZU).—**Great Britain:** *Scotland:* V.C. 96, Easternness: SE of Aviemore, Rothiemurchus Forest, v 1980, *Sherwood & Coppins* (UPS). V.C. 105, West Ross: SE of Shiel Bridge, 1987, *Diederich* 7979 (h).—**Norway:** Sogn og Fjordane, Gulen, Byrknesøy, Gråvika, x 1988, *Tønsberg* (BG); Hordaland, Meland, Holsnøy, Skjeljanger, x 1988, *Tønsberg* (BG).—**Slovenia:** *Pohorje* (Bacher Gebirge): Schutzgebiet Pragozd SE ober Lovrenc na Pohorju, 1000 m, 1993, *Hafellner* 31040 (GZU); SE ober Lovrenc na Pohorju, c. 2.5 km N von Osankarica, W von Obrol, 1200 m, 1993, *Hafellner* 31114 (GZU).—**Spain:** *Navarra:* Belabarce, 1100 m, 1987, *Etayo* 3209 (h); Leiza, Leizalarrea, 470 m, 1987, *Etayo* 3330 (h); valle des Roncal, Isaba, Refugio de Belagua, c. 1000 m, 1985, *Etayo* 4301 (h); Orbaiceta, Irati, Lizardoya, c. 900 m, 1988, *Etayo* 4313 (h).—**Sweden:** Halland, Breared par., Skällas, 1965, *Santesson* 17117 (UPS); Jämtland, Kall par., 11.5 km NW of Anjan, Snadnåset, N of Stortjärnen, 62°46'N, 12°27'E, 430 m, 1987, *Tibell* 17024d (UPS).—**USA:** *Washington:* Clallam Co., between village Neah Bay and Mukkaw Bay, NW of River Waatch, 1 km from Muukaw Bay N, 1993, *Tønsberg* 19350b (BG L-35443); San Juan Co., Lopez Island SE, between MyArdel Bay and Watmough Bay, along and S of Watmough Head Rd, 1998, *Tønsberg* 26936 (BG).

Skyttea hawksworthii Diederich

Lejeunia, n. s. 119: 14 (1986); type: Luxembourg, W of Hunsdorf, on *Verrucaria*, 4 iii 1984, *Diederich* 5099 (IMI 30096—holotypus; hb. Diederich—isotypus).

For a description and illustrations, see Diederich (1986).

Host. A specimen of *Verrucaria* in very poor condition, similar to *V. macrostoma*, but with much narrower ascospores, $18\text{--}24 \times 6\text{--}7 \mu\text{m}$.

Distribution. Luxembourg, known only from the type collection.

Observations. *Skyttea hawksworthii* is very close to *S. spinosa*. The differences between both are given under that species.

***Skyttea lecanorae* Diederich & Etayo sp. nov.**

Skyttea insignis ascomatibus (75–) 90–125 (–150) μm diam., margine 30–50 μm crasso, striato, partim albido, poro parvo, excipulo viridibrunneo, K+ olivaceo, pilis 8–13 μm longis, ascis 35–50 \times 3–4 μm , ascosporis 7–9 \times 3–3.5 μm .

Typus: Norway, Troms, Harstad, N-facing slope of S of lakelet Kasfjordvatn, on *Lecanora* sp. growing on *Alnus incana*, 5 August 1987, Tønsberg 10409b (BG—holotypus).

Ascomata initially immersed, later erumpent, blackish, margin distinctly striate and often appearing whitish, especially when young, (75–)90–125(–150) μm diam.; margin in opened ascomata 30–50 μm thick (surface view, $\times 80$); pore c. 20% of the ascomatal diameter when mature, exceptionally in some overmature ascomata up to 35%. *Exciple* laterally greenish brown (outer layer brownish, without the green pigment), K+ olivaceous, 10–25 μm thick; basal exciple greenish brown, 13–17 μm thick; excipular hairs hyaline to greenish, straight, wall apically not thickened and therefore not refractive, 8–13(–20) \times 1.5–2.5 μm . *Subhymenium* hyaline, 6–10 μm thick. *Hymenium* 45–55 μm thick. *Epihymenium* hyaline to pale greenish. *Paraphyses* filiform, simple or rarely branched, 1.5–2 μm thick. *Asci* subcylindrical, wall apically thicker, 8-spored, 35–50 \times 3–4 μm . *Ascospores* hyaline, ellipsoid, non-septate, 7–9(–13) \times (2–)3–3.5(–4.5) μm .

Hosts. On the thallus and apothecial margin of corticolous *Lecanora* species, including *L. allophana*, *L. chlarotera*, *L. farinaria* and *L. pulicaris*.

Distribution. We have seen material from Finland, Great Britain (Scotland), Norway, Spain, Russia (Siberia), Canary Islands, Canada, USA, Argentina and Uruguay.

Observations. The new species is close to *S. pyrenulae* and to *S. gregaria*. The differences from *S. pyrenulae* are given under that species. Microscopically, both *S. lecanorae* and *S. pyrenulae* are very similar to *S. gregaria*; in that species, the ascospores are 7–8.5 \times 3–3.5 μm , the asci 40–55 \times 6–8 μm , and the excipular hairs 5–20 \times 3–3.5 μm . There are, however, important macroscopical differences: the ascomata in *S. gregaria* are much bigger, (125–)150–210 μm diam., the margin of opened ascomata in surface view ($\times 80$) is 55–85 μm thick, the exciple is 40–50 μm thick, and the ascomata look dark greyish, almost blackish, even when young. *S. lecanorae* should not be confused with *Unguiculariopsis lesdainii* or *U. thallophila*, both

confined to *Lecanora* species, which are distinguished by the reddish brown ascomata and excipular pigments.

Additional specimens examined. **Finland:** Inari-Lapland, Umgebung von Kevo, auf *Lecanora* sp., 196x (full date missing), *Poelt* (GZU).—**Great Britain:** *Scotland:* V.C. 92, South Aberdeen: 9 km ENE of Ballater, Dinnet Oakwood NNR, on *L. chlarotera*, 1994, *Coppins* 16565 (E). V.C. 98, Main Argyll: Tyndrum, Glenorchy, near Invergaunan, 105 m, on *L. pulicaris*, vi 1978, *Coppins* (E). V.C. 104, North Ebuades, Isle of Skye: SW Broadford, Coille Gaireallach, 1987, on *L. chlarotera*, *Diederich* 8148 (h) & *Coppins* 11695 (E); Drinan, v 1987, on *L. chlarotera*, *Diederich* 8212 (h). V.C. 105, West Ross: Torridon, Inveralligan, wood and gorge of Abhainn Alligin, on *L. chlarotera*, 1994, *Coppins* 16403 (E).—**Spain:** *Navarra:* Leiza, on *L. chlarotera*, 1987, *Etayo* 3801 (h); Zugarramurdi, Alkurruntz, on *L. gr. argentata*, 1988, *Etayo* 5201 (h).—**Canary Islands:** *La Palma:* Subida a La Cumbre desde Breña Baja, fayal-brezal, sobre *L. chlarotera* en *Laurus*, 760 m, 1995, *Etayo* 13501 (h).—**Russia:** Baikal Lake region, Baikal'skii Reserve, right bank of Kliuchevaia River before the *Populus* islands, on *L. allophana*, viii 1996, *Urbanavichyus* (LE).—**Canada:** Québec, Gaspésie, Parc National Forillon, 5 km ENE of Gaspé, 'Penouille' peninsula, on *L. pulicaris*, 1997, *Rambold* 6124 (M).—**USA:** *Florida:* Marion Co., Ocala National Forest, NE of Mill Dam Lake, hardwood scrub, on sterile crust, 1987, *Harris* 21072 (NY). *Washington:* Clallam Co., Olympic Nat. Park, Lake Ozette, Tivoli Island, on *L. farinaria*, 1997, *Tansberg* 24861, 24876 (BG L-35318, 35324).—**Argentina:** Buenos Aires, Mar de Plata, Punto Magotes, 1995, *Marbach & Dorsch* (hb. Kalb 32934).—**Uruguay:** Canelones, Parque Nacional de F. D. Roosevelt, on *Leanora*, 1995, *Marbach & Osório* (hb. Kalb 32913).

Skyttea mayrhoferi Diederich & Etayo sp. nov.

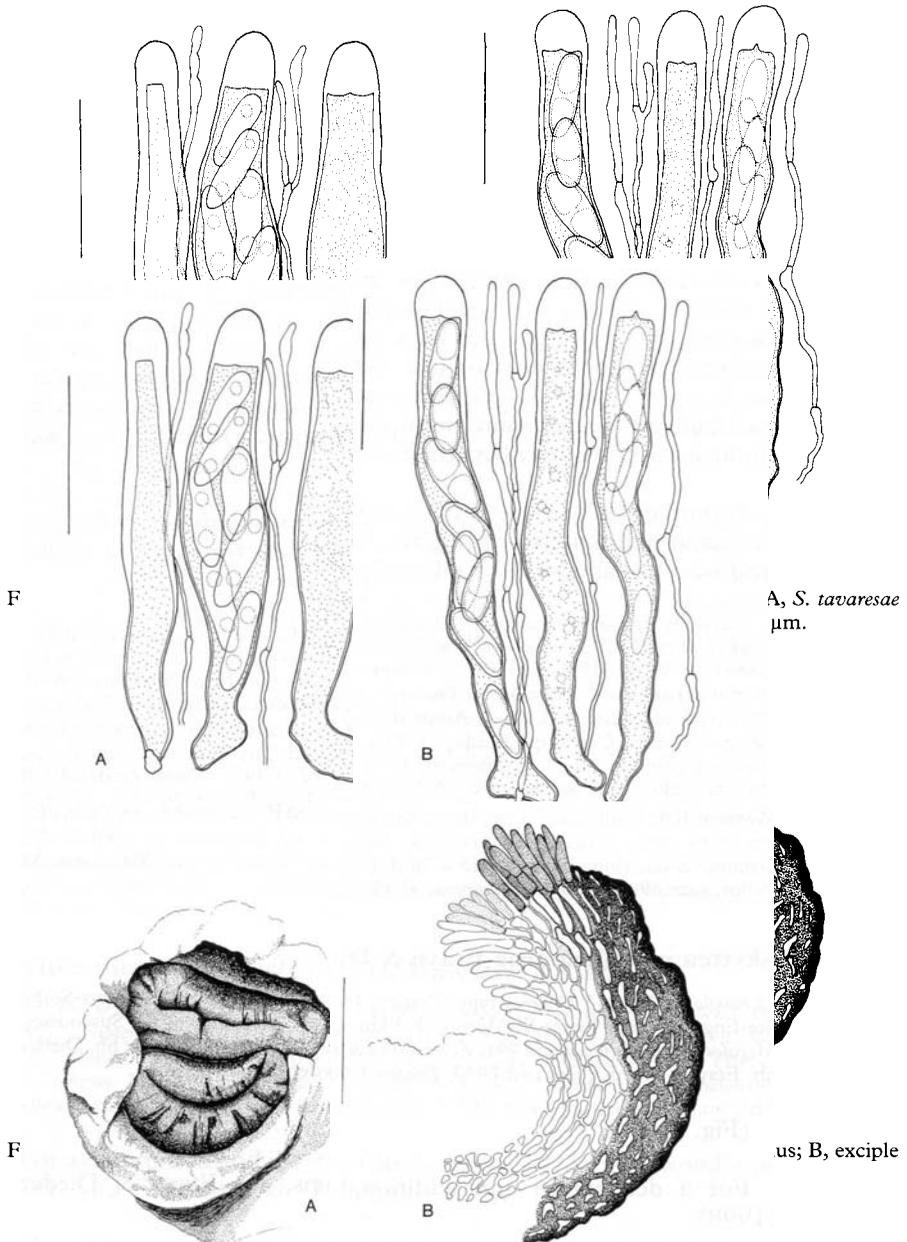
Skyttea insignis ascomatibus 150–225(–500) µm diam., margine 70–105(–150) µm crasso, poro 10–30 µm diam., excipulo viridibrunneo, K+ olivaceo, basaliter pro parte brunneo, K+ violaceo, pilis 15–30 µm longis, ascis 35–55 × 4.5–6.5 µm, ascosporis 6–12 × 3–4 µm.

Typus: New Zealand, Auckland, Kawakawa Bay E of Auckland, Papanui Point, 36°56'S, 175°13'E, 0–20 m, coastal rock, on *Pertusaria melanospora*, 8 January 1985, *Mayrhofer* 5883 & *Samuels* (GZU—holotypus); *ibid.*, *Mayrhofer* 5884 & *Samuels* (GZU, hb. Diederich—topotypi); *ibid.*, 12 January 1985, *Mayrhofer* 5828, *Hertel* 29148, 29155 & *Samuels* (GZU, M—topotypi).

(Figs 2C, 3B, 4)

Ascomata initially immersed, later erumpent, rarely gall-forming, dispersed or aggregated, black, ± roundish, sometimes elongate, 150–225(–300) µm diam., up to 500 µm long if elongate; margin in opened ascomata 70–105 µm thick (× 80), in the largest ascomata even 100–150 µm, striate, sometimes with several deep fissures and appearing cruciate; pore 10–30 µm. *Exciple* laterally greenish to olivaceous, K+ olivaceous brown, 20–45 µm thick, basally greenish brown, with a reddish brown, K+ purple or violet pigment, 25–45 µm thick; excipular hairs olivaceous, straight, wall apically not thickened and therefore not refractive, 15–30 × 3–4 µm. *Subhymenium* hyaline, 10–20 µm thick. *Hymenium* 35–60 µm thick. *Epihymenium* hyaline to pale olivaceous. *Paraphyses* filiform, simple, 1.5–2.5 µm thick. *Asci* subcylindrical, wall apically thicker, (6–)8-spored, 35–55 × 4.5–6.5 µm; ascogenous hyphae with croziers. *Ascospores* hyaline, ellipsoid, non-septate, biguttulate, (5–)6–12 × 3–4(–4.5) µm, exceptionally 1-septate.

Hosts. *Pertusaria* cf. *coccodes* (from Kenya: sterile, isidiate, K+ red), *P. heterochroa*, *P. melanospora* and other *Pertusaria* species (thallus). In some specimens, the fungus has induced the formation of galls.



Distribution. we have seen specimens from Europe (Mallorca), Africa, North, Central and South America, Australia and New Zealand. The species appears to be widespread and possibly cosmopolitan. In Europe, however, where the hosts, species of *Pertusaria*, are common, it seems to be very rare, and possibly restricted to the Mediterranean area.

Observations. The species is mainly characterized by the presence of a reddish brown, K⁺ weakly purple to violet excipular pigment, broad ascospores and large ascomata with a fissured margin, which are often aggregated and of an irregular form. For differences from the similar *S. elachistophora* and *S. gregaria*, see the identification key. The observed variability of the ascospore size is much larger than in the other known species. Some ascospores may become 1-septate.

Etymology. The new species is dedicated to H. Mayrhofer (Graz), who collected rich material during his 1985 and 1992 field trips to New Zealand, and who has allowed us to describe it.

Additional specimens examined (all on *Pertusaria*). **Spain:** Mallorca: between Cala D'Or and Porto Colom, Cala Arsenau, on *Juniperus phoenicea*, on *P. heterochroa*, 1997, van den Boom 18480, 18481, 19482, 18483, 18645 (h).—**Kenya:** Central Prov.: Nanyuki Distr., Mt Kenya, W slope, National Park Road (Naro Moru Track), 0°10'S, 37°13'E, 2900 m, corticolous, on *P. cf. coccodes*, 1970, Santesson 22164 (UPS).—**Australia:** South Australia: Kangaroo Island, mouth of De Male River, 18 km SSE of Cape Borda, 35°43'S, 136°46'E, alt. 20 m, dry forest on rocky slopes, on exposed boulder, on *P. melanospora*, 1994, Streimann 55087 (CBG).—**New Zealand** (all on coastal rocks, on *P. melanospora*): North Island: Wellington, Cape Palliser Road, c. 13 km N of Ngawihi, 1992, Mayrhofer 10.881 (GZU); Mirimar Peninsula E of Wellington, Waser Bay, 1992, Mayrhofer 12.235 (GZU); Titahi Bay of Porirua, 1992, Mayrhofer 12.257 (GZU, hb. Diederich). South Island: South Auckland, Whale Bay, c. 10 km SW of Raglan, 1992, Mayrhofer 12169 (GZU); Marlborough, Whites Bay NE of Rarangi, NE of Blenheim, 1992, Mayrhofer 10.833 (GZU).—**USA:** New Mexico: Santa Fé Co., Cañoncito, on a sterile corticolous thallus (cf. *Pertusaria*), s. d., Sprague (UPS); *ibid.*, s. d., Brandege (UPS: ex hb. Willey in hb. Farlow).—**Mexico:** Baja California Norte, Bahía San Quetin, c. 170 km SSE of Ensenada on Pacific Coast, low playa with scattered low mounds, 10 m, on a cactus, on *Pertusaria* sp. (yellow thallus, 2-spored asci), 1966, Santesson 18373c (UPS).—**Chile:** Juan Fernández Isles: Masafuera, Mono Valley, saxicolous, on *P. melanospora*, 1955, Skottsberg 178 (UPS).

Skyttea megalosporae Etayo & Diederich

Lichenologist 30: 113 (1998); type: France, Pyrénées-Atlantiques, au sud de Tardets-Sorholus, Ste-Engrâce, vers Pierre-St-Martin, à 3 km après la dernière maison, col de Suscouste, sur *Megalospora tuberculosa*, vi 1991, Etayo 5904 & Diederich (MA-Lichen—holotypus; hb. Diederich, hb. Etayo—isotypi); *ibid.*, vii 1990, Diederich 9360 (hb. Diederich—topotypus).

(Fig. 2E)

For a description and additional illustrations, see Etayo & Diederich (1998).

Host. *Megalospora tuberculosa* (thallus).

Distribution. The western French and Spanish Pyrenees (Etayo & Diederich 1998), and Columbia.

Observations. This species has very long ascospores, 22–46 × 2.5–3 µm, which are even longer than those of *S. fusispora* and *S. caesi*. It is distinguished from these two species by falcate to sigmoid or helicoid ascospores with ± pointed ends. In this character it is very similar to some species of

Spirographa, which lack, however, the distinct excipular hairs and the greenish pigment common in *Skyttea* (Etayo & Diederich 1998).

We studied a specimen on a different host which might belong to the same species: **Canada**, Newfoundland, Avalon Peninsula SW, between Point Verde and Cape St Mary's, 47°4'N, 54°5·5'W, alt. 10 m, on *Loxospora cismonica*, vi 1991, Tønsberg 17089a (BG). As the specimen is small, we would prefer, however, to have more material on the same host before deciding if this represents a new species or not.

Another specimen with similar ascospores has been examined: Ecuador, Azuay, c. 35 km S von Cuenca, Waldreste in einem Grasparamo, 3200 m, viii 1987, *Kalb* 18353 (h). The ascomata are superficial, 200–310 µm, irregular in outline due to numerous fissures of the margin, margin 90–100 µm, pore 35–100 µm, exciple greenish, hairs 15–25 µm, ascospores 8 per ascus, sigmoid, with pointed ends, aseptate, 28–34 × 2–2·5 µm. This clearly represents a distinct, undescribed species, with ascomata much larger than in *S. megalosporae*. We do not formally describe it here as the host is still unidentified (*Loxospora* sp. ?). The host is corticolous, crustose, whitish, sorediate, with a few superficial, indistinctly marginate, dark brown apothecia; hymenium hyaline, 65–75 µm, epihymenium bluish green, K –, hypothecium c. 70 µm, dark reddish brown, K –, exciple 55–70 µm, hyaline outside, brownish inside, of strongly gelatinized, radiating hyphae, paraphyses anastomosing, asci clavate to subcylindrical, wall apically KI+ blue (possibly *Lecanora*-type), 8-spored, ascospores hyaline, cylindrical to vermiform, up to 7-septate, 34–43 × 3–3·5 µm.

Additional specimen examined. **Colombia:** Dept. Nariño, Pasto, corregimiento El Encano, verede Sta. Isabel, S lago de La Cocha (Guamues), páramo azonal, 0°59'N, 77°09'W, alt. 2700 m, on *M. tuberculosa*, 1998, *Etayo* 16530 (h, COL).

***Skyttea nitschkei* (Körb.) Sherwood, D. Hawksw. & Coppins**

Trans. Br. mycol. Soc. 75: 488 (1981 [1980]).—*Nesolechia nitschkei* Körb., *Parerg. lich.*: 462 (1865).—*Niptera nitschkei* (Körb.) Rehm, *Rabenh. Krypt.-Fl.* 1: 561 (1892).—*Beloniella nitschkei* (Körb.) Rehm, *Ber. bayer. bot. Ges.* 13: 182 (1912).—*Rhymbocarpus nitschkei* (Körb.) Triebel, *Bibl. Lichenol.* 35: 144 (1989); type: Germany, Münster, Wolbecker Thiergarten, on *Thelotrema lepadinum*, viii 1864, *Nitschke* (L 910.195-559—holotypus; L 910.195-556—isotypus, non vid.).

For a description and illustrations, see Hawksworth (1975), Sherwood *et al.* (1981) and Coppins *et al.* (1991, illustration of asci).

Host. This species is confined to *Thelotrema lepadinum* (thallus and thalline margin of the apothecia), the ascomata usually being aggregated in some parts of the thallus. It is most abundant in ancient woodlands with an oceanic microclimate. The host thallus typically turns brownish around the ascomata of the fungus.

Distribution. We have seen material from Austria, Belgium, Denmark, France, Germany, Great Britain, Ireland, Luxembourg, Spain, Switzerland, Canary Islands, and Canada (see also Diederich 1986). The species has also been mentioned in the literature from Norway, Argentina and Chile

(Sherwood *et al.* 1981; Santesson 1993), but we cannot exclude that some of the specimens cited belong to *S. thelotrematis*, a species known from Europe and South America.

Observations. *Skyttea nitschkei*, which is the type species of the genus *Skyttea*, differs from most other species by the particular excipular pigments (see identification key). Similar pigments are found in the new species *S. carboneae* and *S. tavaresae*. The differences between these three species are explained in the key.

Interestingly, one specimen of *Thelotrema lepadinum* from the French Pyrénées-Atlantiques (Diederich 9342) is infected by two distinct species of *Skyttea*: *S. nitschkei*, with dark brownish ascomata, and *S. thelotrematis* with dark greenish to blackish ascomata, which are whitish around the pore. For the differences between both species, see under *S. thelotrematis*.

Additional specimens examined. **Austria:** *Niederösterreich:* Seetal SE von Lunz, Kurz S hinter dem Mittersee, 780 m, 1981, *Hafellner* 9201 (GZU); Göllergruppe, Südhänge der Weißmauer E von Lahnsattel, 940 m, 1994, *Hafellner* 32476 (GZU); Ybbstaler Alpen, E-Abhänge des Dürrensteins, Urwald Rotwald, Großer Urwald, 1000 m, 1993, *Hafellner* 23631 (GZU); *ibid.*, 1994, *Poelt* (GZU 10-94). *Steiermark:* Salzatal, bei der Einmündung des Krimpen Baches in die Salza, 580 m, 1989, *Hafellner* 24192, 24184, 24185 (GZU); Hochschwab-Gruppe, Fözl NW von Afenz, im untersten Teil des Mitterbachgrabens W vom Gasthof Schwabenbartl, 860 m, 1994, *Hafellner* 32573 (GZU, also distributed in Santesson *Fungi Lichenicoli Exsiccati* 285).—**Denmark:** South Jutland, Lögumkloster, viii 1975, *Christiansen* (GZU).—**France:** *Finistère:* Forêt de Cranou, route forestière de St-Conval, 1960, *Lambinon* 60/683 (LG, sub *T. lepadinum*). *Pyrénées-Atlantiques:* Gorge d'Ehujarre, 1991, *Diederich* 9589 (h) & *Etayo* 1350, 5914, 5966 (h); col de Saucusse, 1991, *Etayo* 5926 (h); gorges du Pihot, D-341 near parking, 1993, *Etayo* 666 (h); gorges de Kakouetta, 1991, *Diederich* 9575 (h) & *Etayo* 12850 (h). *Sarthe:* Parc naturel régional Normandie Maine, Forêt de Perseigne E of Alençon, Vallée d'Enfer, 1980, *Hafellner* 8782 (GZU).—**Germany:** Wolbech prope Münster, s. d., *Lahn* (UPS); Schleswig-Holstein, Kr. Herzogtum Lauenburg, Sachsenwald, Revier Klein Viert, ix 1919, *Ericksen* (HBG).—**Great Britain:** *England:* **V.C. 11,** South Hampshire: New Forest, Frame Wood, 1979, *Hawksworth* 4934 (GZU); New Forest, 1984, *Diederich* 5418 (h). *Scotland:* **V.C. 97,** West Inverness-shire: N side of Loch Sunart, 4–5 km W of Strontian, vi 1992, *Poelt* (GZU); woods at hillside to W of Glenborrodale Castle, vi 1992, *Poelt* (GZU). **V.C. 98,** Argyll Main: Loch Creran, Glasdrum, near Inver, vi 1992, *Poelt* (GZU); *ibid.*, 1976, *Tibell* 6586 (UPS). **V.C. 104,** North Ebudes: Isle of Skye, Tokavaig Wood, 1987, *Diederich* 8032 (h); S of Kyle of Lochalsh, S of Loch Na Béiste, 1987, *Diederich* 8827 (h).—**Ireland:** **V.C. H2,** North Kerry: Near Ladies View S of the Upper Lake of Killarney, 1968, *Santesson* 19662 (UPS); Killarney, Cromaglan Mountain, SW of the top not far from the main road, 1968, *Santesson* 19860, 19871 (UPS).—**Spain:** *Huesca:* Hecho, valle de Hecho, selva de Oza, s. d., *Etayo* 5021 (h). *Navarra:* Vera, Collado de Ibardin, 1987, *Etayo* 2724 (h); Orbaiceta, Lizardoya, 1988, *Etayo* 5927 (h); NW Estella, Sierra de Urbasa, Pto de Urbasa, 1991, *Diederich* 9647 (h).—**Switzerland:** Obwalden, Giswil, Merliwald, close to Wang above Kleinteil, 46°50'N, 8°9'E, 1350 m, 1987, *Moberg* 7315 & *Santesson* 31660 (UPS).—**Canary Islands:** *Tenerife:* Macizo de Anaga, Monte de las Mercedes, c. 900 m, 1989, *Hafellner* 32835, 32869 (GZU).—**Canada:** *Nova Scotia:* Richmond Co., in Cape Breton, 1.5 km NW of North Frambo, 1980, *Maass* (BG).

***Skyttea pyrenulae* Diederich, Etayo & Coppins sp. nov.**

Skyttea insignis ascomatibus 125–160 µm diam., margine 40–50 µm crasso, non striato, poro magno, excipulo viridibrunneo, K+ olivaceo, pilis 4–7 µm longis, ascis 45–60 × 3.5–4.5 µm, ascosporis 8–12 × 2.5–3 µm.

Typus: Great Britain, Scotland, North Ebudes (V.C. 104), Isle of Skye, Sleat Peninsula, Tokavaig Wood, alt. 10–100 m, on *Corylus*, on *Pyrenula occidentalis*, 21 May 1987, *Coppins* 11599 (E—holotypus).

Ascomata initially immersed, later erumpent, blackish, inner border of ascomatal margin whitish due to the excipular hairs, roundish and 125–160 µm diam. or elongate and up to 200 µm; margin in opened ascomata 40–50 µm thick (surface view, $\times 80$); pore up to 50% of the ascomatal diameter when mature. *Exciple* laterally greenish (outer layer darker), K+ olivaceous, except the region near the hairs, which is brownish (green pigment absent) and K–, 40–55 µm thick; basal exciple green, K+ olivaceous, 8–16 µm thick; excipular hairs hyaline, straight, wall apically not thickened and therefore not refractive, $4-7 \times 2-2.5$ µm. *Subhymenium* hyaline, 3–6 µm thick. *Hymenium* 50–65 µm thick. *Ephymenium* hyaline. *Paraphyses* filiform, simple or rarely branched, *c.* 1 µm thick. *Asci* subcylindrical, wall apically thicker, 4–8-spored, $45-60 \times 3.5-4.5$ µm. *Ascospores* hyaline, ellipsoid, non-septate, $8-12 \times 2.5-3$ µm.

Hosts. *Pyrenula occidentalis* (syn. *P. neglecta* auct. eur.) and *Pyrenula* sp.

Distribution. Great Britain (Scotland) and Azores.

Observations. This species is similar to *S. lecanorae*, which differs by the overall smaller dimensions (e.g. ascomata 90–125 µm, hymenium 45–55 µm, asci 35–50 µm long, ascospores 7–9 µm long) [except the hairs, which are slightly longer, 8–13 µm], by the distinctly striate and whitish ascomatal margin, and mainly by the much narrower ascomatal pore in mature ascomata. For differences with *S. gregaria*, see under *S. lecanorae*.

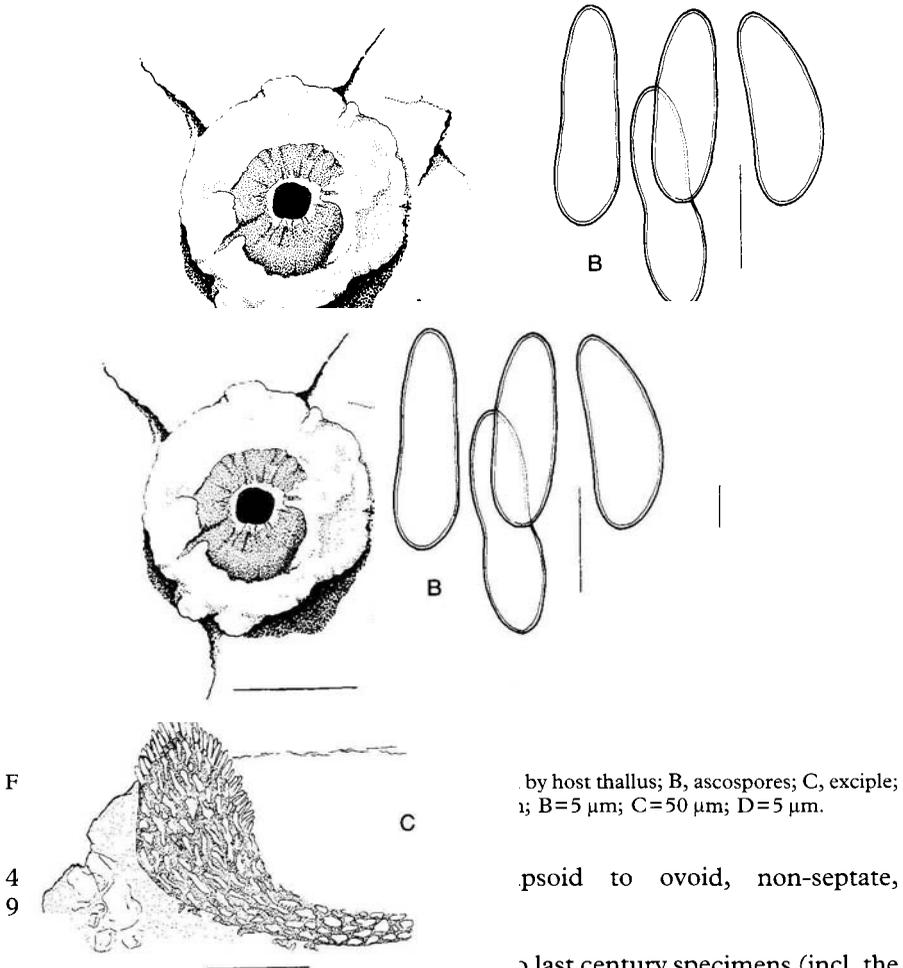
Additional specimens examined. **Great Britain:** *Scotland:* V.C. 97, Westernness: Morvern, N of Glenmorvern Cottage, coastal hazelwood, on *Corylus*, on *P. occidentalis*, 1992, Coppins 15388 (E).—**Azores:** *Faial:* Cabeço dos Trinta, edge of a ravine, *c.* 650 m, on *Ilex*, on *Pyrenula* (sterile), vi 1986, Degelius (UPS).

***Skyttea radiatilis* (Tuck.) R. Sant., Etayo & Diederich comb. nov.**

Gyalecta radiatilis Tuck., *Lich. Calif.*: 30 (1866); type: USA, Rhode Island, North Kingstown, on *Pinus rigida*, on cf. *Loxospora pustulata*, 1865, Bennett (FH—holotypus, vid.).

(Fig. 5)

Ascomata immersed in the host, bordered by the thallus, dispersed or aggregated, blackish, roundish, 100–140 µm diam.; margin in opened ascomata 40–50 µm thick (surface view, $\times 80$), striate, often whitish due to remnants of the host thallus, without any deep fissures; pore 20–35 µm diam. *Exciple*, except at base, internally greenish olivaceous, K+ olivaceous (rarely yellowish brown in pale ascomata), externally darker greyish or olivaceous brown, K+ (sometimes indistinctly) purple to violet, 17–45 µm thick; basal exciple yellowish brown or brownish (no green pigment), K–, 5–25 µm thick; excipular hairs hyaline to olivaceous, septate, straight, wall apically not thickened and therefore not refractive, $10-20 \times 2-3$ µm. *Subhymenium* hyaline, *c.* 10 µm thick. *Hymenium* 50–60 µm thick. *Ephymenium* hyaline. *Paraphyses* filiform, simple to ramified, septate, apically not thickened, 1–1.5 µm thick. *Asci* subcylindrical, wall apically thicker, (4–)8-spored,



F
4
9

by host thallus; B, ascospores; C, exciple;
1; B=5 μm; C=50 μm; D=5 μm.

psoid to ovoid, non-septate,

last century specimens (incl. the holotype) are very much reduced and do not allow a study of the thallus by TLC; however, as the thalli in both specimens react K and KC+ yellow and C-, and strongly resemble recently collected thalli of *L. pustulata*, we consider them as belonging to that species.

Distribution. USA (Arkansas, Kentucky, Massachusetts, North Carolina and Rhode Island).

Observations. Initially, this species was considered to be a lichen belonging to the genus *Gyalecta*. Tuckerman (1882) subsequently recognized that he had described a lichenicolous fungus growing on 'a white thallus with little doubt to be referred to *Pertusaria multipuncta*'. Recently, Santesson (in Esslinger & Egan 1995) pointed out that *Gyalecta radiatilis* is a lichenicolous fungus, perhaps a *Skyttea*. We confirm here that the species is a typical member of

Skyttea, characterized by its large ascospores and small ascomata, bordered by the host thallus.

Lettauia santessonii Ihlen & Tønsberg, another fungus growing on *Loxospora pustulata*, is easily distinguished by ascomata with a \pm flat disc, the absence of excipular hairs, hemi-amyloid asci, and larger ascospores, $14.5\text{--}19 \times 3\text{--}4.5 \mu\text{m}$ (Ihlen & Tønsberg 1996).

Additional specimens examined. **USA:** *Arkansas:* Newton Co., Boston Mountains, Ozark National Forest, Alum Cove Recreation Area, T. 14N, R. 21W, sect. 17, c. 600 m, 1988, *Harris* 21510A (NY). *Kentucky:* Letcher Co., upland oak–red maple woods adjacent to upper section of Bad Branch Nature Preserve, c. 732 m, 1991, *Harris* 27101A (NY). *Massachusetts:* New Bedford, s. d., *Willey* (UPS). *North Carolina:* Macon Co., Sunset Rock, Highlands, c. 3850 ft, 1981, *Harris* 13680A (NY, hb. Diederich); Macon Co., Nantahala National Forest, McDowell Mountain, c. 10 mls S of Franklin and 2 mls N of Georgia state line on SR 1629, $35^{\circ}03'N$, $83^{\circ}22'W$, 640–945 m, 1994, *Harris* 33214 (NY, hb. Diederich).

***Skyttea spinosa* D. Hawksw. & Coppins**

In Hawksworth, *Notes R. bot. Gdn Edinb.* 40: 392 (1982); type: Great Britain, Scotland, Dunbarton (V.C.99), Loch Lomond National Nature Reserve, Shore Wood, on *Verrucaria nigrescens*, 5 ix 1980, *Coppins* 8215 (E—holotypus, non vid.).

For a description and illustrations, see Hawksworth (1982).

Host. *Verrucaria nigrescens* (thallus) (det. B. J. Coppins, pers. comm.), on sandstone rocks near lake shore.

Distribution. Great Britain (Scotland), known only from the type collection.

Observations. This species is similar to *S. hawksworthii*, from which it is distinguished by shorter excipular hairs, which are not visible macroscopically, and also by narrower ascospores. As both species are similar, live on the same host genus and are known only from the type specimen, more material is needed to ascertain if they can really be distinguished.

***Skyttea tavaresae* R. Sant., Etayo & Diederich sp. nov.**

Skyttea insignis ascomatibus 200–300 μm diam., margine 75–100 μm crasso, poro 50–75 μm , excipulo atrogiseo ad fumoso, K+ verdigri, sub subhymenio rufo, K+ dilute purpurea-violaceo, pilis ad 30–48 μm longis, ascis 43–50 \times 5–8 μm , ascosporis 9–12 \times 2.5–3 μm .

Typus: USA, California, Santa Barbara Co. San Miguel Island, SE of the Ranger Station, S of the Camp Site, $34^{\circ}2'3"N$, $120^{\circ}20'7"W$, alt. 140 m, on fence post, on *Pyrrhospora* cf. *quernea*, 17 March 1998, *Tønsberg* 25475 (BG—holotypus; hb. Diederich—isotypus).

(Figs 2A, 3A, 6)

Ascomata dispersed on the host thallus, immersed to superficial, black, (100–)200–300 μm diam.; margin in opened ascomata 75–100 μm thick (surface view $\times 80$), sometimes with deep fissures; pore 50–75 μm diam. *Exciple* laterally hyaline to reddish or violet brown in the inner part, dark grey to brownish grey in the outer part, K+ bright aeruginose green, N+ dark reddish brown, 10–40 μm thick; basal exciple the same colour and reactions,

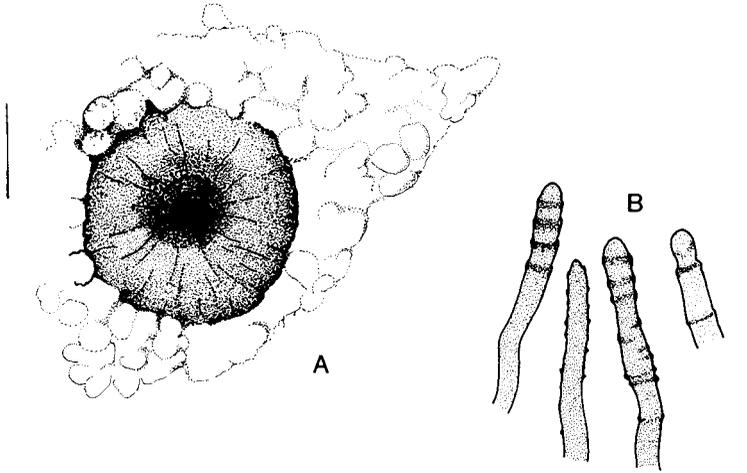


FIG. 6. *Skyttea tavaresae* (Tavares 1419). A, ascoma on *Pyrrhospora* thallus; B, excipular hairs. Scales: A=100 μ m; B=5 μ m.

but just below the subhymenium reddish brown, K+ pale purplish or violet, N- , 15–20 μ m thick; excipular hairs dark greyish brown, K+ bright aeruginose green, N+ dark reddish brown, straight, wall apically not thickened, with irregular, pigmented ring-like structures (see Fig. 6), c. 30–48 \times 2.5–3 μ m. *Subhymenium* hyaline to yellowish, c. 10 μ m thick. *Hymenium* 30–60 μ m thick. *Epihymenium* hyaline. *Paraphyses* filiform, simple, septate, 1.5 μ m thick, apically slightly thicker. *Asci* subcylindrical, wall apically thicker, 8-spored, c. 43–50 \times 5–8 μ m. *Ascospores* hyaline, elongate ellipsoid, 0(–1)-septate, biguttulate, (8–)9–12(–13) \times 2.5–3 μ m.

Host. On the thallus of *Pyrrhospora* cf. *quernea*.

Distribution. Known from two localities in the USA (California).

Observations. This species is mainly characterized by the unusual dark greyish brown exciple, which is K+ bright aeruginose green and N+ dark reddish brown (basally with an additional, reddish brown, K+ purplish or violet pigment), by the long concolorous excipular hairs (hairs are pale greenish or hyaline in most other *Skyttea* species) and the long, but narrow, biguttulate ascospores. The differences with *S. carboneae* and *S. nitschkei* are given in the identification key. The species is named after I. I. Tavares who collected the first specimen of this species and who made it available for study.

We studied a specimen of a similar, but distinct species, growing on *Pertusaria* cf. *santamonicae* [USA, California, Santa Barbara Co., Santa Rosa Island, pass along the main road just SE of Black Mountain, 33°58'45"N, 120°4'30"W, i 1994, T. H. Nash III 32.615 (ASU)]. The ascospores are 8.5–10.5(–11.5) \times 3–3.5 μ m, the ascomata 150–250(–300) μ m in diam., the hairs reach at least 50 μ m and the exciple contains the dark red, K+

aeruginose green pigment. The ascospores are slightly broader than those of *S. tavaresae* and longer than those of *S. carboneae*. Unfortunately, the single specimen is in a very poor condition and cannot be used for a type.

Additional specimen examined. USA: California: Cambria, near Cambria Pines Lodge, on *Pinus radiata*, 1963, *Tavares* 1419 (UC, UPS).

***Skyttea thelotrematis* Diederich & Etayo sp. nov.**

Skyttea insignis ascomatibus 125–250(–325) µm diam., margine 45–60 µm crasso, poro 40–60% ascomatum diam., excipulo viridibrunneo, K+ olivaceo, pilis ad 16 µm longis, ascis 40–50 × 4–6 µm, ascosporis (7·5–)9–10(–11) × (1·7–)2·3–3 µm.

Typus: France, Pyrénées-Atlantiques, au sud de Tardets-Sorholus, Ste-Engrâce, vers Pierre-St-Martin, à 3 km après la dernière maison, c. 1000 m, sur *Abies*, sur *Thelotrema lepadinum*, 26 July 1990, *Diederich* 9342 (LG–holotypus, with *Skyttea mitschkei*).

Ascomata initially immersed, later erumpent, dispersed or aggregated, blackish, but around the pore generally whitish, roundish, 125–250(–325) µm diam.; margin in opened ascomata 45–60 µm thick (× 80), entire, striate, with numerous fissures (5–10 per margin), partly whitish; pore in mature ascomata 40–60% of the ascomatal diameter. *Exciple* laterally greenish to olivaceous, K+ olivaceous brown, of globose to elongate cells of 4–8 µm, basally greenish brown, without a brownish, K+ violet pigment; excipular hairs straight, wall apically not thickened and therefore not refractive, up to 16 µm long. *Subhymenium* hyaline, c. 25 µm thick. *Hymenium* c. 55 µm thick. *Epihymenium* hyaline to pale olivaceous. *Paraphyses* filiform, simple, 1·5–2 µm thick. *Asci* subcylindrical, wall apically thicker, 8-spored, (35–)40–50 × 4–6 µm. *Ascospores* hyaline, narrowly ellipsoid, non-septate, (7·5–)9–10(–11) × (1·7–)2·3–3 µm.

Host. Thelotrema lepadinum (thallus). It is interesting to note that in the Neotropics, where many species of *Thelotrema* occur, the fungus has been found only on *T. lepadinum*.

Distribution. France (western Pyrenees) and Colombia.

Observations. This species is very close to *S. elachistophora* and *S. gregaria*. For differences, see the identification key. It is most likely to be confused with *S. nitschkei*, confined to the same host. *Skyttea nitschkei* has dark brownish ascomata (not blackish), and the surrounding host thallus is often typically reddish brown. Microscopically, *S. nitschkei* is characterized by different pigments.

Additional specimen examined. Columbia: Dept. Nariño, Pasto, bosque de Daza, vía Pasto-Buesaco, 1°12'N, 77°16'W, alt. 2750 m, 1998, *Etayo* 16481 (h, COL).

***Skyttea viridis* D. Hawksw. & Coppins**

In Hawksworth, *Notes R. bot. Gdn Edinb.* 40: 394 (1982); type: Great Britain, Scotland, West Perthshire (V.C. 87), Clackmannan, Alva, Silver Glen, on *Fagus* wood, on cf. *Micarea denigrata*, 23 viii 1981, *Coppins* 8631 (E—holotypus, non vid.).

For a description and illustrations, see Hawksworth (1982).

Host. Probably on the thallus of *Micarea denigrata*.

Distribution. Great Britain (Scotland), known only from the type locality.

Observations. This species is characterized by the very short and narrow ascospores and the large ascomata.

Llimoniella Hafellner & Nav.-Ros.

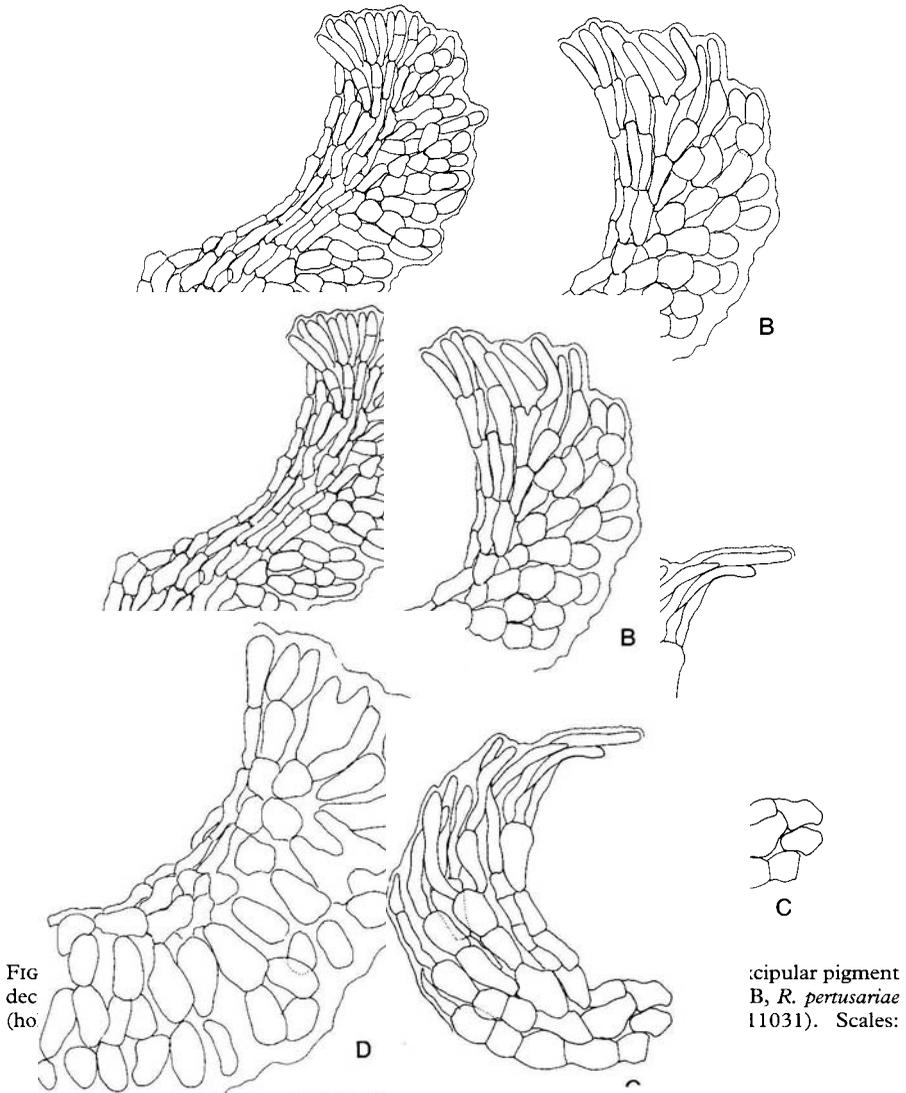
Herzogia 9: 770 (1993); type: *Llimoniella scabridula* (Müll. Arg.) Nav.-Ros. & Hafellner.

Ascomata lichenicolous, commensalistic, black, sessile to shortly pedicellate, marginate, disc plane, slightly concave or becoming convex. *Exciple* formed of dark, thick-walled, catenate, \pm isodiametric cells, the outer cells being often enlarged or swollen (best observed in commercial bleach), without hairs or periphysoids, reddish to purplish brown (see Fig. 7). *Subhymenium* hyaline. *Hymenium* hyaline, KI $-$. *Epihymenium* purplish. *Pigments*: (1) reddish to purplish brown, K $+$ violaceous, N $-$ or greyish brown, in the exciple and epihymenium; (2) pale olivaceous, usually hidden by the darker purplish pigment, K $+$ bright green, N $-$, in the exciple and the hymenium [pigment absent in *L. adnata* and *L. scabridula*]; (3) yellowish or orange, K $-$, N $+$ bright orange, in the excipular and epihymenial gel. *Paraphyses* simple or apically branched, apically indistinctly swollen, without pigments, easily separating in KOH under slight pressure. *Asci* clavate, thin-walled, wall apically hardly thickened, KI $-$, normally 8-spored. *Ascospores* hyaline, 0–3-septate, smooth, without a perispore, ellipsoid, fusiform, cylindrical or sigmoid, 1–2- or multiguttulate. *Conidiomata* known in one single species (*L. vinosa*), pycnidial, globose, erumpent, wall reddish brown, apically greenish brown. *Conidiogenous cells* phialidic, hyaline. *Conidia* bacilliform, hyaline.

Observations. The genus *Llimoniella* was originally introduced for two closely related species, *L. adnata* and *L. scabridula*. Subsequent authors added a number of related, but not congeneric species: *Llimoniella fuscoatrae*, *L. neglecta*, *L. pubescens* and *L. stereocaulorum* belong to *Rhymbocarpus*, and *L. groenlandiae* neither belongs to *Rhymbocarpus* nor to *Llimoniella*, but to *Unguiculariopsis* (see under 'Excluded species').

Llimoniella is characterized by blackish, superficial apothecia with a \pm regular, smooth, striate or scabrous margin lacking hairs and a slightly concave to convex disc; an upper exciple composed of radiating, thick, catenate cells; the combination of very characteristic pigments; thin-walled asci without any hemi-amyloid reactions; and ellipsoid or elongate, straight or curved to sigmoid, 0–3-septate, 1–2- or multiguttulate, hyaline ascospores lacking a distinct perispore. For differences with *Rhymbocarpus*, see the identification key to lichenicolous leotialean fungi below.

Llimoniella pertusariae is the only species of the genus in which we have seen living ascospores. They are multiguttulate, containing hundreds of minuscule



lipid drops. Dead, multiguttulate ascospores have also been observed in *L. pyrenulae*, *L. ramalinae* and *L. vinosa*. In *L. adnata* and *L. scabridula*, the ascospores, observed in water or in KOH, have one or two large lipid drops. This appears to be a useful taxonomic character at species level, which should always be noted in fresh material, or in herbarium specimens which are less than 3 years old.

According to the detailed study of *Pleoscutula arsenii* by Hafellner (1982), that fungus differs from *Llimoniella* in the multispored asci and distinctly curved, 1-septate ascospores with pointed ends. Otherwise, it is very similar to *Llimoniella*, and we wondered if *Pleoscutula* might represent an earlier name for

Llimoniella. However, a careful study of the extremely reduced holotype of *P. arsenii* [MARSS], vid.] confirmed that both genera were distinct. The excipular and ephymenial pigment of *P. arsenii* is dark greyish to olivaceous brown, K – and N –, and none of the characteristic pigments of *Llimoniella* have been observed. Furthermore, the exciple, if observed in commercial bleach (C), is very distinct, formed by loosely interwoven hyphae, similar to that of *Micareia*.

Key to the species of *Llimoniella*

- 1 Ascospores ellipsoid, non-septate, $9-13 \times 4-7 \mu\text{m}$, 1-2-guttulate; K+ green pigment absent; ascomata $200-500 \mu\text{m}$; on terricolous lichens 2
- Ascospores narrowly ellipsoid, elongate, fusiform or sigmoid, septate or not, $12-32 \times 2.5-4 \mu\text{m}$, multiguttulate; K+ green pigment present; on corticolous lichens 3
- 2(1) Ascospores $9-11 \times 4-5 \mu\text{m}$; asci $65-80 \times 7-10 \mu\text{m}$; hymenium up to $90 \mu\text{m}$ tall; ascomatal margin scabrous; on terricolous *Acarospora* **L. scabridula**
- Ascospores $11-13 \times 6-7 \mu\text{m}$; asci $80-90 \times 8-9 \mu\text{m}$; hymenium $100-120 \mu\text{m}$ tall; ascomatal margin \pm smooth; on *Placidium* **L. adnata**
- 3(1) Ascospores non-septate, straight or curved; ascomata mainly $300-500 \mu\text{m}$ 4
- Ascospores 1-3-septate, straight, curved or sigmoid; ascomata mainly $150-350 \mu\text{m}$ 5
- 4(3) Ascomatal margin prominent, smooth or concentrically striate, disc concave; ascospores $12-17 \times 2.5-4 \mu\text{m}$; asci $53-61 \times 7-10 \mu\text{m}$; ascomata dispersed on the thallus of *Pertusaria ophthalmiza*. **L. pertusariae**
- Ascomatal margin less prominent, often not higher than the slightly concave to strongly convex disc, smooth or irregularly fissured, sometimes almost disappearing when old; ascospores $15-25 \times 2.5-3.5 \mu\text{m}$; asci $40-55 \times 5-7 \mu\text{m}$; ascomata aggregated on the thallus of *Pyrenula* (Fig. 8) **L. pyrenulae**
- 5(3) Ascospores 1-septate, straight or slightly curved, $12-16 \times 3-4 \mu\text{m}$; asci $50-63 \times 7-10 \mu\text{m}$; exciple violaceous to purplish brown; on *Ramalina celsatri* (Fig. 9) **L. ramalinae**
- Ascospores 1-3-septate, sigmoid, $15-32 \times 3-4 \mu\text{m}$; asci $52-78 \times 8-11 \mu\text{m}$; exciple wine-red; on *Ochrolechia* **L. vinosa**

Llimoniella adnata Haf. & Nav.-Ros.

Herzogia 9: 773 (1993); type: Spain, prov. Madrid, Gipshügel E von Ciempozuelos, S von Madrid, auf *Placidium squamulosum*, ix 1980, Hafellner 8592 & Crespo (GZU, vid.).

For a description and illustrations, see Hafellner & Navarro-Rosinés (1993).

Hosts. *Placidium* species, including *P. squamulosum*. The ascomata of the fungus all develop on the margin of the lower surface of the host thallus. Macroscopically they appear therefore as growing between the squamules of the lichen.

Distribution. Spain (type locality) and Russia (Siberia, Yakutia).

Observations. This species has the same dark purplish brown, K+ violet excipular and epihymenial pigment as the other *Llimoniella* species recognized here. The K+ green pigment, present in several *Llimoniella* species, is absent in this species and in the type species of the genus, *L. scabridula*. In N, the excipular and epihymenial gel turns deep yellow to orange. Subsequent replacement of N by K turns the exciple brownish, but no purplish or violet reaction has been observed (the K+ violet pigment has been degraded in N). The exciple, observed in C (commercial bleach) is typically that of *Llimoniella*, with enlarged and swollen cells in the outer layer. Most ascospores observed in water or in K have one large lipid drop, rarely two or three smaller drops (see also the ascospores figured by Hafellner & Navarro-Rosinés 1993).

Additional specimens examined. **Russia:** Siberia: Republic Sakha-Yakutiya, Moma District, Yakutiya, 48 km NNW of Chebagalakh settlement, c. 50 km N of Tiubeliakh settlement, right bank of Indigirka river, 65°48'N, 142°53'E, alt. 200–300 m, calcareous rocks with *Larix sibirica* by the river side, on *Placidium* species (incl. *P. squamulosum*), 1992, Zhurbenko 92196, 92198, 92462 (LE, hb. Diederich).

***Llimoniella pertusariae* Diederich & Etayo sp. nov.**

Llimoniella insignis ascomatibus dispersis, superficialibus, atris, 300–600 µm diam., disco concavo, margine prominenti, excipulo pigmento K+ viridi, ascosporis anguste ellipsoideis ad cylindrico-fusiformibus, aseptatis, multiguttulatis, 12–17 × 2.5–4 µm, ascis 53–61 × 7–10 µm.

Typus: USA, Washington, Kittitas Co., 23 km (direct) SSE of Snoqualmie Pass, S of Hwy 90, SW of Kachess Lake, between Yakima River and road FR 4283, 47°16'N, 121°17'E, alt. 680–690 m, on *Acer*, on *Pertusaria ophthalmiza*, 27 September 1997, Tønsberg 25165 (BG-L 36229—holotype).

Ascomata dispersed on the host thallus, superficial, black, initially ± closed, very soon applanate, 300–600 µm diam.; disc exposed, concave to slightly convex; margin prominent, smooth or with many fissures, without hairs. *Exciple* with a dark purplish brown pigment, K+ violet, N+ dark greyish brown, in the upper part also with a pale olivaceous hymenial pigment, K+ dark green (usually not visible due to the strong purplish pigmentation, but easily seen in K), the gelatinous matrix in which the excipular cells are embedded (best seen in the outer layer of the upper exciple) orange, K–, N+ bright yellowish orange, indistinctly prolonged in a stipe, 50–70 µm thick, composed of ± isodiametric cells of 4–7 µm diam., except the outer layer, which consists of radiating cells reaching 12 µm in length. *Subhymenium* hyaline. *Hymenium* ± colourless or pale olivaceous or greenish, K+ green, 85–100 µm tall, KI–. *Epihymenium* orange, partly with an additional purplish pigment, K+ purplish (colour disappears after a short time). *Paraphyses* hyaline, c. 1.5 µm thick, occasionally branched, apically slightly thicker, 2–3 µm. *Asci* claviform to subcylindrical, 53–61 × 7–10 µm, wall apically

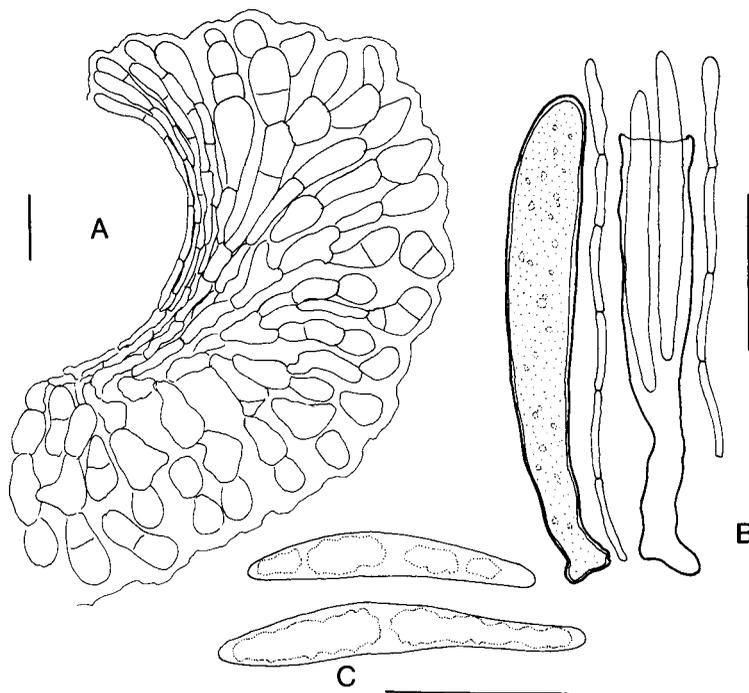


FIG. 8. *Llimoniella pyrenulae* (holotypus). A, exciple (excipular pigment decolourized in C [commercial bleach]), note the paraphysis-like hyphae of the inner exciple; B, young ascus (left), old ascus with ascospores (right) and paraphyses (in H_2O); C, ascospores (in H_2O). Scales: A=20 μm , B & C=10 μm .

not thickened, KI -, 8-spored. *Ascospores* hyaline, narrowly ellipsoid to cylindrical-fusiform, straight or curved, non-septate, multiguttulate [living ascospores!], $12-17 \times 2.5-4 \mu m$.

Host. On the thallus of *Pertusaria ophthalmiza*.

Distribution. USA (Washington) and Canada (Vancouver Island).

Observations. This species is very close to *L. pyrenulae*. For differences, see the identification key.

Additional specimen examined. **Canada:** *British Columbia:* Vancouver Island, Port Renfrew, Botanical Beach, $48^{\circ}31'N$, $124^{\circ}25'W$, alt. 0-50 m, on *Picea*, 1994, *Aptroot* 35367 (h, hb. Diederich).

***Llimoniella pyrenulae* Diederich & Etayo sp. nov.**

A *Llimoniella pertusariae* ascomatibus aggregatis, ascomatis margine minus prominenti, haud alta quam parum concavo ad valde convexo disco, interdum fere evanescenti ubi veterem, ascosporis $15-25 \times 2.5-3.5 \mu m$ et ascis $40-55 \times 5-7 \mu m$ differt.

Typus: Kenya, Eastern prov., Machakos distr., NW of Ngwata, 2°30'S, 38°2'E, alt. 800 m, on the trunk of *Adansonia digitata*, on *Pyrenula*, January 1970, Santesson 20743b (UPS—holotypus; hb. Diederich—isotypus).

(Fig. 8)

Ascomata often aggregated on the host thallus, superficial, narrowly attached to the substratum, black, initially \pm closed, very soon appanate, 200–500 μm diam.; disc exposed, convex, with a rough surface; margin initially prominent, later \pm disappearing, with a few distinct fissures, without hairs. *Exciple* with a dark purplish brown pigment, K+ violet, N+ dark greyish brown, sometimes also with the pale olivaceous hymenial pigment (see below, usually not visible due to the strong purplish pigmentation, but easily seen as dark green in K), the gelatinous matrix in which the excipular cells are embedded (best seen in the outer layer of the upper exciple) orange, K–, N+ bright yellow, paraplectenchymatous, not prolonged in a stipe, 60–80 μm thick, composed of \pm isodiametric cells of 4–7 μm diam., except the outer layer, which consists of radiating cells reaching 12 μm in length. *Subhymenium* hyaline. *Hymenium* with a pale olivaceous to greyish brown pigment, K+ green (pale or dark, depending on the concentration of the pigment), N– or yellowish (the lower part often becoming K+ violet due to the neighbouring excipular pigment), 65–100 μm tall, KI–. *Ephymenium* orange (to brownish), K–, N+ bright yellow, partly also with the dark purplish, K+ violet excipular pigment, or with the olivaceous, K+ dark green hymenial pigment. *Paraphyses* hyaline, 1.5–2.5 μm thick, not or basally branched, apically not or slightly thicker. *Asci* claviform to subcylindrical, 40–55 \times 5–7 μm , wall apically not thickened, KI–, 4–8-spored; ascogenous hyphae with croziers. *Ascospores* hyaline, narrowly ellipsoid to \pm fusiform, straight, non-septate, multiguttulate, 15–25 \times 2.5–3.5 μm .

Hosts. On the thallus and on the perithecia of *Pyrenula* species, including *P. ravenelii*.

Distribution. Australia, Kenya and the USA (Florida and Missouri).

Observations. This species has the typical excipular structure and pigments of the genus *Llimoniella*. The differences from the similar *L. pertusariae* are given in the identification key.

Additional specimens examined. **Australia:** New South Wales: Brown Mtn, c. 30 km SE of Nimmitabel, 1994, Kalb 30448 (h).—**USA:** Florida: Nassau Co., just E of Lofton Creek on Fla. Hwy. A1A, 5.5 ml W of Amelia River (Intracoastal Waterway), on *P. ravenelii*, 1987, Harris 21178 (NY). Missouri: Carter Co., Ozark National Scenic Riverways, Big Spring, trail from 'Boil' to road near bridge over Big Spring Branch, on *P. ravenelii*, 1990, Harris 25510 (NY).

***Llimoniella ramalinae* (Müll. Arg.) Etayo & Diederich comb. nov.**

Patellaria ramalinae Müll. Arg., *Flora, Jena* 66: 79 (1993).—*Scutula ramalinae* (Müll. Arg.) Vouaux, *Bull. Soc. Mycol. France* 29: 430 (1913).—*Skyttea ramalinae* (Müll. Arg.) Triebel, *Bibl. Lichenol.* 48: 169 (1992); type: Australia, Western Australia, Eucla, on *Ramalina ecklonii* var. *membranacea* (syn. *Ramalina celsa*str), 1882, Olivier (G—holotype, vid.).

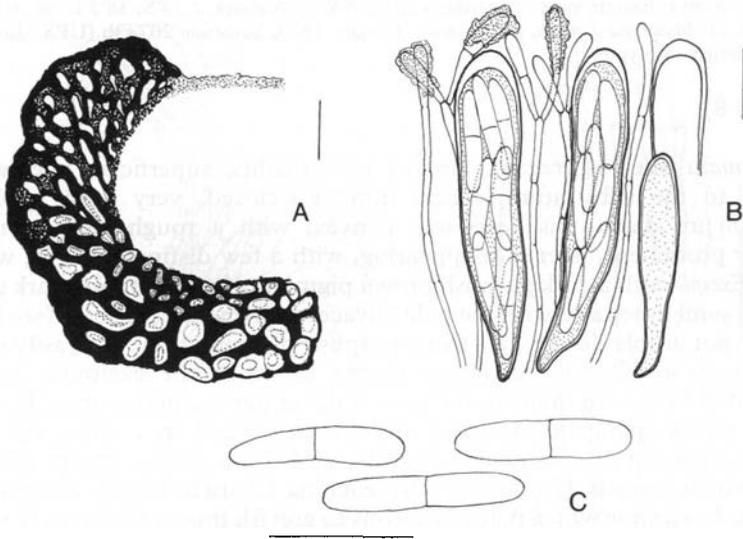


FIG. 9. *Limoniella ramalinae* (holotypus) (in H_2O). A, exciple; B, asci and paraphyses; C, ascospores. Scales: A-C=10 μm .

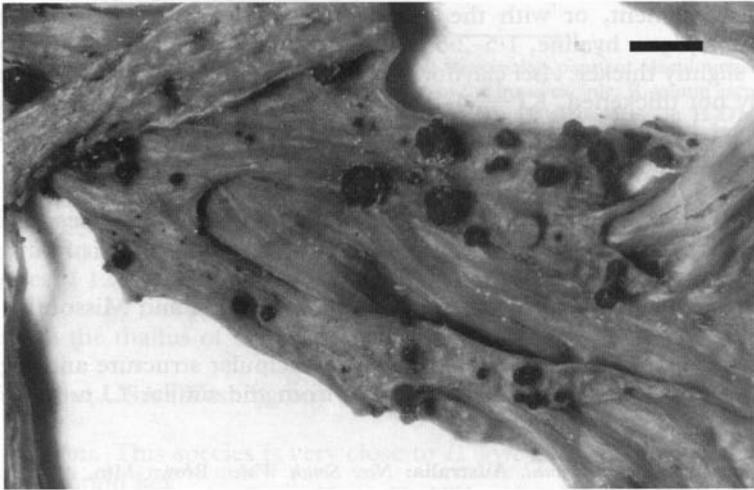


FIG.

(Figs 9 & 10)

Ascomata black, \pm immersed when young, becoming sessile to shortly pedicellate, margin slightly irregular, almost disappearing when old, disc plane, becoming convex, 150–350(–600) μm diam. *Exciple* formed of

dark, thick-walled, conglutinated hyphae, without hairs or periphysoids; lateral exciple violaceous to purplish brown, K+ green or partly violaceous, N- (brown); basal exciple greenish brown, K+ green or violaceous brown, N- (brown). *Hymenium* hyaline or pale violaceous, K- or partly K+ green or violaceous, c. 50 µm tall, KI-. *Epihymenium* red-violaceous, K+ green or partly violaceous, N+ yellowish brown. *Paraphyses* simple or apically branched, apically swollen, without pigments. *Asci* clavate, wall apically not or hardly thickened, with a small but distinct ocular chamber, KI-, 50–63 × 7–10 µm, 8-spored. *Ascospores* hyaline, 1-septate, smooth, without a perispore, cylindrical to narrowly ellipsoid, straight or slightly curved, multiguttulate, (10–)12–16(–17) × 3–4 µm.

Host. Thallus of *Ramalina celastri*. In the recent collection, a mixture of *R. celastri* and *R. inflata* [both identified by N. Stevens], only the thalli of *R. celastri* are parasitized by *L. ramalinae*, whilst those of *R. inflata* are heavily attacked by a lichenicolous species of *Stigmidium* (possibly *Arthopyrenia ramalinae* Müll. Arg.). This indicates that *Llimoniella ramalinae* might be restricted to *Ramalina celastri*.

Distribution. Known from two Australian localities (Victoria and Western Australia).

Observations. Despite its 1-septate ascospores, this species has the same excipular structure, the same pigments and similar ascospores as the other species of *Llimoniella*, and it belongs without any doubts to this genus. In the original description, the ascomata were said to measure 500–800 µm diam., but our observations show that those in the type collection are much smaller, up to 350 µm only. One large ascoma of 600 µm is present in the recent specimen from Victoria.

Additional specimen examined. **Australia:** *Victoria:* Gunnamatta Beach, 38°23'S, 144°45'E, at sea level, s. d., Stevens 7336 (hb. Diederich).

***Llimoniella scabridula* (Müll. Arg.) Nav.-Ros. & Haf.**

In Hafellner & Navarro-Rosinés, *Herzogia* 9: 771 (1993).—*Lecidea scabridula* Müll. Arg., *Bull. Soc. Murith. Valais* 10: 55 (1881); type: Switzerland, Valais, 'pentes gypseuses au-dessus des platrères du Granges', on *Acarospora nodulosa*, s. d., Wolf (G, non vid.).

(Fig. 7D)

For a description and additional illustrations, see Hafellner & Navarro-Rosinés (1993).

Hosts. Terricolous *Acarospora nodulosa* and *A. placodiiformis* (see Hafellner & Navarro-Rosinés 1993).

Distribution. Spain and Switzerland (see Hafellner & Navarro-Rosinés 1993).

Observations. The exciple in this species is dark purplish, K+ purplish violet (after the dissolution of this extra-cellular pigment, the cell walls appear greyish brown), N+ bright pinkish red, then orange red. The hymenium is purplish, K+ violaceous or greyish violaceous, N+ orange. The ascospores are (1-)2-guttulate.

Specimens examined. **Spain:** Zaragoza: Los Monegros, gypsum hill c. 5 km N of Bujaraloz, c. 70 km E of Zaragoza, on *A. placodiiformis*, 1983, Hafellner 23122, Santesson *Fungi Lichenicoli Exsiccati* 211 (hb. Diederich); La Retuerta, Pina de Ebro, on *A. nodulosa*, 1991, Etayo 11031 (h).

Llimoniella vinosa (Holien & Triebel) Diederich & Etayo comb. nov.

Spirographa vinosa Holien & Triebel, *Lichenologist* 28: 307 (1996); type: Norway, S-Trøndelag, Meldal, Urvatnet Nature Reserve, alt. c. 320 m, on thallus of *Ochrolechia juvenalis* [as '*O. cf. pallescens*'], on twigs of *Picea abies*, 19 viii 1993, Holien 5802 (TRH—holotype, vid.; M—isotype, non vid.).

For a description and illustrations, see Holien & Triebel (1996).

Hosts. Following Holien & Triebel (1996) and Holien (1998), the species grows mainly on the thallus and the apothecial margin of *Ochrolechia juvenalis* (in Holien & Triebel 1996 as '*O. cf. pallescens*'), more rarely on *O. gowardii*, and has once been observed on a poorly developed thallus of *Pertusaria cf. borealis*. All hitherto known occurrences are on twigs of *Picea abies* in northern boreal spruce forests. The host thallus often turns yellowish orange in the presence of the fungus.

Distribution. The species is known from several Norwegian localities in Hedmark, Oppland and Sør-Trøndelag.

Observations. The type specimen examined by us is very poor, with only a small number of minuscule, black ascomata developing on the host thallus. The single ascoma examined allowed an accurate study of the pigments, but no asci or ascospores were observed. As the original description is very detailed, we did not examine any further ascomata.

The species was originally described in *Spirographa*, because of the 'odontotremoid ascomata, the thin-walled asci and the sigmoid, septate spores'. However, the ascomata are not odontotremoid (see the discussion under *Skyttea* above), as they are not cleistohymenial and lack periphyses, and the asci are not hemi-amyloid. Also, the ascospores with broad obtuse ends are not those of a species of *Spirographa* with pointed ends. Instead, this is a typical leotialean fungus, which belongs to *Llimoniella*.

The exciple and large parts of the hymenium (especially the epihymenium) have a wine-red, K+ violet, N+ greyish brown pigment, the excipular and epihymenial gel is orange, K- , N+ deep yellowish orange, and an additional excipular and hymenial pigment, which is pale and almost invisible in water (hidden by the dark red pigment), reacts K+ intensively green and N- . This combination of pigments, their location within the ascoma and the excipular structure is typical for *Llimoniella*. The ascomata are only 200–300 µm in diam., which is smaller than in most other known species of the genus, but

otherwise they look perfectly like them. The asci are typically thin-walled, with no hemi-amyloid reaction. The ascospores are narrowly elongate with obtuse ends, similar to those of *L. pyrenulae* (which are straight and non-septate) or *L. ramalinae* (which are straight or slightly curved and 1-septate), but distinctly sigmoid and normally 1–3-septate, and the ascospore cells are multiguttulate [see Fig. 2C in Holien & Triebel (1996)].

This is the only species in the genus in which pycnidial conidiomata have been observed. The conidia are bacilliform, $3\text{--}4 \times 0.5 \mu\text{m}$ (Holien & Triebel 1996).

Rhymbocarpus Zopf

Hedwigia 35: 357 (1896); type: *Rhymbocarpus punctiformis* Zopf.

Ascomata lichenicolous, commensalistic, aggregated or dispersed, immersed to erumpent, but then broadly attached to the substratum, immersed parts hyaline to brown, exposed parts black, 50–250(–350) μm diam.; margin, when ascomata immersed, hardly visible, otherwise often covering the disc, except for a pore-like opening, in some species divided by several deep cruciately arranged fissures when old; disc at least partly exposed when old; hairs absent or present, macroscopically visible or not. *Exciple* basally paraplectenchymatous, of isodiametric cells, hyaline to brown or orange brown, K–, N–; lateral exciple in the upper part of more elongate, narrow cells, which protrude as hairs in some species, brownish, sometimes with an additional greenish, K+ olivaceous, N– pigment. *Hypothecium* indistinct. *Subhymenium* hyaline. *Hymenium* hyaline, KI–. *Epihymenium* greenish, K+ olivaceous, N–. *Paraphyses* simple or branched, septate, apically slightly swollen, without pigments (but surrounded by the greenish epihymenial pigment), easily separating in KOH under slight pressure. *Asci* clavate to subcylindrical, thin-walled, with a single functional wall layer, wall apically not or slightly thickened, I– and KI–, 8-spored. *Ascospores* hyaline, 0(–1)-septate, smooth, without a distinct perispore, ellipsoid to fusiform, straight or slightly curved, with \pm obtuse ends, in at least three species biguttulate. *Conidiomata* known in two species (*R. boomii* and *R. cruciata*), pycnidial, macroscopically almost indistinguishable from closed ascomata and intermixed with them, wall brown (same pigment as the ascomatal wall). *Conidiogenous cells* phialidic, ampulliform, hyaline. *Conidia* subcylindrical to narrowly ellipsoid, basally thickened and truncate, hyaline, simple, smooth-walled.

Observations. Triebel (1989) considered *Rhymbocarpus* to be congeneric with *Skyttea*, and she subsequently transferred several *Skyttea* species to *Rhymbocarpus*. Coppins *et al.* (1991) correctly noticed, however, that these two genera are very distinct. In the type of *Rhymbocarpus*, apothecia are immersed, almost perithecioid, with no or sparse excipular hairs, the reduced exciple is very different (see Fig. 1B, D), the epihymenium distinctly pigmented (brownish to greenish), and the ascus wall not thickened at the apex. *Rhymbocarpus* was retained as *incertae sedis* by Coppins *et al.* (1991), but in our opinion the genus belongs to the *Leotiales*.

Careful studies of numerous lichenicolous leotialean species have led us to conclude that *Skyttea cruciata* is congeneric with *Geltingia stereocaulorum*, *Llimoniella fuscoatrae*, *L. neglecta*, *L. pubescens* and several undescribed taxa. They all share the following characters: ascomata blackish, initially partly immersed, often urceolate, exciple often covering the disc when young, epihymenium with a green, K+ olivaceous pigment (in some species also present in the upper exciple), exciple with a brownish, K- pigment, ascus wall apically not thickened, no reactions with iodine (all parts I- and KI-), paraphyses easily separating in KOH with pressure, ascospores 0(-1)-septate, hyaline, smooth, ellipsoid to fusiform. The exciple is composed of \pm isodiametric cells below, but of narrow, elongate, sometimes almost filiform cells above; these elongate cells are either embedded in a gel and are thus part of the exciple s. str., or they are free and form excipular hairs. We initially hesitated to include species with and without excipular hairs in the same genus, but as both situations have been observed in *R. pertusariae*, described below, in the same specimen and on the same host thallus, it is clear that this character is of a minor taxonomic importance in this group of fungi.

These species differ from *Skyttea* by the apically non-thickened ascus wall, the completely different excipular margin (see Figs 1A, 13) and hairs, the hymenium with paraphyses easily separating in KOH with pressure, the intensively green epihymenium and the different ascomatal opening.

They are very distinct from the known lichenicolous leotialean fungi with excipular hairs, *Echinodiscus lesdainii* (Etayo & Diederich 2000), *Polydesmia lichenis* Huhtinen & R. Sant. (*Hyaloscyphaceae*; Huhtinen & Santesson 1997) and *Unguiculariopsis* spp. (*Hyaloscyphaceae* [H.-O. Baral pers. comm.]; e.g. Rambold & Triebel 1990; Zhuang 1988; see also below). We initially wondered if these species belong to *Llimoniella*, in which two of them were described, and two more have been combined later. The type species of *Llimoniella* and all other species included by us in the same genus, have no excipular hairs, and present a different, reddish, K+ purplish violet excipular pigment, the green, K+ olivaceous epihymenial pigment being absent; the exciple, which is more strongly developed at the base of the ascomata, is entirely composed of \pm isodiametric cells and does not or only hardly covers the ascomatal disc. As some of these differences, such as the different pigmentation, might just be important at specific and not at generic level, we hesitated for a long time in separating the '*Skyttea cruciata*-group' from *Llimoniella*. We believe now that there is a strong case in favour of this separation. The technique required consists of examining apothecial sections in C (commercial bleach), which lets the dark excipular pigments disappear completely, allowing an accurate study of the excipular structure. A detailed study of most species involved confirmed that the excipular structure is clearly different in these two groups of fungi (see Figs 7, 8). The outer excipular cells in *Llimoniella* are \pm isodiametric, often \pm swollen, whilst those in the '*S. cruciata*-group' are narrowly elongate. These \pm linear outer excipular cells in the latter group may well be interpreted as excipular hairs, which in some species are free and visible, whilst in others they are embedded in an excipular gel, the exciple thus appearing as devoid of hairs.

We concluded that the ‘*S. cruciata*-group’ represented a genus distinct from *Llimoniella*. Superficially, it does not look like *Rhymbocarpus geographici*, but microscopically, these fungi are extremely similar. In both *S. cruciata* (and relatives) and *R. geographici*, we observed the same asci, ascospores and paraphyses, the same (negative) iodine reactions, the same green, K+ olivaceous epihymenial pigment (sometimes also present in the upper exciple), the same brownish, K- excipular pigment (sometimes obscured by the additional green pigment), which is pale brown (i.e. less concentrated) in the immersed condition, and dark brown (i.e. strongly concentrated) when exposed, the same elongate cells of the upper exciple, excipular hairs which might be absent or present, even within the same specimen, and ascomata which are at least partly immersed when young, with a ± important tendency to become superficial later.

The main differences are the degree of immersion in the host thallus and of the development of the exciple. However, we believe that the development of the exciple is a result of the degree of immersion: in *Rhymbocarpus geographici*, young ascomata are completely immersed, and the exciple is reduced and pale; older ascomata are partly superficial (e.g. 20%), and the exposed parts of the exciple become thicker and blackish, often covering the disc. In *Rhymbocarpus makarovae*, described below, young ascomata are immersed, the exciple being reduced with only the upper part blackish; older, almost completely superficial ascomata are entirely dark, with an often remarkably developed exciple. In the species of the *S. cruciata*-group, ascomata are partly or completely exposed from a very early stage of their development, and the exciple is well developed and dark from the beginning.

We conclude that all these species are congeneric, and that the apparent differences in the development of the exciple and the excipular hairs, in the immersion of the ascomata and in the concentration of the excipular pigments are of a minor systematic importance. These species have to be included in *Rhymbocarpus*, which is the only generic name available.

Key to the species of *Rhymbocarpus*

- 1 Ascomata ± immersed, almost perithecioid; margin indistinct, at least when young; disc punctiform (Figs 1B, 11, 13) 2
- Ascomata erumpent to superficial, with a distinct margin (Figs 12, 14) 5
- 2(1) Ascomata remaining immersed, even when mature, up to 120 µm diam.; margin hardly visible. 3
- Ascomata usually erumpent, developing a thick, black margin when old, mostly 100–200 µm diam. 4
- 3(2) Ascospores 8–10.5 × 3–4 µm; ascomatal margin without hairs; on *Dirina ceratoniae*. **R. boomii**
- Ascospores 11–12 × 4–5 µm; ascomatal margin sometimes with short hairs; on *Rhizocarpon* **R. geographici**

- 4(2) Ascomata, when mature, deeply cruciate; margin divided by 3 or 4 deep fissures, almost completely covering the disc, except when old; ascospores $9-12(-13) \times 3-4(-4.5) \mu\text{m}$; on *Lecidea fuscoatra* **R. fuscoatrae**
 Ascomatal margin, when old, not deeply fissured; ascospores $7-10 \times 3-4 \mu\text{m}$; on *Porpidia* **R. makarovae**
- 5(1) Ascomatal margin with hairs (Figs 1A, 14 p. p.) (in *R. cruciatus* only visible in microscopical section) 6
 Ascomatal margin without hairs (Fig. 14 p. p.) 8
- 6(5) Ascospores narrowly ellipsoid to fusiform, $10-15 \times 2-3.5 \mu\text{m}$; ascomata with or without hairs; on *Pertusaria panyrga* (Fig. 14) **R. pertusariae**
 Ascospores ellipsoid, mostly under $9 \mu\text{m}$ 7
- 7(6) Exciple entirely covered by hairs; ascomatal margin usually without, or with inconspicuous fissures; ascospores $5.5-9 \times 2.5-3.2 \mu\text{m}$; green pigment present in the epihymenium and the upper exciple; on *Lepraria lobificans* and *Lepraria* sp. **R. pubescens**
 Hairs restricted to the excipular margin; ascomatal margin often divided by a few deep fissures; ascospores $7-8.5(-10.5) \times (2.5-3-3.5) \mu\text{m}$; green pigment only present in the epihymenium, exciple entirely brown; on *Diploicia canescens* **R. cruciatus**
- 8(5) Ascospores $15-17(-20) \times 2.5-3 \mu\text{m}$; on *Stereocaulon* **R. stereocaulorum**
 Ascospores shorter 9
- 9(8) Ascomata deeply cruciate; margin divided by 3 or 4 deep fissures, almost completely covering the disc, except when old; ascospores $9-12(-13) \times 3-4(-4.5) \mu\text{m}$; on *Lecidea fuscoatra* **R. fuscoatrae**
 Ascomata not cruciate, margin not, or not deeply fissured. . . . 10
- 10(9) Ascospores $10-15 \times 2-3.5 \mu\text{m}$ (Fig. 14); on *Pertusaria panyrga* **R. pertusariae**
 Ascospores shorter 11
- 11(10) Ascomata partly immersed when young, soon superficial; ascospores $(8-9-11(-14) \times 2-3(-3.5) \mu\text{m}$; asci $35-45 \times 6.5-8 \mu\text{m}$; on the *Lepraria neglecta*-group **R. neglectus**
 Ascomata immersed, almost perithecioid when young (Fig. 13), later erumpent to superficial; ascospores $7-10 \times 3-4 \mu\text{m}$; asci $47-57 \times 6-8 \mu\text{m}$; on *Porpidia* **R. makarovae**

Rhymbocarpus boomii Etayo & Diederich sp. nov.

A Rhymbocarpus boomii ascosporis parvioribus, $8-10.5 \times 3-4 \mu\text{m}$ differt.

Typus: Spain, Mallorca, between Cala D'Or and Porto Colom, Cala Arsenau (Cala Sanau) coastal area, 20 m, on *Juniperus phoenicea*, mixed with *Pinus halepensis*, *Pistacia* and *Olea*, on *Dirina ceratoniae*, 3 April 1997, van den Boom 18478 (MA-Lich—holotypus; hb. Etayo—isotypus).

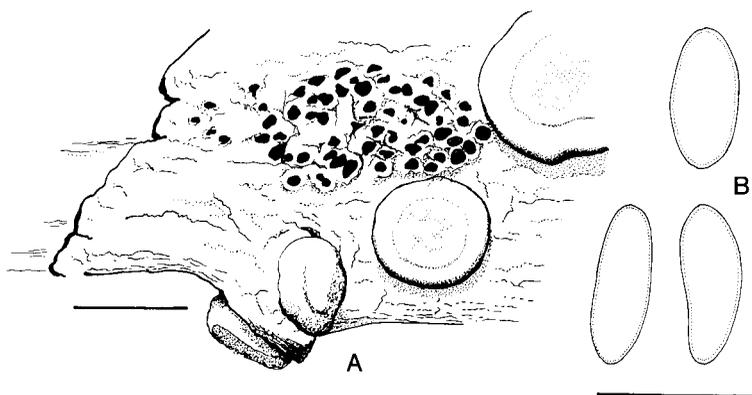


FIG. 11. *Rhymbocarpus boomii* (holotypus). A, ascomata on thallus of *Dirina ceratomiae*; B, ascospores. Scales: A=1 mm; B=10 µm.

(Fig. 11)

Ascomata aggregated to almost confluent on the thallus and the apothecial margin of the host, at first completely immersed, \pm perithecioid, breaking through the cortex of the lichen, becoming apothecioid when mature, but remaining immersed, black, margin not prominent, thin and smooth, concolorous to the disc, 100–120 µm diam. *Exciple* basally hyaline to greenish, laterally greyish to brownish green, K – or more intensively brownish, N+ olivaceous brown, composed of several rows of elongate cells; excipular hairs absent. *Subhymenium* 5–10 µm. *Hymenium* hyaline, 55–60 µm. *Epihymenium* greenish. *Paraphyses* simple or branched, hyaline, not or slightly swollen at the apices, 1.5–2 µm thick. *Asci* cylindrical, wall apically not thickened, I – and KI –, 8-spored, 48–55 × 6–7 µm. *Ascospores* ellipsoid, straight or slightly curved, simple, hyaline, smooth, with obtuse ends, 8–10.5 × 3–4 µm. *Conidiomata* pycnidial, similar to perithecioid apothecia and intermixed with them. *Pycnidial wall* the same colour as the exciple. *Conidiogenous cells* phialidic, ampulliform, hyaline, 4–5 × 2.5–3 µm. *Conidia* subcylindrical to narrowly ellipsoid, basally thickened and truncate, hyaline, simple, smooth-walled, 5–8 × 0.5–1 µm.

Host. Thallus and apothecial margin of epiphytic *Dirina ceratomiae*.

Distribution. Known only from the type locality in Mallorca (Spain).

Observations. *Rhymbocarpus boomii* is similar in habitus to the type species, *R. geographicus*, because of the small, aggregate and immersed ascomata and the same kind of exciple. It is distinguished from the latter species by the smaller ascospores, the absence of excipular hairs and the different host (it is the only known species in the genus growing on a host with *Trentepohlia*).

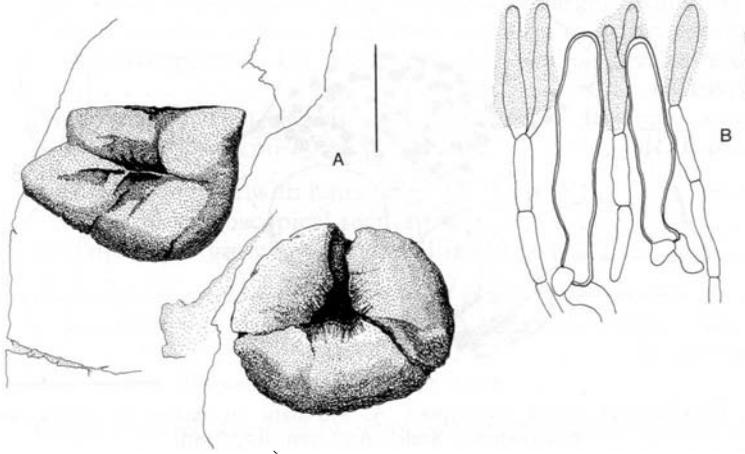


FIG. 12. *Rhymbocarpus cruciatus* (Santesson 15584b). A, apothecium (right) and conidioma (left); B, asci with croziers and paraphyses. Scales: A=100 μ m; B=10 μ m.

The new species is named after our friend, P. van den Boom (Son, Netherlands), who collected the material and allowed us to describe it in this paper.

***Rhymbocarpus cruciatus* (Sherwood, D. Hawksw. & Coppins) Etayo & Diederich comb. nov.**

Skyttea cruciata Sherwood, D. Hawksw. & Coppins, *Trans. Br. mycol. Soc.* 75: 484 (1981 [‘1980’]); type: Ireland, Co. Kerry, Dingle Peninsula, near Ballyoughteragh, N of Ballyferriter, on saxicolous *Diploicia canescens*, 9 viii 1978, *Poelt* (GZU—holotypus, vid.).

(Figs 1A, 12)

For additional illustrations, see Sherwood *et al.* (1981: Figs 1B, 3).

Ascomata dispersed, immersed to erumpent, broadly attached to the substratum, black, 150–250 μ m diam., initially almost closed, except for a pore-like opening, covered by the exciple which divides by 3–4 deep cruciately arranged fissures in older ascomata, hairs not visible. *Exciple* brown to orange brown, K⁻, paraplectenchymatous, not prolonged in a stipe, laterally 15–20 μ m; hairs hyaline to brown, smooth, septate, restricted to the excipular margin, up to 20 \times 2.5 μ m. *Hymenium* with paraphyses easily separating. *Epihymenium* green, K⁺ olivaceous. *Paraphyses* septate, hyaline, 2–2.5 μ m thick, simple or sometimes branched (mainly near the apex), apically slightly thicker and greenish. *Asci* subcylindrical, 30–46 \times 5.5–7 μ m, wall apically not thickened, KI⁻, 8-spored; ascogenous hyphae with croziers. *Ascospores* hyaline, ellipsoid, non-septate, biguttulate, 7–8.5(–10.5) \times (2.5–)3–3.5 μ m. *Conidiomata* rare, almost indistinguishable from cruciate ascomata.

Host. Thallus of corticolous and saxicolous *Diploicia canescens*.

Distribution. Great Britain, Ireland, Canary Islands and Morocco.

Additional specimens examined (the specimens from V.C. 14 and 89, and from Jersey examined by B. J. Coppins). **Great Britain:** *England:* V.C. 1, West Cornwall, Isles of Scilly: St Mary's, 1963, *Samesson* 15584b, 15858c, 15634, 16182, 16113b (UPS). V.C. 3, South Devon: Kingsbridge, Slapton, 1971, *Poelt* 10527, 10541 (GZU). V.C. 14, East Sussex: Icklesham churchyard, on *Ulmus*, iv 1972, *Coppins* (E). V.C. 113, Channel Isles: Jersey, 1860, *Mrs McKenzie* (E). *Scotland:* V.C. 89, East Perthshire: Kinnoull Hill, [on basaltic rock], iv 1856, *Lindsay* (E).—**Canary Islands:** *El Hierro:* La Dehesa, El Sabinal, Valle Quemado N vom Santuario Virgen de los Reyes, 550 m, 1995, *Hafellner* 37012 (GZU) (also distributed in *Santesson Fungi Lichenicoli Exs* 284 [GZU], hb. Diederich!).—**Morocco:** 8 km S de Sidi Ifni, 1981, *Crespo* (hb. Hafellner 9133 [GZU]).

***Rhymbocarpus fuscoatrae* (Hafellner) Diederich & Etayo comb. nov.**

Llimoniella fuscoatrae Hafellner, *Herzogia* 12: 136 (1996); type: Canary Islands, la Gomera, Alto de Cherelepin N ober der Straße von San Sebastian nach Valle Gran Rey, 28°6'5"N, 17°15'30"W, c. 1340 m, auf den Felsköpfen am Grat, auf *Lecidea fuscoatra*, 10 ii 1991, *Hafellner* 34166 (GZU—holotypus, vid.).

For a description and illustrations, see Hafellner (1996c).

Host. *Lecidea fuscoatra* (thallus).

Distribution. Hafellner (1996c) reported this species from the Canary Islands (La Gomera, La Palma and Tenerife) and Madeira.

Observations. Macroscopically, the ascomata of this species do not look at all like a species of *Llimoniella*. Instead, they are reminiscent of the deeply cruciate ascomata of *Rhymbocarpus cruciatus*, in which the disc is covered by the thick margin, which divides by a few deep fissures into 3 or 4 ± equal parts. Only in older ascomata does the disc become exposed. Very young, developing ascomata are completely immersed, almost perithecioid, as in *R. boomii*, *R. geographicum* or *R. makarovae*. Some old ascomata reach a diameter of 350 µm, which is larger than in the other known species of the genus; this size is mainly due to the very thick, often irregular margin. The epihymenium is olivaceous green, K – (olivaceous), which is characteristic for species of *Rhymbocarpus*, and the exciple dark brown, K+ reddish brown, with a greenish tinge in the upper layer close to the epihymenium. The exciple, observed in C (commercial bleach), is typically that of a *Rhymbocarpus*, with narrow, elongate, ± linear, septate, radiating hyphae; excipular hairs are absent. The ascospores are biguttulate.

***Rhymbocarpus geographicum* (J. Steiner) Vouaux**

Bull. Soc. Mycol. France 29: 419 (1913).—*Nesolechia geographicum* J. Steiner, *Beitr. zur Lichfl. Griech. und Egypt. Griech. Pentelikon, Sitzungsber. Akad. Wissensch. Wien, math.-naturw. Kl.* 102 (1): 161 (1893).—*Phacopsis geographicum* (J. Steiner) Keissl., *Rabenh. Krypt.-Fl.* 8: 67 (1930); type: Greece, on the summit of Mt Pentelikon, on *Rhizocarpon geographicum*, Steiner (type lost: W-, WU-, fide Triebel 1989: 143); neotype: holotype specimen of *Rhymbocarpus punctiformis* Zopf, designated here.

Rhymocarpus punctiformis Zopf, *Hedwigia* 35: 357 (1896); type: Italy, S. Tirol, St Ulrich in Gröden, on *Rhizocarpon geographicum*, viii 1895, Arnold (M—holotypus, vid.); *ibid.*, 10 viii 1898, Arnold *Lichenes exs.* 1772 (UPS—topotypus, vid.); *ibid.* ['Bolzano, Val Gardena (Grödner Tal), Ortisei (St Ulrich), 2–2.2 km NEE of centre, road 242 Ponte Gardena (Waidbruck)—Ortisei'], on *R. geographicum*, ix 1991, Triebel & Rambold 5968, 5969, 5973, 5974, 5975 (M—topotypi, vid.).

(Fig. 1B)

For an illustration of the asci and ascospores, see Coppins *et al.* (1991).

Ascomata aggregated in decolourized or bullate areoles of the host, at first immersed and ± perithecioid, becoming apothecioid when mature, normally remaining immersed, even when mature, rarely slightly erumpent, black; margin hardly visible, 50–120 µm diam. *Exciple* hyaline, except the upper part close to the epihymenium, which is greenish brown, composed of several rows of cells which are ± subglobose in the lower part and elongate in the upper part, 10–15 µm thick at the base and up to 30 µm above; excipular hairs absent or sparse, hyaline, tapered towards the apex, simple or with one septum. *Subhymenium* and *hymenium* hyaline. *Epihymenium* brownish to greenish. All parts KI –. *Paraphyses* simple to branched, hyaline, septate, slightly swollen at the apices. *Asci* elongate clavate, with a single functional wall layer, wall apically not thickened, I – and KI –, 8-spored. *Ascospores* ellipsoid, straight or slightly curved, simple, hyaline, smooth, with obtuse ends, 11–12 × 4–5 µm.

Hosts. *Rhizocarpon atroflavescens*, *R. geminatum* and *R. geographicum*.

Distribution. Greece, Italy and Sweden.

Observations. The descriptions of *R. geographicum* and *R. punctiformis* are extremely close. As both taxa have been collected on the same host species, they most probably represent the same species. As the type of *Nesolechia geographicum* is lost, we neotypify that name herewith on the type specimen of *Rhymocarpus punctiformis* to irrevocably fix the two names together.

Additional specimens examined. **Sweden:** Härjedalen, Tännäs par., Mt Ashögen, southern slope, 950 m, on *R. atroflavescens*, 1975, Santesson 26333 (UPS); Torne Lappmark, the Torneträsk Area, S of the railway station of Abisko, on *R. geminatum*, 1959, Santesson 13456a (UPS).

***Rhymocarpus makarovae* Diederich & Etayo sp. nov.**

Rhymocarpus insignis ascomatibus immersis ad erumpentibus, atris, primo clausis, demum aperientibus, 100–200 µm, margine glabro, 3–4 profundis fissuris diviso ubi vetere, ascosporis ellipsoideis, aseptatis, 7–10 × 3–4 µm.

Typus: Russia, eastern coast of Chukchi Peninsula, Lavrentiya Bay, near Cape Krauze, on *Porpidia* sp., 10 July 1973, Makarova (LE—holotypus)

(Fig. 13)

Ascomata aggregated, immersed to erumpent, broadly attached to the substratum, black, ± shiny, initially ± closed, 100–200 µm diam.; margin, when old, divided by 3–4 deep cruciately arranged fissures, without excipular

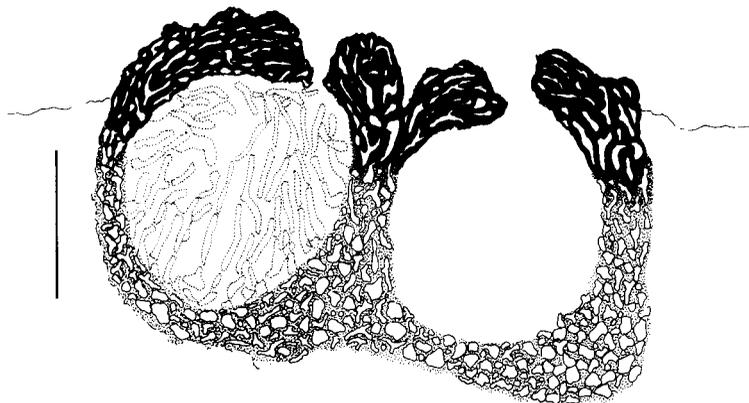


FIG. 13. *Rhymbocarpus makarovae* (holotypus). Two young, almost perithecioid ascomata, immersed in the thallus of *Porpidia* sp. Scale = 50 μm .

hairs. *Exciple* orange brown to greyish brown, K⁻, paraplectenchymatous, not prolonged in a stipe, laterally 15–60 μm thick (up to 60 μm in old ascomata), composed of elongate cells of 10–17 \times 4–5.5 μm , basally thinner, pale or dark brown, of isodiametric cells of 5.5–7 μm diam., with cell walls strongly gelatinized. *Hymenium* with paraphyses easily separating. *Epihymenium* with a greenish, K⁺ olivaceous pigment, often appearing as olivaceous as intermixed with the brownish excipular pigment. *Paraphyses* septate, hyaline, c. 2 μm thick, regularly branched, apically not or slightly thicker. *Asci* cylindrical, 47–57 \times 6–8 μm , apically not thickened, KI⁻, 8-spored. *Ascospores* hyaline, ellipsoid, non-septate, 7–10 \times 3–4 μm .

Hosts. Thallus of unidentified *Porpidia* species (thallus esorediate, with apothecia).

Distribution. Russia, known from two localities in eastern Siberia (Chukchi Peninsula).

Observations. Young ascomata of this species are \pm immersed and almost perithecioid, like those of *R. geographicus*, whilst older ones may be completely superficial, with a well-developed margin, as in *R. cruciatus* or *R. neglectus*.

The new species is dedicated to I. I. Makarova, an outstanding collector of lichens in the Russian Arctic and particularly on the Chukchi Peninsula.

Additional specimen examined. **Russia:** eastern coast of Chukchi Peninsula, near Inchoun settlement, on *Porpidia* sp., vii 1975, *Makarova* (LE).

***Rhymbocarpus neglectus* (Vain.) Diederich & Etayo comb. nov.**

Nesolechia neglecta Vain., *Acta Soc. Fauna Flora Fenn.* 57 (2): 418 (1934).—*Limoniella neglecta* (Vain.) Triebel & Rambold, *Bibl. Lichenol.* 53: 154 (1993); type: Finland, Nylandia, Helsinki, Samalilla kalliolla, on *Lepraria neglecta*, 1872, *Lang* (= *Vainio*) (TUR-VAINIO 25372—lectotype, selected by Kümmerling *et al.* 1993: 154, non vid.).

(Fig. 7A)

For a description and additional illustrations, see Kümmerling *et al.* (1993: 154–157).

Hosts. Species of the *Lepraria neglecta*-group, including *L. caesioalba*, *L. neglecta* and *L. cacuminum* (Kümmerling *et al.* 1993).

Distribution. Austria, France, Great Britain, Norway, Portugal, Russia, Slovakia, Sweden, Greenland and the USA (Kümmerling *et al.* 1993).

Observations. The ascospores in this species are biguttulate.

Specimens examined. **Austria:** Salzburg: Pinzgau, Hohe Tauern, Granatspitz-Gruppe, Tauern Kogel S ober dem Weißsee, am E-Grat W ober dem Kaiser Tauern, 2550–2650 m, auf *L. neglecta*, 1996, Hafellner 37910 (h).—**Great Britain:** England: V.C. 3, South Devon: Dartmoor, Black Tor Copse, on *Lepraria*, 1986, Giavarini (E, hb. Diederich). **Scotland:** V.C. 108, W Sutherland: Stoer Peninsula, Culkein, on *Lepraria*, v 1985, Woods (E).—**Portugal:** Serra da Estrela, 5 km SW of Manteigas, 1 km N of Curral do Martins, on *Lepraria*, 1998, van den Boom 20423 (h).—**Sweden:** Uppland: Funbo par., on *L. neglecta*, 1955, Santesson 11146, Santesson Fungi Lichenicoli Exsiccati 269 (hb. Diederich).

Rhymbocarpus pertusariae Diederich, Zhurb. & Etayo sp. nov.

Rhymbocarpus insignis ascomatibus erumpentibus, atris, primo clausis, demum applanatis, 100–250 µm, disco exposito, margine prominenti, interdum pubescenti, ascosporis anguste ellipsoideis ad fusiformibus vel bacilliformibus, 0–1-septatis, 10–15 × 2–3.5 µm.

Typus: Sweden, Torne Lappmark, the Torneträsk Area, Abisko, Paddos, alt. c. 630 m, on open calcareous rocks, on *Pertusaria panyrga*, 29 August 1959, Santesson 13473 a (UPS—holotypus; hb. Diederich—isotypus).

(Figs 7B, 14)

Ascomata aggregated, immersed to erumpent, broadly attached to the substratum, black, initially ± closed, later applanate, disc exposed and margin prominent, 100–250 µm diam.; margin, when old, entire or with several deep fissures, but thinner than in *R. cruciatus* and not appearing cruciate, not, or rarely entirely, covered by hairs. *Exciple* with a dark brown pigment, K–, N–, mainly located in the outer layer, and a greenish pigment, K+ olivaceous, N–, present in the whole exciple, but best visible in the inner layer, paraplectenchymatous, indistinctly prolonged in a stipe, laterally 35–45 µm thick, composed of elongate cells of 7–12 × 4–6 µm, basally c. 45 µm thick, of isodiametric cells of 7–10 µm diam., with cell walls strongly gelatinized; excipular hairs, when present, hyaline to dark brownish green, occasionally 1–2-septate, thin-walled, base not distinctly thickened, 13–35 × 2–3 µm. *Subhymenium* hyaline, 10–20 µm thick. *Hymenium* hyaline, 55–65 µm tall, KI–, with paraphyses easily separating. *Epihymenium* with a greenish pigment, K+ olivaceous, N–. *Paraphyses* septate, hyaline, c. 2 µm thick, regularly branched, apically not or slightly thicker. *Asci* claviform to subcylindrical, 36–53 × 6–9 µm, wall apically not thickened, KI–, 8-spored; ascogenous hyphae with croziers. *Ascospores* hyaline, narrowly ellipsoid to

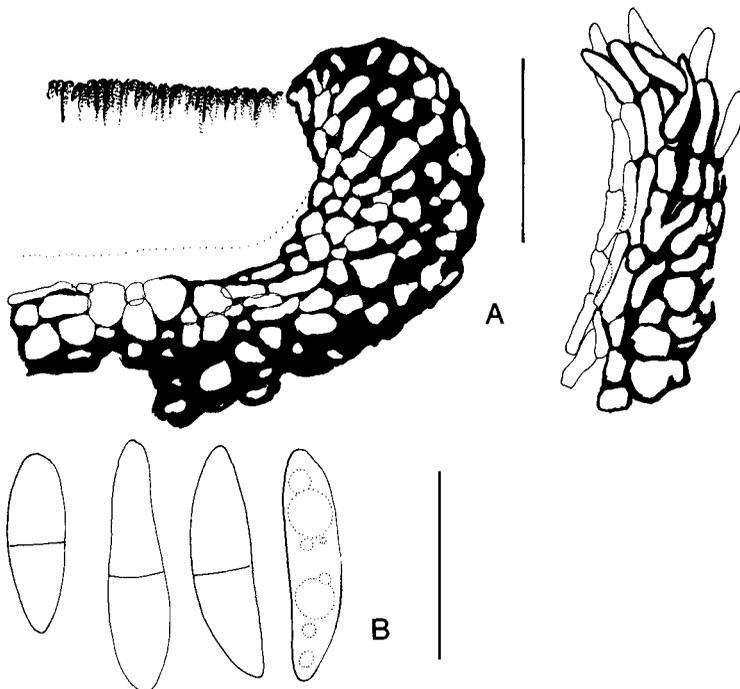


FIG. 14. *Rhymbocarpus pertusariae* (Zhurbenko 9462) (in H₂O). A, exciple and epihymenium of an old ascoma (left), and a young ascoma with excipular hairs (right); B, 0–1-septate ascospores. Scales: A=50 μ m; B=10 μ m.

\pm fusiform, or almost bacilliform, 0–1 septate, 10–15 \times 2–3.5 μ m, dead cells (observed in K) with one or several small or large guttules.

Host. Thallus of muscicolous *Pertusaria panyrga*.

Distribution. Sweden and Russia (Taymir Peninsula).

Observations. The ascomata in the type collection are devoid of excipular hairs. In the Russian specimen, most ascomata have no hairs, but some (mainly younger, less exposed ascomata) are pubescent (easily visible with a binocular microscope). When the ascomata are hairy, the new species resembles *R. pubescens*; however, the older ascomata are more applanate, the disc more visible, the hairs disappearing or becoming indistinct, and the margin sometimes with distinct deep fissures. The main microscopical differences are the shorter, ellipsoid ascospores in *R. pubescens*, which are 5.5–9 \times 2.5–3.2 μ m (Etayo & Diederich 1998). *Rhymbocarpus pertusariae* and *R. pubescens* are the only known species in the genus with hairs (when present) covering the entire exciple, and with an important percentage of ascospores developing one septum. When the hairs are absent, as in the type specimen,

the species is similar to *R. neglectus*, which usually has shorter ascospores (see identification key).

Lecidea pertusaricola Jatta, described from Italy on *Pertusaria pertusa*, might represent an older name for this species. However, the original description is absolutely insufficient (Vouaux 1912–14), and the type specimen has never been re-examined.

Additional specimen examined. **Russia:** Taymir Peninsula, region of Lewinson-Lessing Lake, vii 1994, Zhurbenko 9462 (LE).

**Rhymbocarpus pubescens (Etayo & Diederich) Diederich & Etayo
comb. nov.**

Llimoniella pubescens Etayo & Diederich, *Lichenologist* **30**: 108 (1998); type: Spain, Navarra, alto de Lizarraga, 900 m, on *Fagus*, on *Lepraria lobificans*, iv 1992, Etayo 3052 (MA-Lichen—holotypus; LG, hb. Diederich, hb. Etayo—isotypi).

For a description and illustrations, see Etayo & Diederich (1998).

Hosts. Etayo & Diederich (1998) studied several specimens on *Lepraria* sp., including *L. lobificans*.

Distribution. Great Britain (Scotland), Spain (Pyrenees) and Papua New Guinea (Etayo & Diederich 1998).

Rhymbocarpus stereocaulorum (Alstrup & D. Hawksw.) Etayo & Diederich comb. nov.

Geltlingia stereocaulorum Alstrup & D. Hawksw., *Meddr Grønland, Biosci.* **31**: 34 (1990).—*Llimoniella stereocaulorum* (Alstrup & D. Hawksw.) Hafellner, in Zhurbenko & Santesson, *Herzogia* **12**: 155 (1996); type: Greenland, Godthåb (Nuuk), on *Stereocaulon*, vii 1946, Christiansen 5547 (C—holotypus, vid.).

(Fig. 7C)

For a description and additional illustrations, see Alstrup & Hawksworth (1990).

Hosts. *Stereocaulon* species, including *S. rivulorum*.

Distribution. Greenland, Norway and Russia.

Observations. The hymenium is olivaceous green, K+ olivaceous (to brownish), and the exciple olivaceous green when young and brownish when old. When young, the outer exciple consists of elongate, terminal cells, embedded in gel (similar to hairs) (see Fig. 7C). The ascospores are often larger than indicated in the original account, reaching 20 µm in length.

Additional specimens examined. **Norway:** Oppland, Vågå par., Åbakken, N of Lake Vågavatn, on *S. rivulorum*, 1961, Santesson 14241 (UPS, hb. Diederich).—**Russia:** NW Siberia: T'umenskaia oblast', Gvdan Peninsula, Chuhor'-Yakha River, 69°7'N, 74°40'E, on *Stereocaulon*, vii 1991, Andreev (UPS [dupl. from LE]).

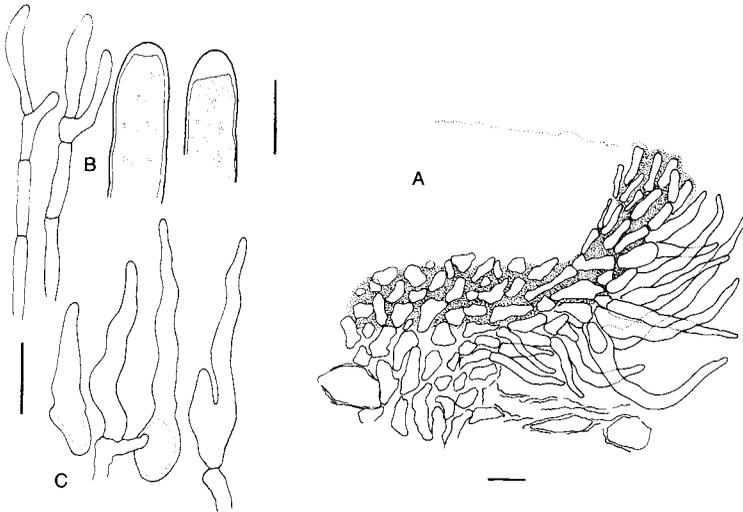


FIG. 15. *Unguiculariopsis acrocordiae*. A, ascomatal section in LCB (*Hafellner* 31378); B & C, (isotypus, hb. Diederich): B, paraphyses and ascus tip (in KOH); C, excipular hairs. Scales: A–C=10 μ m.

Excluded species

***Unguiculariopsis acrocordiae* (Diederich) Diederich & Etayo
comb. nov.**

Skyttea acrocordiae Diederich, *Lejeunia*, n. s. 119: 12 (1986); type: Belgium, Etalle, au SE de Buzenol, vallée de la Rouge-Eau, en aval du passage de la route d’Etalle à St-Léger, sur *Quercus* et *Acer*, sur *Acrocordia gemmata*, 19 vi 1984, Diederich 5566, Sérusiaux & Rose (IMI 300097—holotypus; hb. Diederich—isotypus).

(Fig. 15)

For additional illustrations, see Diederich (1986).

Ascomata slightly immersed to superficial, brownish red, initially \pm closed, becoming expanded, 100–200 μ m diam.; when mature, disc \pm plane to slightly convex, margin prominent or not, covered by white hairs ($\times 40$). *Exciple* reddish to orange brown, pigment K+ reddish, N–, paraplectenchymatous, cells subglobose, with conglutinate walls; excipular hairs hyaline, \pm straight, without an apical hook, 25–50 \times 2.5–5.5 μ m. *Subhymenium*, *hymenium* and *epihymenium* hyaline or pale. *Paraphyses* hyaline, filiform, septate, not rarely branched in the upper part, apically not or slightly thickened. *Asci* clavate to subcylindrical, wall thickened near the apex, without or with an indistinct ocular chamber, I– and KI–, 8-spored, 22–45 \times 4–8 μ m. *Ascospores* hyaline, simple, ellipsoid, smooth-walled, without a distinct perispore, 5.5–7.5 \times 2.5–3 μ m. *Conidiomata* not seen.

Host. Commensalistic on *Acrocordia gemmata* (thallus).

Distribution. Austria, Belgium, France, Spain (Navarro-Rosinés *et al.* 1994) and Ukraine (B. J. Coppins, pers. comm.).

Observations. *Unguiculariopsis acrocordiae* clearly does not belong to *Skyttea* s. str. It strongly resembles other species of *Unguiculariopsis*, but is distinguished by straight, apically not hooked excipular hairs and asci with a thickened apex. However, at least four other lichenicolous species of *Unguiculariopsis* with straight (not hooked) excipular hairs are known: *U. lesdainii*, treated in detail below, *U. lobariellum* S. Kondr. & D. J. Galloway (see Kondratyuk & Galloway 1995), *U. refractiva* (see Coppins 1998), and *U. manriquei* Etayo (see Etayo & Diederich 1996). The hairs in *U. acrocordiae* are quite variable, and some have a distinctly swollen base, which is characteristic for most species of *Unguiculariopsis*.

The structure of the ascus apex is also, in our opinion, variable in this genus. In a specimen of *U. thallophila* (Coppins 156), we observed that most asci have no apical wall thickening when studied in KI, whilst others in the same apothecium have a thickened wall, some with an indistinct internal ocular chamber. In *U. acrocordiae*, the wall is generally thicker at the apex, with sometimes an ocular chamber visible.

A strong argument to consider *U. acrocordiae*, *U. lesdainii*, *U. lettaui*, *U. thallophila* and *U. refractiva* as congeneric is the presence of the same excipular pigment, which is orange brown, when observed in water, becomes darker reddish to purplish in K, and N – (or more bright orange).

For all these reasons we are convinced that *U. acrocordiae* belongs to *Unguiculariopsis* s. str. *Unguiculariopsis acrocordiae* is a minuscule, but very distinct species with reddish, ± applanate apothecia and a hairy margin, confined to *Acrocordia gemmata*. It can hardly be confused with any other lichenicolous fungus, and it is the only known fungus growing on *A. gemmata*.

Additional specimens examined. **Austria:** Burgenland: Südburgenland, Günser Gebirge, im engen Taleinschnitt zwischen Markt Neuhodis und Althodis, 380 m, 1991, Hafellner 31378 (GZU); Südburgenland, Tal des Rodlingerbaches S von Tschaterberg, c. 1 km NW vom Stausee, 250 m, 1992, Hafellner 29329 (GZU); Tobaj N von Güssing, S-exponierte Hänge des Tobajer Berges, 250 m, 1990, Hafellner 24958 (GZU).—**France:** Orne: S. loc., s. d., Olivier *Lich. exs.* 245 (as '*Verrucaria gemmata*') (LUX).

***Unguiculariopsis groenlandiae* (Alstrup & D. Hawksw.) Etayo & Diederich comb. nov.**

Geltlingia groenlandiae Alstrup & D. Hawksw., *Meddr Grønland, Biosci.* 31: 33 (1990).—*Llimoniella groenlandiae* (Alstrup & D. Hawksw.) Triebel & Hafellner, in Kümmerling *et al.*, *Bibl. Lichenol.* 53: 156 (1993); type: Greenland, Narssaq d., 1 km S of Qagssiarssuk, 61°8'N, 45°32'W, alt. 140 m, on *Caloplaca citrina* s. l., 1980, Alstrup 801120 (C—holotype, vid.).

(Fig. 16A & B)

For a description and additional illustrations, see Alstrup & Hawksworth (1990).

Hosts. Commensalistic on *Caloplaca citrina* s. lat., *Fulgensia bracteata* and *F. fulgens* (thallus). An additional specimen of *U. groenlandiae*, mentioned by

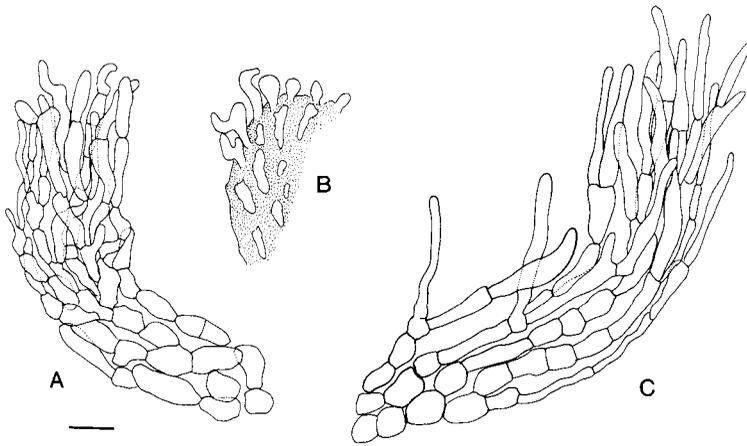


FIG. 16. Exciple of *Unguiculariopsis* species. A & B, *U. groenlandiae* (Alstrup 91072); C, *U. lesdainii* (Fries). A & C, examined in C (commercial bleach); B, in water. Scale = 10 μ m.

Alstrup & Hawksworth (1990) on *Lepraria neglecta*, proved to be typical *Rhymbocarpus neglectus* on *Lepraria cacuminum* (Kümmerling *et al.* 1993).

Distribution. Known from Greenland and Sweden.

Observations. *Unguiculariopsis groenlandiae* strongly differs from other species of *Unguiculariopsis* by the apparent absence of excipular hairs. However, all the other characters show that the species is very close to this genus: the reddish brown exciple and orange epihymenium (same pigment as in other *Unguiculariopsis* species), the 2(–4)-guttulate ascospores, the thin-walled asci, the typical paraphyses and the excipular anatomy. Furthermore, a careful microscopical examination of thin excipular sections in water revealed small, simple, straight to curved, hyaline hairs, which are just a few μ m long. When examined in commercial bleach (C), the exciple appears to be composed of paraplectenchymatous cells basally and of elongate, catenate cells in the upper part. As the material examined is very small and possibly in a poor condition, we conclude that *U. groenlandiae* does belong to *Unguiculariopsis*, but that the hairs are poorly developed in the specimens available.

Additional specimens examined. **Greenland:** SW, Sondre Stromfjord Airport, S-slope of Mt Hassel, NE of airport, 150 m, on a sterile thallus of *Fulgensia bracteata*, 1991, Alstrup 91072 (C 1212).—**Sweden:** Gotland, Lummelunda-Nyhamn, on *F. fulgens*, xi 1999, Kummer (h).

***Unguiculariopsis lesdainii* (Vouaux) Etayo & Diederich comb. nov.**

Nesolechia lesdainii Vouaux [as '*lesdaini*'], in Bouly de Lesdain, *Rech. lich. env. Dunkerque*: 272 (1910).—*Mollisia lesdainii* (Vouaux) Vouaux, *Bull. Soc. Mycol. France* 30: 180 (1914).—*Skyttea lesdainii* (Vouaux) W. Y. Zhuang & Korf, *Mycotaxon* 34: 648 (1989); type: France, dépt Nord, Dunkerque, on *Salix*, on *Lecanora saligna* (sub *L. effusa*), 23 ix 1903, Vouaux (hb. Rondon—holotypus, non vid.).

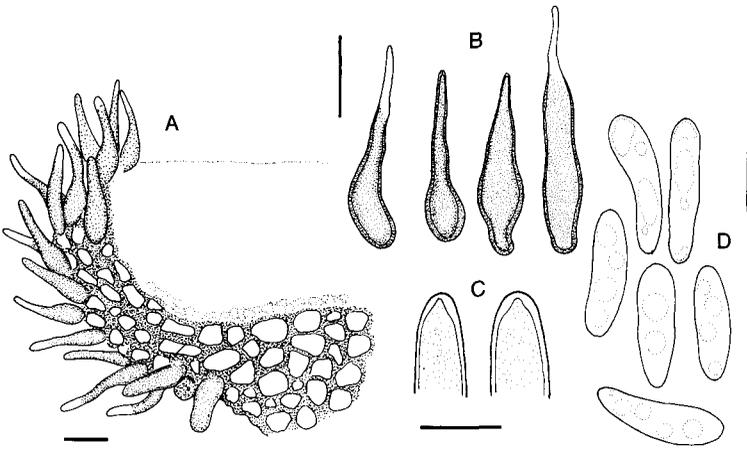


FIG. 17. A–D, *Unguiculariopsis lesdainii* (Earland–Bennett). A, ascomatal section showing the exciple; B, excipular hairs; C, ascus tip (in KOH); D, ascospores. Scales: A–C=10 μ m; D=5 μ m.

(Figs 16C, 17)

For additional illustrations, see Zhuang & Korf (1989).

Ascomata slightly immersed to superficial, reddish to dark greyish brown, initially \pm closed, becoming expanded; when mature, cupulate, 150–270 μ m; margin often irregular, undulating, covered by whitish hairs ($\times 40$). *Exciple* reddish to orange brown, pigment K+ reddish, N–, paraplectenchymatous, cells subglobose, with conglutinate walls; excipular hairs hyaline to brownish, \pm straight, without an apical hook, (10–)17–30 \times 3.5–4 μ m, covered by minuscule granules dissolving in K. *Subhymenium*, *hymenium* and *epihymenium* hyaline or pale. *Paraphyses* hyaline, filiform, septate, not or rarely branched, apically not or slightly thickened. *Asci* clavate to subcylindrical, wall thickened near the apex, with a distinct ocular chamber, I– and KI–, 27–34 \times 4.5–6 μ m. *Ascospores* hyaline, simple, ellipsoid, smooth-walled, without a distinct perispore, 5–7 \times 2–2.5 μ m. *Conidiomata* not seen.

Host. Commensalistic on *Lecanora saligna* (syn. *L. effusa*).

Distribution. Denmark, France, Great Britain and Sweden.

Observations. *Unguiculariopsis lesdainii* has been combined into the genus *Skyttea* (Zhang & Korf 1989), but, with the current circumscription of the genus, it can hardly stay there because of different asci, exciple, excipular hairs, pigments, etc.

Zhang & Korf (1989) suggested a close relationship of *U. lesdainii* with *Rhymbocarpus cruciatus*. However, the latter species is distinguished by asci with no apical wall thickening, black ascomata, a dark exciple with longer cells, very different excipular hairs restricted to the excipular margin and not visible

macroscopically, different pigments, etc. These two species clearly belong to distinct genera.

Like *U. acrocordiae*, *U. lesdainii* is distinguished from typical species of *Unguiculariopsis* by apparently different asci (with a distinct ocular chamber) and different excipular hairs (without a hooked apex). However, asci with an ocular chamber have also been observed by us in *U. thallophila*, several species are known in *Unguiculariopsis* with straight excipular hairs, and all these species have the same excipular pigments (see above, under *U. acrocordiae*).

The type specimen was described by Vouaux (1912–14) as devoid of excipular hairs. Later Zhuang & Korf (1989) examined the type and found hairs only on the inner face of the margin. The Swedish specimen studied by us is also almost devoid of such hairs. The study of abundant, well-developed material recently collected in Great Britain proved the presence of hairs growing on the complete margin, including the lower parts. These hairs are ampulliform below, but not hooked, they are covered by minuscule granules dissolving in K [a character also known from a fungicolous species, *U. hysterigena* (Berk. & Broome) Korf, see Zhuang 1988], and the apex is subhyaline or concolorous with the brown base.

Although the monographer of *Unguiculariopsis*, W.-y. Zhuang, discarded *U. lesdainii* from that genus after studying the holotype (Zhuang & Korf 1989), we are convinced that *U. lesdainii* is a typical member of *Unguiculariopsis* s. str.

Unguiculariopsis lesdainii seems to be restricted to *Lecanora saligna*. A similar species, *U. thallophila*, also grows on *Lecanora* species (mainly on *L. carpinea* and *L. chlarotera*, but never on *L. saligna*) and might be confused with it. *U. lesdainii* has cupulate apothecia with an almost completely exposed disc, and a thin, often irregular, undulate margin, whereas the apothecia of *U. thallophila* are urceolate, almost completely closed, the disc only visible through a small opening, and the margin much thicker. As mentioned above, *U. lesdainii* is furthermore distinguished by different excipular hairs and asci.

Specimens examined (all on *L. saligna*). **Denmark:** S Zealand, Barse, W of Præstø, Broskov, 1971, *Christiansen* 6717 (UPS).—**Great Britain:** *England:* V.C. 18, South Essex: Basildon, Vange, parish church, iii 1982, *Earland-Bennett* (E, hb. Diederich). V.C. 64, Mid-west Yorkshire: Bolton Abbey, v 1979, *Seaward* (E).—**Sweden:** Skåne, on '*Lecanora sarcopsis*', s. d., *Fries* (UPS).

Unguiculariopsis lettaui (Grumann) Coppins

In Rambold, G. & Triebel, D., *Notes R. bot. Gdn Edinb.* **46:** 387 (1990).—*Pyrenopeziza lettaui* Grumann, *Bot. Jahrb.* **80:** 140 (1960).—*Skyttea lettaui* (Grumann) D. Hawksw., *Notes RBG Edinb.* **40:** 396 (1982); type: Germany, Schwarzwald, Gersbacher Wald, Fetzenberg, 900 m, on *Acer*, on *Evernia prunastri*, 15 ix 1913, *Lettau* (B—holotypus, non vid.).

Lichen stictoceros Sm. & Sowerby, *Engl. Bot.* **19:** t. 1353 (1804).—*Evernia prunastri* (L.) Ach. var. *stictocera* (Sm. & Sowerby) Ach., *Lich. univ.*: 85 (1810).—*Evernia stictoceros* (Sm. & Sowerby) Sm. & Sowerby, *Engl. Bot.*, ed. 2: 67 (1844); type: Great Britain, South Devon (V.C. 3), Exmouth Warren, *Brodie* (BM—lectotype, selected here, vid.).

For a description and illustrations, see Grumann (1960) and Coppins (1988).

Host. *Evernia prunastri*, forming conspicuous galls on the host thallus.

Distribution. Austria, France (Corsica), Germany, Great Britain (incl. Jersey), Italy, Spain, Sweden, Turkey and Canary Islands (Coppins 1988; Hafellner 1994b, 1995, 1996a; Hafellner & Türk 1995; Santesson 1993, Santesson *Fungi Lichenicoli Exs.* 41).

Observations. The galls associated with *Unguiculariopsis lettaui* look very similar to basidiomata of some lichenicolous heterobasidiomycetes, but no basidia, basidiospores or hyphae with clamp connections could be found. They are herewith considered as galls caused by *U. lettaui*.

The *Lichen stictoceros*, introduced for a specimen of *Evernia prunastri* with strange 'tubercles', has often been misunderstood and used in various ways. Most lichenologists used this name either for specimens of *E. prunastri* with no lichenicolous fungus, or for specimens bearing dark reddish brown gall-like structures on the thallus. Keissler (1958) considered this name as applying to a thallus of *E. prunastri* with pycnidia. Grumann (1960) gives a short historical survey of the different opinions, and he described a new ascomycete growing on dark galls of *E. prunastri*, *Pyrenopeziza lettaui*. In order to safeguard Grumann's epithet, Hawksworth (1982) suggested *Lichen stictoceros* be lectotypified by the host, but did not formally do so.

According to the original description, *Lichen stictoceros* represents *Evernia prunastri* 'bearing minute black terminal tubercles'. The terminal branches are 'often dotted with little dark specks, and each tipped with a minute, black, convex, smooth tubercle'. The original illustration shows on the bottom left the tip of a branch with several black minute dots looking like pycnidia and a terminal 'tubercle'. Examination of an isotype in BM proved that it represents a typical thallus of *Evernia prunastri* with no lichenicolous fungus. The terminal 'tubercles' seen on some branches are simply a dark brown pigmentation of the cortex. Grumann (1960) mentions the presence of a further isotype collection in UPS, showing 'Tuberkeln' and apothecia, but no such specimen could be located during a visit by the first author to that herbarium. B. J. Coppins kindly informed us about an additional specimen in E, collected on 29 ix 1803 by G. Don or by Brodie, which probably represents an isotype; some pieces do have the 'tubercles' as figured by Sowerby and described by Smith, and these are the conidiomata of *Lichenocodium erodens* M. S. Christ. & D. Hawksw. At least three other specimens (from hb. G. Davies, E. Forster and H. B. Holl) kept in BM and named *Evernia prunastri* var. *stictoceros* are from the type locality and represent either isotypes or topotypes; they all represent *Evernia prunastri* with no lichenicolous fungus. In order to safeguard the names *Pyrenopeziza lettaui* and *Lichenocodium erodens*, we herewith lectotypify the name *Lichen stictoceros* on the isotype from BM collected by Brodie.

The name *Lichen stictoceros* is consequently a later synonym of *Evernia prunastri*. This is in full accordance with the proposal of Hawksworth (1982) to lectotypify *Lichen stictoceros* 'by the host rather than by the fungus attacking it'.

Specimens examined. **Austria:** *Kärnten:* Gailtaler Alpen, Gailtal, bei Weidenburg, viii 1959, Grumann (UPS—paratypus of *Unguiculariopsis lettaui*); *Tirol:* Lechtaler Alpen, Paßhöhe unmittelbar östlich Kelmten an der Straße von Berwang nach Namlos, 1988, Feuerer 8630/1 (h,

hb. Diederich).—**France**: *Gironde*: Périgord, near Bordeaux, Lösse, 1993, *Izquierdo* (hb. Etayo 12074).—**Great Britain**: *England*: **V.C. 4**, North Devon: SE of Hartland, Hartland Forest, 1963, *Nordin* 1922-b (UPS). **V.C. 113**, Channel Isles: Jersey, Slopes of the Quenvais, on sand-hills, Larbaletstier, *Lich. Caesar. et Sarg.* 59, 1867 (BM!), sub *Evernia prunastri* var. *stictocera*; an additional specimen from the same collection, but not distributed in the exsiccata is also attacked by *U. lettaui*.—**Italy**: *Region Trentino-Alto Adige*, Provinz Trient, Valda, 1986, *Feuerer* 25289 (h); *Toscana*, Siena prov., Chianti, SE of Radda in Vhianti, 1985, *Coppins* 12002 (E, UPS).—**Spain**: *Andalucía*: NW of Cordoba, near El Rosal, 1985, *Sérusiaux* 7193 (LG, hb. Diederich). *Galicia*: Lugo, Sierra de Caurel, Puente en Pista de Seoane a Visuña, 1988, *Alvarez* 1153 (h). *Navarra*: Ibiricu, 1992, *Etayo* 3061, 3064 (h, hb. Diederich); Abárzuza, track to Iranzu, 1993, *Etayo* 3362 (h); Leazcue, 1996, *Etayo* 13792 (h). *Málaga*: Ronda, Sa de las Nieves, Cortijo de los Quejigales, 1994, *Etayo* 12079 (h).—**Sweden**: *Ostergothia*, Omberg, *Acharius* (UPS L-01297). *Uppland*: Vänge par., Jobsbo, 1961, *Nordin* 133-b (UPS); Lagga par., Norredatorp, 1952, *Santesson* (UPS); Funbo par., Lövestahagen, 1952, *Santesson Fungi Lichenicoli Exs.* 41 (UPS).—**Turkey**: Süd-Anatolien, c. 15 km E von Antalya, ix 1989, *Wehling* (hb. Lumbsch & Mietzsch 7057).—**Canary Islands**: *La Palma*: Track from Cumbre to Cabeza de Vaca, 1995, *Etayo* 13478 (h).

Minuscule, applanate to strongly convex, reddish brown galls, 0.1–0.3 mm diam., are frequent on European specimens of *Evernia divaricata* and *E. prunastri*. They clearly differ from the galls induced by *U. lettaui* and resemble basidiomata of some lichenicolous heterobasidiomycetes. One specimen from Luxembourg was erroneously considered as representing immature material of *Tremella coppinsii* Diederich & G. Marson (Diederich 1989). However, microscopical studies of numerous specimens proved that no basidiomycete is present in these galls, the origin of which is therefore unknown at present [they should not be confused with *Tremella everniae* Diederich, producing very different galls on *Evernia mesomorpha* (Diederich 1996)].

Selected specimens of these sterile galls (mostly on *E. prunastri*). **Finland**: Savonia borealis, Pielavesi, Säviä, on *E. divaricata*, ii 1947, *Huuskonen* (LG).—**France**: *Landes*: Bias, 1994, *Izquierdo* (hb. Etayo 13010). *Pyrénées-Atlantiques*: S of St-Jean-Pied-de-Port, Forêt d'Iraty, 1990 and 1991, *Diederich* 9214, 9693 (h) & *Etayo* 5921 (h).—**Great Britain**: *England*: **V.C. 28**, West Norfolk: Sheringham Park, vii 1988, *Hitch* (hb. Diederich).—**Luxembourg**: 2 km N of Bigonville, 1992, *Diederich* 4815 (h); 1 km E of Esch-sur-Sûre, 1992, *Diederich* 4827 (h); Godbrange, 1986, *Diederich* 8974 (h).—**Spain**: *Cádiz*: Jerez de la Frontera, Mojón de la Vibora, 1994, *Etayo* 12449 (h). *Cantabria*: Argüebanes, 1992, *Etayo* 790 (h). *Navarra*: N of Ochagavía, Forêt d'Iraty, 1991, *Diederich* 9684 (h) & *Etayo* 5932 (h).—**Sweden**: *Öland*: Böda par., Byxelkrok, 1983, *Löfgren* 1532 (UPS). *Uppland*: Almunge par., Länna, 1981, *Löfgren* 1204 (UPS); Uppsala, Bondkyrka, Vårdsåtra, 1954, *Santesson* 10001 (UPS). *Västmanland*: Ångsö par., 1984, *Santesson* 31074b (UPS).

Unguiculariopsis refractiva (Coppins) Coppins

In Rambold, G. & Triebel, D., *Notes R. bot. Gdn Edinb.* **46**: 386 (1990).—*Skyttea refractiva* Coppins, *Notes RBG Edinb.* **45**: 171 (1988); type: Great Britain, England, V.C. 26, East Suffolk, Lakenheath Warren, on *Mycobilimbia lobulata*, viii 1985, *Giavarini* (E—holotypus, non vid.).

For a description and illustrations, see Coppins (1988).

Hosts. Commensalistic on the thallus of *Mycobilimbia lobulata* and *M. sabuletorum*.

Distribution. This species was known from Great Britain and Luxembourg (Coppins 1988). M. Zhurbenko (St Petersburg) kindly informed us about an

additional collection of this species on *Mycobilimbia* cf. *lobulata* from **Russia**: Severnaya Zemlya, northern extremity of Bolshevik Is., vii 1996, *Zhurbenko* 96131 (LE 207715).

Unguiculariopsis thallophila (P. Karst.) W. Y. Zhuang

Mycotaxon 32: 62 (1988).—*Trochila thallophila* P. Karst., *Fungi fenn. exs.*, cent. 9, no. 823 (1869).—*Mollisia thallophila* (P. Karst.) P. Karst., *Bidr. Kännedom Finlands Natur Folk* 19: 205 (1871).—*Pyrenopeziza thallophila* (P. Karst.) Sacc., *Syll. Fung.* 8: 370 (1889).—*Skyttea thallophila* (P. Karst.) Sherwood & D. Hawksw., in Sherwood *et al.*, *Trans. Br. mycol. Soc.* 75: 489 (1981 [1980]); type: Finland, Tavastia australis, Tammela, Mustiala, on *Lecanora carpinea*, xii 1868, *Karsten, Fungi Fenniae Exs.* 823 (H—holotypus, non vid.; UPS—isotypus vid.).

Lecidea cristata Leight., *Lich. Fl. Br.*, ed. 1: 356 (1871).—*Catillaria cristata* (Leight.) Arnold, *Flora* 57: 99 (1874).—*Scutula cristata* (Leight.) Sacc. & D. Sacc., *Syll. Fung.* 18: 175 (1906).—*Biatorina cristata* (Leight.) A. L. Sm., *Monogr. Br. Lich.*, ed. 1, 2: 132 (1911); type: Great Britain, Barmouth, N Wales, parasitic on *L. glaucoma* Ach. [= *Lecanora subcarnea*], vi 1856, *W. A. Leighton*, Nr. 878' (E—isotype?, absent in BM, examined by Rambold & Triebel 1992; 164; Triebel 1998, *in litt.*).

For a description and illustrations, see Hawksworth (1980a) and Zhuang (1988). The differences with *U. lesdainii* are discussed under that species.

Hosts. Mainly on the thallus and the apothecial margin of *Lecanora carpinea*, also on *L. chlarotera* agg., *L. leptyroides*, *L. septentrionalis* and *L. subcarnea*, always commensalistic. Reports on lichens belonging to other genera are almost certainly misidentifications of other species.

Distribution. Austria, Finland, France, Germany, Great Britain, Norway, Spain (incl. Mallorca), Sweden, Canary Islands (Bricaud *et al.*, 1993; Etayo 1996; Hafellner 1993, 1995, 1996a; Hafellner & Türk 1995; Hawksworth 1980a; Santesson 1960, 1993; Santesson *Fungi Lichenicoli Exs.* 224).

Specimens examined. **Austria:** Steirmark, Gurktaler Alps, Paalgraben S of Stadl an der Mur, c. 1 km S of Kaltwasser, on *L. carpinea*, 1989, *Hafellner* 23720, Santesson *Fungi Lichenicoli Exs.* 300 (hb. Diederich!).—**Great Britain:** Scotland: V.C. 88, Mid Perthshire: Balliemore, by B847 to Struan, on *L. chlarotera* agg., 1974, *Coppins* 156 (E). V.C. 104, North Ebudus: Isle of Skye, 5 km SW of Broadford, Coille Gaireallach, on *L. chlarotera*, 1985, *Coppins* 11694 (E).—**Sweden:** Uppland: Alsike par., Lunsen, on *L. carpinea*, 1947, *Santesson* (UPS); Jumkil par., Holmstävrenen, on *L. carpinea*, 1961, *Santesson* 14070 (UPS).

A Key to the lichenicolous genera of Ostropales and Leotiales

The key includes most known lichenicolous taxa of the Ostropales and Leotiales. For genera including also non-lichenicolous species, the characters used in the key are those of the lichenicolous species. The following species, which are poorly known or of unknown affinities, are not included in the key:

Hymenobia insidiosa Nyl. [see Eriksson & Hawksworth (1991) for a nomenclatural discussion], a taxon of unknown affinities, might be related to the Ostropales (Triebel 1989, sub *Hymenobiella aporea* (Nyl.) Triebel).

Lachnella tetraspora (Henn.) Vouaux (syn. *Solenopeziza tetraspora* Henn.), collected on *Physcia integrata* in tropical Africa, has superficial, urceolate, hairy, yellowish ascomata of 200 µm, subclaviform, 4-spored asci, and 1-septate, fusiform, hyaline ascospores with pointed ends (Vouaux 1914). It might be identical to the specimen of *Skyttea* aff. *fusispora* on *Physcia* studied above (see under *S. fusispora*). Unfortunately, the type specimen could not be located and seems to be lost in B or HBG.

Mollisia collematis Boud., collected on *Collema* in France, has superficial apothecia of 300–500 µm, with a grey disc, a margin which is whitish internally, and blackish, with hairs externally, claviform asci, filiform, septate paraphyses, and ovoid, hyaline, simple ascospores, 7–8 × 3–4 µm (Vouaux 1914).

Niptera lichenicola (Speg.) Sacc. (syn. *Pyrenopeziza lichenicola* Speg.), collected on *Flavoparmelia caperata* in Italy, has blackish, subspherical to discoid ascomata of 100–125 µm, a black, pseudoparenchymatous exciple, claviform to ellipsoid, thick-walled, 8-spored asci, no paraphyses, an ascus apex becoming blue with iodine, ovoid, hyaline, 1-septate ascospores, constricted at the septum, unequal cells, with a distinct perispore when young (Vouaux 1914).

Stictis cladoniae (Rehm) Sacc. (syn. *Schmitzomia cladoniae* Rehm) has been studied by Sherwood (1977), who excluded it from the genus *Stictis*, and who suggested that it does not belong to the Ostropales because of its asci that appear bitunicate. The exciple illustrated by Sherwood (1977: fig. 61) resembles that of *Lethariicola* or *Nanostictis*, but the ascospores are filiform and non-septate.

Thamnogalla crombiei (Mudd) D. Hawksw., a species discussed by Hawksworth (1980a), Hafellner & Sancho (1990) and Hoffmann (1999), is likely to belong to the Leotiales, but no material has been examined by us.

- 1 Ascomata cleistohymenial, i.e. initially closed, hymenium completely covered by the exciple which later opens by an often irregular pore, becoming apothecoid; inner layer of exciple with periphyses; exciple without hairs; hymenium and asci normally KI+ blue (rarely only ascus wall KI+ bluish); ascus wall apically distinctly thickened, ocular chamber present; ascospores 1- to several-septate or submuriform, or cylindrical to filiform with several septa (Ostropales, *Odontotremataceae*). 2
- 2 Ascomata initially not completely closed, hymenium not, or only partly covered by the exciple, often urceolate (in dry specimens); periphyses absent; exciple with or without hairs; hymenium KI – ; asci generally KI – (but wall bluish in *Phaeopyxis punctum*) or with a KI+ blue apical ring (*Bryoscyphus*, *Pezizella*, *Polydesmia*); ascus wall apically thin or thick, with or without an ocular chamber; ascospores 0–1(–3)-septate, ellipsoid, rarely sigmoid to helioid or vermiform (mostly Leotiales; note that amongst non-lichenicolous

- leotialean fungi, some taxa have cleistohymenial ascomata or periphyses) 3
- 2(1) Ascospores ellipsoid to elongate, transseptate or submuriform; ascomata dark coloured (see also Sherwood-Pike 1987: 146–148; Lumbsch & Hawksworth 1990) (Fig. 1C) **Lethariicola**
 Ascospores thread-like to vermiform, straight, 3–7 septate, at least 30 µm long; ascomata pale, whitish; exciple hyaline or pale (see Christiansen 1954; Alstrup 1985; Sherwood-Pike 1985; Etayo & Diederich 1996) **Nanostictis**
- 3(1) Ascospores sigmoid to helicoid, 1-septate, with pointed ends, 22–45 × 1.5–2.5 µm; asci (8–)16–32-spored; ascomata immersed, without hairs (see Sherwood-Pike 1987: 170–172, sub *Pleospilis*; Holien & Triebel 1996) (Leotiales?) **Spirographa**
 Ascospores different (if narrowly elongate and with pointed ends, then ascomata with excipular hairs; see *Skyttea megalosporae*, Fig. 2E); asci usually (4–)8-spored (if multispored, then ascomata superficial; see *Pleoscutula*); ascomata rarely immersed, mostly erumpent or superficial (Leotiales) 4
- 4(3) Ascospores 1–3-septate; excipular hairs present, hyaline, thin, undulating or interwoven; ascomata whitish (see Huhtinen & Santesson 1997) **Polydesmia**
 Ascospores 0–1(–3)-septate; if constantly 1–3-septate, then exciple without hairs; ascomata pinkish, brownish, pale orange, greyish or blackish. 5
- 5(4) Ascomata in section pale, with a violet, K+ greyish blue, N+ reddish orange pigment; exciple thin, with hairs; paraphyses intermixed with hairs resembling those of the exciple; ascus apex thin-walled, I– (Etayo & Diederich 2000) **Echinodiscus**
 Ascomata different, without violet pigment, and without hymenial hairs 6
- 6(5) Ascomata pale coloured 7
 Ascomata dark coloured 9
- 7(6) Ascospores 1-septate; ascomata distinctly stipitate, pale orange; stipe up to 1.5 mm high and 0.8 mm thick; disc flat to cupulate, up to 1.5 mm; exciple reduced; asci with an I+ blue ring (see Alstrup & Cole 1998). **Bryoscyphus**
 Ascospores aseptate; ascomata not or shortly stipitate 8
- 8(7) Ascomata arthonioid, immarginate, sessile; ascus apex I– (see Hawksworth & Santesson 1988). **Skyttella**
 Ascomata with a distinct margin, shortly stalked; ascus apex with an I+ blue ring (at least in *P. epithallina*; to be checked in *P. ucrainica*), ascospores 2-guttulate (see Hawksworth 1980a, 1983; Kondratyuk & Galloway 1995) **Pezizella**

[Whether *Pezizella epithallina* (W. Phillips & Plowr.) Sacc. or *P. ucrainica* S. Kondrat. belong to *Calycina* Gray (= *Pezizella* Fuckel, fide Baral 1994: 122) remains to be resolved.]

- 9(6) Ascospores uniseriate, shortly ellipsoid to subglobose, with a verruculose perispore, with one large guttule; asci elongate cylindrical, wall apically slightly thickened, with a distinct ocular chamber (see Alstrup & Hawksworth 1990; Rambold & Triebel 1990; Hafellner & Navarro-Rosinés 1993) **Geltungia**
 Ascospores not uniseriate, (elongate), ellipsoid or fusiform, smooth-walled, mostly with 2 or more guttules (but with 1 guttule in *Llimoniella adnata*); asci clavate to cylindrical, wall apically thin or thickened, with or without an ocular chamber 10
- 10(9) Excipular hairs present (but reduced in *U. groenlandiae*), with narrow to pointed, sometimes hooked apices and a swollen base (Figs 15, 17) **and** ascomata reddish to dark brownish (excipular pigment orange brown, K+ reddish to purplish, N-; greenish pigment absent); ascospores usually biguttulate; ascus wall I- **Unguiculariopsis**
 Excipular hairs absent or present, but then ascomata blackish, with green or K+ green excipular or epihymenial pigments, hairs with rounded apices, base not swollen (Figs 1A, D, 4-6, 14) . . . 11
- 11(10) Asci elongate cylindrical, wall laterally thin, apically distinctly thickened, bi-convex, with a small, often indistinct ocular chamber (Fig. 3); ascospores biguttulate (Fig. 2); excipular margin with cylindrical hairs (Figs 1D, 4-6) **Skyttea**
 Asci clavate to clavate-cylindrical, wall apically thin or slightly thickened, sometimes with an ocular chamber; excipular margin with or without hairs 12
- 12(11) Pigments of epihymenium, exciple and hypothecium coarsely granular, brown to violet brown; ascus wall I- or I+ bluish, apically distinctly thickened (see Rambold & Triebel 1990) **Phaeopyxis**
 Pigments not coarsely granular; ascus wall I- , apically not or slightly thickened 13
- 13(12) Asci multispored; ascospores 1-septate, distinctly curved, with acute ends; disc slightly concave, partly covered by the exciple; exciple and epihymenium dark greyish or olivaceous brown, K-, N-, without greenish pigments, without hairs; exciple (observed in C) of loosely interwoven hyphae (see Hafellner 1982, and introduction to *Llimoniella*) **Pleoscutula**
 Asci 8-spored; ascospores 0(-3)-septate, with rounded ends; exciple of radiating, ± catenate cells 14
- 14(13) Ascomata indistinctly limited, plane, immersed, roundish to elongate, brownish black, sometimes confluent, up to 450 µm,

resembling ascomata of *Arthonia*; epihymenium and exciple greenish to olivaceous; excipular hairs absent; ascospores multiguttulate (see Rambold & Triebel 1990; Baral & Marson, unpublished) . . .

. **Gelatinopsis**
 Ascomata usually superficial and with a raised margin, at least when mature; if completely immersed, then almost perithecioid and disc punctiform 15

15(14) Epihymenium, and occasionally exciple, with a greenish K+ olivaceous pigment; lower exciple of isodiametric cells, upper exciple of elongate, narrow, almost filiform cells (Fig. 7A–C), which, in some species, are prolonged into hair-like processes (either embedded in the excipular gel, or free and forming hairs) (Figs 1A, 14); ascomata mostly 50–250 µm diam., usually partly immersed (mainly when young), with a punctiform disc (Figs 1B, 11, 13), later in most species superficial, the disc often partly or mostly covered by the exciple (Figs 1A, 12); ascospores biguttulate (observed in at least three species) **Rhymbocarpus**

Ascomata in section without such a greenish pigment, exciple in most species dark purplish, K+ purplish violet, often with an additional, K+ bright green pigment; exciple entirely of isodiametric cells (Figs 7D, 8); excipular hairs absent (Fig. 9); ascomata mostly 200–500 µm diam., superficial; ascomatal disc exposed (except when young), often becoming convex; ascospores 1–2-guttulate in two species, multiguttulate in the other species . . . **Limoniella**

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