Lichenologist **30**(3): 231–244 (1998)
Article No. li980133

TWO NEW SPECIES OF THE LICHEN GENUS *IMMERSARIA* (*PORPIDIACEAE*)

V. CALATAYUD* and G. RAMBOLD‡

Abstract: *Immersaria olivacea*, its lichenicolous fungus *Polycoccum decolorans*, and *Immersaria mehadiana* are described as new species from Spain and Romania, respectively. A new combination, *Immersaria cupreoatra* is proposed, and a revised concept of the genera *Bellemerea* and *Immersaria* is supplied.

Introduction

In recent years, several crustose lichens with aspicilioid apothecia have been recognized as members of the *Porpidiaceae*. Besides a few monotypic genera restricted to the Southern Hemisphere (e.g. Hertel 1984; Brusse 1988; Malcolm *et al.* 1995), the genera *Amygdalaria*, *Bellemerea*, and *Immersaria* belong here. *Immersaria* has been described with the following combination of character states: brown thallus, areoles with a flat to concave surface, immersed apothecia, with a more or less strongly reduced proper margin and with a greenish-blackish pigmented parathecial crown, which during ontogeny is mostly separated by a fissure from the areole from which it was originated (Rambold 1989). Esnault & Roux (1987) characterized this type of margin as ' a bord d'aspect propre, se décollant souvent du thalle '. After searching through rich material of *I. athroocarpa* (Ach.) Rambold & Pietschm., however, it became obvious that some specimens exist that show no distinct proper apothecial margin and have no fissures between the apothecial disc and the surrounding areole. These observations support the decision of Barbero *et al.* (1990) to transfer *Amygdalaria tellensis* Esnault & Cl. Roux as *I. usbekica* (Hertel) M. Barbero, Nav.-Ros. & Cl. Roux to *Immersaria* and thus enlarge the genus concept. Since then, *Immersaria* has included taxa with obligatory cryptolecanorine apothecial margins beside taxa with reduced lecideine margins.

Up to now, only three species have been referred to *Immersaria*, the two mentioned before and *I. carbonoidea* (J. W. Thomson) Esnault & Cl. Roux, known from North America (Thomson 1972; Barbero *et al.* 1990). In the present paper, two further species of *Immersaria* are described as new: *I. olivacea* and *I. mehadiana*. In addition, *Bellemerea cupreoatra* (Nyl.) Clauzade & Cl. Roux is transferred to *Immersaria*, and the delimitation of both genera is discussed. A *Polycoccum* species found when studying the lichenicolous fungi

*CEAM, Parc Tecnològic, C/4, Sector Oest, 46980 Paterna, València, Spain. E-mail: vicent@ceam.es
‡Institut für Systematische Botanik der Universität München, Menzinger Str. 67, D–80638 München, Germany. E-mail: rambold@botanik.biologie.uni-muenchen.de

0024–2829/98/030231+14 $25.00/0

growing on taxa of this group of lichens also turned out to be a new species and is consequently described below.

Materials and Methods

Specimens from BCC, GZU, H, M and VAB-lich. were investigated. Sections were made by hand or by freezing microtome, mounted in water or in iodine–potassium iodide solution (1%) [=Lugol's solution (Merck 9261)] ' I ' or diluted iodine–potassium iodide solution (0·15%) ' I_d ', and examined by means of standard light microscopic techniques. ' K/I ' indicates pretreatment with KOH before I. Chemical features were examined by thin-layer chromatography (TLC) following Culberson & Kristinsson (1970), Culberson (1972, 1974) and Culberson & Johnson (1982), and some specimens were also analysed by mass spectrometry (MS). Material for co-chromatography: 4-*O*-demethylplanaic acid (from *Lecidea lithophila* (Ach.) Ach.—Hertel, *Lecideac. Exs.* 268, M).

Besides the material of *Immersaria olivacea*, *I. mehadiana* and *I. cupreoatra* reported below, the following specimens were examined for comparison:

Amylora cervinocuprea: **Switzerland**: Graubünden, Samnaungruppe, Fimbertal, E der Heidelberger Hütte, gegen [Piz] Davo Sassè, alt. *c.* 2400 m, 1960, *J. Poelt, A. Schröppel & M. Steiner* (M).

Bellemerea alpina: **Sweden:** *Torne Lappmark:* Gem. Kiruna, Torneträsk-Gebiet, Gipfel des Laktatjåkko, 1400 m, 1967, *H. Hertel* 7643 (M).—**Austria:** *Salzburg:* Radstädter Tauern, südl. oberhalb der Paßhöhe des Radstädter Tauernpasses, 1800 m, 1967, *H. Hertel* 8096 (M).

Immersaria athroocarpa: **Austria:** *Tirol:* Kitzbühler Alpen, Gebiet des Kleinen Rettenstein W Paß Thurn, Gipfelgrat des Kleinen Rettenstein, 2100–2217 m, 1989, *F. Schuhwerk* 2270 (M).

Immersaria carbonoidea: **Canada:** *British Columbia:* Queen Charlotte Islands, Moresby Island, San Cristoval Range, SSE of Mount Laysen, 3·1 km E of end of S of Sunday Inlet, on ridge top Elev. 762–914 m, 1988, *I. M. Brodo* 26828 (M).

Immersaria usbekica: **Spain:** *Catalunya*, Lleida, Segarra, Sanaüja, al N del poble, U.T.M. 31TCG53–CG54–CG63 [*c.* 41°53'N, 1°11'E], 500 m, infected by *Muellerella pygmaea* var. *pygmaea*, 1989, *P. Navarro-Rosinés* (BCC).

The Species

Immersaria cupreoatra (Nyl.) Calatayud & Rambold comb. nov.

Lecanora cupreoatra Nyl., *Lichenes Lapponiae orientalis*: 181 (1866).

Lecanora cupreoatra (*Bellemerea cupreoatra* (Nyl.) Clauzade & Cl. Roux) is most closely related to *I. mehadiana* and is therefore transferred to *Immersaria*. It has been lectotypified recently (Rambold 1994). The species is characterized by a brown thallus with flat to concave areoles, a distinct epinecral layer, a strongly developed hypothallus, the presence of gyrophoric acid, a brown epihymenium and non-amyloid ascospores. Unfortunately, mature ascospores could not be detected in the original material. Morphologically and chemically identical specimens, however, revealed that the ascospore walls of this species are not amyloid, in contrast to the true representatives of *Bellemerea*. Material of *I. cupreoatra* examined derived from various localities in Europe, that is Russia, Italy (Sicilia), Macedonia, and from Asia (Mongolia). The ecology and distribution of this species is rather unclear.

Specimens examined: **Russia:** Kareliae Ladogensis, in latere meridionali montis Liikolanmäki prope oppid. Sortvala, 1874, *J. P. Norrlin* (Norrlin & Nylander *Herb. Lich. Fenn.* 245, M).—**Italy:** Sicilia, Prov. Palermo, Le Madonie, an der Straße von Piano Battaglia nach Petralia, Bosco

Pomieri, *c.* 1300 m, 1988, *J. Poelt* (GZU).—**Macedonia:** Nordhänge des Pelister SW Bitola, auf Blöcken auf einer Waldwiese in der *Pinus peuce*-Stufe, 1971, *J. Poelt* 10176 (M).—**Mongolia:** Chanteij, Gorchin-Ama, 1978, *S. Huneck & U. Cogt* MUR 100 (GZU).

Immersaria mehadiana Calatayud & Rambold sp. nov.

Immersariae cupreoatrae similis est, sed thallo acido 4-*O*-demethylplanaico continente differt.

Typus: Romania, Caraş-Severin Comitat, Mehadia [=*c.* 168 m], Strájoţ Mtn, rock-flow on W-exposed slope *c.* 100 m above the village, *c.* 44°53′N, 22°20′E, *c.* 300 m, on horizontal and inclined surfaces of trachytic boulders below *Acer campestre*, *Cornus mas*, *Syringa vulgaris* etc., partly infected by *Muellerella pygmaea* var. *pygmaea*, 10 August 1994, *G. Rambold* (M—holotypus, isotypi, chemotype I: containing 4-*O*-demethylplanaic acid).

Thallus crustose, regularly areolate, up to several centimetres in diameter, brown. *Areoles* flat to slightly concave, *c.* 0·4–0·8(–1·0) mm diam.; areole margin whitish, sometimes slightly elevated. Hypothallus greyish, more or less distinct between the areoles. In section, thallus *c.* 0·2–0·3 mm thick; epinecral layer up to 20 µm high, sometimes indistinct; (pheno-)cortical layer 10–25 µm thick; uppermost cells brown. Algae trebouxioid, 8–15 µm diam. Medulla I+ violet, partly I −; hyphae *c.* 4 µm thick.

Apothecia immersed, one per areole, 0·2–0·3(–0·4) mm diam., round, irregularly distributed over the thallus. *Disc* flat, brownish black, with epruinose surface. *Margin* homologous to and of the same appearance as the areole margin. *Excipulum* reduced; tissue at the lateral sides of the hymenium corresponding to the phenocortical and algal layer of the vegetative areole, and to hypothecial hyphal cells when the apothecia reach the margin of the areole. *Hypothecium* colourless, *c.* 50 µm, containing algal cells in the lower parts. *Hymenium* colourless, *c.* 100–110 µm, I+ blue, I_d+ blue. *Epihymenium* brown, *c.* 10 µm. *Paraphyses* branched and anastomosing, *c.* 3 µm diam. (lumina 1·5–2 µm); apical cells (3·5–)4–5 µm (lumina 2–3 µm). *Asci* of *Porpidia*-type, clavate, 8-spored, *c.* 100 × 25 µm; amyloid wall layer *c.* 1·5–2·5 µm thick, I+ orange–red, I_d+ orange–yellow; non-amyloid wall layer *c.* 1 µm thick. *Ascospores* ellipsoid, colourless, non-septate, halonate, rarely non-halonate, not amyloid, *c.* 16–17 × 8–9 µm.

Conidiomata immersed, mostly at the centre of the areoles; ostiole sometimes prominent. *Conidia* acrogenously developed, bacilliform, 4·5–5 × 1–1·5 µm.

Chemistry. Two chemotypes were observed: (I) 4-*O*-demethylplanaic acid; (II) unknown A (R_f classes: A: 5; B: 3; C: 5) and unknown B (R_f classes: A: 3; B: 3; C: 2). The brown pigment of the epihymenium does not react with HCl.

Etymology. The epithet '*mehadiana*' refers to the type locality, the village Mehadía (Banat, Romania).

Habitat and distribution. Immersaria mehadiana is so far known from only three localities in the Banat region, Romania (Fig. 3). The major collections distributed in three exsiccatae derive from one and the same locality, Strájoţ mountain, above the village of Mehadia. It was found growing on horizontal

and inclined surfaces of trachytic boulders and rocks. As indicated on the labels of the collections of Lojka (' Hungary '), this area once belonged to Hungary (1748–1918).

Remarks. Despite the number of specimens examined, this material sporulated very badly, and only a limited number of ascospores could be measured. *Immersaria mehadiana* is closely related to *I. cupreoatra* and mainly distinguished by the presence of 4-*O*-demethylplanaic acid, whereas the latter species produces gyrophoric acid as the major substance. Both secondary metabolites are biosynthetically remote from one another. Although both the tridepside, gyrophoric acid, and the depside, 4-*O*-demethylplanaic acid, are para-depsides, the individual benzenoid moieties incorporate quite distinctive polypeptide chains, comprising 8-carbon and 12-carbon chains, respectively. However, not only are the mono-nuclear precursors of these two depsides quite dissimilar, but the observed secondary biosynthetic processes are also distinctive. Thus, the biosynthesis of 4-*O*-demethylplanaic acid involves simple depside formation (rather than a formation of a tridepside) and *O*-methylation of the 2-hydroxy group, a process not involved in the production of gyrophoric acid. Hence, one can conclude that *I. mehadiana* and *I. cupreoatra* are not mere chemotypes. These chemical differences are regarded as taxonomically relevant and suitable for distinguishing the two taxa at species level. Although there is no information available on the biosynthetic processes involved in the production of the unknown substances A and B, samples containing these substances are referred to *I. mehadiana*, because they are identical and were collected together with typical specimens of this species containing 4-*O*-demethylplanaic acid.

Additional specimens examined:

Chemotype I: 4-O-demethylplanaic acid: **Romania:** Caraş-Severin Comitat; ' Szöveny [Comitat] ', supra lapides quarzoso-trachyticos montis ' Strozsucz ' [=Strájoţ] prope Mehadiam, [*c.* 44°53′N, 22°20′E], [no date], *H. Lojka* (Lojka, *Fl. Exs. Austro-Hungarica* 751, as *Lecanora cupreoatra*, GZU, M); Auf dem Berge Strazsucz [=Strájoţ] bei Mehádia im Szórényer Comitate, 1877, *H. Lojka* (Lojka, *Lich. Regni Hungarici Exs.* 44, M); An Quarztrachyt-Blöcken eines Gerölles am Berge Strazsucz [=Strájoţ] ober dem Dorfe Mehádia, 1885, *H. Lojka* (Arnold, *Lich. Exs.* 1114, as *Aspicilia cupreoatra*, M); in monte Treskovacz prope Szvinica [=Szinice] ad Danubium inferiorem, [*c.* 44°28′N, 22°06′E], 1874, *H. Lojka* 2602 (M); Mehadía, Strájoţ Mtn, rock-flow on W-exposed slope *c.* 100 m above the village, with *Acer campestre*, *Cornus mas*, *Syringa vulgaris*, etc. 44°53′N, 22°20′E, *c.* 300 m, 1994, *G. Rambold* 6043a (M).

Chemotype II: unknown A and B: **Romania:** Caraş-Severin Comitat: ' Comitat Szöreny ', supra saxa quarzoso-trachytica montis ' Strazsucz ' [=Strájoţ] prope pagum Mehádia, 1877, *H. Lojka* (Lojka, *Lich. Regni Hungarici Exs.* 44, as *Lecanora cupreoatra*, M—with *Muellerella pygmaea* var. *pygmaea*—); Ad saxa arenaria conglom., prope Trikuli ad Danubium inferiorem [locality not localizable], 1874, *H. Lojka* 2644 (M); Mehadía, Strájoţ Mtn, rock-flow on W-exposed slope *c.* 100 m above the village, with *Acer campestre*, *Cornus mas*, *Syringa vulgaris* etc. 44°53′N, 22°20′E, *c.* 300 m, on horizontal and inclined surfaces of trachytic boulders and rocks, 1994, *G. Rambold* 6043b (M).

Immersaria olivacea Calatayud & Rambold sp. nov.

Lichen saxicola. Thallus crustaceus, areolatus, colorem olivaceam prevalet, corticatus. Apothecia nigra, immersa, 0·2–0·4 mm in diametro, plus minusque marginata. Epihymenium atrovenetum. Paraphyses ramosae anastomosantesque. Asci typi ' *Porpidia* ', octospori. Ascosporae hyalinae, simplices vel 1-septatae, ellipsoideae, aliquando juveniliter halonatae, 9–14 × 4–7 µm. Conidia simplicia, clavata ad pyriformia, basim truncata, 6–10 × 3–5 µm.

Typus: Spain, Castelló province, Benicàssim, Parreta Alta., U.T.M. 31TBE4538 [40°3′8″N, 1°0′38″E], on sandstones, 390 m, 22 April 1993, *V. Calatayud* 2952 (VAB-lich.—holotypus; M—isotypus).

Thallus crustose, areolate, up to several centimetres in diameter, colour predominantly olivaceous, varying from pale brown to brownish green, sometimes with a slight bluish tinge. *Areoles* flat to slightly concave, 0·3–0·6 mm diam.; margins usually slightly elevated. Hypothallus dark brownish green, more or less distinct between the areoles. In section, thallus *c.* 0·2–0·3 mm thick; epinecral layer up to 17(–25) µm high; (pheno-)cortical layer 30–50 µm thick; uppermost cells pale brown; an amorphous layer of a bluish green pigment also usually present in the cortex, especially in those areoles or parts of areoles that are more distinctly greenish; at the lateral sides of the areoles, cells darker, 4–6 µm diam., dark bluish green or dark brownish green. Algae trebouxioid, 6–15 µm diam. Medulla incorporating abundant crystals and mineral debris, I − ; hyphae 2–4 µm thick.

Apothecia immersed, mostly one per areole, 0·2–0·4 mm diam., rounded or somewhat angular. *Disc* flat to slightly convex, black, epruinose. *Margin* homologous to and of the same appearance as the areole margin. *Excipulum* usually very reduced in those parts of the apothecia attached to the areoles, better developed in parts of the apothecia reaching the margins of the areoles or in occasionally isolated apothecia, of the same appearance as the areole margin, of conglutinated hyphae with the wall dark bluish green or dark brownish green. *Hypothecium* colourless or slightly pale brown, 75–125(–140) µm, not containing algal cells in the lower parts. *Hymenium* colourless or sometimes progressively bluish green towards the upper part, 50–90 µm, I+ blue, I_d+ blue. *Epihymenium* dark bluish green, *c.* 10 µm. *Paraphyses* branched and anastomosing, 2–3 µm diam. (lumina 1·5–2 µm), slightly swollen at apices; apical cells 3–4·5 µm diam. (lumina 2·5–3 µm). *Asci* of *Porpidia*-type, clavate, 8-spored, 40–55 × 12–18 µm; amyloid wall layer *c.* 2 µm thick, I+ orange–red, I_d+ pale orange–yellow; non-amyloid wall layer *c.* 1 µm thick. *Ascospores* ellipsoid, colourless, simple or 1-septate, occasionally halonate when young, not amyloid, 9–14 × 4–7 µm.

Conidiomata immersed, upper part dark bluish or brownish green, 60–110 µm; wall colourless or slightly pale brown. *Conidiogenous cells* in a single layer, obpyriform to cylindrical, 7–12 × 3–4 µm. *Conidia* acrogenously developed, clavate to pyriform, simple, hyaline, truncate at the base, guttulate, 6–10 × 3–5 µm.

Chemistry. No lichen substances detected by TLC or trace amounts of stictic acid (3 specimens analysed). The green pigment of the epihymenium, margin of the areoles and upper part of the conidiomata reacts HCl+ blue (*Lecidea*-green).

Etymology. The epithet *olivacea* (Latin *olivaceus*, resembling the tint of a ripe olive, a mixture of brown and green) refers to the predominantly olivaceous colour of the thallus of this species.

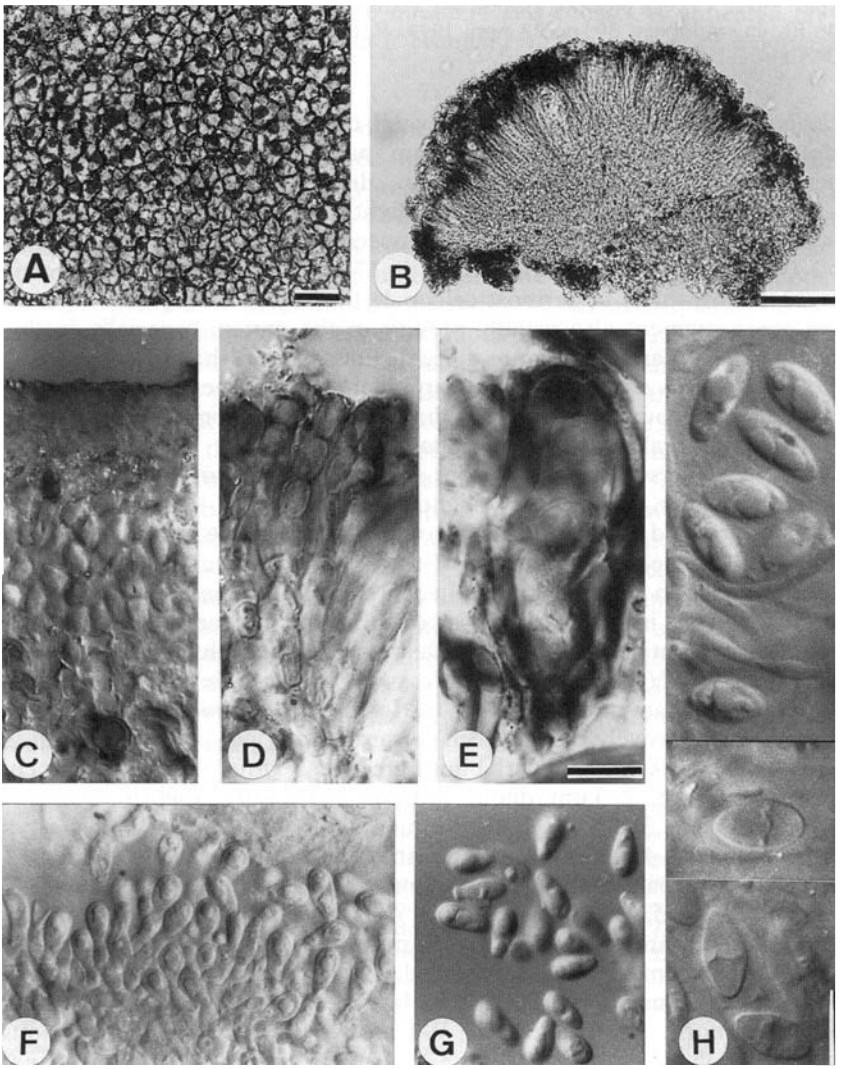

FIG. 1. *Immersaria olivacea* (holotype). A, habit; B, section of an apothecium; C, vertical section of the cortex; note the epinecral layer; D, paraphyses; E, young ascus, after treatment with K/I; F, conidiogenous cells bearing conidia; G, conidia; H, ascospores, three of them septate. Scales: A=1 mm; B=100 μm; C, D, E=10 μm; F, G, H=10 μm.

Habitat and distribution. The new species is so far known only from three localities at low altitudes (not higher than 700 m) in, eastern Spain (Fig. 3). These localities have a typically Mediterranean climate, with a pronounced dry period in summer and, according to the typology proposed by Rivas-Martínez (1987), they belong to the thermomediterranean and lower meso-mediterranean vegetation belts. The main dominant plants in these zones were *Pinus halepensis* and *Quercus coccifera*, together with some thermophilous

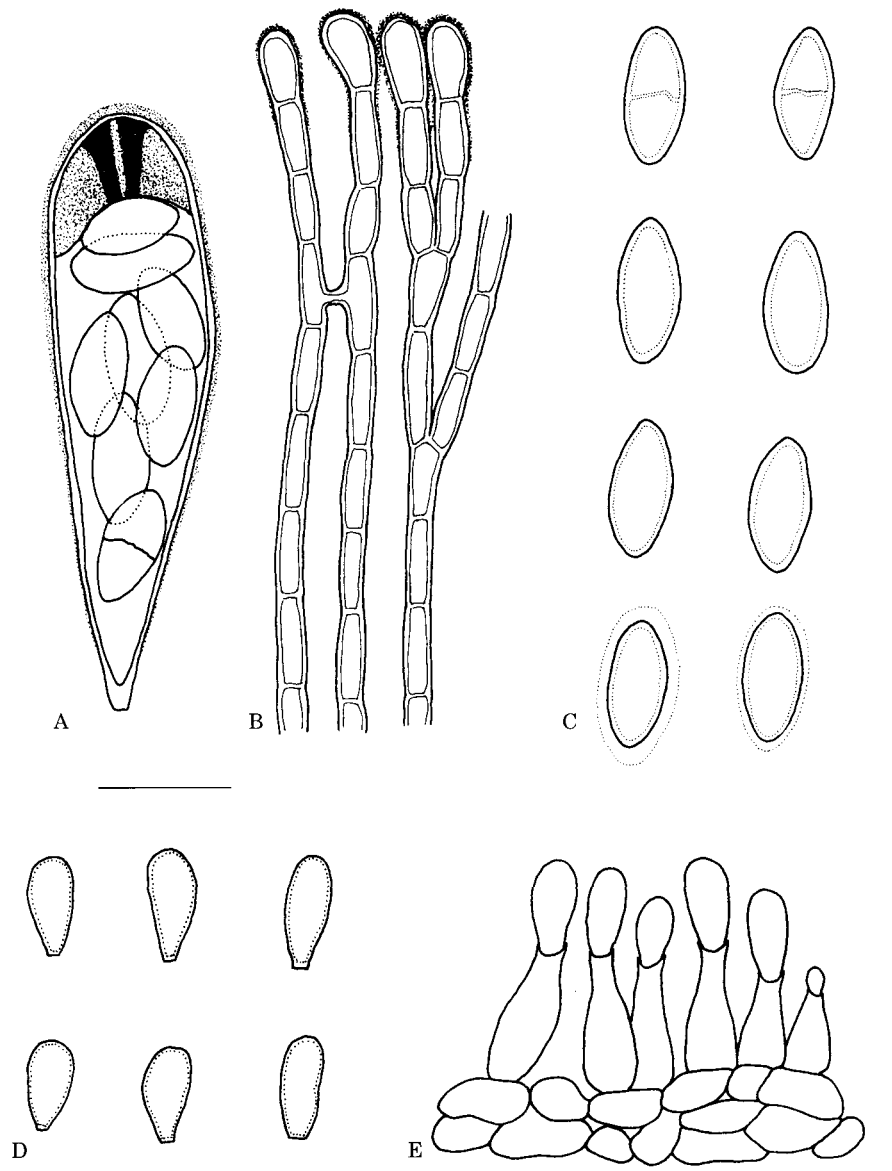

FIG. 2. *Immersaria olivacea* (holotype). A, ascus; B, paraphyses; C, ascospores; D, conidia; E, conidiogenous cells bearing conidia. Scale: 10 μm.

evergreen shrubs, such as *Pistacia lentiscus*, *Rhamnus lycioides* ssp. *angustifolia* and *Ulex parviflorus*. The substrata on which the specimens were collected were red sandstones of the Buntsandstein (Triassic), a characteristic type of siliceous rock, the lichens of which have been previously studied in similar territories (Calatayud & Barreno 1994). *Immersaria olivacea* was collected on

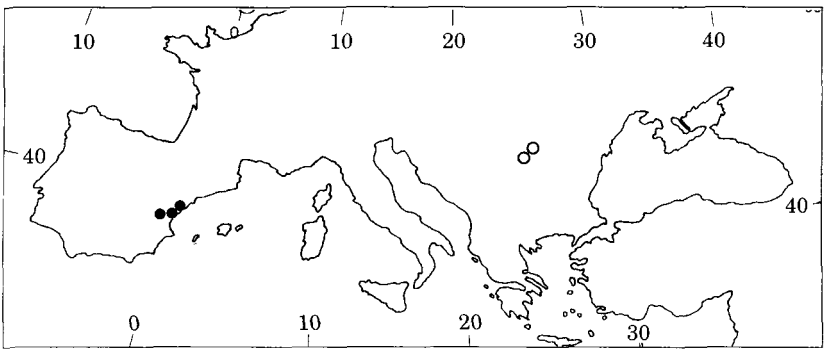

FIG. 3. Distribution of *Immersaria mehadiana* (open circles) and *Immersaria olivacea* (solid circles).

weakly inclined rocks in clearings of the vegetation, fairly to intensely sun-exposed, close the ground and enriched with bases due to the vicinity of calcareous substrata. The new species was associated with *Aspicilia contorta* ssp. *hoffmanniana*, *A. intermutans*, *Buellia dispersa*, *Caloplaca irrubescens*, *C. subpallida*, *C. pyrithrella*, *Lecanora albescens*, *Lecidella carpathica* and *Rhizocarpon disporum*. When growing close to small rain tracks with periodic percolation of water, *Lichinella stipatula* and *Peltula euploca* may also occur together with *I. olivacea*. Colonies of free-living cyanobacteria were also frequently observed between and on the areoles of the new species, but there does not seem to be a regular connection between both organisms, such as that reported for other species (Poelt & Mayrhofer 1988).

Remarks. The structure of the thallus of *I. olivacea* shows the characteristic pattern of the genus, with flat or slightly concave areoles and a well-developed epinecral layer (Fig. 1). Compared to other species of the genus, *I. olivacea* shows a characteristic olivaceous colour due to the deposition of a bluish green pigment in the cortex. The uneven distribution of this pigment within the thallus and even within each single areole has the effect that some parts of the thallus and/or of the areoles are more distinctly green than others, which in the absence of this pigment are brown. Whitish patches are also sometimes observed in the material examined, but they are produced by infection with the parasitic fungus *Polycoccum decolorans*. Typically, the apothecia have a very reduced exciple, but in those parts in which they are not attached to the areole (e.g. margins of the areoles or in isolated apothecia) the exciple is well developed. A single apothecium may therefore have one part with a very reduced exciple, similar to that occurring in ' cryptolecanorine ' apothecia, and other parts with a well-developed dark exciple as in ' cryptolecideine ' apothecia. As we have also observed in other species of this genus, the examination of mature ascospores was frequently difficult due to rather poor sporulation of the material. The ascospores are mostly simple, but 1-septate ascospores, with an irregularly curved septum, have been regularly observed, and in some specimens represent up to 25% of the overall ascospores examined. Septate ascospores have not been previously reported in other members of *Immersaria*.

The shape and size of the conidia of *I. olivacea* is also very remarkable, since in all the species of *Immersaria* in which conidia are known, they are bacilliform. These conidia are similar to those of the lichenicolous genus of coelomycetes *Vouauxiomyces*, but the authors are convinced that they belong to the lichen because of the accumulation in the upper part of the conidiomata of the same dark bluish green pigment found in the exciple of the apothecia. This type of conidium is also very unusual among lecideoid lichens, since in these groups conidia are usually cylindrical, ellipsoid, fusiform or filiform, with a breadth normally varying between *c.* 0·5 and *c.* 1·5 μm (Rambold 1989). *Immersaria olivacea* is easily separated from the rest of the species of the genus by its olivaceous thallus, small and occasionally 1-septate ascospores and characteristic conidia (Table 1).

Additional specimens examined: **Spain:**, València province, Chelva, U.T.M. 30SXK7303 [39°45′29″N, 0°58′50″W], on sandstone, 700 m alt, 1993, *V. Calatayud* 7603 (VAB-lich.); *ibid.*, 1995, *V. Calatayud* 7605 (VAB-lich.); Castelló province, Almenara, La Frontera, U.T.M. 30SYK3405 [39°45′41″N, 0°16′6″W], on sandstone, 230 m alt, 1993, *V. Calatayud* 7203 (VAB-lich.).

Lichenicolous fungi

In the material examined, two taxa of lichenicolous fungi have been recognised. *Muellerella pygmaea* (Körb.) D. Hawksw. var. *pygmaea* was growing on *I. cupreoatra*, *I. mehadiana* and *I. usbekica*, and some samples of *I. olivacea* from the collection gathered at Chelva were infected by a new species of *Polycoccum*, which is described below.

Polycoccum decolorans Calatayud & Triebel sp. nov.

Fungus in thallis lichenis *Immersaria olivacea* vigens. Differt a speciei *Polycoccum sporastatiae* ascomatibus minoribus et sporibus (16–)18–22 × 6–8 μm magnis.

Typus: Spain, València province, Chelva, U.T.M. 30SXK7303 [40°3′8″N, 1°0′38″E], parasitic on *Immersaria olivacea*, on sandstones, 700 m, 1 November 1993, *V. Calatayud* 7711 (VAB-lich.—holotypus, isotypi; M—isotypus).

Ascomata perithecioid, globose to pyriform, occurring in groups of up to 8 ascomata, more or less completely immersed in the thallus of *I. olivacea*, 75–150 μm diam. The infected areoles are bleached by the presence of the parasite and become slightly bullate. Ascomatal wall slightly thickened near the ostiole, apically up to 25 μm thick, brown to dark brown, at the base brown to pale brown, pseudoparenchymatous (textura angularis with wall pigments somewhat irregularly distributed), *c.* 15 μm thick, composed of 3–6 cell layers. Cells *c.* 4–7 μm diam. Ostiolar elements not visible. Interascal elements numerous, septate, branched and anastomosing, *c.* 2–2·5 μm thick (lumina 1·5–2 μm). *Asci* subcylindrical to elongate–clavate, short-stalked, bitunicate, fissitunicate, with a weakly developed ocular chamber, 6–8-spored, *c.* 65–80 × 13–15 μm; not reacting in Lugol's iodine solution. *Ascospores* distichously arranged, ellipsoid to oblong, obtuse, 1-septate, not constricted at the septum, the lower cell somewhat attenuated, halonate when young, later becoming dark (green–)brown, often with one oil drop per cell, thick-walled, with rugose perispore, (16–)18–22 × 6–8 μm.

TABLE 1. *The main distinguishing characters between the species of* Immersaria

Characters	*I. athroocarpa*	*I. carbonoidea*	*I. cupreoatra*	*I. mehadiana*	*I. olivacea*	*I. usbekica*
Thallus colour	Brown	Brown	Brown	Brown	Olivaceous	Brown
Subhymenial algae present	–	–	±	+	–	–
Iodine reaction of the medulla	+	+	±	±	–	+
Apothecial margin	Crypto-lecideine	Crypto-lecideine	Crypto-lecanorine	Crypto-lecanorine	Crypto-lecanorine/-lecideine	Crypto-lecanorine/-lecideine
Hypothecium pigmentation	±	+	–	–	–	–
Epihymenium pigmentation	Olivaceous, brownish	Brown	Brown	Brown	Dark bluish green	Olivaceous, grey
Ascospore septation and size (μm)	Simple, 13–19·3 × 7–9·5	Simple, 12–12.5 × 6.5–7.5*	Simple, (no measurements)	Simple, *c.* 16–17 × 8–9	Simple or 1-septate, 9–14 × 4–7	Simple, 13–23 × 7–13
Conidia	Bacilliform	Bacilliform	Bacilliform	Bacilliform	Clavate to pyriform	Bacilliform
Chemistry	Confluentic acid syndrome	Traces of norstictic acid	Gyrophoric acid	4-*O*-demethylplanaic acid or unknown A and B	No substances or traces of stictic acid	Confluentic/ gyrophoric acid syndrome
Distribution	World-wide	N-America	Eurasia	SE-Europe	Spain	N-Africa, Europe, Asia

*According to Thomson (1972), ascospores not found in the material examined.

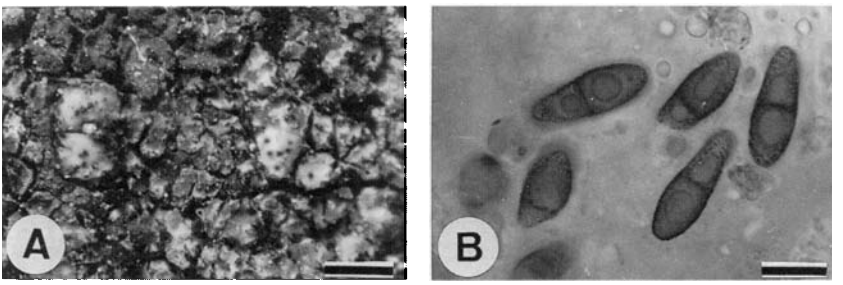

FIG. 4. *Polycoccum decolorans* (holotype). A, thallus of *Immersaria olivacea* infected by the fungus; note the bleached and slightly bullate areoles; B, ascospores. Scales: A=0·5 mm; B=10 μm.

Conidiomata pycnidial, *Phoma*-like, immersed, 45–70 μm diam. Conidiomatal wall slightly thickened above, dark brown, *c.* 10–15 μm thick, composed of 3–4 cell layers. Cells *c.* 3–4 μm diam. *Conidiogenous cells* lining the internal cavity, colourless, obpyriform to cylindrical, 7–10 × 2·5–3 μm, conidiogenesis enteroblastic. *Conidia* colourless, bacilliform, 5–7 × 1–2 μm.

Vegetative hyphae mainly colourless. Some short brown hyphae (*c.* 4 μm) might be observed originating from the upper part of the ascomata.

Etymology. The epithet '*decolorans*' refers to the loss of colour in the host thallus caused by the infection of this lichenicolous fungus.

Remarks. Polycoccum decolorans mostly resembles *Polycoccum sporastatiae* (Anzi) Arnold, which is found on *Sporastatia asiatica*, *S. polyspora* and *S. testudinea* (Grube & Poelt 1993). Common features are the completely immersed pseudothecia, the ascomatal wall structure, the firstly halonate and then dark (green–)brown distinctly verrucose ascospores with one oil drop per cell and the causing of certain discoloration of the host thallus. In *P. sporastatiae* we found also conidiomata with conidia of similar shape and size as in *P. decolorans*. However, the ascomata of *P. sporastatiae* are up to 300 μm diam., the ascospores measure 18–23(–25) × 7–10(–11) μm (see also Hawksworth & Diederich 1988) and the conidiomata are up to 150 μm diam.

Muellerella pygmaea var. *pygmaea* has also been found on *I. cupreoatra*, *I. mehadiana* and *I. usbekica*. This variety has been found so far also on host species of *Porpidiaceae*, all belonging to *Bellemerea* in its new delimitation: *B. alpina* (Sommerf.) Clauzade & Cl. Roux, *B. cinereorufescens* (Ach.) Clauzade & Cl. Roux, and *B. subcandida* (Arnold) Hafellner & Cl. Roux (Triebel 1989). *Muellerella pygmaea* var. *athallina* (Müll. Arg.) Triebel is known to grow on *I. athroocarpa*, and some other genera of the *Porpidiaceae* such as *Clauzadea*, *Farnoldia*, *Porpidia*, and *Stenhammarella*. This variety, however, does not occur on *Bellemerea*. This means that the host selection of these lichenicolous fungi cannot be used as a supporting argument in favour of the generic delimitation of *Bellemerea* and *Immersaria* as presented here. However, it should be considered that there are some more cases known where the host selection of *Muellerella pygmaea* does not reflect the circumspection of a host genus, for example of *Caloplaca* (Triebel 1989: 154, fig. 19).

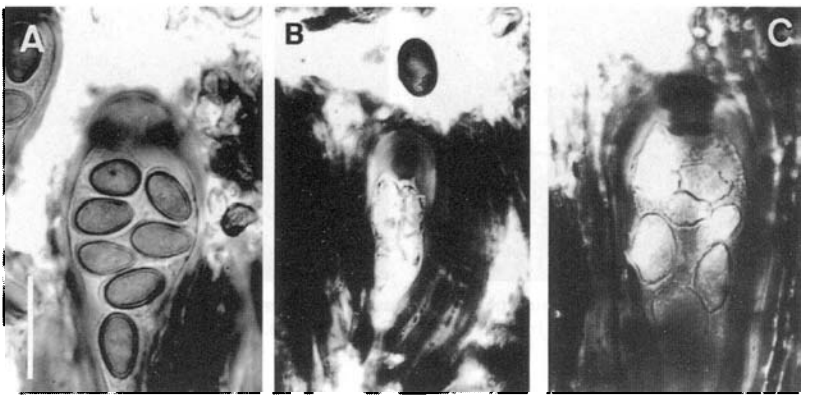

FIG. 5. The asci in Lugol's solution of A, *Amylora cervinocuprea* (Switzerland, Graubünden, 1960, *J. Poelt, A. Schröppel & M. Steiner*, M); B, *Bellemerea alpina* (*H. Hertel* 8096, M); C, *Immersaria athroocarpa* (*F. Schuhwerk* 2270, M). Scale: 10 μm.

TABLE 2. *The main distinguishing characters between the species of* Bellemerea *and* Immersaria

Characters	*Bellemerea*	*Immersaria*
Areole surface	Flat to convex	Flat to concave
Areole pigmentation	Not brown	Brown or olivaceous
Epinecral layer	Absent	Present
Iodine reaction of the medulla	Strongly violet	Violet to negative
Tholus structure	*Bellemerea*-type	*Porpidia*-type
Ascospore wall	Amyloid	Not amyloid

Discussion

A closer examination of the ascus structures of *Bellemarea alpina* and related taxa revealed that the tholus exhibits a relatively diffuse amyloid tube (Fig. 5), which may look rather atypical for *Porpidiaceae* in individual specimens. In such samples, the inner non-amyloid channel of the axial tube is the only visible structure within a bluish tholus. Clauzade & Roux (1984) already have discussed the variation of amyloid tube structures in this genus.

The exclusion of *I. cupreoatra* from *Bellemerea* entails a restricted concept of that genus (Table 2). *Bellemerea* is defined by the following combination of character states: thallus whitish, greyish, ochraceous to rusty coloured, without a distinct epinecral layer, with β-orcinol depsidones (norstictic acid chemosyndrome) in most species, asci of *Bellemerea*-type, which is similar but not equivalent to the *Porpidia*-type and shows a less distinct tube structure, ascospores with amyloid inner wall layer and distinctly halonate perispore structure. The members of the genus usually occur in arctic–alpine habitats. Poelt (1994) discussed the morphological variation of its members (not of *B. cupreoatra*) and pointed out that all these species except *B. subsorediza* (Lynge) R. Sant. are connected by intermediate forms, which may underline

the homogeneity of the genus. In a fertile specimen of *B. subsorediza*, we observed amyloid ascospores in asci with a tube-like amyloid structure. This might confirm the actual generic status of this species.

Conclusions

The genus *Immersaria* in its new delimitation (Tables 1 & 2) includes taxa having a brown or olivaceous thallus, areoles with a mostly concave upper surface and a more or less thick epinecral layer. All have immersed apothecia, *Porpidia*-type asci (Fig. 5), and non-amyloid ascospores. Areoles with concave surface occur in various species or genera with immersed apothecia (e.g. also in species of *Acarospora*); however, these two character states are not strictly correlated.

In *I. cupreoatra* and *I. mehadiana*, subhymenial algal cells may occur. The occurrence of subhymenial algae seems to be correlated with the occurrence of a brown epihymenial pigment. In specimens with a greenish or blackish epihymenium, subhymenial algal cells are lacking. The greenish pigment (' *Lecidea*-green ') seems to absorb considerable amounts of light of photosynthetically relevant wavelengths.

The two types of ascomata marginations, ' cryptolecideine ' beside ' cryptolecanorine ', observed within *Immersaria* seem not to be basically different. The differences concern only the fact that in apothecia with ' cryptolecideine ' margins (e.g. in *I. athroocarpa*), the medullary tissue lateral to the hymenium becomes separated during ontogeny from adjacent parts of the ' parental ' areole, whereas it remains coherent in the ' cryptolecanorine ' apothecia (e.g. in *I. usbekica*). These differences are regarded as being ontogenetically related and intermediate stages have been observed in both species [e.g. in Arnold, *Lich. Exs.* no. 1659, M of *I. athroocarpa* and in the isotype specimen (M) of *Amygdalaria tellensis* (=*I. usbekica*)]. The transfer of *A. tellensis* to *Immersaria* (as *I. usbekica*) by Barbero *et al.* (1990), therefore, is regarded as consistent, and the inclusion of *I. cupreoatra* and *I. mehadiana* in *Immersaria*, as justified. Both types of margination have also been observed in *I. olivacea* even in the same ascoma; e.g. in ascomata not completely surrounded by the areole those parts of the ascomata attached to the areole show a very reduced exciple as in ' cryptolecanorine ' ascomata, whereas in detached parts a well-developed dark exciple usually evolves, as in ' cryptolecideine ' ascomata. An overview on the variation of margination types in *Porpidiaceae* is given by Rambold *et al.* (1990).

The ascus structure of *Amylora cervinocuprea* (Arnold) Rambold, hitherto placed in the synonymy of *Bellemerea cupreoatra*, has recently been recognized as different from the *Porpidia*-type by Rambold (1994). It exhibits certain similarities to the *Rimularia*-type, having an amyloid cap and amyloid lateral parts of the apical ascus wall layers.

The inclusion of *I. olivacea* enlarges the concept of *Immersaria* to accommodate also facultatively 1-septate ascospores and clavate to pyriform conidia.

We are most grateful to J. A. Elix (Canberra) for reviewing the manuscript, advice, and help with the chemistry, to D. Triebel (München), E. Barreno (València) and V. J. Rico (Madrid) for comments on the text, to I. Sebek (München) for technical assistance, to K. Vánky

(Tübingen) for information about collecting localities in Romania, and J. Esnault (Acigne), P. Navarro-Rosinés (Barcelona) and the curators of the herbaria for loaning material. C. Trescolí, V. Calatayud Ros and A. Lorente (València) are also thanked for their help collecting material of *Immersaria olivacea*. G.R. thanks Nicolae and Maria Brancu (Mehadía) for their hospitality during his stay in Romania. This research was supported by the Deutsche Forschungsgemeinschaft (Ra 731/1-2) and by the Spanish DGCYT (PB96-1115-C04-01).

References

Barbero, M., Navarro-Rosinés, P. & Roux, C. (1990) *Immersaria usbekica* (Hertel) Barbero, Nav.-Ros. et Roux comb. nov. [=*Amygdalaria tellensis* Esnault et Roux]. *Bulletin de la Société Linnéenne de Provence* **41:** 139–142.

Brusse F. (1988) *Schizodiscus*, a new porpidioid lichen genus from the Drakensberg. *Bothalia* **18:** 94–96.

Calatayud, V. & Barreno, E. (1994) Contribution to the lichen floristics of eastern Spain—I. Silicicolous lichens and their lichenicolous fungi of Serra d'Espadà (Castelló). *Cryptogamie, Bryologie et Lichénologie* **15:** 23–41.

Clauzade, G. & Roux, C. (1984) Les genres *Aspicilia* Massal. et *Bellemerea* Hafellner et Roux. *Bulletin de la Société Botanique du Centre-Ouest, Nouvelle Serie* **15:** 127–141.

Culberson, C. F. (1972) Improved conditions and new data for the thin layer chromatographic method. *Journal of Chromatography* **72:** 113–125.

Culberson, C. F. (1974) Conditions for the use of Merck silica gel 60 F 254 plates in the standardized thin-layer chromatographic technique for lichen products. *Journal of Chromatography* **97:** 107–108.

Culberson, C. F. & Johnson, A. (1982) Substitution of methyl *tert.*-butyl ether for diethyl ether in the standardized thin-layer chromatographic method for lichen products. *Journal of Chromatography* **238:** 483–487.

Culberson, C. F. & Kristinsson, H. (1970) A standardized method for the identification of lichen products. *Journal of Chromatography* **46:** 85–93.

Esnault, J. & Roux, C. (1987) *Amygdalaria tellensis* (lichens), nouvelle espèce du Tell Algérien. *Anales del Jardín Botánico de Madrid* **44:** 211–225.

Grube, M. & Poelt, J. (1993) Beiträge zur Kenntnis der Flechtenflora des Himalaya X. *Sporastatia testudinea*, ihre Variabilität, ihre Ökologie und ihre Parasiten in Hochasien. *Fragmenta floristica et geobotanica supplementum* **2**(1): 113–122.

Hawksworth, D. L. & Diederich, P. (1988) A synopsis of the genus *Polycoccum* (Dothideales), with a key to the accepted species. *Transactions of the British Mycological Society* **90:** 293–312.

Hertel, H. (1984) Über saxicole, lecideoide Flechten der Subantarktis. In: *Beiträge zur Lichenologie, Festschrift J. Poelt* (H. Hertel & F. Oberwinkler, eds). *Beihefte zur Nova Hedwigia* **79:** 399–499.

Malcolm, W. M., Elix, J. A. & Owe-Larsson, B. (1995) *Labyrintha implexa* (*Porpidiaceae*), a new genus and species from New Zealand. *Lichenologist* **27:** 241–248.

Poelt, J. (1994) Different species types in lichenized ascomycetes. In: *Ascomycete Systematics* (D. L. Hawksworth, ed.). *Nato ASI Series, Series A: Life Sciences* **269:** 273–278.

Poelt, J. & Mayrhofer, H. (1988) Über Cyanotrophie bei Flechten. *Plant Systematics and Evolution* **158:** 265–281.

Rambold, G. (1989) A monograph of the saxicolous lecideoid lichens of Australia (excl. Tasmania). *Bibliotheca Lichenologica* **34:** 1–345.

Rambold, G. (1994) *Amylora*, a new genus in the *Rimulariaceae*. *Bulletin de la Société Linnéenne de Provence* **45:** 343–348.

Rambold, G., Hertel, H. & Triebel, D. (1990) *Koerberiella wimmeriana* (Lecanorales, Porpidiaceae) and its lichenicolous fungi. *Lichenologist* **22:** 225–240.

Rivas-Martínez, S. (1987) *Memoria del mapa de series de vegetación de España*. Madrid: ICONA, ser. Técnica.

Thomson, J. W. (1972) Two new species of *Lecidea* and one of *Lecanora* from North America from the north slope of Alaska. *Bryologist* **75:** 355–359.

Triebel, D. (1989) Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. *Bibliotheca Lichenologica* **35:** 1–278.

Accepted for publication 11 *February* 1998