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Morphology, chemistry and distribution of *Melanelia sorediella* (*Parmeliaceae*) and similar species in the Iberian Peninsula

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Abstract: Lichen material from the Iberian Peninsula of *Melanelia commixta*, *M. hepatizon* and *M. sorediella* has been studied and compared on the basis of morphology, chemistry, habitat and distribution. The new combination *Melanelia sorediella* is proposed and *Cetraria commixta* f. *sorediella* is lectotypified. Chemotypes I and III have been detected in *M. commixta*. *Melanelia sorediella* is characterized mainly by the formation of pycnoisidia and soralia-like structures in the lamina and margins of the thallus and by the absence of pseudocyphellae and apothecia. The pycnoisidium is here described as a combination of isidia-like proliferations of the thallus surface containing pycnidia, carrying algae and acting as vegetative symbiotic propagules. Non detached pycnoisidia grow into lobuli in central parts of the thallus, regenerating it. Pycnoisidia, soralia-like areas and lobuli are formed as a consequence of pycnidia development. *Melanelia sorediella* is morphologically and chemically close to *M. commixta* and is currently known from mountains of central and south-west Europe where it grows on acid rocks. In south-western Europe, the meridional limit of the distribution of the three species studied seems to be located in the mountains of the central part of the Iberian Peninsula (Sistema Central Ibérico). Relevant data on the three species are provided and a key is also included.

Key words: Andorra, *Melanelia commixta*, *M. hepatizon*, *M. sorediella*, Portugal, pycnoisidia, Spain, taxonomy

Introduction

According to Kärnefelt *et al.* (1992) and Thell (1995*a*, 1996), the *Cetraria commixta* group includes foliose saxicolous lichen species, restricted to the Northern Hemisphere and characterized by marginal and laminal emergent pycnidia and also marginal to laminal apothecia, broadly clavate asci with a broad axial body and thick paraplectenchymatous cortex. Recently, four species included in the group, *Melanelia agnata* (Nyl.) A. Thell, *M. commixta* (Nyl.) A. Thell, *M. culbersonii* (Hale) A. Thell and *M. hepatizon* (Ach.) A. Thell, were transferred by Thell (1995*a*) from *Cetraria* Ach. to *Melanelia* Essl., based mainly on their reproductive, morphological and anatomical characters. These taxa included in the *M. commixta* group, therefore, show morphological similarities with *M. stygia* (L.) Essl., the type species of the genus *Melanelia*, with laminal immersed pycnidia (Esslinger 1977; Thell 1995*a*). However, differences in the type of conidia have been reported and bifusiform conidia have been described in *M. agnata*, *M. culbersonii*, *M. hepatizon* and *M. stygia* whilst citriform conidia have been observed in *M. commixta* (Thell 1995*a*, 1995*b*). Recent phylogenetic studies based on molecular, morphological and chemical data, have shown the *M. commixta* group to be polyphyletic with *M. commixta* in a

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different clade from *M. hepatizon* and *M. stygia* (Thell *et al.* 2002; Blanco *et al.* 2004).

During our studies on different species of *Parmelia* s. lat. from Spain (Rico *et al.* 1992; Muñoz *et al.* 1993; Rico & Manrique 1995, 1997) and also floristic work on lichens from the upper belt of the Serra da Estrêla in Portugal (van den Boom & Jansen 2002), we have found a brown saxicolous silicicolous lichen with a parmelioid thallus which develops a peculiar kind of asexual propagule. Following Hillmann (1936) and Poelt & Vězda (1981) this material corresponds with the concept of *Cetraria commixta* (Nyl.) Th. Fr. f. *sorediella* Lettau, a sterile and poorly known taxon in Europe, related to *Melanelia commixta*. Subsequently, *C. commixta* f. *sorediella* was transferred by Hafellner & Türk (2001) to *Melanelia commixta* var. *sorediella* (Lettau) Hafellner & Türk. We introduce here the new term pycnoisidia for the characteristic isidia-like asexual propagules of this lichen, whose formation is induced by the development of conidiomata, carrying algal cells in the process. The pycnoisidia develop profusely in well-delimited soralia-like areas on the upper side and margins of the thallus. Vegetative symbiotic propagules are especially important not only from a biological point of view, but also in taxonomy and nomenclature (Poelt 1995; Büdel & Scheidegger 1996).

In this paper the taxonomic status of *Cetraria commixta* f. *sorediella* is raised to species level and a new combination is proposed, based principally on the presence of pycnoisidia and absence of pseudocyphellae and apothecia. The development of pycnoisidia is described and illustrated in detail. A taxonomic revision of all the Iberian species belonging to the artificial *Melanelia commixta* group is also presented, including *M. commixta*, *M. hepatizon* and the newly combined species, *M. sorediella*. The study emphasizes the differential characteristics of the three species, based mainly on morphology and structures of the thallus, type of reproduction, chemistry, habitat and distribution within the Iberian Peninsula. In order to clarify and facilitate comparisons of their differential characteristics, detailed descriptions of the three treated species are presented.

Materials and Methods

More than 125 herbarium specimens from B, BCC, GDA, LEB, LISU, MACB, MAF and SANT and from the private collections of J. Etayo (hb. Etayo, Pamplona) and P. P. G. van den Boom (hb. v. d. Boom, Son) were studied. Following Llimona & Hladun (2001) and except for *Melanelia sorediella*, listed synonyms are those from the Iberian literature (Andorra, Portugal, Spain and the Balearic Islands). For more synonyms from elsewhere see Zahlbruckner (1930). The description of the species and the data included in the key are based on the Iberian material studied, except for *M. sorediella*, in which the type specimen has also been included. For comparison of descriptive details and illustrations on the treated species, see Hillmann (1936), Tavares (1945) and Thell (1995*a*). Current mycological terminology is used following Kirk *et al.* (2001) and Thell (1995*b*) for pycnoconidia. Phytoclimatic terminology follows Rivas-Martínez (1987). The distribution maps, with country and province political divisions, are based on a UTM grid projection and include all the Iberian material studied here. Iberian records or bibliographic compilations prior to 1900 (*cf.* Llimona & Hladun 2001) were considered doubtful and excluded, unless the materials were available. Routine optical analyses were carried out using a Zeiss (47 50 52) stereomicroscope and a Nikon Optiphot AFX-II microscope. Sections were hand-cut or, for optical photomicrographs, cut by hand or on a freeze microtome (Sartorius Werke A.G.-MI 27) and then mounted in distilled water or in lactophenol cotton blue solution (Merck 1.13741.0100). All microscopic measurements were made in water. Extreme values have been noted between brackets when they represented no more than 10% of the measurements. Samples of some specimens were sputter coated with gold (E5000C-P53) and examined in an ISI-SX-25 SEM, particularly to view the pored epicortex (*cf.* Hale 1981), but no images are included here.

The standard methods of thin layer chromatography (TLC) (Culberson & Ammann 1979; Culberson *et al.* 1981; Culberson & Johnson 1982; Orange *et al.* 2001) were used for identification of lichen substances. Selected material was analyzed by high performance liquid chromatography (HPLC), according to Rico *et al.* (1992) and Feige *et al.* (1993). The chemical references used for TLC and HPLC analysis were: atranorin, chloratranorin and stictic acid: Sigma Chemical Co.; norstictic acid: *Pleurosticta acetabulum* (Neck.) Elix & Lumbsch (MAF); α-collatolic, 4-*O*-methylphysodic, alectoronic and physodic acids: *Cetrelia chicitae* (W. L. Culb.) W. L. Culb. & C. F. Culb. (MAF), *Xanthoparmelia glabrans* (Nyl.) O. Blanco, A. Crespo, Elix, D. Hawksw. & Lumbsch (MAF) and *Tephromela atra* (Huds.) Hafellner (MAF).

Specimens used for comparison. Melanelia commixta (chemotype I: α-collatolic acid as main substance).

Finland: *Nylandia*: Ruotsinpyhtää (Strömfors), Söderby-Kungshamm, ad rupem in silva, 29 vii 1949, *V. Räsänen* [MAF, sub *Cetraria fahlunensis* (L.) Schaer.]. *Varsinais-Suomi*: (Ab) Raisio, on sunny granite rock, 19 viii 1965, *T. Laine* (MAF, sub *Cetraria commixta*).—**France:** *Vosges*: Au Tanet, supra rupes graniticas in alpinis, *J. Harmand* [Harmand, *Lich. Gall. Rar. Exs.* 35] (B, sub *Platysma commixtum* Nyl.).—**Slovakia:** *Vysoké Tatry*: NW of Poprad, NNW of Stary Smokovec, path from Slavkovská vyhliadka to Slavkovsky stit, mountain ridge, SE slope, N exp. Vertical and sloping rock, 2100 m, 1994, *P. P. G. van den Boom* 15649 (hb. v. d. Boom).—**Sweden:** *Västra Götaland*: Bohuslän, Hülesdalen, pas. Odsmål, in rupe, 18 viii 1918, *H. Magnusson* (B, sub *C. commixta*).—**Switzerland:** *Graubünden*, *Ober Engadin*: Pontresina-Chünetta, über Felsen, 1950 m, viii 1912, *G. Lettau* (B, sub *C. commixta*).

Melanelia commixta (chemotype III: without lichen substances). **Norway:** *Nordland*: Lofoten Island, 28 vii 1988, *A. Belio & L. G. Sancho* (MAF, sub *Cetraria hepatizon*).—**Sweden:** *Torne Lappmark*: Kärkevagge 2 km S of Laktatjakka station, 800–850 m, 68°25′N/ 18°20′E, 25 viii 1992, *L. G. Sancho* (MAF, sub *C. commixta*).

Melanelia hepatizon (stictic acid as main substance). **Austria:** *Salzburg*: Lungau, Schladminger Tauern, path from Prebersee to Preberkessel, E of the Preberhalterhütte, 1810 m, 47°12′N/13°52′E, MTB 8749, on garnet-mica-schist, 21 vi 1997, *R. Türk* [Obermayer, *Lichenoth. Graec.* 108] (MAF).—**Canada:** *British Columbia*: Trophy Mountains, *c.* 2300 m, 51°46′N/ 119°54′W, 24 viii 1994, *L. G. Sancho* [MAF, sub *C. hepatizon* (Ach.) Vain.].—**Finland:** *Ostrobotnia borealis*: Simo, Pahnila, ad saxa aprica prope agrum, 10 vi 1946, *V. Räsänen* [Räsänen, *Lichenoth. Fenn.* 89] (B, sub *C. hepatizon*).—**France:** *Vosges*: Hohreck, sobre pedres exposades, 9 ix 1971, *X. Llimona* (BCC).—**Greenland:** *Qeqertarsuaq (Disko)*: Mudderbugten, Kûgkâp kûa, 50 m, 69°43′N/51°58′W, on soil and stones rather weakly influenced by guano in old river bed, 19 vii 1975, *V. Alstrup* [Hansen, *Lich. Groenl. Exs.* 193] (B, sub *C. hepatizon*).—**Italy:** *Vercelli*: nelle frane dei monti tra Riva ed Allagna in Valsesia, *A. Carestia* [Baglietto, Cesati & Notaris, *Erb. Critt. Ital. Ser. I* 517] (B, sub *Parmelia fahlunensis*).—**Norway:** *Nordland*: Lofoten Island, 28 vii 1988, *A. Belio & L. G. Sancho* (MAF, sub *C. hepatizon*).—**Romania:** *Carpatii Meridionali*: comit. Hunyad in Transsylvania, in valle "Riu sor" infra alpem Retyezát, super saxum micaceoeschistosum decompositum, 15 vii 1886, *H. Lojka* [Lojka, *Lichenoth. Univ.* 214] (B, sub *P. commixtum*).—**Slovakia:** *Vysoké Tatry*: NW of Poprad, NNW of Stary Smokovec, 1800 m, blockstream, on NE slope, on granite under overhang, 1994, *P. P. G. van den Boom* 15629 (hb. v. d. Boom, sub *C. hepatizon*).—**Sweden:** *Torne Lappmark*: Torne Träsk area, Pathkatterjakk Station to Katterjame Lake, 600 m, 68°85′N/18°08′E, low alpine belt, 26 viii 1992, *L. G. Sancho* (MAF, sub *C. hepatizon*).—**Switzerland:** *Graubünden*, *Ober Engadin*: Rosegtal b. Pontresina, a. Blöcken, Silikatgestein, 1900 m, vi 1913, *G. Lettau* (B, sub *C. hepatizon*).—**USA:** *Alaska*: North Slope Borough, Brooks Range, Anaktuvuk Pass, 800 m, 68°8′0″N / 151°45′0″W, wet tundra, on non calcareous rock, 1976, *T. H. Nash III* 13210 [Anonymous, *Lich. Exs. Arizona State Univ.* 320] (MAF).

Tuckermanopsis chlorophylla (Willd. in Humb.) Hale in Egan (protolichesterinic acid complex). **Italy:** *Calabria*: Cosenza, Sila Piccola, 100 m, 11 vii 1988, *L. G. Sancho* [MAF, sub *Cetraria chlorophylla* (Willd.) Vain.].—**Spain:** *Castilla y León*, *León*: Sancedo, sobre *Castanea*, *A. Terrón* (MAF, sub *C. chlorophylla*). *Galicia*, *Orense*: Montes de Invernadeiro, sobre *Quercus* sp., 21 vi 1973, *S. Castroviejo & A. Crespo* (MAF, sub *C. chlorophylla*). *Madrid*: El Berrueco, 930 m, sobre *Cistus ladanifer*, 3 i 1980, *J. Silva* (MAF, sub *C. chlorophylla*); San Lorenzo de El Escorial, Abantos, sobre *Pinus*, 10 x 1973, *A. Crespo* (MAF, sub *C. chlorophylla*).

Key to the *Melanelia* species studied in the Iberian Peninsula

1. Pycnoconidia citriform; medulla K −, C −, KC − or KC+ rose-red, Pd −; without lichen substances or with α-collatolic acid as main substance 2
Pycnoconidia bifusiform; medulla K+ yellow to red or dirty brown (crystals), C −, KC+ yellow to dirty brown-rose, Pd+ orange; with stictic and norstictic acids as main substances . . . . **M. hepatizon**

2(1) Thallus with marginal and laminal pycnoisidia, clustering in soralia-like areas; pseudocyphellae absent; apothecia lacking; medulla KC+ rose-red; with α-collatolic acid as main substance . . . . **M. sorediella**
Thallus without pycnoisidia; pseudocyphellae marginal to rarely laminal; rarely with apothecia . . . . **M. commixta** (for chemotypes see 3)

3(2) Medulla KC+ rose-red; with α-collatolic acid as main substance . . . . **M. commixta—Chemotype I**
Medulla KC −; without lichen substances . . **M. commixta—Chemotype III**

The Species

Melanelia commixta (Nyl.) A. Thell

Nova Hedwigia **60:** 417 (1995).—*Platysma commixtum* Nyl., *Syn. meth. lich.* **1**(2)**:** 310 (1860) (basionym).—*Cetraria commixta* (Nyl.) Th. Fr., *Lichenogr. scand.* **1:** 109 (1871); type: Finland, Nyland, Helsingfors, 1860, *W. Nylander* (H—lectotype, not seen; *cf.* Thell 1995*a*: 417).

Lichen fahlunensis L., *Sp. pl.* **2:** 1143 (1753), *nom. rej.* [=*Melanelia stygia* (L.) Essl.; *cf.* Greuter *et al.* 2000: 394; Jørgensen *et al.* 1994: 307, 375].—*Parmelia fahlunensis* (L.) Ach., *Methodus***:** 203 (1803).—*Imbricaria fahlunensis* (L.) DC. in Lam. & DC., *Fl. franç.* **2:** 395 (1805).—*Platysma fahlunense* (L.) Nyl., *Syn. meth. lich.* **1**(2)**:** 309 (1860); type: Habitat in Europae rupibus nudis (LINN 1273.70—lectotype, not seen; *cf.* Jørgensen *et al.* 1994: 307, 375; Greuter *et al.* 2000: 394).

(Fig. 1A)

Thallus foliose, lobate, loosely adnate, 1–8(–15) cm diam., up to 215 µm thick; upper surface brown to dark brown-black, rather glossy; lower surface whitish, whitish brown, pale brown, reddish brown or somewhat darker in parts; on siliceous rocks, rare on silicicolous bryophytes and or as an epiphyte. *Lobes* 1·5–25 mm long, 0·25–3·25 mm broad, irregularly divided and branched, plane to concave or sometimes convex, often imbricate, axils angular or rounded, margins sometimes distinct, tips often ascending, lower surface somewhat irregularly wrinkled. *Rhizinae* sparse, simple or rarely irregularly branched, marginal to laminal, pale brown to moderately brown or brown-black. *Algae* chlorococcoid, cells 7–14 µm diameter. *Pseudocyphellae* 0·05–0·15 mm long, rounded to elongate or irregular, whitish to obscure, on the margin of lobes, very rarely laminal. *Upper cortex* paraplectenchymatous, up to 5 layers of cells, outer cells with dark brown caps, 15–35 µm thick; epicortex not pored. *Lower cortex* paraplectenchymatous, up to 4 layers of cells, 12–35 µm thick. *Medulla* grey to hyaline, of mesodermatous hyphae up to 5 µm diameter, walls with irregular granules dissolving totally or partially in KOH.

Apothecia rare in the Iberian material (8 specimens of 45), lecanorine, marginal to terminal, up to 6 mm in diameter. *Hymenium* hyaline, 40–50 µm thick. *Pseudocyphellae* up to 2 mm long, rounded to elongate or irregular, whitish to obscure, on the upper and lower surface of apothecial margin. *Asci* broadly clavate, 8-spored, *Lecanora*-type, with an amyloid outer gel, a small amyloid tholus with a broad axial body and ocular chamber. *Ascospores* simple, hyaline, ellipsoidal to elongate, (6–)7–9(–10) × 4–5(–6) µm.

Pycnidia frequent, marginal to rarely laminal and also on the apothecial margin, rarely immersed to sessile or on simple to ramified thallus projections, up to 0·6 mm long, apices black, globose to elliptical, up to 225 µm in diameter, without cortical tissue beneath, wall with more than one layer. *Pycnoconidia* citriform, 3·5–7 × (1–)1·5–2(–3)µm.

Chemistry and spot tests. Chemotype I: α-collatolic acid as major substance, alectoronic, 4-*O*-methylphysodic and sometimes physodic acids as minor substances, atranorin, chloratranorin and four unidentified substances in traces or absent; cortex HNO_3-; medulla K −, C −, KC+ rose-red, Pd −, I −. Chemotype III: with no secondary compounds; cortex HNO_3-; medulla K −, C −, KC −, Pd −, I −.

Distribution and habitat. *Melanelia commixta* is a holartic species, extending from North America to Europe (Esslinger & Egan 1995; Thell 1995*a*). This silicicolous species shows an arctic to alpine distribution and is mainly found in humid sites of the subalpine to alpine belts of central and northern Europe, where it is considered much rarer than *M. hepatizon* (Poelt & Vězda 1981; Nimis 1993; Wirth 1995; Thell 1995*a*).

In the Iberian Peninsula, *Melanelia commixta* is a species from medium to high altitudes, ranging from 1500 to 2350 m, on acid rocks and gravel in open and ± humid places. It prefers horizontal to slightly inclined sunny rock surfaces, between the ground and the rock apices. Sometimes it colonizes moving blocks in block streams or, more rarely, boulders slightly exposed to the wind. It has been cited in Portugal as an epiphyte on *Erica* spp. and *Juniperus communis* L. (Tavares 1945, sub *Cetraria commixta*; Terrón *et al.* 2000*b*, sub *C. commixta*; van den Boom & Jansen 2002), and also in some cases growing among saxicolous mosses. According to the material studied, it represents a locally common species that has been found in the supramediterranean to the cryoromediterranean belts of the Mediterranean region (Beira Alta province in Portugal; Ávila, León, Madrid, Orense, Segovia and Zamora provinces in Spain) and in the montane to the alpine belts of the Eurosiberian region (Minho in Portugal; Asturias and Palencia in Spain). The materials cited by Casares & Llimona (1982, sub *C. commixta*) from Sierra Nevada (Granada, SE Spain) and by Azuaga & Gómez-Bolea (2000, sub *C. commixta*) from Andorra, corresponds to *Cornicularia normoerica* (Gunnerus) Du Rietz and *Melanelia hepatizon* respectively. Unfortunately, it was not possible for us to check the records reported from Zaragoza province in Spain by Navás (1903, sub *Parmelia fahlunensis*). Consequently, our current data indicate that the meridional limit of the distribution of *M. commixta* in south-western Europe (Fig. 1A) seems to be the central mountains of the Iberian Peninsula (Sistema Central Ibérico).

Remarks. According to Kärnefelt *et al.* (1992) and Thell (1995*a*), three different chemotypes are recognized in *Melanelia commixta*: chemotype I with α-collatolic acid as main substance, chemotype II with alectoronic acid and chemotype III with no secondary compounds. Only chemotypes I and III have been detected in the Iberian material examined so far. No significant correlations between distribution, morphology and chemistry have been found within the species.

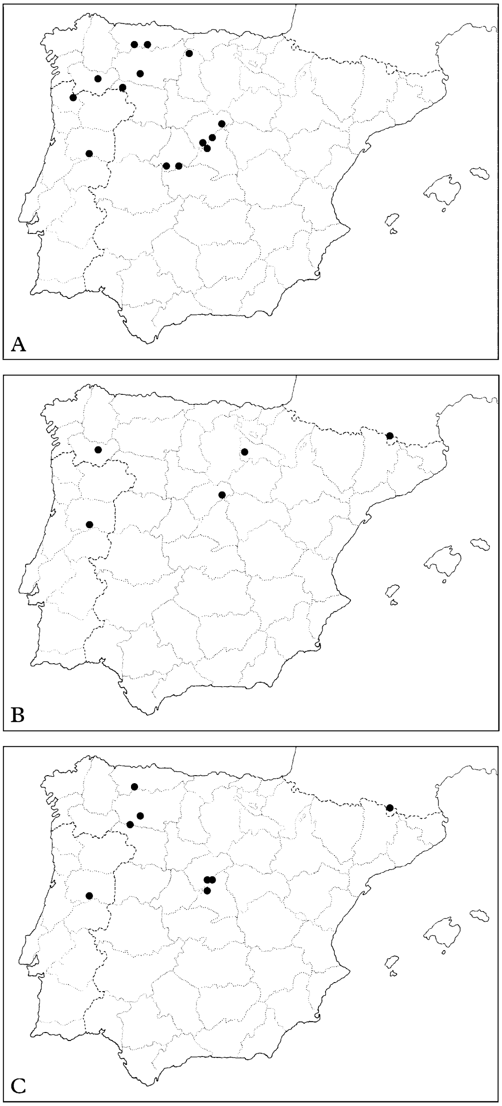


FIG. 1. Distribution of the species of the *Melanelia commixta* group in the Iberian Peninsula. A, *Melanelia commixta*; B, *M. hepatizon*; C, *M. sorediella*.

Selected specimens examined. Chemotype I (α-collatolic acid as main substance). **Portugal:** *Beira Alta*: Serra da Estrêla, a SW da Lagoa Comprida, 1650 m, sôbre o granito, 17 vii 1942, *R. T. Palhinha* (LISU-C. N. Tavares 140, sub *Cetraria commixta*); *ibid.*, desde o Curral do Martins até à Ribeira das Naves, sôbre o granito exposto, 1944, *C. N. Tavares* 139 (LISU, sub *C. commixta*); *ibid.*, entre a Lagoa Comprida e a Escura, *c.* 1600 m, sôbre o granito, 1947, *C. N. Tavares* 2234 (LISU, sub *C. commixta*); *ibid.*, Morro fronteiro à Nave de San António, sôbre o granito, 1949, *C. N. Tavares* 3122 (LISU, sub *C. commixta*); *ibid.*, subida a la Torre, 1650 m, 17 vii 1983, *P. Coello* (MAF, sub *C. commixta*); *ibid.*, pico da Estrêla, cerca del Alto da Torre, 1990 m, 29TPE16, granito, orientación NE, 6 vi 1990, *J. M. Pizarro & S. Sardinero* (MAF, sub *C. commixta*); *ibid.*, SE of Lagoa Comprida, near fte. dos Perus, 1850 m, on horizontal surface of exposed granite boulder, 1997, *P. P. G. van den Boom* 19054 (hb. v. d. Boom, sub *C. commixta*). *Minho*: Serra do Gerês, Carris, *c.* 1500 m, sôbre o granito, 1948, *C. N. Tavares* 2473 (LISU, sub *C. commixta*).—**Spain:** *Asturias*: puerto de Somiedo, laderas de Vega Cimera, 1500 m, sobre cuarcitas, 13 x 1978, *V. M. Vázquez* (MAF, sub *C. commixta*). Cangas de Narcea, puerto de Leitariegos, 1850 m, 6 ix 1980, *A. Crespo*, *L. G. Sancho*, *E. Barreno*, *V. J. Rico*, *A. G. Bueno & V. M. Vázquez* (MAF, sub *C. commixta*); *ibid.*, ascensión al pico de Cueto de Arbás desde el puerto de Leitariegos, 1900 m, 29TQH16, sobre cuarcitas en orientación N, 10 vi 1990, *V. J. Rico* (MAF, sub *C. commixta*). *Castilla y León*, *Ávila*: Sierra de Gredos, Risco del Francés, 2200 m, 30 vii 1983, *L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, puerto de Mijares, 1800 m, 16 x 1984, *L. G. Sancho* (MAF, sub *C. commixta*). *Castilla y León*, *León*: Macizo de El Teleno, collado de El Palo, 1900 m, 29TQG1292, sobre cuarcita, or NE, 1988, *A. Terrón* 1233, 1241 (LEB, sub *C. commixta*); *ibid.*, ascensión al pico de El Teleno, 2080 m, 29TQG1492, sobre cuarcita, en cueva, 1989, *A. Terrón* 1153/1, 1520 (LEB, sub *C. commixta*); *ibid.*, pico de El Teleno, 2185 m, 29TQG1491, sobre cuarcita, en superficie horizontal de cima, 1989, *A. Terrón* 28 (LEB, sub *C. commixta*); *ibid.*, proximidades del pico de El Teleno, 2185 m, 29TQG1491, sobre cuarcita, en cueva, 1989, *A. Terrón* 344 (LEB, sub *C. commixta*). *Castilla y León*, *Palencia*: Fuentes Carrionas, pico de Curavacas, 2300 m, 30TUN66, sobre conglomerado silíceo, 7 vii 1991, *A. Terrón & M. E. López de Silanes* (SANT). *Castilla y León*, *Segovia*: Sierra de Guadarrama, N of Pto. de Navacerrada, 1800 m, in sloping *Pinus* forest, on shaded granite, 18 viii 1987, *P. P. G. van den Boom* 6093 (hb. v. d. Boom, sub *C. commixta*); *ibid.*, La Pinareja, 2180 m, 21 vii 1984, *L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, umbría de Siete Picos, 1850 m, 30TVL37, granito en orientación N, pinar de *Pinus sylvestris*, 9 viii 2001, *A. R. Burgaz* (MACB, sub *C. commixta*). Cerezo de Arriba, Sierra de Ayllón, pico de El Lobo, 2200 m, 1985, esquistos y cuarcitas, zona protegida, ladera N, *E. Manrique* mo-11-65, 11-66, 11-68 (MAF, sub *C. commixta*); *ibid.*, 2270 m, 30TVL6059, esquistos, 5 v 1980, *V. J. Rico* (MAF, sub *C. commixta*); *ibid.*, 18 vi 1980, *V. J. Rico, E. Barreno & L. G. Sancho* (MAF, sub *C. commixta*). *Galicia*, *Orense*: Montes de Invernadeiro, Fial de las Corzas, 1548 m, cuarcitas y esquistos, rocas planas, 13 vii 1988, *R. Carballal* (SANT, sub *C. commixta*). *Madrid*: Sierra de Guadarrama, pico de Cabezas de Hierro, 2200 m, 20 viii 1983, *L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, pico de El Escaparate, 1900 m, 20 xi 1981, *L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, 10 ix 1985, *L. G. Sancho* [Casares, *Exs. Permut. Lichenol. Fasc. II* 39] (MACB, MAF, sub *C. commixta*); *ibid.*, Manzanares el Real, proximidades del pico de La Bola del Mundo, 2220 m, gneis, 1987, *V. J. Rico* 1239/31, 1239/32 *& E. Manrique* (MAF, sub *C. commixta*).

Chemotype III (without secondary compounds). **Spain:** *Asturias*: puerto de Leitariegos, Laguna de Arbás, 1900 m, 6 ix 1980, *A. Crespo*, *L. G. Sancho*, *E. Barreno*, *V. J. Rico*, *A. G. Bueno & V. M. Vázquez* (MAF, sub *C. commixta*). *Castilla y León*, *Palencia*: Fuentes Carrionas, pico de Curavacas, 1900 m, 30TUN66, sobre conglomerado, 3 ix 1990, *A. Terrón* (LEB, sub *C. commixta*); *ibid.*, 2000 m, 30TUN66, sobre conglomerado silíceo, 9 ix 1990, *A. Terrón* (LEB, sub *C. commixta*). *Castilla y León*, *Segovia*: Cerezo de Arriba, Sierra de Ayllón, cercanías del pico de El Lobo, Alto de Las Mesas, 1950 m, 30TVL5959, esquistos soleados, 18 vi 1980, *V. J. Rico*, *E. Barreno & L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, estación de esquí de La Pinilla, Gran Plató, 1850 m, 30TVL6060, esquistos, 17 vii 1981, *V. J. Rico* (MAF, sub *C. commixta*); *ibid.*, pico de El Lobo, 2200 m, esquistos y cuarcitas, zona protegida, ladera N, 1985 *E. Manrique* mo-11-67 (MAF, sub *C. commixta*). La Granja, carretera del puerto de Navacerrada al puerto de Cotos, km 45, Loma del Noruego, 1940 m, 30TVL1716, pinar de *Pinus sylvestris*, sobre granito, 2000, *V. J. Rico* 3561 (MAF). *Castilla y León*, *Zamora*: Parque Natural del Lago de Sanabria, Lagunas de Padornelo, 1700 m, 29TPG7860, on rocks, 1998, *M. P. Jones* 1520 (MAF, sub *Cetraria hepatizon* and sub *C. commixta*). *Madrid*: Sierra de Guadarrama, Valdemartín, 2200 m, 3 viii 1985, *E. Manrique & L. G. Sancho* (MAF, sub *C. commixta*); *ibid.*, pico de Los Claveles, 2350 m, sobre gneis, repisa orientada al E, 1985, *E. Manrique* mo-30-8-35 *& L. G. Sancho* (MAF, sub *C. commixta*).

Melanelia hepatizon (Ach.) A. Thell

Nova Hedwigia **60:** 419 (1995).—*Lichen hepatizon* Ach., *Lichenogr. suec. prodr.***:** 110 (1799) [1798] (basionym).—*Parmelia fahlunensis* var. *hepatizon* (Ach.) Ach., *Methodus***:** 203 (1803).—*Cetraria hepatizon* (Ach.) Vain., *Természetrajzi Füz.* **22:** 278 (1899); type: Sweden, Härjedalen, Tännäs, mt. Gruvvålen, near Lake Glimsjön, *c.* 2 km. NE of Hotel Ramundberget, *c.* 920 m, 62°52′N/12°25′E, on exposed schists in the subalpine region, 12 viii 1988, *R. Santesson* 32495 (UPS—neotype, not seen; *cf.* Thell 1995*a*: 419).

(Fig. 1B)

Thallus foliose, lobate, loosely adnate, 1–8 cm diameter, up to 350 µm thick; upper surface greenish brown to dark brown or black, glossy to mat; lower surface dark brown-black, mat, somewhat pale at the margin; on siliceous rocks, rare on silicicolous bryophytes. *Lobes* 3–14 mm long, 0·25–2·5 mm broad irregularly divided and branched, often concave, often imbricate, axils angular or rounded, margins often distinct, sometimes with proliferating secondary lobes. *Rhizinae* scattered, laminal to marginal, simple to irregularly branched, black. *Algae* chlorococcoid, cells 7–12 µm diameter. *Pseudocyphellae* 0·1–0·5 mm long, rounded to elongate and irregular, whitish to obscure, marginal and rarely laminal. *Upper* *cortex* paraplectenchymatous, up to 4 layers of cells, outer cells with dark brown caps, 10–30 µm thick; epicortex pored. *Lower cortex* paraplectenchymatous, up to 4 layers of cells, 12–25 µm thick. *Medulla* hyaline to grey, of mesodermatous to leptodermatous hyphae up to 4 µm diam., walls commonly with irregular granules dissolving totally or partially in KOH.

Apothecia absent in the Iberian material.

Pycnidia frequent, marginal to laminal, immersed to frequently sessile or on simple to ramified thallus projections up to 0·3 mm long, often grouped forming gall-like areas, apices black, globose to elliptical, up to 200 µm in diameter, without cortical tissue beneath, wall with more than one layer. *Pycnoconidia* bifusiform, dumb-bell shaped, 4–7 × 1–1·5 µm.

Chemistry and spot tests. Stictic and norstictic acids as major substances, cryptostictic, menegazziaic and constictic acids as minor substances, atranorin, chloratranorin and two unidentified substances (probably related to the stictic chemosyndrome) in traces or absent. Cortex HNO_3-; medulla K+ yellow to red or dirty brown (crystals), C−, KC+ yellow to dirty brown-rose, Pd+ orange, I−.

Distribution and habitat. *Melanelia hepatizon* is a circumpolar, arctic and alpine silicicolous species extending from North America (Esslinger & Egan 1995) to Greenland, Europe, Russia (Thell 1995*a*), the Himalayas (Wei 1991; Thell 1995*a*) and Japan (Kurokawa 2003). It is usually found in the upper montane to the alpine belts of central and northern Europe (Poelt & Vězda 1981; Nimis 1993; Wirth 1995), but seems to be less frequent in the Mediterranean mountains (Nimis 1993).

In the Iberian Peninsula it is a rare species, growing from 1500 to 2878 m, mainly on N-facing, open wind-exposed siliceous and wetted rocks (occasionally on silicicolous mosses), from the upper supramediterranean to the cryoromediterranean belts of the Mediterranean region (Beira Alta province in Portugal; La Rioja, Orense and Segovia provinces in Spain) and from the alpine belt of the Eurosiberian region (Ordino in Andorra). It seems to be more limited to windy, humid or hyperhumid exposed sites than are *Melanelia commixta* and *M. sorediella* (*cf.* Wirth 1972). It was not possible for us to check the records reported from the provinces of Ávila (Sancho 1986, sub *Cetraria hepatizon*) and León (Terrón *et al.* 2000*a*, sub *C. hepatizon*) in Spain. Taking into account the material studied, the meridional limit of the distribution of *M. hepatizon* in south-western Europe (Fig. 1B) could be established in the central mountains (Sistema Central Ibérico) of the Iberian Peninsula.

Remarks. In comparison with the extra Iberian material, the thalli of the Iberian specimens studied of *Melanelia hepatizon* are smaller and sterile, although they are well characterized by their chemistry, dark brown to black lower surface, pored epicortex, pycnidia on marginal projections and bifusiform pycnoconidia.

Selected specimens examined. **Andorra:** *Ordino*: Serra de Tristaina, Cim del Pic de Tristaina, 2878 m, 31TCH7623, vii 1998, *A. Gómez-Bolea & T. Azuaga* (BCC, sub *Cetraria commixta*).—**Portugal:** *Beira-Alta*: Serra da Estrêla, 9·5 km SSW of Manteigas, Cantaro Raso, steep N facing granite, 1900 m, 1998, *P. P. G. van den Boom* 20274 (hb. v.d. Boom).—**Spain:** *Castilla y León*, *Segovia*: Cerezo de Arriba, Sierra de Ayllón, pico de El Lobo, 2270 m, 30TVL6059, esquistos soleados, 12 vii 1979, *V. J. Rico* (MAF, sub *Cetraria hepatizon*); *ibid.*, 18 vi 1980, *V. J. Rico*, *E. Barreno & L. G. Sancho* (MAF, sub *C. hepatizon*). *Galicia*, *Orense*: Montes de Invernadeiro, Altos de Guasenza, en la cumbre, 1500 m, 29TPG3472, pizarras, 13 vii 1988, *R. Carballal* (SANT, sub *C. hepatizon*). *La Rioja*: Sierra de San Lorenzo, monte cercano al pico de San Lorenzo, 2000 m, 30TWM07, cresta vertical y venteada, *J. Etayo* 10435 (hb. Etayo, sub *C. hepatizon*).

Melanelia sorediella (Lettau) V. J. Rico, van den Boom & Barrasa comb. et stat. nov.

Cetraria commixta (Nyl.) Th. Fr. f. *sorediella* Lettau, *Hedwigia* **60:** 119 (1918) (basionym).—*Cetraria fahlunensis* (L.) Schaer. var. *sorediella* (Lettau) Räsänen, *Kuopion Luonnon Ystäväin Yhdistyksen julkaisuja ser. B*, **2**, no. **6:** 38 (1952).—*Cetraria sorediella* (Lettau) V. J. Rico in Reisinger & Bresinsky (eds.) *comb. inval.*, *Abstracts IMC IV* (*Regensburg*)**:** 49 (1990) [Art. 33.2, basionym

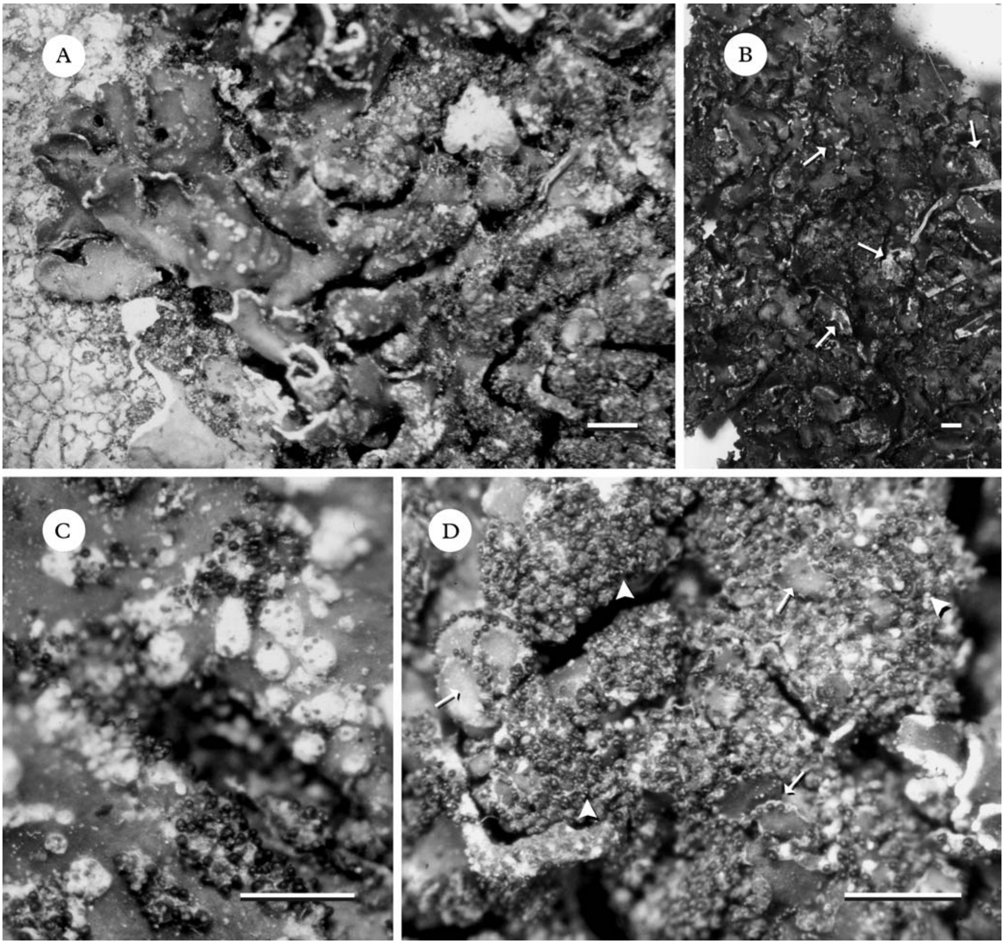


FIG. 2. *Melanelia sorediella*. A, habit (*Rico* 1239, MAF); B, part of thallus showing whitish soralia-like areas (arrows) (lectotype, B-1305); C, laminal soralia-like areas and pycnoisidia with darker tips (*Rico* 1239, MAF); D, central part of the thallus showing profusely developed pycnoisidia (arrow heads) in transition to young lobuli (arrows) (*Rico* 1239, MAF). Scales: A–D = 1 mm.

not indicated and reference omitted].—*Cetraria sorediella* (Lettau) V. J. Rico & Manrique in Randlane & Saag *comb. inval.*, *Mycotaxon* **47:** 401 (1993) [Art. 33.2, basionym not indicated and reference omitted; *cf.* Randlane *et al.* 1997: 119].—*Melanelia commixta* (Nyl.) A. Thell var. *sorediella* (Lettau) Hafellner & Türk, *Stapfia* **76:** 153 (2001).—*Melanelia sorediella* (Lettau) van den Boom & J. Jansen *comb. inval.*, *Österr. Z. Pilzk.* **11:** 25 (2002) [Art. 33.2, basionym not indicated and reference omitted]; type: [Switzerland: Graubünden, Ober] Engadin, Chünetta b. Pontresina, ü. Fels', Urgestein, 2000 m, viii 1912, *G. Lettau* (B 13052—lectotypus!, here designated: from five thalli, the separated specimen).

(Figs 1C, 2 & 3)

Thallus foliose, lobate, loosely to moderately adnate, sometimes firmly attached on rock, 1–12(–16) cm diameter, up to 370 µm thick; upper surface medium brown to dark brown, mat to somewhat glossy; lower surface pale brown, reddish brown to dark brown-black, somewhat black in parts and pale at the margin; on siliceous rocks, rare on silicicolous bryophytes. *Lobes* 1–30 mm long, 0·25–5 mm broad, irregularly divided and branched, concave or convex to sometimes flat, often imbricate, axils rounded to angular, tips often ascending, lower surface somewhat wrinkled. *Pycnoisidia* conspicuous and very frequent especially towards the thallus centre, marginal and laminal, sessile or forming simple to rarely ramified projections up to 0·7 mm, with dark brown to black tips, clustering in soralia-like areas; white soralia-like areas, with exposed medulla, appear after pycnoisidia detachment; in the thallus centre, non-detached pycnoisidia grow into frequently ascending imbricate lobuli. *Rhizinae* sparse, simple or rarely irregularly branched, marginal to laminal, pale brown to black. *Algae* chlorococcoid, cells 6–14 µm diameter. *Upper cortex* paraplectenchymatous, up to 6 layers of cells, outer cells with dark brown caps, 20–40 µm thick; epicortex not pored. *Lower cortex* paraplectenchymatous, up to 5 layers of cells, 20–50 µm thick. *Medulla* grey to hyaline, of mesodermatous hyphae up to 5 µm diameter, walls with irregular granules dissolving totally or partially in KOH.

Apothecia not known.

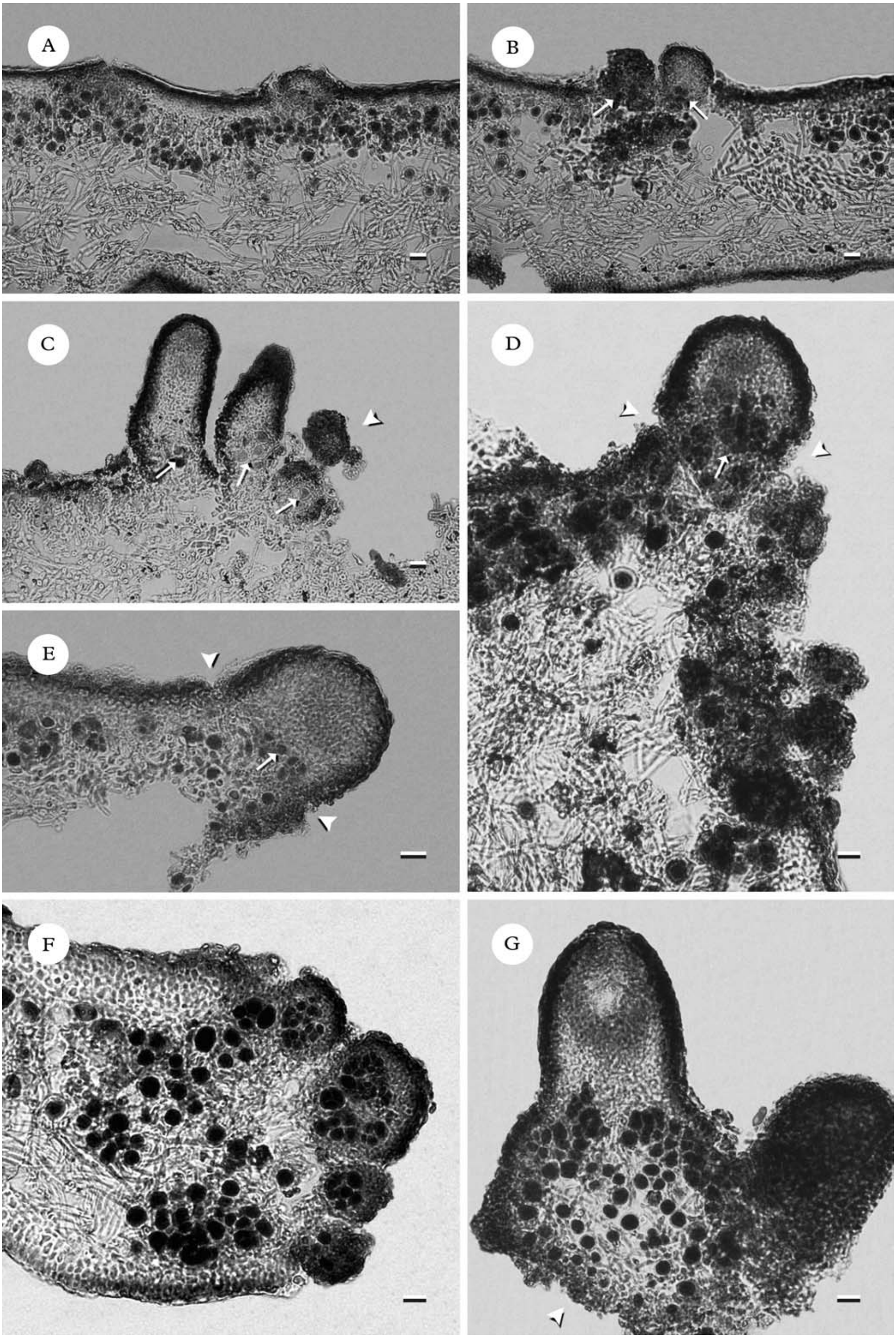
Pycnidia numerous, inducing the formation of pycnoisidia, up to 200 µm diam., globose to elliptical, tips brown-black to black, with algal cells beneath, wall with more than one layer. *Pycnoconidia* citriform, sometimes slightly curved, 4–6(–7) × (1–) 1·5–2 µm.

Chemistry and spot tests. Alectoronic, α-collatolic and 4-*O*-methylphysodic acids as major substances, physodic acid as minor substance, atranorin, chloratranorin and five unidentified substances in traces or absent; cortex HNO_3-; medulla K − , C − , KC+ rose-red, Pd − , I − .

Distribution and habitat. According to our data, *Melanelia sorediella* has a limited distribution and is currently known from the Schwarzwald in Germany (Poelt & Vězda 1981), the Alps in Austria (Hafellner & Türk 2001) and Switzerland (Lettau 1918, type locality) to the Pyrenees (Andorra) and the siliceous high mountains of the north-west quadrant of the Iberian Peninsula (Portugal and Spain). It is an orophilous lichen, living on open ± humid acid rocks.

In the Iberian Peninsula, *Melanelia sorediella* seems to be restricted to the oromediterranean and cryoromediterranean belts of the Mediterranean region (Beira Alta province in Portugal; León, Madrid, Segovia and Zamora in Spain) and to the subalpine to alpine belts of the Eurosiberian region (Ordino in Andorra; Asturias in Spain). It has a peculiar ecology, growing from 1650 to 2480 m altitude, on moving, medium to large sized block stream rocks in talus slopes or in polished glacier moraines. More rarely, it grows on low rocky outcrops. *Melanelia sorediella* is especially frequent on ± horizontal or vertical surfaces of block streams with large boulders of the Sistema Central Ibérico, in Spain and Portugal (van den Boom & Jansen 2002), where it develops the biggest thalli and in a few sites lives side by side with *M. commixta*. On exposed rock outcrops, it prefers to grow between the ground and the apices, covering ± vertical and narrow protected rock fissures. In all cases, the sites are sunny, slightly to moderately exposed to the wind and covered by snow in winter; in some cases it grows on silicicolous mosses. Currently, and just like the two other species studied, the meridional limit of the distribution of *M. sorediella* in south-western Europe (Fig. 1C) seems to be the central mountains of the Iberian Peninsula (Sistema Central Ibérico).

Remarks. Looking at the upper thallus surface of *Melanelia sorediella*, both the lamina and the lobe margins are profusely covered by whitish soralia-like areas, strongly associated with darker brown to black tips of isidia-like outgrowths (Fig. 2). The isidia-like outgrowths correspond to detachable pycnidia (Fig. 2C), in different developmental stages, with hyphae and algal cells at the base (Figs 3C–G). The soralia-like areas are interruptions in the cortex with loosely packed medullar hyphae, resulting from the detachment of those pycnidia with algae (Fig. 2C), which probably suggested the original epithet of the taxon (Lettau 1918; Hillman 1936). We have called these novel structures that can serve for vegetative symbiotic reproduction, pycnoisidia. The


A
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term may also be given to the type of diaspore produced by a combination of corticated budding proliferations of the thallus surface with pycnidia (Poelt 1980, 1995). The absence of apothecia and pseudocyphellae and the production of pycnoisidia associated with soralia-like areas, are the most characteristic features of *M. sorediella*. A description of the development of pycnoisidia is given in the following section.

Development of pycnoisidia. The upper cortex of the dorsiventrally structured foliose thallus of *Melanelia sorediella* is frequently interrupted by the development of pycnidia, in the lamina as well as in the margins (Figs 2 & 3). In the lamina, the pycnidial primordia, strongly stained with lactophenol cotton blue, grow out from the upper algal layer by breaking and degenerating parts of both, upper cortex and epicortex (Figs 3A & B). Some algal cells are trapped in the pycnidial primordia, forming the pycnoisidia. In the margins of the lobes, which are active pseudomeristematic growth areas in macrolichens (Honegger 1996), the pycnidial primordia grow out from the cortical layer, and soon the cortex degenerates around its base (Fig. 3E). Again, some algal cells are included at the base of the generative pycnidial tissue. During their development and growth, the already organized pycnoisidia, both laminal and marginal, tend to lie, sessile or shortly peltate, on thallus projections, always carrying corticated fragments of thallus with algal cells beneath them (Figs 3C, D & G). The pycnoisidia cluster in delimited areas of the lichen surface and margins, taking on the appearance of punctiform or diffuse isidiate-sorediate zones, especially in earlier stages (Fig. 2C). Finally, the pycnoisidia break off and can function as vegetative symbiotic diaspores.

After successive pycnoisidium formation and further detachment, the soralia-like areas appear naked, as more or less large fissures with only loosely packed medullar hyphae, exposed to external environmental conditions (Fig. 2C). In the margins of these fissures, where algal cells and cortex remnants already exist, new pycnoisidia may develop, increasing their size and merging together with other fissures. Such areas of exposed medulla probably act as pseudocyphellae. Although this cortical degeneration is produced to different extents, we have never observed it to occur without the involvement of the conidiomata.

The detachment of pycnoisidia is probably a consequence of their own developmental process plus external agents. In this way, the pycnoisidia might have a dual vegetative function: (i) production and dispersion of conidia, although most of the pycnoisidia observed have immature or closed pycnidia and only large pycnoisidia have mature ones (Fig. 3G), and (ii) the simultaneous dispersion of algal cells and fungal hyphae.

In older central parts of the *Melanelia sorediella* thallus, the pycnoisidia that have still not detached alter their primary functions and begin to grow again. They become larger and form detachable thallus scales (Fig. 2D). These scales continue their

FIG. 3. *Melanelia sorediella*, thallus cross-sections in lactophenol cotton blue of different developmental stages of detachable pycnoisidia, showing the accompanying algae (arrows) and the pycnidial generative tissue (darker stained hyphae) (*Rico* 1239, MAF). A, early laminal pycnidial primordia breaking the upper cortex, showing some algal cells included in the generative tissue; B, young laminal pycnoisidia, carrying algae at the base; C, laminal pycnoisidia with algae at the base, the pycnidia are still immature and new pycnoisidia grow near the exposed medulla (arrow head) after some pycnoisidia have broken off; D, laminal pycnoisidium showing the rupture zone with degenerating upper cortex (arrow heads), new propagules are in formation probably involving pycnidial generative tissues and algal cells (granules in centre-right); E, marginal pycnoisidium showing the rupture zone with degenerating cortex (arrow heads); F, marginal formation with new intensely stained pycnoisidia after detachment of older ones, note that before cutting the propagule tips appear black coloured; G, large pycnoisidium of thallus centre in transition to a lobulus, showing a pseudocorticated layer (arrow head) and mature pycnidium. Scales: A–G = 10 μm.

growth, transforming into more or less ascending lobuli, producing at the same time new marginal pycnoisidia (Fig. 2D). In some cases the lobuli completely cover the centre of the thallus, and replace the older parts underneath. Thus, the development of new lobuli in this way is here related to regeneration processes in older central parts of the *M. sorediella* thallus. Similar regeneration structures, but involving non-detachable pycnidia, have been previously described in *Cetraria islandica* (L.) Ach. (Jahns & Schuster 1981; Jahns 1988).

During the development of pycnoisidia, the upper cortex of the normal thallus degenerates and is replaced by the pycnidial wall (darker than cortex) and by a pigmented new cortex, probably for algal protection. After detachment of pycnoisidia, and if algal cells are available, new pycnoisidia will be secondarily produced (Figs 3D & F). In these cases and in earlier developmental stages, it is difficult to see whether the new outgrowths with algae and hyphae, include within them pycnidial primordia. Although the production of 'simple' isidia, blastidia or soralia cannot be excluded, the colour of the bud apices, dark brown to black and always darker than the thallus surface, suggests that earlier stages of pycnidial development are involved. Moreover, the pycnidia seem to be the active inducers of the development and production of pycnoisidia and always participate in the construction of all the structures described here.

Summarizing, from the edges to the centre of the *M. sorediella* thallus, one can see a marginal zone of young and entire lobes, mainly without warts and cortex interruptions, followed by a broad portion of the thallus with detachable pycnoisidia and soralia-like areas (with pseudocyphellae function) that increasingly cover the lamina and lobe margins. Finally this broad portion is progressively replaced by a zone in which pycnoisidia gradually grow into profuse lobuli (Fig. 2A). The new lobuli grow into new small thalli, overgrowing one another and covering the old thallus. The multifunctional ability of the propagative and regenerative thallus structures of *M. sorediella* described above seems to be clear (Ott *et al.* 1993). It is important to note that in the sterile lichen *M. sorediella*, the transformation of thallus organs into one another follows certain patterns, which have also been observed in other *Parmeliaceae* (Beltman 1978). In this way, we can see similarities between the development of the *M. sorediella* organs described above and the growth processes of the isidia, pseudocyphellae and lobuli observed in *Parmelia saxatilis* (L.) Ach. (Jahns 1984), but in contrast to *P. saxatilis*, in *M. sorediella* the conidiomata development induces the process.

In addition, we have observed in *Tuckermannopsis chlorophylla* pycnoisidia similar to those described above in *M. sorediella*. Although Beltman (1978) does not indicate any relationship between the so called sorediate-isidiate structures of the thallus margins of *T. chlorophylla* with pycnidia development [Beltman 1978: 117; sub *Cetraria scutata* (Wulfen) Poetsch], in the figures of the species (*loc. cit.* plate 42) ostiolate pycnidia can be seen in soredia-like areas. The pycnoisidia probably develop in other *Parmeliaceae* species, especially in cetrarioid groups, but more detailed studies are needed.

We can hypothesize that the development of pycnoisidia in the sterile lichen *M. sorediella*, is probably related to its life strategy (Jahns & Ott 1997). The lichen prefers to grow on moving blocks of screes or talus slopes above the tree level, which have a poorly developed lichen flora (van den Boom & Jansen 2002). In those talus slopes, rocks and blocks are subjected to the action of physical weathering processes, and the consequential fragmented blocks are relatively easily transported, carrying lichens and offering new free rock surfaces for lichen colonization. So, the function of pycnoisidia seems to be to provide propagules with a fast growth rate for thallus regeneration and recolonization in movable substrata of neighbouring rock surfaces.

In some species of cetrarioid *Parmeliaceae*, occasionally soredia occur, apparently induced by external causes, such as infections from lichenicolous fungi (Kärnefelt 1979, 1986). In this way, the lichenicolous hyphomycete *Taeniolella rolfii* Diederich & Zhurb. was described as the inducer of the formation of 'dark soralia' in the lichen *Cetraria nigricans* Nyl. (Diederich & Zhurbenko 1997). In a subsequent work (Diederich & Zhurbenko 2001), it was reported as a widespread lichenicolous fungus in northern Europe and Canada producing soralia-like infections on several species of *Cetraria* and on *Cetrariella delisei* (Bory ex Schaer.) Kärnefelt & A. Thell. Consequently we searched for that possibility in our species. However, using the morphological and chemical methods described above, no infections were observed inducing the formation of pycnoisidia in the thallus of *M. sorediella*. Moreover, we did not find any lichenicolous fungi in the specimens studied.

Additional specimens examined. **Andorra:** *Ordino*: estación de esquí Ordino-Arcalis, final de la pista, Port de Rat, laderas pedregosas del Estany de Port de Rat, 31TCH7520, 2480 m, sobre rocas pizarroso-esquistosas, 2002, *V. J. Rico* 3618 (MAF).—**Portugal:** *Beira Alta*: Serra da Estrêla, pico da Estrêla, cerca del Alto da Torre, 1980 m, sobre granito, exposición NE, 6 vi 1990, *J. M. Pizarro & S. Sardinero* (MAF, sub *Cetraria commixta* f. *sorediella*); *ibid*., 9·5 km SSW of Manteigas, Cantaro Raso, 1850 m, 29TPE194649, 7°35·6′W/40°19·5′N, NNE exposed granite blockstream, 1998, *P. P. G. van den Boom* 20319 (hb. v. d. Boom, sub *C. commixta* f. *sorediella*). – **Spain:** *Asturias*: Cangas de Narcea, puerto de Leitariegos, 1850 m, 6 ix 1980, *A. Crespo*, *E. Barreno*, *A. G. Bueno*, *L. G. Sancho & V. J. Rico* (MAF, sub *Cetraria commixta*); *ibid*., cercanías, 1650 m, 29TQH06, sobre cuarcita, orientación N, 10 vi 1990, *V. J. Rico* (MAF, sub *C. commixta* f. *sorediella*); *ibid*., ascensión al pico de Cueto de Arbas desde el puerto de Leitariegos, 1900 m, 29TQH16, sobre cuarcitas, orientación N, 10 vi 1990, *V. J. Rico* (MAF, sub *C. commixta* f. *sorediella*). *Castilla y León*, *León*: Macizo de El Teleno, ascensión al pico de El Teleno, 2080 m, 29TQG1492, sobre cuarcita, en cueva, 15 v 1989, *A. Terrón* 1153/2, 1157 (LEB, sub *C. commixta* and *C. commixta* f. *sorediella*); *ibid*., alto de El Palo, 1900 m, 29TQG1192, sobre areniscas, superficie horizontal de cima, 1989, *A. Terrón* 653 (LEB, sub *C. commixta*). *Castilla y León*, *Segovia*: Sierra Guadarrama, N of Pto de Navacerrada, 1800 m, in sloping *Pinus* forest, on shaded granite, 1987, *P. P. G. van den Boom* 6235 (hb. v. d. Boom, sub *C. commixta* f. *sorediella*). La Granja, carretera del puerto de Navacerrada al puerto de Cotos, km 45, Loma del Noruego, 1940 m, 30TVL1716, pinar de *Pinus sylvestris*, sobre granito, 2000, *V. J. Rico* 3515 (MAF). *Castilla y León*, *Zamora*: Galende, Sierra de La Cabrera, alrededores de la Laguna de los Peces, 1690 m, 30TPG8771, sobre pizarras soleadas, 1999, *V. J. Rico* 3382 (MAF, hb. v. d. Boom). *Madrid*: Sierra de Guadarrama, pico de El Escaparate, 1900 m, granito, 20 xi 1981, *L. G. Sancho* (MACB, MAF, sub *C. commixta*); *ibid*., pico de Cabezas de Hierro, 2200 m, granito, 20 viii 1983, *L. G. Sancho* (MAF, sub *C. commixta*); *ibid*., Manzanares el Real, alrededores del pico de La Bola del Mundo, 2220 m, 30TVL177156, sobre gneises soleados, 1987, *V. J. Rico* 1239/1-30 & *E. Manrique* (MAF, TU, hb. v. d. Boom).

Discussion

In the Iberian Peninsula, we have distinguished three different species within the *Melanelia commixta* group based on morphology, reproductive mode, chemistry and distribution. The two most common species are *M. commixta* and *M. sorediella* while *M. hepatizon* is less frequent. The three species show similar distributions and are found at altitudes from 1500 m upwards, on exposed acid rocks in the mountains of the centre and north of the Iberian Peninsula (Fig. 1).

From the examination of more than 125 herbarium specimens from the Iberian Peninsula and from other sites of Europe and North America, *Melanelia hepatizon* can be clearly differentiated from *M. commixta* and *M. sorediella*. This agrees with previous phylogenetic studies based on molecular, morphological and chemical features, in which *M. hepatizon* and *M. commixta* have been shown to be only distantly related (Thell *et al.* 2002; Blanco *et al.* 2004); *Melanelia commixta*, together with the genus *Cetrariella* Kärnefelt & A. Thell, being placed in a separate clade from *M. hepatizon* (Thell *et. al.* 2002). Although *M. commixta* has been transferred from *Cetraria* to *Melanelia* (Thell 1995*a*), mainly on the basis of external morphological similarities, we have observed some noteworthy differences in the type of conidia, reproductive mode and chemistry that also suggest a different generic placement for *M. commixta* (and *M. sorediella*). The Iberian specimens of *Melanelia commixta* studied are characterized by the following features: apothecia rarely present, surface with pseudocyphellae and without pores, lower side light coloured, conidiomata more abundant on the margins than on the surface and conidia citriform (3·5–7 × (1–)1·5–2(–3) µm). Moreover two chemical races have been found: one of them without lichen substances (Chemotype III) and another accumulating α-collatolic acid (orcinol depsidone) as main substance and sometimes showing traces of atranorin (Chemotype I). In contrast, *M. hepatizon* has the following features: thallus sterile, lower side black, surface with pseudocyphellae, epicortex with pores, conidiomata abundant on the margins and the surface, conidia bifusiform with two dumb-bell-shaped swellings (4–7 × 1–1·5 µm) and with stictic and norstictic acids (β-orcinol depsidones) as main substances.

When comparing *Melanelia sorediella* with *M. commixta*, some differences are also evident. Thus in *M. sorediella*, the lobes are thicker and not always divided and may be concave and also convex in the same specimen, the thallus is slightly thicker (up to 320 µm) lacking true pseudocyphellae and no apothecia have been observed. In addition, *M. sorediella* clearly differs from *M. hepatizon* not only in the morphology of thallus surface and absence of true pseudocyphellae but also in the type of conidia and chemistry. Furthermore, one of the principal differences between *M. sorediella* and the other two species refers to the presence of symbiotic vegetative propagules, here named pycnoisidia. These structures are commonly grouped forming zones similar to soralia and arise from the profuse development of conidiomata.

In spite of the differences mentioned above, *Melanelia commixta* is close to *M. sorediella* when taking into account the similarities in the type of conidia (*cf.* Thell 1995*a*), epicortex without pores and chemistry. Moreover, in a few sites in the Iberian Peninsula both taxa were sometimes found living together (Fig. 1A & C). Consequently, and on the basis of its reproductive mode, these species could be considered as a 'species-pair' or 'Artenpaar' in the sense of Poelt (1972). Recent studies, mainly based on molecular data, have criticized the species-pairs concept in lichenized fungi. Molecular analyses based on ITS sequences, carried out in *Arthoniales* and *Physciaceae* have demonstrated that the so-called species-pairs are not monophyletic (Lhotander *et al.* 1998*a*, 1998*b*; Cubero *et al.* 2004). Furthermore, the species-pairs concept was also studied using β-tubulin, ITS and group I intron sequences in *Physcia aipolia* (Ehrh. ex Humb.) Fürnr. (sexual) and *P. caesia* (Hoffm.) Fürnr. (asexual). The results obtained from combined sequences suggested both taxa to be conspecific (Myllys *et al.* 2001). Similar results were obtained in *Usnea florida* (L.) Weber ex F. H. Wigg. (sexual) and *U. subfloridana* Stirt. (mainly asexual) (Articus *et al.* 2002). However, in the case of recently diverged species, a single locus such as ITS, seems not to be sufficient evidence to reject species based on morphology, reproductive mode or chemistry and the use of several genetic loci has been suggested to delimit species according to a phylogenetic species concept. For a better understanding of the species concept in lichenized fungi, these phylogenetic species should be corroborated with morphological, chemical and ecological and biogeographical evidence (Grube & Kroken 2000). In the same way, some studies using gene genealogies of 6 and 12 loci have been carried out in order to recognize species boundaries in the genus *Letharia* (Th. Fr.) Zahlbr. (Kroken & Taylor 2001). In this study, not only was a species pair recognized but at least six phylogenetic species were found within the genus *Letharia*: one species was exclusively sexual, three species were sexual and isidiate and two sorediate.

Although no phylogenetic molecular analyses have been made in our study, *Melanelia commixta* and *M. sorediella* can be considered as two separate species based on their type of reproduction and thallus morphology. *Melanelia commixta* is a sexual species in which no soralia are formed and *M. sorediella* is asexual in which the most noteworthy morphological feature is the formation of pycnoisidia grouped in soralia-like structures in the thallus. A similar variation in reproductive structures has also been reported in other foliose lichens such as *Xanthoria* (Fr.) Th. Fr., *Hypogymnia* (Nyl.)

Nyl. and *Parmelia* s. lat., as well as in other cetrarioid (Thell 1996) and umbilicarioid lichens (Codogno *et al.* 1989), with important taxonomic and nomenclatural implications (Poelt 1995).

According to Thell *et al.* (2002), *Melanelia commixta* (and probably *M. sorediella*) is phylogenetically close to the genus *Cetrariella*. However, a new generic placement for the former species could be proposed on the basis of the following features: foliose thallus, citriform conidia, α-collatolic and alectoronic acids as major substances, and saxicolous silicicolous habitat. Although *M. commixta* has been recently transferred to *Cetrariella* (Thell *et al.* 2004), only further phylogenetic studies will show whether *Cetrariella* will survive as a separate genus.

Conclusions

Three species, *Melanelia hepatizon*, *M. commixta* and *M. sorediella*, can be recognised in the *Melanelia commixta* group in the Iberian Peninsula. *Melanelia hepatizon* is clearly distinguished from *M. commixta* and *M. sorediella* by the presence of bifusiform conidia, pored epicortex and stictic and norstictic acids. According to Thell *et al.* (2002), these morphological and chemical features would indicate that *M. commixta* group is polyphyletic. *Melanelia sorediella* is considered here as a different species from *M. commixta*, mainly because of the absence of pseudocyphellae and apothecia, and the development of pycnoisidia in the thallus; a new type of vegetative propagule named and described here. The pycnoisidia of *M. sorediella*, are induced by the development of pycnidia, which include algae and vegetative hyphae. The surrounding cortex then degenerates and facilitates the breaking off of the pycnoisidia. Soralia-like areas are a consequence of pycnoisidia development. In older parts of the thallus, non-detached pycnoisidia develop into lobuli and then into secondary thallus, thus regenerating it. Pycnoisidia act as propagules that can be involved in a rapid recolonization of mobile substrata and rock surfaces. Two chemotypes (I: α-collatolic as main substance; III: without lichen substances) have been detected in the Iberian specimens of *M. commixta* examined. In south-western Europe, the meridional limit of the distribution of the three species studied, *M. hepatizon*, *M. commixta* and *M. sorediella*, seems to be located in the mountains of the central part of the Iberian Peninsula (Sistema Central Ibérico). The morphological, chemical and biogeographical observations presented indicate that *M. commixta* and *M. sorediella* represent two different species that could also correspond to two phylogenetic species. However, this matter should be corroborated with molecular phylogenetic analyses.

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