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Miriquidica invadens, an obligate youth parasite on *Sporastatia*, with remarks and a key to species of the *M. griseoatra* group

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Abstract: The new species *Miriquidica invadens* Hafellner, Obermayer & Tretiach is described and reported from Austria, Bulgaria, Italy, Switzerland, France and Spain. From a morphological point of view the species belongs to the *M. griseoatra* group, in which it is, so far, the only constantly lichenicolous taxon. Chemically it is characterized by the regular presence of miriquidic acid, stictic acid, and constictic acid (in variable amounts). It starts its ontogenetic life cycle as an obligate youth parasite on *Sporastatia*, usually *S. polyspora*.

Morpho-anatomical treatments of other species of the *Miriquidica griseoatra* group occurring in Europe, based on the examination of type material, are also presented. According to the characters exhibited by the lectotype of *Lecidea contigua* var. *griseoatra* Flot., *M. griseoatra* (Flot.) Hertel & Rambold is the correct name for a montane species with subdivided areoles and immersed, laterally adnate apothecia with a pigmented hypothecium. Specimens exhibiting this set of characters were usually named *M. obnubila* auct. According to the characters observed on the lectotype of *Lecidea* (*Biatora*) *obnubila* Th. Fr. & Hellb., *M. obnubila* (Th. Fr. & Hellb.) Hertel & Rambold is a species with sessile apothecia with a hyaline hypothecium. *Lecidea subplumbea* Anzi does not constitute a heterotypic synonym of *Lecidea griseoatra* (Flot.) Schaer. but is the legitimate name at the species level for *Miriquidica griseoatra* sensu auct., and therefore *M. subplumbea* (Anzi) Cl. Roux is the correct name for that taxon. *Lecidea inserena* Nyl. is confirmed as a heterotypic synonym of *Lecidea subplumbea* Anzi. *Lecidea plumbea* Garov. ex A. Massal. is an earlier heterotypic synonym of *Miriquidica limitata* Hertel & Rambold and, therefore, the new combination *M. plumbea* (Garov. ex A. Massal.) Hafellner, Obermayer & Tretiach is introduced.

Lectotypes are designated for *Lecidea contigua* var. *griseoatra* Flot., *Lecidea inserena* Nyl., *Lecidea obnubila* Th. Fr. & Hellb., *Lecidea plumbea* Garov. ex A. Massal., and *Lecidea subplumbea* Anzi. A key to the taxa of the *M. griseoatra*-group and other *Miriquidica* taxa with a grey thallus is provided.

Key words: Holarctic, *Lecanorales*, lichenicolous lichens, lichenized Ascomycota, mycota of the Alps

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Introduction

The genus *Miriquidica* was introduced by Hertel & Rambold (1987) for a group of mainly *Lecidea*-like saxicolous lichens, most of them with non-carbonized apothecia, *Lecanora*-type asci and frequently with the presence of miriquidic acid and related compounds in the thallus. In the Zahlbrucknerian system, *Miriquidica* species were formerly scattered in the genera *Lecidea*, *Lecanora*, *Lecidella*, and *Aspicilia*. Detailed generic descriptions can be read either in the protologue or in the revision of the sorediate taxa (Owe-Larsson & Rambold 2001), or in the regional treatments by Andreev (2004), Nash *et al.* (2004), and Giavarini *et al.* (2009). The genus is generally accepted in floras and checklists, although its relation to *Protoparmelia* needs a critical re-evaluation because some of the species in both genera exhibit striking similarities in morpho-anatomical characters and secondary thallus chemistry. The major taxonomic problems

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in *Miriquidica* have already been settled by Hertel & Rambold (1987). Since then, additions to the taxonomy of the genus have been published by Rambold & Schwab (1990), Hertel (1991), Timdal (1993), Rambold *et al.* (1996), Andreev (2001, 2004), Owe-Larsson & Rambold (2001), Hertel & Andreev (2003), Nash *et al.* (2004), Fryday (2008), Lendemer & Knudsen (2008), and Øvstedal *et al.* (2009).

Although most of the specimens collected in the Holarctic should be identifiable with the key compiled by Andreev (2004), the taxonomy of one of the distinguishable species groups, the taxa around *M. griseoatra* auct., was not previously well settled. The term '*M. griseoatra* group' is applied here to include all taxa with a more or less dark grey, areolate, spreading thallus and black apothecia. Although no phylogenetic analysis has been undertaken to date, we are confident that in such a study these species will be shown to belong to one clade.

Commonly, only *M. leucophaea* (Flörke ex Rabenh.) Hertel & Rambold, with a pale, whitish grey thallus and brown to black-brown apothecia but otherwise similar morphology and anatomy, is easily distinguishable in the group. Even *M. griseoatra* itself remained unevaluated due to the lack of authentic material accessible to revisers. On the other hand, two names are commonly given as purported heterotypic synonyms of *M. griseoatra* auct.: *Lecidea subplumbea* Anzi and *Lecidea inserena* Nyl., although, as no type material had been available for previous monographers, some doubt remained for these proposed synonymies.

The application of the name *Lecidea subplumbea* was previously entirely unresolved. Because two chemical strains had been detected within *M. griseoatra* auct. (in the delimitation of Hertel & Rambold 1987), some authors argued that *Lecidea subplumbea* might be a possible name for strain 2 (chem.: miriquidic, stictic) (Hertel & Rambold 1987; Andreev 2004: 23), although they had indicated that the only material of Anzi at their disposal (Anzi, *Lich. Rar. Langob.* no. 573) pertained to strain 1.

During fieldwork, we regularly came across a lichenicolous *Miriquidica*, all our attempts at the identification of which failed. Lichenicolous behaviour is well known in *Miriquidica* (for an overview see Rambold & Triebel 1992). Namely, for *M. intrudens* parasitism was documented by several authors and from many localities (see e.g., Owe-Larsson & Rambold 2001) and in this species it is regarded as more or less obligate. For some additional *Miriquidica* species, including taxa of the *M. griseoatra* group, facultative parasitism is occasionally mentioned in the literature. As far as we could trace, the first person who pointed to the presence of a lichenicolous lichen species that would currently be classified in *Miriquidica* was Minks (1896: 85). He investigated a specimen from Tyrol (Austria) of what he had determined as "*Lecidea inserena* Nyl." on "*Lecidea cinerea* (Schaer.)" [i.e., *Sporastatia polyspora* (Nyl.) Grummann]. Further notes on lichenicolous growth of taxa in this species group were published by Hertel (1970: 428, sub *Lecidea subplumbea* on supposed *Lecidea* sp.) and Obermayer (1993: 130, sub *Miriquidica* sp. 1 on *Sporastatia polyspora*).

Recent re-examination of type material of *Lecidea subplumbea* Anzi and *Lecidea plumbea* Garov. ex A. Massal. gave us the opportunity to resolve the problem of our unidentified collections of the parasitic *Miriquidica* sp., along with other problems concerning the nomenclature and delimitation of taxa within the *M. griseoatra* group. A morpho-anatomical and chemotaxonomic study has thus been carried out, and extended to include further representatives of the genus.

Material and Methods

More than 400 specimens were used for the study. External morphology was examined with a dissecting microscope (WILD M3, 6, ×4 – 40), and anatomical studies of the thallus and the ascomata were carried out using a compound microscope (LEICA DMRE, ×100 – 1000). Sectioning was performed with a freezing microtome (LEITZ, sections of 12–15 mm) but hand-cut sections were also used, especially for ascus analysis. Preparations were mounted in water and, when necessary, treated with lactic acid-cotton blue (MERCK

13741) for added contrast. Amyloid reactions in hymenia were observed both progressively and regressively by the use of Lugol's reagent (MERCK 9261). Conidiogenesis of pycnoconidia was studied in erythrosin B (ALDRICH 19,826-9) in 10% ammonia. Sections were not pretreated with KOH, unless otherwise stated. Measurements refer to dimensions in tap water.

Secondary chemistry was investigated by TLC (Culberson 1972; Culberson & Ammann 1979; Culberson & Johnson 1982) and substances are noted in square brackets. Other microchemical tests follow Orange *et al.* (2001). For identification of lichen substances, the catalogue compiled by Elix & Ernst-Russell (1993) has been used. Chemical analyses were performed by W. Obermayer if not otherwise stated.

Abbreviations for institutional herbaria follow Holmgren *et al.* (1990). Author's abbreviations are those proposed by Brummitt & Powell (1992).

Other abbreviations: cs – constictic acid, l – lobaric acid, m – miriquidic acid or miriquidic acid syndrome, n – norstictic acid, p – protocetraric acid, s – stictic or stictic acid syndrome, u – unknown substance, 0 – no lichen substance detected; J. H. – J. Hafellner.

In addition to the specimens cited together with the treated species, the following material has been used for comparision (label data shortened, lichen compounds analysed by TLC):

Miriquidica atrofulva (Sommerf.) A. J. Schwab & Rambold. **Austria:** *Salzburg*: Schladminger Tauern, Lungau, Zinkwand, 47°16′10″N / 13°40′55″E, 2300 m, GF 8748/1, 1995, *J. H.* 50390 & *M. Möslinger* (GZU) [s]. *Steiermark* (*Styria*): Schladminger Tauern, Giglachseen S. Schladming, Vetternkar ESE Ignaz-Mattis-Hütte, Sauberg, 47°16′40″N / 13°40′10″E, 2190 m, GF 8748/1, 1993, *J. H.* 50146 & *M. Möslinger* (GZU) [s].

Miriquidica complanata (Körb.) Hertel & Rambold. **Austria:** *Tirol* (*Tyrol*): Ötztaler Alpen, Kaunertal, S. Gepatschhaus, Weg zur Rauhekopfhütte, 2200–2500 m, GF 9130, 1972, *J. Poelt* (GZU) [m]. *Salzburg*: Schladminger Tauern, Lungau, Lessachtal, von Lasshofer Hütte zum Landschitzsee, 1300 m, GF 8748, 1981, *J. Poelt* (GZU) [m]. *Kärnten* (*Carinthia*): Hohe Tauern, Kreuzeck-Gruppe, Turgger Alm gegen Schwarzsteinwände, 46°43′N / 13°09′E, 2000–2100 m, GF 9244/2, 1994, *J. Poelt* (GZU) [m]. *Steiermark* (*Styria*): Schladminger Tauern, NW Ignaz-Mattis-Hütte gegen Kampzähne, 2050–2150 m, GF 8747, 1991, *J. Poelt* (GZU) [m].—**Germany:** *Baden-Württemberg*: Schwarzwald, Belchen, W. Belchenhaus, 1300–1350 m, 1967, *J. Poelt* 4647 & *V. Wirth* (GZU) [m].—**Norway:** *Telemark*: Haukelifjell bei Vågslid, bei Haukeliseter, 1976, *A. Buschardt* & *J. Poelt* (GZU) [m]. Note: Thallus infested by *Endococcus complanatae*.—**Great Britain:** *Scotland*: V. C. 97, Westerness, Morvern, below Coire an Lagain, 1992, *B. Coppins*, *B. W. James* & *J. Poelt* Sc 92/230 (GZU) [m].—**Greenland:** Godhavn, at Arctic Station, N of Lange Kær, 69°15′N / 53°32′W, 40 m, 1952, *P. Gelting* 18146 (GZU) [m].

Miriquidica deusta (Stenh.) Hertel & Rambold. **Finland:** Schärenhof um Turku, Korppo / Utterskär, 1965, *J. Poelt* 1783 (GZU) [l, u].—**France:** *Korsika*: Dept. Haute-Corse, Golo Tal, *c.* 5 km E Ponte Leccia, 170 m, 1993, *H. Mayrhofer* & *J. Prügger* (GZU) [l, u].—**Italy:** *Sardinien*: Prov. Nuoro, Monte del Gennargentu, Bruncu Spina, Punta Paulinou, 1700–1790 m, 1985, *P. L. Nimis* & *J. Poelt* (GZU) [l, u].—**Slovakia:** *Stiavnické Vrchy*: Kamenné More, Kamenna bei Vyhne, 330–490 m, 1993, *I. Pišút* & *J. Poelt* 93-460 (GZU) [l, u].—**Sweden:** *Uppland*: Stockholms skärgård, Runmarö, 1927, *E. P. Vrang* (GZU) [l, u]. *Bohuslän*: Koster-Archipel SW Strömstad, Sör-Koster, Straße Bergdalen – Ekenäs, 58°53′N / 11°01′E, 1990, *J. Poelt* (GZU) [l, u].

Miriquidica garovaglii (Schaer.) Hertel & Rambold. **Austria:** *Vorarlberg*: Rätikon, Kreuzspitze, WSW Schruns, 2280–2353 m, 1986, *J. Poelt* (GZU) [m, s, c]. *Kärnten* (*Carinthia*): Gurktaler Alpen, Schoberriegel, SE Turracherhöhe, 2150 m, GF 9049, [host: *Aspicilia* spec.], 1985, *H. Mayrhofer*, *J. Poelt et al.* (GZU) [m, s]. *Steiermark* (*Styria*): Seckauer Tauern, Hämmerkogel N Seckau, ober Goldlacke, 47°20′30″N / 14°45′05″E, 2100 m, GF 8654/4, 2001, *J. H.* 57567 (GZU) [m, s].—**Svalbard:** *Spitzbergen*, Adventfjorden, Longyearbyen, Trollsteinen-Gipfelmassiv, 800 m, 1974, *H. Ullrich* (GZU) [m, s], anal. by S. Kojetinsky.

Miriquidica instrata (Nyl.) Hertel & Rambold. **Austria:** *Kärnten (Carinthia)*: NP Hohe Tauern, Schober-Gruppe, Gradental W Döllach, bei Ad. Noßberger Hütte, [46°57′20″N / 12°46′50″E], 2500 m, GF 9042/2, [host: *Aspicilia* spec.], 1988, *J. H.* 23051 & *M. Walther* (GZU) [m]. *Steiermark (Styria)*: Gurktaler Alpen, Turracherhöhe, N Turrachsee, 46°55′30″N / 13°52′40″E, 1850 m, GF 9049/3, [host: *Aspicilia* spec.], 2002, *J. H.* 64129 (GZU) [m].—**France:** *Korsika*: Dept. Haute-Corse: von Corte nach Ajaccio, 1,5 km S Venaco, 460 m, [host: *Rhizocarpon* subgen. *Rhizocarpon* spec.], 1993, *J. H.* 31840 (GZU) [m].

Miriquidica intrudens (H. Magn.) Hertel & Rambold. **Austria:** *Kärnten* (*Carinthia*): Saualpe W Wolfsberg, Sandkogel, Wirtsofen NNE Offnerhütte, 46°51′05″N / 14°41′00″E, 1730 m, GF 9154/1, [host: *Rhizocarpon geographicum*], 2009, *J. H.* 75066 & *L. Muggia* (GZU) [m]. *Steiermark* (*Styria*): Wölzer Tauern, Greim 11 km NW Oberwölz, 47°14′50″N / 14°09′05″E, 2470 m, GF 8750/4, [host: *Rhizocarpon geographicum*], 2006, *J. H.* 69938 & *L. Muggia* (GZU) [m].—**Italy:** *Piemonte*, Prov. Torino, Alpi Cozie, W Pinerolo, Punta Cialáncia S Perero, 44°53′00″N / 07°07′20″E, 2350 m, [host: *Lecidea* spec.], 2001, *J. H.* 69360 (GZU) [m]. *Trentino-Alto Adige*, Prov. Trento, Central Alps, Ortler-group (Stelvio-group), 8 km N Cógolo, La Cascata S Lago Lungo, 46°25′30″N / 10°41′00″E, 2575 m, [host: *Lecanora polytropa*], 2006, *J. H.* 69324 (with L. Muggia & M. Tretiach) (GZU) [m].

Miriquidica leucophaea (Flörke ex Rabenh.) Hertel & Rambold. **Austria:** *Tirol* (*Tyrol*): [Kitzbühler Alpen], Weg zum Roßgrubkogel, 6000 Fuß, [W] Pass Thurn, 1873, *F. Arnold* (M) [m]. *Kärnten* (*Carinthia*): Saualpe W Wolfsberg, zwischen Ladinger Spitz und Gertrusk, Kaiserofen, 46°51′25″N / 14°38′45″E, 2030 m, GF 9153/2, 2012, *J. H.* 80769 (GZU) [m]. *Steiermark* (*Styria*): Gleinalpe, Roßbachalpe S Gleinalmsattel, 1650–1750 m, 1981, *J. Poelt* (GZU) [m].—**France:** *Dept. Cantal, Auvergne*: Monts du Cantal, Puy de Peyre-Arse, 1760 m, 1980, *A. Bellemère* & *J. H.* 9475 (GZU) [m]. *Dept. Haute Savoie*, Montblanc-Gruppe, St. Ger-

vais, Les Contamines-Montjoie, N.D. de la Gorge, gegen Aig. des Glaciers, 1100–1400 m, 1981, *J. Poelt* (GZU) [m], *anal. S. Kojetinsky*.—**Norway:** *Hordaland*: Insel Sotra SW Bergen, Glesvaer, Gem. Sund, 1976, *A. Buschardt et al.* (GZU) [m], anal. S. Kojetinsky.—**Great Britain:** *Scotland*: V. C. 88, Mid Perthshire, Glen Lochay, Meall nan Subh, Grid 27(NN)/45.39, 770 m, 1991, *A. M. Fryday* 2106 (E) [m, u].

Miriquidica lulensis (Hellb.) Hertel & Rambold. **Sweden:** *Schwedisch-Lappland*: Vassijaure, 68°N, 800 m, 1925, *E. Frey* (G) [n]; as admixture: *Miriquidica nigroleprosa* [m].

Miriquidica nigroleprosa (Vain.) Hertel & Rambold var. *nigroleprosa*. **Austria:** *Kärnten* (*Carinthia*): Saualpe W Wolfsberg, Sandkogel NW Offnerhütte, 46°51′15″N / 14°39′50″E, 2010 m, GF 9153/2, [host: *Rhizocarpon geographicum*], 2009, *J. H.* 73440 & *L. Muggia* (GZU) [m]. *Steiermark* (*Styria*): Wölzer Tauern, Rettlkirchspitze NW Oberwölz, NE-Grat SW Neunkirchner Hütte, 47°15′45″N / 14°08′05″E, 2300 m, GF 8750/2, [host: *Rhizocarpon geographicum*], 2002, *J. H.* 68146 & *J. Miadlikowska* (GZU) [m].—**Italy:** *Calabria*: Prov. Reggio di Calabria, Aspromonte, Pietra Impiccata, 1700–1750 m, 1988, *J. Poelt* (GZU) [m].—**Switzerland:** *Kanton Bern*: Berner [Bernese] Alps, Grimselpass c. 20 km SE Meiringen, trail to Husegghütte, 46°33′35″N / 08°19′40″E, 2350 m, 2006, *J. H.* 69316 (GZU) [m].—**Canada:** *British Columbia*: Whistler Mountain, Mountain Hemlock zone, 50°07′N / 122°58′W, 1800–2000 m, 1994, *T. Goward* & *J. Poelt* (GZU) [m].

Miriquidica pulvinatula (Arnold) Hertel & Rambold. **Austria:** *Tirol* (*Tyrol*): Gurgl im Ötztal, Hohe Mut, 1877, *Arnold* (M, topotype) [m]. [no stictic!]; *ibid.*, 2350 m, 1878, *Arnold* = Arnold, *Lich. exs.* no. 758 sub *Lecidella pulvinatula* (M, lectotype) [m]. [no stictic!].

Miriquidica ventosa (Vain.) Timdal. **Russia:** *Magadanskaya oblast*: Yagodnisnki region, 20 km SSE Orotukan, 62°6′N / 151°51′E, 1992, *M. P. Zhurbenko* 92152 (GZU) [m].

Sporastatia testudinea (Ach.) A. Massal. **Austria:** *Steiermark* (*Styria*): Seckauer Tauern, Speikbichl S Mautern, 47°21′30″N / 14°49′00″E, 1870 m, GF 8654/2, 2000, *J. H.* 51653 & *A. Hafellner* (GZU); Gleinalpe, Speikkogel S St. Michael, 47°13′40″N / 15°02′55″E, 1980 m, GF 8756/3, 2000, *J. H.* 52103 & *A. Hafellner* (GZU).

Sporastatia polyspora (Nyl.) Grummann. **Austria:** *Steiermark* (*Styria*): Wölzer Tauern, Greim, 11 km NW Oberwölz, 47°14′50″N / 14°09′05″E, 2470 m, GF 8750/4, 2006, *J. H.* 67965 & *L. Muggia* (GZU). – Additionally the host lichen of the following specimens cited under *Miriquidica invadens* has been used for a screening of lichen compounds: *Hafellner* 23960, 26169, 57316, 57569, 62326, 75908, 80296. *Rechinger* 1684, *Tretiach* 38912.

Results

Miriquidica griseoatra (Flot.) Hertel & Rambold

Mitt. Bot. Staatssamml. München **23:** 385 (1987) [non *sensu* Hertel & Rambold nec *sensu* auct.].—*Lecidea contigua* var. *griseoatra* Flot., *Flora (Regensburg)* **11:** 676 (1828).—*Lecidea griseoatra* (Flot.) Schaer., *Enum. Lich. Europ.*: 101 (1850); type: [Czech Republic: Riesengebirge], "im Aupengrunde, 1824, *J. v. Flotow*" (Flotow 1828: 676). = Flotow, *Lich. exs.* no. 210, distributed as *Lecidea panaeola* [sic!] var. *griseoatra* (UPS—lectotype!, designated here). Secondary chemistry of type specimen: miriquidic acid (by TLC).

(Fig. 1)

Thallus dark grey, sometimes with brownish tinge, areolate, spreading, up to 5 cm diam. *Areolae* densely arranged, verrucose to subsquamulose, flat to subconvex, *c.* 0·5–1·5 mm diam., the older ones with a net of shallow fissures subdividing each areole into *c.* 5–10–20 portions, those *c.* 0·2–0·3 mm in diam. *Hypothallus* in between areoles indistinct.

Apothecia subsessile, tightly adpressed or laterally attached to the areoles and then not distinctly protruding above the thallus surface, flat and marginate when young, later more or less convex and virtually immarginate, 0·35–0·80 mm diam., solitary or laterally attached in groups of *c.* 2–5. *Excipulum* in the upper parts externally olive green-black and internally paler, basally red-brown to violet-black. *Hypothecium* red-brown to dark violet-brown, K+ purple-brown. *Hymenium* hyaline, 70–90 µm high, upper 10–15 µm pale olive to blue-green forming an epihymenial layer; *paraphyses* mostly simple, *c.* 70–90 µm long and 1·5–2·0 µm thick; apical cells hardly to slightly enlarged, up to 3 µm diam., embedded in pigmented gel. *Asci* of *Lecanora*-type, 8-spored, 50–65 × 12–15 µm, outer wall layer and tholus except the central body I(Lugol)+ blue; *ascospores* hyaline, non-septate, ellipsoid, (13–)14–16(–17) × (4·0–)4·5–6·0 µm, length-breadth ratio *c.* 2·5–2·9.

Secondary chemistry. Cortex K–, P–, C–, medulla K–, P–, C–, containing miriquidic acid (number of specimens investigated: 14).

Notes. The peculiar subdivided areoles and fusing apothecia were perfectly described by Flotow (l. c.:. . .“Sie hat dunkelgraue geschwollene feinrunzelige und gefaltete oder warzig-geballte Areolen, und sitzende zerstreute oder zusammenfliessende unförmig geballte schwarze Keimfrüchte,. . .”). His observation (a sufficiently powerful microscope was evi-

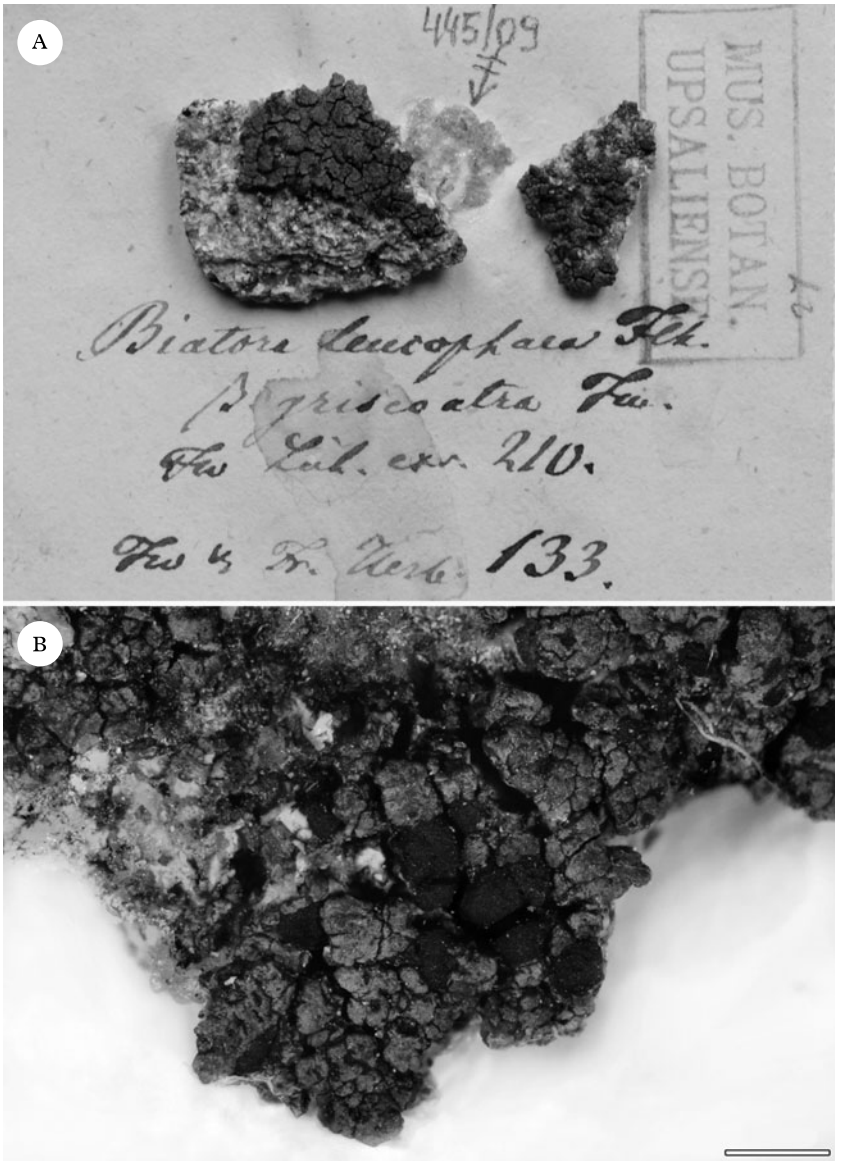

FIG. 1. *Miriquidica griseoatra.* A, lectotype specimen of *Lecidea contigua* var. *griseoatra* (UPS); B, close-up of the more richly fruiting piece to the right. Scale: B = 1 mm.

dently not available for Flotow at that time) that the apothecia are white inside does not necessarily mean that he saw an unpigmented hypothecium, because he compared the taxon with *Porpidia macrocarpa* (sub *Lecidea contigua*) and *Amygdalaria panaeola* (sub *Lecidea p.*), both of which have a strongly carbonized exciple.

Because the herbarium of Flotow, originally housed in Berlin, was destroyed in 1943 (Grummann 1974), the only authentic material of *Lecidea contigua* var. *griseoatra* is evidently the exsiccate Flotow, *Lich. exs.* no. 210. Of this exsiccate, the specimen preserved in UPS has been re-examined and is here selected as lectotype. The lectotype

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consists of two pieces of rock most likely representing fragments of a single thallus. Whereas thallus features are more clearly visible on the left piece, apothecia are better developed on the one on the right. However, the lichen present is not that which is generally understood as *Miriquidica griseoatra* but is a species with peculiar areole features and semi-immersed, laterally attached apothecia exhibiting a pigmented hypothecium in longitudinal sections (Fig. 1B). A comparable set of characters is recorded for *M. obnubila* auct. Interestingly, the lectotype of *Lecidea griseoatra* (Flot.) Schaer. was revised as "*M. obnubila sensu* Hertel & Rambold" (S. Kojetinsky, on an annotation slip), a synonymization that we also considered for some time. However, after having studied authentic material of *Lecidea obnubila* Th. Fr. & Hellb., we see enough differences to distinguish the two species (see also below under *M. obnubila*).

Although the name *Miriquidica griseoatra* is frequently used in floras and checklists in the sense applied here (compare description above), it is the correct name for a relatively rare species that has seldom been distinguished in the past. Therefore, without a reinvestigation of the specimens, it will be difficult to assign previous records of *M. griseoatra* to the correct species.

As a consequence of the revised application of the name *M. griseoatra*, the relatively common species to which this name was previously applied (*M. griseoatra sensu auct.*, apothecia with hyaline hypothecium) needs a new name, and *M. subplumbea* (Anzi) Cl. Roux (Roux *et al.* 2011) is available. *Miriquidica subplumbea* s. str. has an identical thalline chemistry and is also morpho-anatomically rather similar to *M. griseoatra*. The distinguishing characters are the, at least partly, red-brown hypothecium of *M. griseoatra* (hyaline in *M. subplumbea*), the subdivided thallus areoles of *M. griseoatra* (hardly divided in *M. subplumbea*) and the larger ascospores of *M. griseoatra*. Furthermore, the two species evidently have different ecologies (see the treatments of both species).

Two further *Miriquidica* species with apothecia exhibiting a pigmented hypothecium are distinguished. Of these, *M. plumbeoatra* is the only one with a thallus lacking lichen substances in an amount high enough to be detected by TLC (Owe-Larsson & Rambold 2001). However, it is unlikely that *M. plumbeoatra* represents the lichen substance deficient strain of *M. griseoatra* s. str., because the ascospore size is significantly different in these two taxa. The other species, the Himalayan *M. molybdochroa* (Hertel) Hertel & Rambold (not studied by us), shares an identical profile of lichen substances with *M. griseoatra*, both having the miriquidic acid syndrome without further lichen acids. *Miriquidica molybdochroa* is similar to *M. griseoatra* in the shape and position of apothecia, but in the former species the ascospores are reported to be broader and its areoles apparently look different (Hertel 1977).

A strongly pigmented hypothecium is also reported for *M. obnubila* (Hertel & Rambold 1987; Andreev 2004). However, Fries (1874: 459) described the hypothecium of *Lecidea obnubila* as colourless and this is true for the lectotype studied by us. *Miriquidica obnubila* s. str. with its scattered flat to convex, basally constricted, not subdivided, areoles and its sessile, basally constricted, distinctly marginate apothecia looks quite different from *M. griseoatra* (see below).

Ecology. Judging from where the species has been collected, the site characteristics mentioned on the labels, and the autecology of accompanying species found on the specimens, *M. griseoatra* s. str. is a boreal-montane to temperate-lower alpine species, with a preference for long-time moist habitats, such as rocks close to waterfalls, boulders in or near snow beds, and similar sites.

Accompanying species. The lectotype specimen of *M. griseoatra* consists only of thallus portions on two small pieces of rock and there is no further lichen species present. On specimens from the Scottish Highlands we noted *Rhizocarpon badioatrum* and *Lecanora leptacina* (on *Coppins* 13822). Many small thalli of *Lecanora leptacina*, lichenicolous on *Miriquidica griseoatra*, are also present on the samples of Havaas, *Lich. Norveg. Occid.* no.

293 studied by us. A similar set of species, including some basiphilous ones, was reported by Gilbert & Fox (1985) from snow beds on the Cairngorm plateau in Scotland.

Distribution. Because we here apply a different species concept from that commonly used, distributional data from the literature are difficult to interpret. We have seen material from the Czech Republic, Norway, Poland, Sweden, and Great Britain (Scotland).

Exsiccata examined. Flotow, *Lich. exs.* no. 210 sub *Lecidea panaeola* var. *griseoatra* (UPS). Havaas, *Lich. Norveg. Occid.* no. 293 sub *Biatora griseoatra* (GZU, W). Malme, *Lich. Suec. Exs.* no. 719 sub *Lecidea subplumbea* (GZU).

Specimens investigated [non type material, (label data shortened, lichen compounds analysed by TLC)]. **Czech Republic:** *Tatra Magna*: in valle Velká Studená dolina, 1950 m, 1935, *J. Suza* (M) [m].—**Norway:** Möre, Nordal hd, near Trollstien, 850 m, 1947, *A. H. Magnusson* (G) [m]. *Hordaland*: Smøreggfjellet in par. Granvinensi, 700–750 m, 1950, *J. J. Havaas* = Havaas, *Lich. Norveg. Occid.* no. 293 (GZU, W) [m].—**Poland:** Sudeten, *Körber* (B) [m]; Riesengebirge, *Körber* (B) [m].—**Sweden:** *Jämtland*: Undersåker, Vällista, 1917, *G. O. A. Malme* & *E. P. Vrang* = Malme, *Lich. Suec. Exs.* no. 719 (GZU) [m].—**Great Britain:** *Scotland*: **(V. C. 87)**, Westerness: Ben Nevis range, Aonach Mór, Seang Aonach Mór, ridge S of summit, Grid 27/19.72, 1090–1200 m, 1990, *B. J. Coppins* 13822 et al. (E) [m]; *ibid.*, Creag Meagaidh, Grid 27(NN)/40.87, 1150 m, 1994, *A. M. Fryday* (E) [m]. **V. C. 88**, Mid-Perthshire: Ben Lawers, "Crater" gully, Grid 27/637.412, 1180 m, 1986, *B. J. Coppins* 11446 et al. (E) [m, u]; *ibid.*, N ridge, Grid 27(NN)/63.41, 1150 m, 1989, *A. M. Fryday* s.n. (E, 2 specimens) [m]. [**V. C. 94**, Banffshire:] Cairngorm, above Lochan Buidhe, Grid 28/983.015, 1983, *B. W. Fox* 1915 (E) [m]. [**V. C. 96** East Inverness-shire:] Cairngorm, Ciste Mhearad, Grid 38/012.046, 1116 m, 1983, *B. W. Fox* (E) [m]. **V. C. 106**, West Ross: 18 km SE Ullapool, Beinn Dearg, NE slope, Grid 28/26.81, 1984, *B. J. Coppins* 10523 et al. (E) [m].

Lichenicolous fungi. None recorded.

Miriquidica invadens Hafellner, Obermayer & Tretiach sp. nov.

MycoBank No.: MB 804718

Miriquidicae subplumbeae similis sed thallus griseus ad olivaceogriseus ad fuscogriseus. Ceterum ab ea differt ascosporis aliquot minoribus et acidum sticticum ut substantiam alteram continens, ergo medulla Pd+ aurantiaca. Habitat primum constanter supra thallum *Sporastatiae* (plerumque *S. polysporae*), ubi insulas magnas format, demum partim solutus.

Typus: Austria, Steiermark (Styria), Steirisches Randgebirge, Stubalpe, Ameringkogel-Massiv E von Obdach, obere Abhänge in das NE-exponierte Kar zwischen Ameringkogel und Größenberg, 47°04′30″N, 14°48′15″E, *c.* 2050–2100 m, GF 8954/2, Gneisschrofen umgeben von alpinen Rasen, an Steilflächen, auf *Sporastatia polyspora*, 28 July 1990, *J. Hafellner* 23960 & *W. Obermayer* (GZU— holotypus; GZU, CANB, M, NY, UPS, E, G—isotypi = Obermayer, *Dupla Graecensia Lichenum* no. adhuc ined.). Secondary chemistry of type collection: miriquidic acid, stictic acid, constictic acid (by TLC).

(Figs 2A & B, 3A–C 4A–F)

Thallus grey and matt to olive-grey to brownish grey and then somewhat glossy due to the presence of an epinecral layer above the cortex, areolate, spreading, up to *c.* 6 cm diam. *Areolae* smooth or superficially somewhat subdivided, subconvex to convex, *c.* 0·7–1·5 mm diam. *Hypothallus* indistinct. Invading thalli of *Sporastatia*; older thalli of *M. invadens* sometimes starting to crumble from the centre.

Apothecia black, tightly adpressed or marginally attached to areoles and semi-immersed (but not aspicilioid), 0·2–0·5(–0·8) mm diam, plane to subconvex, with persistent thin somewhat glossy margin. *Excipulum* externally red-brown occasionally with shades of violet, merging to olive-brown in the upper part, internally paler to subhyaline. *Hypothecium* hyaline (sometimes slightly brownish at the base). *Hymenium* hyaline, 40–55 µm high, upper 10–15 µm greyish-brownish to dark olive-brown forming an epihymenial layer; *paraphyses* mostly simple or with few ramifications in the upper part, *c.* 50 µm long and 1–2 µm thick; apical cells hardly or slightly enlarged, up to 3–4 µm diam., embedded in pigmented gel ("Pigmenthaubentype" *sensu* Kilias 1981). *Asci* of *Lecanora*-type, broadly cylindrical to subclavate, 8-spored, 35–45 × 12–16(–18) µm, external ascal wall layer and tholus except the axial body I(Lugol)+ blue; *ascospores* hyaline, non-septate, ellipsoid, 9–11(–12) × 4·5–5·5(–6·0) µm, length-breadth ratio *c.* 2·0–2·4.

Pycnoconidia filiform, curved or straight, 20–30(–40) × *c.* 1 µm.

Secondary chemistry. Cortex K–, P–, C–, medulla K+ yellow, P+ orange-red, containing miriquidic acid and stictic acid (plus

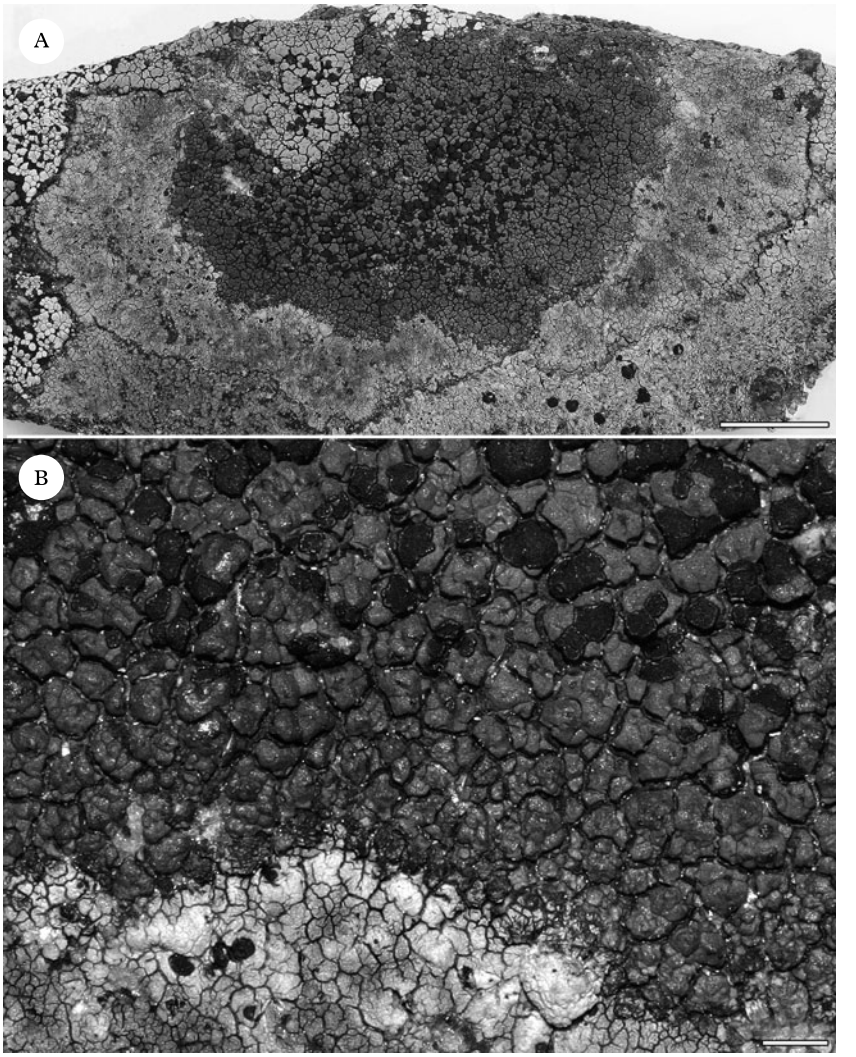

FIG. 2. *Miriquidica invadens*, holotype (GZU). A, habit; B, close-up of the marginal part with the host (*Sporastatia polyspora*) at the bottom. Scales: A = 1 cm; B = 1 mm.

accessory compounds, of which constictic acid is often present in detectable amounts) in the thallus (number of specimens investigated: 71). Coloration of pigmented parts of apothecial sections K+ intensifying. On TLC plates a further spot (5-*O*-methylhiascic acid) may occur, but belongs to the host (see below under Notes).

Notes. The morpho-anatomical characters of *Miriquidica invadens* place it in the *Miriquidica griseoatra* group. As this is a taxonomically difficult group, and type material of some of the species involved had not previously been reinvestigated, we faced a rather confusing situation concerning the applicability of some of the old names.

Initially, we saw a candidate in *Lecidea subplumbea* Anzi, a view supported by the redescription of this taxon given by Hertel (1970: 428). However, after a revision of the

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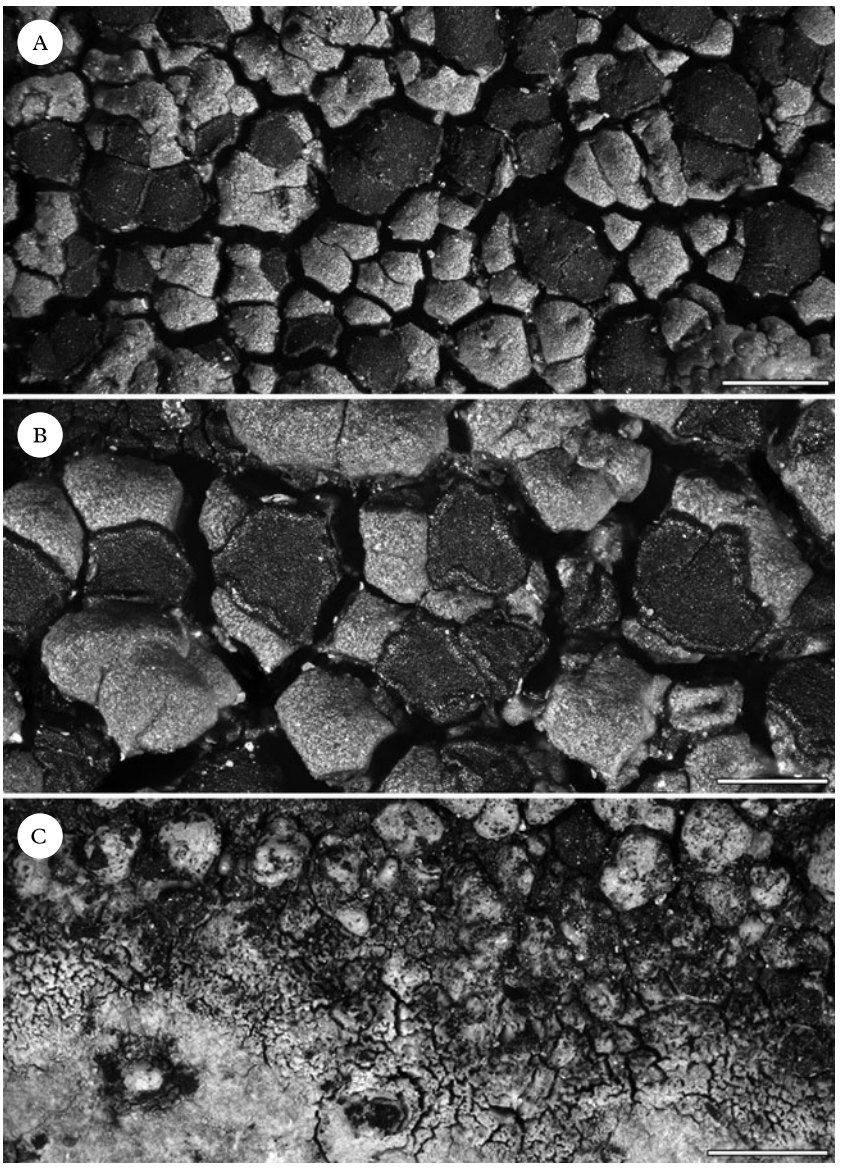

FIG. 3. *Miriquidica invadens*. A & B, close-up of fertile parts of the thallus (holotype, GZU); C, 'combat zone' of *Miriquidica invadens* (above) and its host *Sporastatia polyspora* (below) (*Frey* 1093, G). Scales: A & C = 1 mm; B = 0·5 mm.

specimen upon which that description was based and a reinvestigation of the type specimen of *Lecidea subplumbea*, we now know that Hertel's species treatment refers to *Miriquidica invadens* and that *M. subplumbea* is a different species (see below). The host on the collection used by Hertel for his treatment is not a *Lecidea*, as supposed by him, but sterile *Sporastatia polyspora*, as indicated by its secondary chemistry and features of the areoles.

Hertel & Rambold (1987: 385) and Andreev (2004: 23) mention a red-violet or

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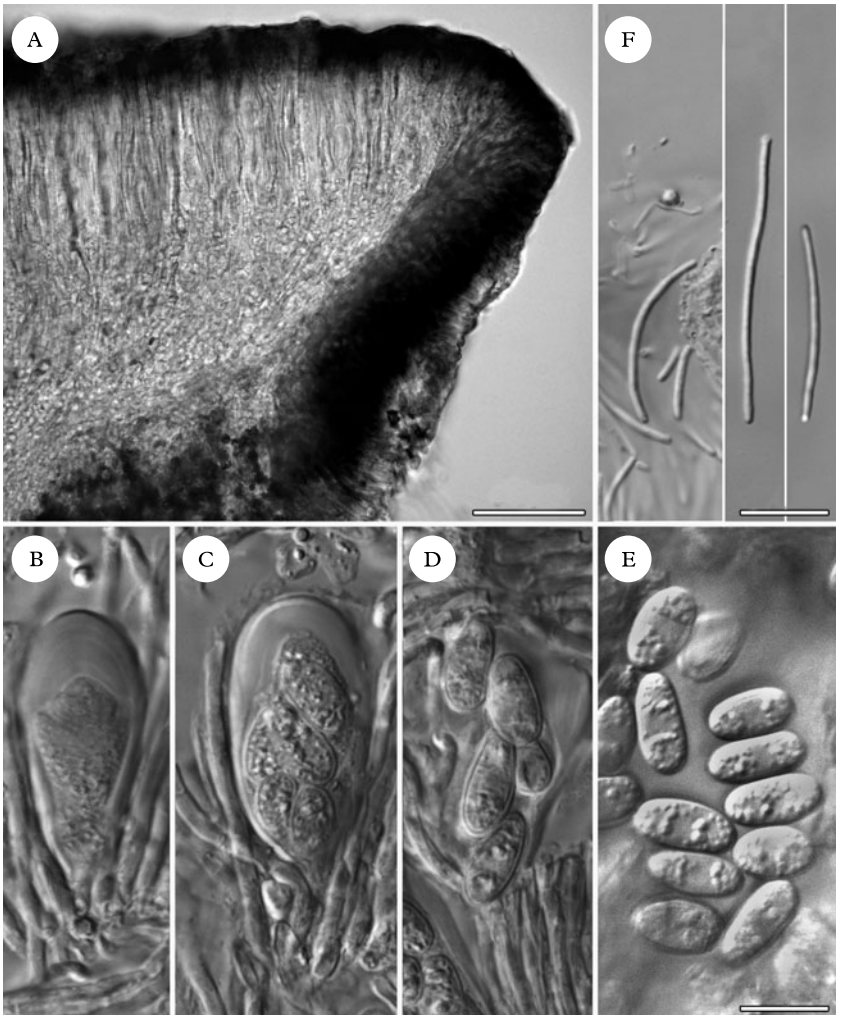

FIG. 4. *Miriquidica invadens*, holotype (GZU). A, longitudinal section of the marginal part of an apothecium; B, immature ascus; C, semi-mature ascus; D & E, ascospores; F, pycnoconidia. Scales: A = 50 μm; B–F = 10 μm.

violet-brown lower part of the exciplum and external part of the hypothecium as characteristic for "forms of *M. griseoatra* [sensu auct.]" called "*Lecidea subplumbea*" or "*Miriquidica griseoatra* chemotype 2" by them. At the same time, such specimens should have somewhat narrower ascospores and contain stictic acid in addition to miriquidic acid. Comparative studies of a larger number of specimens of *M. invadens* have shown that shades of violet are not always detectable in the lower outer part of the exciple (as already admitted by Hertel & Rambold 1987) and that the ascospores are not narrower; their size, in general, being somewhat smaller. Therefore a fragmentary specimen of a dark grey *Miriquidica* (without the edge of the thallus and the host *Sporastatia polyspora* present on the sample) might be difficult to determine by morpho-anatomical characters alone. The only reliable difference between the morphologically similar *M. subplumbea*

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and *M. invadens* is secondary chemistry (TLC or Pd-reaction), as the medulla is Pd− (stictic acid lacking) in the former species, and Pd+ orange-red (stictic acid present) in the latter. The parasitism of *M. invadens* was not recognized by previous collectors. This was even the case with such experienced lichenologists as F. Arnold, who collected typical material of *M. invadens* from at least two localities in Tyrol but in none of the corresponding "Lichenologische Ausflüge" (Arnold 1877: 551, 1893: 379 sub *Lecidea inserena* var./f. *subplumbea*) is the parasitism on *S. polyspora* mentioned.

The first person to report on the presence of a lichenicolous lichen of the genus *Miriquidica* on *Sporastatia polyspora* was Minks (1896: 85, sub *Lecidea inserena*), who recognized this parasitism when he studied a specimen from Tyrol. Later, Obermayer (1993: 130, sub *Miriquidica* spec. #1) pointed to the existence of such a lichenicolous species when working on the lichen flora of the Seetaler Alpen in Styria. At that time we had already studied the rich population at the type locality and were aware of the existence of a further *Miriquidica* species that we could not then name.

One of the species with which *M invadens* is confused, *M. subplumbea* s. str. (syn. *M. griseoatra sensu auct.*), is occasionally found upon *Acarospora fuscata*, *Lecanora polytropa*, *Lecidea* sp. and *Rhizocarpon* sp., but finally always becomes independent (Hertel & Rambold 1987: 385; Rambold & Triebel 1992: 113). The other species with which *M invadens* is confused, *M. griseoatra* (Flot.) Hertel & Rambold s. str., has not been reliably reported to occur on other lichens.

Miriquidica invadens occurs in two morphotypes, one with medium to dark grey, matt areoles and semi-immersed apothecia similar to *M. subplumbea*, and one with olive to brownish grey, somewhat glossy areoles and more or less sessile apothecia recalling those of *M. obnubila*. As we regularly saw intermediate forms and could not find a clearly discriminating character, we decided to regard this as intraspecific variability. Areole colour and surface characteristics may depend on a variably developed epineural layer, and the position of the apothecia may vary with thallus age and thickness.

Until recently, gyrophoric acid has been considered as being the main chemical substance in the genus *Sporastatia*, and this incorrect information is also given in several well-known lichen floras [e.g., Great Britain (Gilbert & Coppins 2009: 850), North America (Brodo *et al.* 2001: 659) or south-western Germany (Wirth 1995*b*: 867)]. By contrast, in the Svalbard flora (Øvstedal *et al.* 2009: 340) 5-*O*-methylhiascic acid is reported as the main secondary compound for *S. polyspora* (additionally with gyrophoric acid as the second major compound and lecanoric acid in traces), *S. testudinea* (additionally with gyrophoric acid as minor compound and lecanoric acid in traces), and an undescribed member of the genus (additionally with gyrophoric acid in traces). A first screening of material from the Alps confirms 5-*O*-methylhiascic acid as being the major compound in both *S. testudinea* and *S. polyspora*. Interestingly, alpine material of *S. polyspora* chemically matches the undescribed *Sporastatia* sp. from Svalbard.

Ecology. *Miriquidica invadens* starts its life cycle as a parasitic lichen on thalli of *Sporastatia polyspora* (rarely upon *S. testudinea*) when the host grows on (sub)vertical to overhanging siliceous rocks. In very young infections the areolae of *M. invadens* develop on, or are laterally adpressed to, areolae of the host, rarely also on apothecia. Under the dissecting microscope it can be seen that host areolae are often gradually overtaken by the invader. In an advanced stage the host thalli may be almost completely replaced by *M. invadens* thalli so that areolae of *M. invadens* may then be bordered by bare rock or thalli of lichens other than *Sporastatia*, which we never found attacked by the *Miriquidica*. In the field it is normally quite easy to demonstrate that the host is still present. In herbarium specimens that do not contain entire thalli, the parasitism may be less obvious. For example, on both duplicates of Arnold, *Lich. exs.* no. 757 that we restudied, only a few areolae of the host could be detected (and it is possible that other samples of the

exsiccata may have no host left), and on the otherwise typical specimen *Frey* 349 from Piz Nuna there is no host at all.

Accompanying species. Being a constantly lichenicolous species, the host *Sporastatia polyspora* is almost always present on the rock samples. However, as *Sporastatia polyspora* usually develops relatively large thalli, the rock pieces frequently do not have further lichen species present.

The type collection consists of one holotype and seven isotypes constituting the exsiccate number cited above. On the entire collection, besides *M. invadens* and its host, only *Aspilidea myrinii, Rhizocarpon geographicum, Lecanora polytropa, Lecidea confluens, Lecidea lapicida* coll., and *Miriquidica* sp. (not yet identified, possibly another undescribed species) grow on the rock pieces. Furthermore, on each specimen we noticed at least several ascomata of *Polycoccum sporastatiae* as an additional inhabitant of *Sporastatia polyspora* and some of the thalli of accompanying species are infested with strains of *Muellerella pygmaea* coll. *Diploschistes scruposus*, *Fuscidea kochiana*, *Ophioparma ventosa*, *Parmelia omphalodes*, *Pertusaria corallina*, *Tephromela atra*, and *Varicellaria lactea* have been sampled in the close neighbourhood of the type locality (specimens in GZU).

A screening of the selected specimens cited below for additional taxa growing on the same rock pieces resulted in the following list: *Bellemerea alpina, Calvitimela armeniaca, Carbonea vorticosa, Fuscidea kochiana, Lecanora alpigena, L. intricata, L. polytropa, Lecidea confluens, L. lapicida* coll., *Rhizocarpon alpicola, R. geographicum, Tremolecia atrata,* and *Umbilicaria cylindrica*.

Sporastatia polyspora and *Lecanora marginata* (sub *Lecida elata*) are the diagnostic species of the silicicolous lichen community *Sporastatietum polysporae* (nom. mut. for *Biatorelletum cinereae* Frey 1923). Other epilithic crusts present with high reliability are the common species *Fuscidea kochiana*, *Lecidea confluens*, *Ophioparma ventosa*, *Protoparmelia badia*, *Psorinia conglomerata*, *Rhizocarpon geographicum*, and *R. alpicola* (Klement 1955: 49).

Distribution. The species is widely distributed in the Alps and also known from the mountain ranges on the Iberian Peninsula and the Balkan Peninsula. It is so far known from Austria, Bulgaria, France, Italy, Switzerland and Spain. As it constantly starts its development on *Sporastatia*, a genus with an arctic-alpine distribution pattern, *Miriquidica invadens* is restricted in Central Europe to high altitudes from the lower alpine to the nival belt, mostly above an altitude of 2000 m, never below 1600 m. On the other hand, both *Sporastatia* species have a much wider distribution range and are known from the Arctic, as well as many orobiomes on both hemispheres. Therefore, we would not be surprised if it can be shown that *M. invadens* has a much wider distribution range than so far documented.

Exsiccata examined. Obermayer, *Dupla Graec. Lich.* no. adhuc ined. (GZU, CANB, M, NY, UPS, E, G) type collection; Hafellner, *Lichenicolous Biota* no. adhuc ined. (BCN, BR, CANB, E, GZU, LE, M, NY, PRM, UPS) paratype collection; Hafellner, *Lichenicolous Biota* no. adhuc ined. (BR, CANB, GZU, NY, UPS) paratype collection; Arnold, *Lich. exs.* no. 757, sub *Lecidella inserena* (G, 2 specimens, M, 2 specimens, W).

Specimens investigated (paratypes): (label data shortened, all specimens on *Sporastatia polyspora* unless otherwise stated). **Austria:** *Tirol* (*Tyrol*): [Verwallgruppe], gegen Hochkor [Hochkarspitze] S St. Anton am Arlberg, 1892, *F. Arnold* (M, 2 specimens) [m, s]; [Ötztaler Alpen], Kaunergrat, Madatschjoch, 3100 m, 1953, *J. Poelt* (GZU) [m, s, c]; *ibid.*, Hohe Mut, Gurgl im Ötztal, 1877, *F. Arnold* (M) [m, s, c]; [Stubaier Alpen], ober dem Weißbach, Rosskogel bei Innsbruck, 1875, *F. Arnold* (M, 5 specimens) [m, s, c]. *Salzburg*, NP Hohe Tauern, Goldberggruppe, Vorderer Gesselkopf, Westgrat 2950 m, GF 8944/3, 1994, *J. H.* 33237 (GZU) [m, s, u]. *Kärnten* (*Carinthia*): Saualpe W Wolfsberg, Forstalpe, N-Rücken, 46°54′10″N / 14°39′55″E, 1950 m, GF 9053/4, 2011, *J. H.* 79177 & *A. Hafellner* = Hafellner, *Lichenicolous Biota* no. adhuc ined. (GZU) [m, s, c]; *ibid.*, Forstalpe, E-Rücken, Forstofen (Kote 1967), 46°53′25″N / 14°40′10″E, 1955 m, GF 9154/1, 2011, *J. H.* 78162 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, zwischen Kienberg und Forstalpe, Kar über Schmiedbauerhütte, 46°53′30″N / 14°39′00″E, 2030 m, GF 9153/2, 2012, *J. H.* 80204 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, Kienberg, Drei Öfen, 46°53′00″N / 14°38′55″E, 2040 m, GF 9153/2, 2012, *J. H.* 80296 & *A. Hafellner* (GZU) [m, s, u]; Saualpe, zwischen Ladinger Spitz und Gertrusk, Kaiserofen, 46°51′25″N / 14°38′45″E, 2030 m, GF 9153/2, 2012, *J. H.* 80781 (GZU) [m, s]; Koralpe E Wolfsberg, Großes Kar, Bergrücken Großer Speikkogel – Steinschneider, 46°47′35″N / 14°57′55″E, 1950 m, GF 9255/2, 2012, *J. H.* et al. 80153 (GZU) [m, s, c];

ibid., Großes Kar, Fuß der NE-Hänge des Großen Speikkogel, 46°47′30″N / 14°58′15″E, 1980 m, GF 9255/2, 2008, *J. H.* 71167 et al. (GZU) [m, s, c]; *ibid.*, 11,5 km NE St. Paul im Lavanttal, Krakaberg SE Koralpenhaus, 46°46′50″N / 14°58′15″E, 2070 m, GF 9255/2, 2007, *J. H.* 68498 *et al.* (GZU) [m, s, c]; *ibid.*, Moschkogel, NE über Grillitschhütte, 46°49′25″N / 14°59′25″E, 1800 m, GF 9155/4, 2007, *J. H.* 70198 & *L. Muggia* (GZU) [m, s, c]; Karnische Alpen, Raudenspitz E ober Hochweißsteinhaus, Gipfel, 2500 m, 46°38′50″N / 12°45′45″E, GF 9342/4, 1996, *J. H.* 39002 (GZU) [m, s, c]; *ibid.*, Steinkarspitz[e] über Maria Luggau im Lesachtal, 2450 m, 1967, *I. Hertel* & *H. Hertel* 8903 (M) [m, s, c]. *Steiermark* (*Styria*), Schladminger Tauern, Zinkwand S Schladming, Nordosthänge SW ober Keinprecht-Hütte, 47°16′25″N / 13°41′20″E, 2100 m, GF 8748/1, 1998, *J. H.* 45719 (GZU) [m, s, c]; *ibid.*, Deneck S über St. Nikolai im Sölktal, S-Grat, 47°17′15″N / 14°03′05″E, 2420 m, GF 8750/1, 2009, *J. H.* 74341 (GZU) [m, s, c]; Wölzer Tauern, Rettlkirchspitze NW Oberwölz, NE-Grat SW über Neunkirchner Hütte, 47°15′45″N / 14°08′05″E, 2300 m, GF 8750/2, 2002, *J. H.* 68159 & *J. Miadlikowska* (GZU) [m, s, c, u]; *ibid.*, Greim ca. 11 km NW Oberwölz, Gipfel, 47°14′50″N / 14°09′05″E, 2470 m, GF 8750/4, 2006, *J. H.* 67975 & *L. Muggia* = Hafellner, *Lichenicolous Biota* no. adhuc ined. (GZU) [m, s, c]; *ibid.*, Planneralpe, zwischen Franzosenkreuz und Vorderer Gstemmerspitze, 47°25′10″N / 14°11′30″E, 2050 m, GF 8551/3, 1998, *J. H.* 45644 (GZU) [m, s, c]; *ibid.*, Großer Rotbühel S Planneralpe, Gipfel, 47°23′35″N / 14°12′30″E, 2000 m, GF 8651/1, 2012, *J. H.* 80091 & *L. Muggia* (GZU) [m, s, c]; *ibid.*, Hochschwung W Hohentauern, W Vorgipfel, 47°24′30″N / 14°20′10″E, 2180 m, GF 8552/3, 1996, *J. H.* 50087a, b (GZU) [m, s, c]; *ibid.*, Berge 5 km SW Pusterwald, Schießeck, N Vorgipfel (wo Gipfelkreuz), 47°16′43″N / 14°19′25″E, 2250 m, GF 8751/2, 2009, *J. H.* & *A. Hafellner* 73384 (GZU) [m, s, c]; *ibid.*, Rottenmanner Tauern, Großer Bösenstein, Gipfel, 47°26′35″N / 14°24′15″E, 2445 m, GF 8552/3, 2003, *J. H.* 68226 (GZU) [m, s, c]; Seckauer Tauern, Triebener Tauern, S ober Hohentauern, zwischen Wirtstörl und Geierkogel, 47°24′10″N / 14°29′50″E, 2150 m, GF 8552/4, 1996, *J. H.* 48962 (GZU) [m, s, c]; *ibid.*, Schleifkogel ENE St. Johann am Tauern, Gipfel, 47°22′10″N / 14°29′55″E, 2060 m, GF 8652/2, 2001, *J. H.* 57316 (GZU) [m, s]; *ibid.*, Großer Ringkogel NW Knittelfeld, Gipfel, 47°19′15″N / 14°37′20″E, 2270 m, GF 8653/4, 1999, *J. H.* 49679 (GZU) [m, s]; *ibid.*, Geierhaupt 10 km S Wald am Schoberpaß, Gipfel, 47°22′30″N / 14°38′15′E, 2410 m, GF 8653/2, 1997, *J. H.* 43683 & *A. Hafellner* (GZU) [m, s]; *ibid.*, Geierhaupt, NE vom Gipfel gegen Grieskogel, 47°22′40″N / 14°38′15′E, 2350 m, GF 8653/2, 1997, *J. H.* 43670 & *A. Hafellner* (GZU) [m, s]; *ibid.*, Hochreichhart NE Ingeringsee, NW Knittelfeld, Gipfel, 2410 m, 47°21′45″N / 14°40′55″E, GF 8654/1, 2001, *J. H.* 56163 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, Brandstätterkogel E Ingeringsee, NW Knittelfeld, Gipfel, 47°21′10″N / 14°42′00″E, 2230 m, GF 8654/1, 1999, *J. H.* 48490 (GZU) [m, s, c]; *ibid.*, Maierangerkogel E Ingeringsee, NW Knittelfeld, Gipfel, 47°20′55″N / 14°42′45″E, 2350 m, GF 8654/3, 2001, *J. H.* 57346 (GZU) [m, s]; *ibid.*, 2005, *J. H.* 64188 (GZU) [m, s]; *ibid.*, Seckauer Zinken N Seckau (SW Mautern), Gipfel, 47°20′20″N / 14°44′10″E, 2395 m, GF 8654/3, 1997, *J. H.* 43781 & *J. Kocourková* (GZU) [m, s]; *ibid.*, Seckauer Zinken, NE-Grat, gegenüber Hämmerkogel, 47°20′30″N / 14°44′30″E, 2250 m, GF 8654/3, 1997, *J. H.* 43846 & *J. Kocourková* (GZU) [m, s, c]; *ibid.*, Hämmerkogel N Seckau, über Goldlacke, 47°20′30″N / 14°45′05″E, 2100 m, GF 8654/4, 2001, *J. H.* 57569 (GZU) [m, s, c]; *ibid.*, Schwaigerhöhe N Seckau, Gipfel, 47°20′20″N / 14°46′E, 2150 m, GF 8654/4, 1998, *J. H.* 45642 & *J. Miadlikowska* (GZU) [m, s, c]; Gurktaler Alpen, Eisenhut ESE Turrach, Gipfel, 46°57′10″N / 13°55′40″E, 2430 m, GF 9049/2, 2002, *J. H.* 61548 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, Kirbisch 11 km SW Murau, über St. Lorenzen, Gipfel, 47°03′05″N / 14°03′05″E, 2100 m, GF 8950/1, 2003, *J. H.* 62326 (GZU) [m, s]; Seetaler Alpen, Wenzelalpe, NE-Rücken, Erslstand, 47°06′50″N / 14°32′50″E, 2110 m, GF 8853/3, 2010, *J. H.* 75908 (GZU) [m, s, c]; *ibid.*, Zirbitzkogel-Massiv SW Judenburg, Kreiskogel, E-exp. Abbrüche, 2200 m, GF 8953/1, 1990, *J. H.* 26169 & *W. Obermayer* (GZU) [m, s, c]; *ibid.*, Zirbitzkogel E Neumarkt, Kar zwischen Scharfes Eck und Zirbitzkogel, 2280 m, GF 8953, 1985, *J. H.* 13487 (GZU) [m, s, c]; Koralpe, Seespitz, SE-Hänge 46°47′20″N / 14°58′45″E, 2050 m, GF 9255/2, 2000, *J. H.* 53145 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, W Deutschlandsberg, Seespitz, E-Hänge gegen Seekar, 46°47′25″N / 14°58′48″E, 2050 m, GF 9255/2, 2008, *J. H.* 72390 & *L. Muggia* (GZU) [m, s, c]; Stubalpe, Ameringkogel E Obdach, Gipfel, 47°04′23″N / 14°48′30″E, 2160 m, GF 8954/2, 2005, *J. H.* 64303 (GZU) [m, s, c, u]; *ibid.*, Ameringkogel-Massiv E Obdach, Weißenstein, S-Hänge, 47°03′55″N / 14°48′30″E, 2100 m, GF 8954/2, 2005, *J. H.* 65179 (GZU) [m, s, c]; *ibid.*, zwischen Speikkogel und Weißenstein, 2020–2030 m, GF 8954, 1985, *K. Kalb* & *J. Poelt* (GZU) [m, s]; Gleinalpe, Speikkogel S St. Michael, N Abhänge, 47°13′40″N / 15°02′55″E, 1980 m, GF 8756/3, 2000, *J. H.* 52121 & *A. Hafellner* (GZU) [m, s, c]; *ibid.*, S St. Michael, zwischen Kreuzsattel und Eiblkogel, 47°15′10″N / 15°05′25″E, 1780 m, GF 8756/4, 2001, *J. H.* 57457 (GZU) [m, s]; Fischbacher Alpen, Stuhleck N Rettenegg, Steinkorb, 47°34′15″N / 15°47′20″E, 1700 m, GF 8460/2, 2000, *J. H.* 50936 (GZU) [m, s, c]. *Niederösterreich (Lower Austria)*, Steirisches Randgebirge, Wechsel W Mönichkirchen, Hochwechsel, unter Wetterkogler Haus, 1690 m, GF 8461/4, 1995, *J. H.* 35973 (GZU) [m, s, c].—**Bulgaria:** Montes Rhodope occidentals [= Rila Mts.], in summo monte Musallah, *c.* 3000 m [=Musala, 2925 m]. 1930, *K. H. Rechinger* 1684 (W) [m, s], anal. by S. Kojetinsky.—**France:** *Dauphiné*: Lautaret, Pyramide du Laurichard, Gipfel, 2770 m, 1932, *E. Frey* 1093 & *A. Schmidt* (G) [m, s, c].—**Italy:** *Piemonte*: Prov. Cuneo, Alpi Marittime, Rocca dell' Abisso W Colle di Tenda, N below summit, 44°08'35"N / 07°30'15"E, 2750 m, 2000, *P. L. Nimis* 34369, 34346 & *M. Tretiach* (TSB) [m, s, c]; *ibid.*, Alpi Liguri, N ridge of Monte Saccarello, W Monesi, crest N Monumento al Redentore, 44°03'40"N / 07°42'55"E, 2200 m, 2000, *P. L. Nimis* 33723 & *M. Tretiach* (TSB)

[m, s, c]; *ibid.*, Alpi Cozie, crest SW Colle dell' Agnello, 44°40′50″N / 06°58′30″E, 2900 m, 2000, *P. L. Nimis* 33126 & *M. Tretiach* (TSB) [m, s, c]; Prov. Torino, Alpi Cozie, montains W Pinerolo, Punta Cialáncia S Perero, 44°53′00″N / 07°07′20″E, 2350 m, 2001, *J. H.* 69356 (GZU) [m, s, c]; *Lombardia*: [Prov. Brescia, Adamello-group], Parco Reg. dell'Adamello, Val Bona, Passo di Vall Fredda, [45°55′30″N / 10°24′10″E], 2400 m, 2006, *M. Tretiach* 38911, 38913 (TSB, 2 specimens) [m, s, c]; *ibid.*, *M. Tretiach* 38912 (TSB) [m, s, c, u], *Trentino-Alto Adige*: Prov. Trento, Ortler-group (Stelvio-group), 8 km N Cógolo, La Cascata S Lago Lungo, summit, 46°25′30″N / 10°41′00″E, 2575 m, 2006, *J. H.* 69344 (GZU) [m, s, c]. *Friuli-Venezia Giulia*: Prov. Udine, Carnic Alps, Monte Fleons (Raudenspitz), crest W below summit, 46°38′45″N/12°45′10″E, 2400 m, 1996, *J. H.* 39060 (GZU) [m, s, c]; *ibid.*, giogaia dei Fleons, sentiero vs. la cima, 2400 m, 26. VII. 1995, *M. Tretiach* (TSB) [m, s, c]; *ibid.*, Monte Fleons (Raudenspitz), summit, 46°38′50″N/12°45′45″E, 2500 m, 1996, *J. H.* 38989 (GZU) [m, s, c]; *ibid.*, Mt. Crostis N Comeglians, Grat W Gipfel, 2240 m, 1994, *J. H.* 39870 (GZU) [m, s, c]; *ibid.*, Monte Crostis, 2200 m, on *Sporastatia testudinea* (!),1993, *M. Tretiach* 17851, 17852 (TSB, 2 specimens) [m, s, c].—**Spain:** *Prov. Madrid*: Sierra de Guadarrama, Peñalara above Puerto de los Cotos, ober Laguna Grande, 2100–2200 m, 1980, *J. H.* 10552 (GZU) [m, s, c].—**Switzerland:** *Kanton Bern*: Berner Alps, Grimselpass *c.* 20 km SE Meiringen, trail to Husegghütte, 46°33′35″N / 08°19′40″E, 2350 m, 2006, *J. H.* 69317 (GZU) [m, s, c, u]; *ibid.*, on *Sporastatia testudinea* (!), *J. H.* 69315 (GZU) [m, s, c]. *Kanton Graubünden*, Silvretta-Gruppe, SW Heidelberger Hütte, Val Fenga, Weg zum Fimberferner, 2400 m, 1967, *J. Poelt* 9578 (GZU) [m, s, c]; Rhätische Alpen, von Albula Pass-Straße zur Fuorcla Carap alv, 2050–2200 m, 1980, *J. Poelt* (GZU) [m, s, c]; Rätien, Umbrail, Muranza, Las Plattas, 2400 m, 1927, *E. Frey* 158/59 (G) [m, s, c]; [Sesvenna Range], Piz Nuna, Gipfelgrat, 3100 m, 1928, *E. Frey* 349 (G) [m, s, c].

Further specimens investigated (non type material): **Austria:** *Tirol (Tyrol)*: Kühkampleseck E Gurgl, 2300 m, 1878, Arnold = Arnold, *Lich. exs.* no. 757 (G, M, W) [m, s, c]. Note: No host may be present on some of the duplicates and then parasitism is not evident. *Kärnten (Carinthia)*: Kreuzeck-Gruppe, Kleines Kreuzeck, 2400 m, 1987, *W. Petutschnig* (GZU) [m, s, c]. Note: No host present on the piece of rock.

Lichenicolous fungi. The lichenicolous *Miriquidica invadens* itself seems not to be a very suitable substratum for lichenicolous fungi. Only a strain of *Muellerella pygmaea* (Körb.) D. Hawksw. has so far been detected on some specimens. Using the key offered by Triebel (1989), the strain would key as *M. p.* var. *athallina*, for which *Miriquidica invadens* would be an additional host. However, we regard the lichenicolous fungi which key out under this name as a difficult, still unresolved swarm of taxa.

Specimen seen [all on *Miriquidica invadens* (th.)]. **Austria:** *Kärnten* (*Carinthia*): Saualpe W Wolfsberg, Forstalpe, 46°54′10″N / 14°39′55″E, 1950 m, GF 9053/4, 2011, *J. H.* 79181 & *A. Hafellner* (GZU). *Steiermark* (*Styria*): Wölzer Tauern, Rettlkirchspitze NW Oberwölz, NE-Grat SW Neunkirchner Hütte, 47°15′45″N / 14°08′05″E, 2300 m, GF 8750/2, 2002, *J. H.* 68162 & *J. Miadlikowska* (GZU); *ibid.*, Greim ca. 11 km NW Oberwölz, Gipfel, 47°14′50″N / 14°09′05″E, 2470 m, GF 8750/4, 2006, *J. H.* 67977 & *L. Muggia* (GZU); Seckauer Tauern, Maierangerkogel E Ingeringsee, NW Knittelfeld, Gipfel, 47°20′55″N / 14°42′45″E, 2350 m, GF 8654/3, 2005, *J. H.* 64186 (GZU).

Another good candidate of a fungus capable of attacking *M. invadens* is *Endococcus complanatae* Arnold because this species sometimes infests other *Miriquidica* species. Frequently the host, *Sporastatia polyspora*, was also infected by *Polycoccum sporastatiae* (Anzi) Arnold in addition to *Miriquidica invadens* (e.g., type collection of *Miriquidica invadens*, specimens *Hafellner* 43670, 43781, 50087, 52121, 56136, 57346, 62326, *Tretiach* 38912).

Miriquidica obnubila (Th. Fr. & Hellb.) Hertel & Rambold

Mitt. Bot. Staatssamml. München **23:** 389 (1987) sed non *M. obnubila sensu* Hertel & Rambold.—*Lecidea* (*Biatora*) *obnubila* Th. Fr. & Hellb. in Th. Fr., *Lichenogr. Scand.* **1:** 459 (1874); type: Sweden, Lapponiae lulensis, Njåmmelst, ad rupes duriores, 1864, *P. J. Hellbom* (M—lectotype, designated here!). Secondary chemistry of type specimen: miriquidic acid (by TLC).

(Fig. 5A–C)

Thallus grey, areolate, spreading, up to 5 cm diam. *Areolae* dispersed to moderately densely arranged on a black hypothallus, flattened to convex, basally somewhat constricted, *c.* 0·4–1·2 mm diam. *Hypothallus* distinct in between the separated areoles, black.

Apothecia black, sessile, 0·5–1·0 mm diam., with consistently flat discs and persistent prominent margin. *Excipulum* externally red-brown to purple-brown, internally distinctly paler to subhyaline. *Hypothecium* hyaline. *Hymenium* hyaline, 60–70 μm high, upper 10–15 μm olivaceous blue-green to purplish blue forming an epihymenial layer; *paraphyses* mostly unbranched, 60–70 μm long and 1·5–2·0 μm thick; apical cells slightly enlarged, up to 3 μm diam., embedded in pigmented gel. *Asci* of *Lecanora*-type, 8-spored, broadly cylindrical to subclavate, 45–55 × 14–18 μm, outer wall layer and

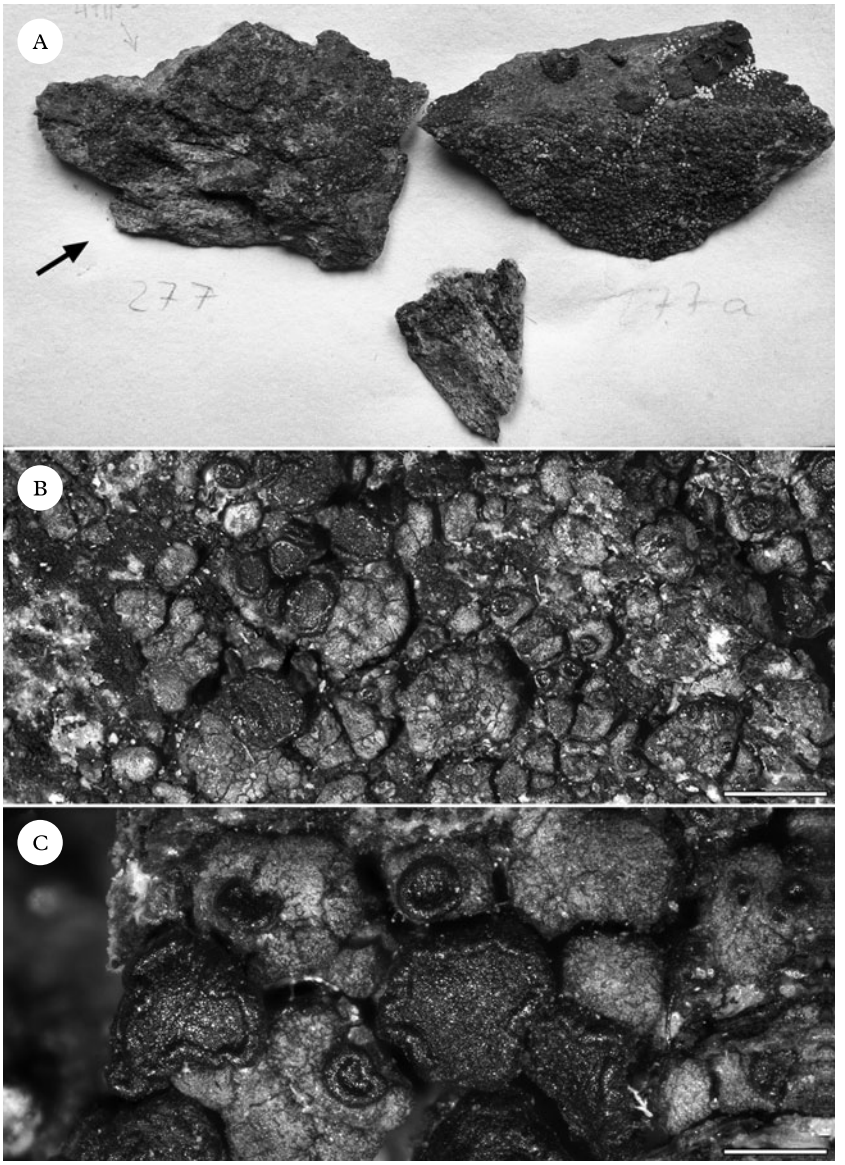

FIG. 5. *Miriquidica obnubila*, lectotype of *Lecidea* (*Biatora*) *obnubila* (M). A, type specimen with the left piece marked by an arrow as lectotype s. str. (for details see text); B & C, close-ups of fertile thallus parts of the lectotype. Scales: B = 1 mm; C = 0·4 mm.

tholus except the central body I(Lugol)+ blue; *ascospores* hyaline, non-septate, ellipsoid, 14–17 × 5–6 µm, length-breadth ratio *c*. 2·5–2·7.

Secondary chemistry. Cortex K−, P−, C−, medulla K−, P−, C−, containing miriquidic acid in the thallus (by TLC, number of specimens investigated: 1).

Notes. The lectotype in Munich (M) consists of three rock pieces, of which the lichen developed on the piece mounted on the left side and the smaller piece in the middle fit

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perfectly with the protologue, and these are, therefore, designated as the lectotype. Fries (l. c.) states that the hypothecium is not coloured and this is what we observed on apothecial sections from the lectotype. The piece on the right side evidently belongs to a different species as the apothecia exhibit a brown hypothecium. It may in fact come from a different locality, as the rock texture and mineral content as seen under the dissecting microscope are quite different from the piece on the left side. A specimen with identical label data to the lectotype is housed in Stockholm (S). This specimen agrees morpho-anatomically with that of the specimen on the right side of the lectotype collection, and consequently, as the characters of the specimen are not in accordance with the protologue, is not considered by us as part of the type collection.

As Hertel & Rambold (l. c.) consistently state that the hypothecium of *M. obnubila* should be pigmented brown, we suppose that their concept of *M. obnubila* was based on a reinvestigation of the lichen present on the piece of rock mounted on the right side (specimen in M). From our observations we conclude that *M. obnubila* s. str. is not conspecific with *M. obnubila sensu* Hertel & Rambold. Here we apply the name in the original sense, whereas *M. obnubila sensu* Hertel & Rambold (with brown hypothecium; full description in, e.g., Andreev 2004: 31–32) is likely to be identical with *M. griseoatra* s. str. (non *sensu M. griseoatra* auct. which is *M. subplumbea*) (see above under *M. griseoatra*).

Of the characters visible under the hand lens or a dissecting microscope, the sessile apothecia with their persistently prominent margins appear to be diagnostic compared with other species of the *M. griseoatra* group. Assuming that these features can be confirmed to be consistent in additional specimens, they would be the best characters to distinguish *M. obnubila* from the otherwise rather similar *M. subplumbea*, which has an identical secondary chemistry.

Ecology. Apart from the habitat of siliceous rock under the climatic conditions of northern Scandinavia, nothing else is known about the ecological setting in which the species can be found.

Accompanying species. None recorded, none present on the lectotype s. str.

Distribution. For the reason stated above, distributional data are difficult to interpret. Andreev (2004) reported the species additionally for Finland, Russia, Greenland and mainland North America but these records may also refer to *M. griseoatra* s. str.

Exsiccata examined. None
Additional specimens investigated. -
Lichenicolous fungi. None observed and none recorded.

Miriquidica plumbea (Garov. ex A. Massal.) Hafellner, Obermayer & Tretiach comb. nov.

MycoBank No.: MB 804719

Lecidea plumbea Garov. ex A. Massal., *Ricerche sull'autonomia dei licheni crostosi*: 74 (1852). Garovaglio, *Delectus Specierum novarum, Sect. II*: 19 (1838) (description without name). Garovaglio, *Catalogo di alcune crittogame, Parte II*: 49 (1838) (description without name). Garovaglio, *Saggio d'un prospetto delle piante crittogame della Lombardia*: 335 (1844) (nomen nudum, no reference to an earlier description). Garovaglio, *Della distribuzione geografica dei licheni di Lombardia*: 16, 29, (1864) (name and bibliography).

Cited localities: Garovaglio (1838*a*), p. 19: "ad rupes micaceas ventis quam maxime obnoxias in Monte Legnone paulo supra dictas Alpi di Delebio". —Garovaglio (1838*b*), p. 49: "M. Legnone". Massalongo (1852), p. 74: "Vive sulle roccie [sic] granitiche schistose nel M. Lineone presso Como"; type: [Italy], ad saxa schistosa in monte Lineone, *Garovaglio* (VER—lectotype!; VER—isolectotype!, lectotype designated here). Secondary chemistry of type specimen: miriquidic acid, protocetraric acid (by TLC).

Miriquidica limitata Hertel & Rambold, *Mitt. Bot. Staatssamml. München* **23:** 387 (1987); typus: Austria, Tirol, Kühtai ("Kühthei"), "Gneisfelsen zwischen den beiden Finsterthaler Seen, 7000′, VIII. 1872", *F. Arnold* (M—holotype!). Secondary chemistry of type specimen: miriquidic acid, protocetraric acid (by TLC).

(Figs 6A–C, 7A & B)

Thallus grey, areolate, up to 3(–5) cm diam., with an attenuated and somewhat effigurate marginal zone where not in contact with other lichens. *Areolae* flat to subconvex, *c.* (0·2–)0·4–1·0 mm diam. *Hypothallus* occasionally distinct on edges without contact with other crustose lichens, mostly black.

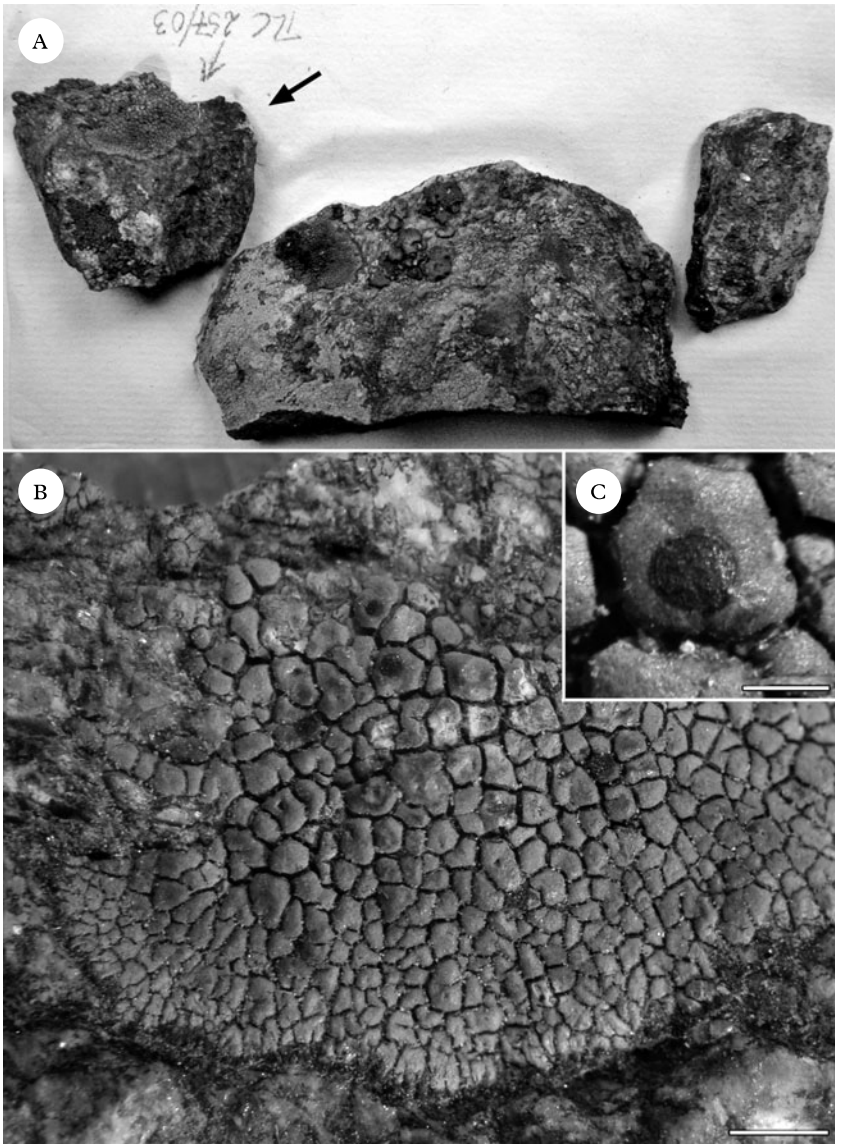

FIG. 6. *Miriquidica plumbea*, lectotype of *Lecidea plumbea* (VER). A, type specimen with the left piece marked by an arrow as lectotype; B, habit of the thallus; C, close-up of one areole with immersed apothecium. Scales: B = 2 mm; C = 0·5 mm.

Apothecia black, aspicilioid and roundish when young, later lecideoid and semi-immersed at edges of thallus areolae, mostly with polygonal outline, with thin, sharp margin, (more rarely apothecia becoming convex and margin then virtually excluded), 0·6–1·2 mm diam. *Excipulum* in the upper part externally dark olive-brown, internally hyaline to brownish, inspersed with granules. *Hypothecium* hyaline. *Hymenium* hyaline, 50–70 µm high, upper 10–15 µm pigmented in various shades of olive-brown forming an

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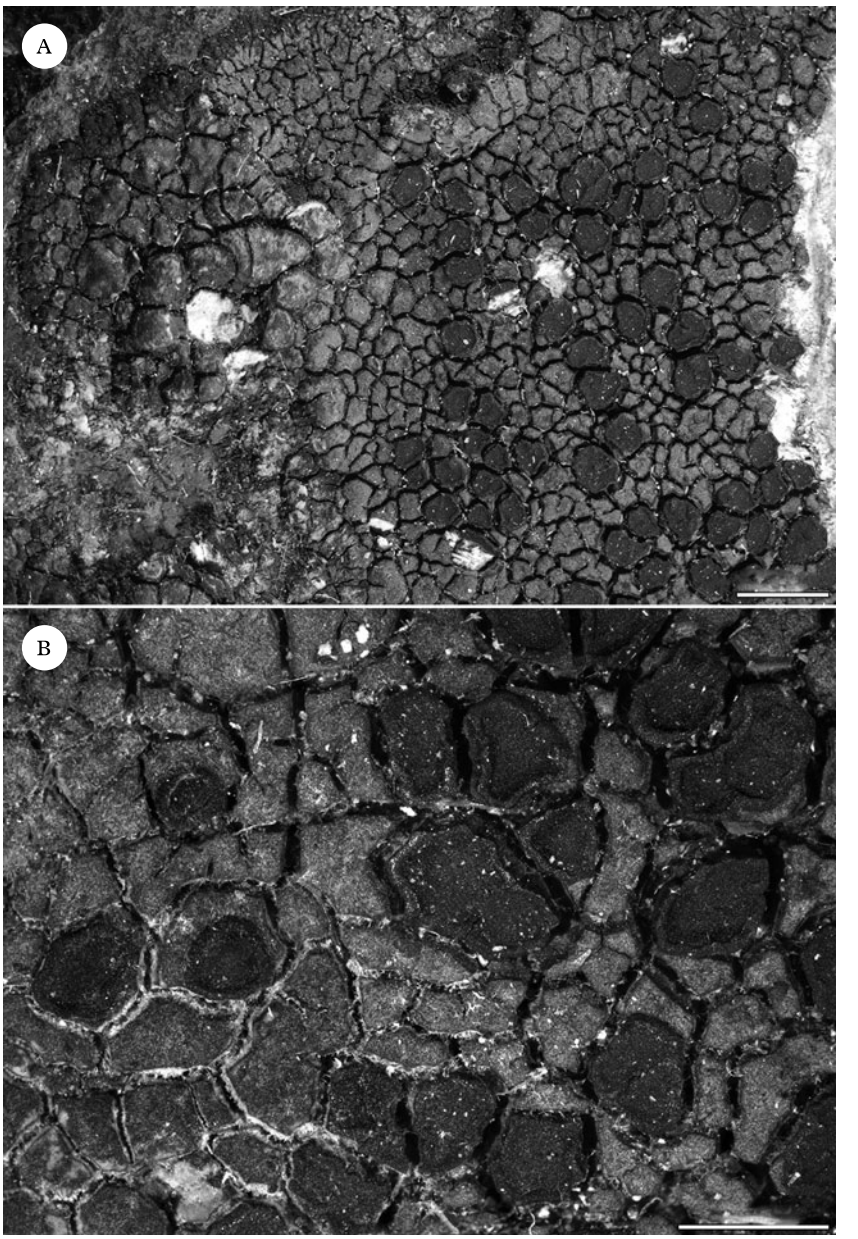

FIG. 7. *Miriquidica plumbea*, holotype of the heterotypic synonym *M. limitata* (M). A, part of the thallus; B, close-up of apothecia. Scales: A = 2 mm; B = 1 mm.

epihymenial layer; *paraphyses* mostly simple, *c.* 50–70 µm long and 1·5–2·0 µm thick; apical cells hardly to slightly enlarged, up to 4 µm diam., embedded in pigmented gel. *Asci* of *Lecanora*-type, 8-spored, 40–55 × 12–16 µm, outer wall layer and tholus except the central body I(Lugol)+ blue; *ascospores* hyaline, non-septate, ellipsoid, (9–)10–13 × 4–

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5 µm, length-breadth ratio *c*. 2·5–2·7 (9–12 × 3–5 µm sec. Hertel & Rambold 1987).

Pycnoconidia filiform, arcuate, 18–25 × *c*. 1 µm.

Secondary chemistry. Cortex K−, P−, C−, medulla K−, P+ orange-red, C−, miriquidic acid, protocetraric acid in the thallus (by TLC, number of specimens investigated: 11).

Notes. Although Massalongo assigned the species to Garovaglio, according to the code (ICN Art. 46.2) the author of the taxon is Massalongo, because the validating description was evidently written by him, whereas Garovaglio contributed the name and the specimen ("SINON. *Lecidea plumbea Garov*! *secund*. *specim*. *missum*.").

The habitus of *M*. *plumbea* recalls that of *Schaereria fuscocinerea* (Nyl.) Clauzade & Cl. Roux, especially when thalli are young and most of the apothecia are still immersed in the areolae and more or less aspicilioid. But these two species are easily separated by hymenial characters (character states of *S*. *fuscocinerea* in brackets), such as consistency (elements easily separating in squash preparations) and height (*c*. 100 µm high) of hymenium, ascus shape (subcylindrical) and construction of ascus tip (tholus lacking or little developed, not distinctly amyloid), epihymenial pigments (green with purple-violet granules), and secondary chemistry of the thallus (gyrophoric acid, C+ red).

A glossy black prothallus, as mentioned in the protologue of *M*. *limitata* (Hertel & Rambold, l. c.) and regarded as diagnostic to distinguish *M*. *griseoatra* auct. (i.e., *M*. *subplumbea*), can only be expected when the *Miriquidica*-thalli have developed on rock surfaces without contact with other crustose lichen thalli. Edges in contact with other crustose lichen thalli lack such a conspicuous prothallus and this can even be seen on the holotype of *M*. *limitata*. We also saw thalli lacking a conspicuous prothallus, the formation of which may depend on how fast a thallus grows.

Ecology. According to the label data of the specimens investigated, *M*. *plumbea* is an alpine to subnival species, confined to steep or overhanging faces of hard siliceous rocks often with a high content of iron.

Accompanying species. Only one species is mentioned as growing together with *M*. *plumbea* in the literature, *Dimelaena oreina*: "[. . .] cum *Par*. *oreina*" (Garovaglio 1838*a*: 19); "[. . .] associato alla *Parm*. *Oreina*" (Garovaglio 1838*b*: 49). On the specimens studied by us we noted: *Rhizocarpon geographicum* on the lectotype of *L*. *plumbea*; *Tremolecia atrata*, *Rhizocarpon geographicum* agg., *Miriquidica garovaglii*, *Miriquidica* sp. (tiny thallus), and *Immersaria athroocarpa* on the holotype of *M*. *limitata*; *Lecanora orbicularis*, *Psorinia conglomerata*, *Rhizocarpon geographicum*, and *Umbilicaria cylindrica* on *Hafellner* 30159; *Lecanora orbicularis*, *Pleopsidium chlorophanum* on specimen from Mohrenköpfe; *Lecanora polytropa*, *Lecidea lapicida*, *Miriquidica intrudens*, *Rhizocarpon geographicum*, *Schaereria fuscocinerea*, *Umbilicaria cylindrica* on specimen from Rosegtal.

Distribution. The species is so far only known from a few localities in the Alps in Italy, Switzerland and Austria. It is mentioned in neither the checklist for France (Roux 2012) nor in that for Switzerland (Clerc 2004). Hence the specimen cited below appears to be a new record for Switzerland.

Exsiccata examined. Anzi, *Lich*. *Rar*. *Langob*. *exs*. no. 154, sub *Lecidea plumbea* (MOD, PAV). Material purportedly distributed in: S. Garovaglio, *Lichenotheca Italica* Ed. I, deca IV, no. 10 (1838) [Note: no printed labels, thus irrelevant for nomenclatural questions (VER)].

Other exsiccata not yet examined. *Lichenotheca Italica* Ed. II, deca XIII, no. 5 (1846) [fide Garovaglio 1838*a*: 19; Garovaglio 1864: 28 (see also Tomaselli 1946); *Lich*. *Com*. no. 140 [fide Garovaglio 1838*b*: 49]. None of these exsiccates was traced by one of us (M.T.) in Italian herbaria.

Specimens investigated (non type material, label data shortened): **Austria:** *Tirol* (*Tyrol*): Samnaun-Gruppe, Furgler W Serfaus, zwischen Furgler Joch und Gipfel, [47°02′40″N / 10°30′50″E], 2800–2900 m, GF 8929, 1991, *J*. *H*. 30159 (GZU) [m, p]; [Tuxer Alpen], Glungezer, Mohrenköpfe, 1899, without collector (W) [m, p].—**Italy:** *Piemonte*: Prov. Cuneo, Alpi Marittime, Rocca dell' Abisso W of Colle di Tenda, N below summit, 44°08′35″N / 07°30′15″E, 2750 m, 2000, *J*. *H*. 41493 & *A*. *Hafellner* (GZU) [m, p]; *ibid*., *Tretiach*

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34093, 34476 (TSB) [m, p]; [prov. Vercelli], presso l'ospizio della Valdobbia [now Rifugio Ospizio Sottile], 1863, *Baglietto* (MOD) [m, p]. *Lombardia*: [Prov. Brescia], Parco Regionale dell'Adamello, Passo di Gallinera, 2006, *M. Tretiach* (TSB) [m, p]. *Friuli-Venezia Giulia*: Prov. Udine, [Southern Alps], Alpi Carniche, Monte Crostis, 2200 m, 1993, *M. Tretiach* (TSB) [m, p]; *ibid.*, giogaia dei Fleons, 2400 m, 1995, *M. Tretiach* 26470 (TSB) [m, p].—**Switzerland:** [*Kanton Graubünden*]: Schweizer Alpen, Rosegtal bei Pontresina, 1900 m, 1913, *G. Lettau* (B) [m, p].

Lichenicolous fungi. Only a strain of *Muellerella pygmaea* (Körb.) D. Hawksw. has so far been detected on some specimens (*Hafellner* 30159).

Miriquidica plumbeoatra (Vain.) A. J. Schwab & Rambold

Rambold & Schwab, *Nordic J. Bot.* **10:** 121 (1990).—*Lecidea plumbeoatra* Vain., *Acta Soc. Fauna Flora Fenn.* **10:** 82 (1883); type: [Finland], Karelia borealis, Nurmes, ad saxa granitica littoralia in insula Kynsisaari lacus Pielisjärvi, 1875, *E. Vainio* (TUR—holotype) n.v., reinvestigated by Rambold & Schwab (1990: 121). Note: the type locality is situated in Finland and not in Russia ("USSR") as Rambold & Schwab (l. c.) had argued.

[Fig. 1F (habitus) (Andreev 2004: 35)]

Thallus dark grey, often rusty or with brownish tinge, areolate, spreading. *Areolae* dispersed to densely arranged, *c.* 0·2–1·0 mm diam. *Hypothallus* obvious between dispersed areoles and at the margin.

Apothecia immersed to semi-immersed, 0·4–1·0 µm diam., plane and with thin margin when young, later slightly convex and margin virtually excluded. *Excipulum* externally greenish brown, internally brown. *Hypothecium* reddish brown to violet-brown. *Hymenium* hyaline, 40–55 µm high, upper 10–15 µm in shades of olive-brown forming an epihymenial layer; *paraphyses* mostly unbranched, 40–55 µm long and 1·5–2·0 µm thick; apical cells hardly or slightly enlarged, up to 4 µm diam. *Asci* of *Lecanora*-type, 8-spored, 40–50 × 12–15 µm, outer wall layer and tholus except the central body I(Lugol)+ blue; *ascospores* hyaline, non-septate, broadly ellipsoid, 8–11 × 4·5–7·0 µm, length-breadth ratio usually < 2.

Secondary chemistry. Cortex K−, P−, C−, medulla K−, P−, C−, no lichen substances in the thallus (by TLC, number of specimens investigated: 2).

For detailed descriptions see Rambold & Schwab (1990: 121) and Andreev (2004: 33).

Notes. The species is the only taxon in the *M. griseoatra* group lacking lichen substances (at least when analyzed with TLC). It is rather similar to *M. griseoatra* s. str. both in morpho-anatomy and ecology, but that species contains miriquidic acid in the thallus and exhibits significantly larger ascospores.

Ecology. The species grows on occasionally inundated siliceous rocks near rivers and waterfalls or other long-time moist habitats, such as boulders in or near snow beds.

Accompanying species. None observed.

Distribution. The species has so far only been recorded from a few localities in Fennoscandia, north-western Russia, Kamchatka and North America (Rambold & Schwab 1990; Andreev 2004).

Exsiccata examined. Malme, *Lich. Suec. exs.* no. 947a sub *Lecidea plumbeoatra* (GZU); Malme, *Lich. Suec. exs.* no. 947b sub *Lecidea plumbeoatra* (GZU).

Specimens investigated (non type material, label data shortened): **Sweden:** *Torne Lappmark*: Jukkasjärvi, Abiskojokk, 1919, *A. H. Magnusson* = Malme, *Lich. Suec. exs.* no. 947a (GZU) [0]; Jukkasjärvi, Vassitjåkko, 1921, *A. H. Magnusson* = Malme, *Lich. Suec. exs.* no. 947b (GZU) [0].

Lichenicolous fungi. None recorded. None seen by us.

Miriquidica subplumbea (Anzi) Cl. Roux

Roux *et al.*, *Bull. Soc. Linn. Provence, no. spec.* **14:** 108 (2011).—*Lecidea subplumbea* Anzi, *Atti Soc. Ital. Sci. Nat.* **11:** 169 (1868); type: "Sulle rupi micaceo-schistose, al termine della vegetazione arborea, nell'alpe Cerasina in Valfurva: rara." (Anzi 1868: 169). [Italy], Alpe Cerasina, *Anzi* (hb. Baglietto in MOD—lectotype!, designated here). Secondary chemistry of type specimen: miriquidic acid (by TLC).

Miriquidica griseoatra sensu auct. non (Flot.) Hertel & Rambold (see above).

Lecidea inserena Nyl., *Flora* **52:** 84 (1869); type: "at saxa granitosa in Scotia (Crombie)" (Nylander 1869: 84). [United Kingdom, Scotland], Scotia, 1868, *J. M. Crombie* (H-Nyl. 16530—lectotype!, designated here). Secondary chemistry of type specimen: miriquidic acid (by TLC).

(Figs 8A–C, 9A–C)

Thallus lead grey to dark grey, matt, areolate, usually rather thick, up to several cm diam. *Areolae* dense, verrucose, not or only

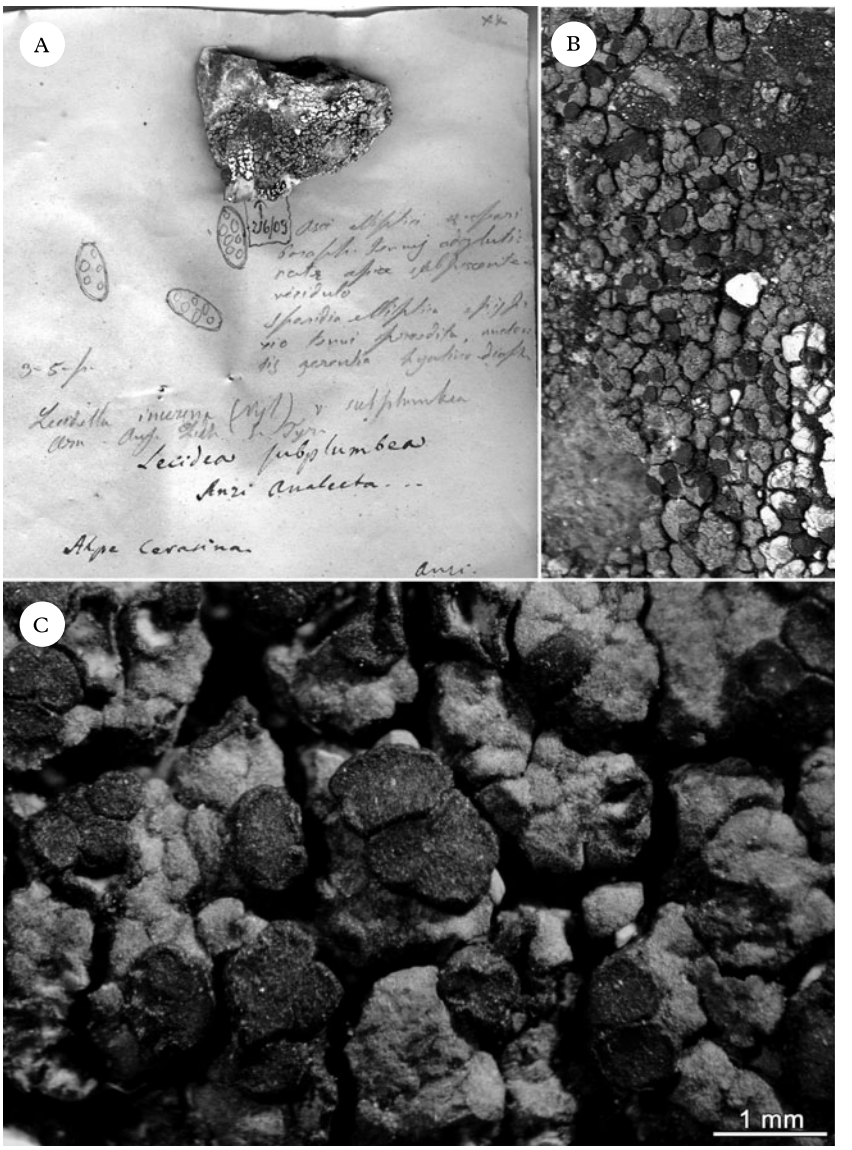

FIG. 8. *Miriquidica subplumbea*, lectotype of *Lecidea subplumbea* (MOD). A, entire specimen; B, part of the thallus; C, close-up of fertile part of the thallus. Scale: C = 1mm.

somewhat subdivided, up to 1·5 mm diam, plane to slightly convex. *Hypothallus* usually indistinct.

Apothecia often not very numerous, black, 0·5–1·2 mm diam., laterally attached to areoles, subsessile, plane and marginate when young, later convex and virtually immarginate. *Excipulum* externally blue-green to olive-brown, internally brownish to almost hyaline. *Hypothecium* hyaline. *Hymenium* hyaline, 55–65 µm high, upper 10–15 µm olive-green to greenish brown forming an epihymenial layer; *paraphyses* mostly unbranched, 55–65 µm long and 1·5–2·0 µm

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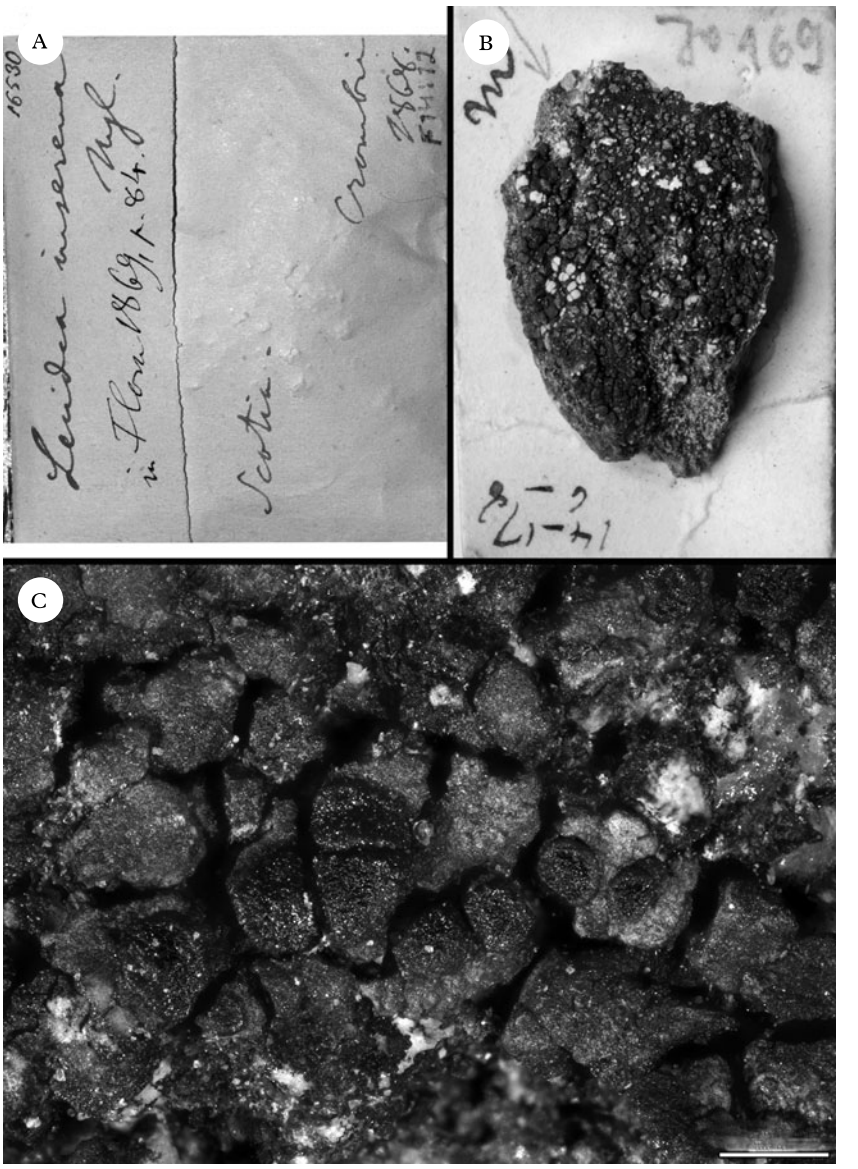

FIG. 9. *Miriquidica subplumbea*, lectotype of the heterotypic synonym *Lecidea inserena* (H-Nyl). A, envelope; B, entire specimen; C, close-up of fertile part of the thallus. Scale: C = 0·5 mm.

thick; apical cells hardly or slightly enlarged and then up to 4 µm diam. *Asci* of *Lecanora*-type, 8-spored, 40–50 × 14–18 µm, outer wall layer and tholus except the central body I(Lugol)+ blue; *ascospore*s hyaline, non-septate, ellipsoid, 10–13 × 5–6(–7) µm, length-breadth ratio *c.* 2·0–2·3 (see also e.g., Andreev 2004: 22–23 or Giavarini *et al.* 2009: 609, both sub *M. griseoatra*).

Secondary chemistry. Cortex K–, P–, C–, medulla K–, P–, C–, containing miriquidic acid (number of specimens investigated: 39).

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Notes. The morphology and anatomy of *Lecidea subplumbea* was correctly described by Anzi (l. c.). The lectotype of *Lecidea subplumbea* Anzi consists of one piece of rock bearing a single thallus. The major part shows well-developed, partly fertile areoles with only a few areoles exhibiting a superficially damaged surface due to feeding activity of gastropods or insects. The edge of the thallus is partly present. There is no indication of parasitic behaviour of the species. No areolae of *Sporastatia polyspora* are discernible on the entire specimen. Accompaning species are *Rhizocarpon geographicum* and *Varicellaria lactea*.

As a consequence of our reinvestigation of type specimens of various *Miriquidica* species, *M. subplumbea* herewith replaces *M. griseoatra* auct., that is, it has to be applied to a species in a concept different to that proposed by Hertel & Rambold (1987).

When Hertel (1970: 428) gave a description of supposed *Lecidea subplumbea*, that concept was not based on the type or other authentic material but on a specimen collected by Poelt in eastern Switzerland (see above under *Miriquidica invadens*). The host on this collection is not a *Lecidea* as argued by Hertel, but *Sporastatia polyspora*, the typical host of *M. invadens*.

Lecidea subplumbea sensu Hertel is a different species. It was also called "*Miriquidica griseoatra* chemotype 2" (miriquidic acid + stictic acid, Hertel & Rambold 1987) whereas "*Miriquidica griseoatra* chemotype 1" (miriquidic acid alone) is the secondary chemistry of both *M. griseoatra* (Flot.) Hertel & Rambold and *M. griseoatra* auct. (here treated as *M. subplumbea*). *Lecidea subplumbea* has been listed among the synonyms of *M. griseoatra* by Andreev (2004: 22), without any indication of doubt. However, Andreev (l. c.) states that "forms with red-violet or violet-brown lower part of the excipulum and the external part of the hypothecium are known as *Lecidea subplumbea*". He also noticed narrower ascospores and a secondary chemistry with stictic acid as typical for that "form". This is obviously based on observations already published by Hertel & Rambold (1987: 385). Although Hertel & Rambold (1987) did not mention a lichenicolous behaviour, according to the given characters and the material studied (e.g., the already mentioned specimen collected by J. Poelt and several further specimens preserved in M) it is almost certain that *Lecidea subplumbea* auct. (="*M. griseoatra* chemotype 2", Hertel & Rambold 1987) is the same as *Miriquidica invadens* (see above).

Miriquidica invadens is morpho-anatomically similar to *M. subplumbea* s. str., but can be distinguished from that species by its different thallus chemistry [*M. invadens* constantly containing miriquidic, stictic, (+ constictic) acids] and its autecology (*M. invadens* being constantly parasitic on *Sporastatia*, mostly *S. polyspora*). Also similar to *M. subplumbea* is *M. griseoatra* s. str., which is easily distinguished by either the colour of the hypothecium (brown in *M. griseoatra*) or ascospore size (larger in *M. griseoatra*).

The type specimen of *Lecidea inserena* Nyl., originating from Scotland, has also previously been reinvestigated by Hertel & Rambold (1987), who suggested the synonymization with *Miriquidica griseoatra* [*sensu auct.*].

Ecology. *Miriquidica subplumbea* grows on exposed acidic siliceous rocks in cold environments. According to Wirth (1995*a*: 427, sub *M. leucophaea* var. *griseoatra*), it prefers stands exposed to wind, light and rain. Its ecology is given as similar to *Miriquidica nigroleprosa*. From our field studies in the Alps we can confirm this, but find *M. nigroleprosa* more frequently on steeper rock faces.

The species is occasionally found growing upon *Acarospora fuscata*, *Lecanora polytropa*, *Lecidea* spp. or *Rhizocarpon* spp., but finally always becomes independent (Hertel & Rambold 1987: 385, sub *M. griseoatra*; Rambold & Triebel 1992: 113, sub *M. griseoatra*). Thus it evidently has no clear association with a specific host lichen. In the material studied by us, we have not detected a clear case where *M. subplumbea* behaves as a parasitic species.

Accompanying species. Species growing with *M. subplumbea* on the herbarium material

studied by us included: *Lecanora intricata*, *Ophioparma ventosa*, *Protoparmelia badia*, *Rhizocarpon geographicum* on *Hafellner* 59161; *Brodoa intestiniformis*, *Lecanora intricata*, *Rhizocarpon geographicum*, *Schaereria fuscocinerea* on *Mayrhofer* 1807; *Calvitimela armeniaca*, *Lecidea lapicida*, *Ophioparma ventosa*, *Protoparmelia badia*, *Pseudephebe pubescens*, *Rhizocarpon geographicum* on *Hafellner* 67954; *Calvitimela aglaea*, *Candelariella vitellina*, *Lecanora intricata*, *Lecanora polytropa*, *Miriquidica leucophaea*, *Rimularia furvella*, *Rhizocarpon geographicum*, *Umbilicaria cylindrica* on *Hafellner* 79721; *Lecanora intricata*, *Miriquidica nigroleprosa*, *Ophioparma ventosa*, *Protoparmelia badia*, *Rhizocarpon geographicum*, *Umbilicaria cylindrica* on *Hafellner* 80177; *Lecanora intricata*, *Lecanora polytropa*, *Lecidea lapicida*, *Rhizocarpon geographicum*, and *Umbilicaria cylindrica* on *Fryday* 2108.

Distribution. *Miriquidica subplumbea* s. str. is evidently widely distributed in Eurasia and North America (Andreev 2004, sub *M. griseoatra*) and seems to be the most common species of the *M. griseoatra* group. Nimis (1993, sub *M. griseoatra*) calls it a boreal-montane species, and Wirth (1995*a*, sub *M. leucophaea* var. *griseoatra*) gives the geobotanical characteristics as "boreal-central European·high montane". However, as *M. griseoatra* s. str. and *M. subplumbea* have often been confused, literature data are difficult to interpret. *Miriquidica subplumbea* seems to be much more common in the boreal zone in mid to moderately high elevations (see e.g., Santesson *et al*. 2004: 211, sub *M. griseoatra*) than in mid elevations in Central Europe where it is quite frequent in the lower alpine belt (see e.g., Lisická 2005, sub *M. griseoatra*; specimens cited below). On the other hand, it remains unclear how many of the earlier high altitude records refer to misidentified samples of *M. invadens*, for which the lichenicolous behaviour was not recognized (see above).

Exsiccata examined. Anzi, *Lich. Rar. Langob. exs*. no. 573, sub *Lecidea subplumbea* (PAV, G). Arnold, *Lich. exs*. no. 714, sub *Lecidella inserena* var. *subplumbea* (G, GZU, M, W). Leighton, *Lich. Brit. exs*. no. 188, sub *Lecidea tenebrosa* (M).

Specimens investigated (non type material, label data shortened), **Austria:** *Tirol* (*Tyrol*): [Ötztaler Alpen], Ötztal, Gurgl, 1900 m, 1877, *F. Arnold* = Arnold, *Lich. exs*. no. 714 (G, GZU, M, W) [m]; *ibid.*, Pitztal, Mittelberg, Mittagskogel, 1875, *F. Arnold* (M) [m]; [Stubaier Alpen], Kühtai [Kühthei], 1872, *F. Arnold* (M) [m]; *ibid.*, zwischen Kühtai [Kühthei] und den Finstertaler Seen, 1874, *F. Arnold* (M) [m]; *ibid.*, Kühtai [Kühthei], Finstertaler Seen, 1872, *F. Arnold* (M) [m]; *ibid.*, ober Weißbach, Rosskogel bei Innsbruck, 1875, *F. Arnold* (M, 2 specimens) [m]; *ibid.*, Inzinger Alpe, 1876, *F. Arnold* (M) [m]; [Kitzbühler Alpen], Kleinen Rettenstein, [W über] Pass Thurn, 1871, *F. Arnold* (M, 2 specimens) [m]; *ibid.*, Roßgrubkogel, Kleiner Rettenstein, 1871, *F. Arnold* (M) [m]. Note: assoc. species: *Miriquidica nigroleprosa*. *Salzburg*: Hohe Tauern, Glockner-Gruppe, Kleiner Schmiedinger N Schmiedinger Scharte, W Krefelder Hütte, über Kaprun, 2700–2739 m, GF 8742, 1973, *J. Poelt* (GZU) [m]. *Kärnten* (*Carinthia*): NP Hohe Tauern, Schober-Gruppe, Fleckenkopf gegen Egger Wiesen, NW Döllach, [46°59′40″N / 12°50′30″E], 2060–2100 m, GF 9043/1, 1988, *J. H.* 21133 & *M. Walther* (GZU); *ibid.*, Gradental W Döllach, SW Graden Alm, [46°58′05″N / 12°48′50″E], ca. 1750 m, 1988, *J. H.* 21906 & *M. Walther* (GZU) [m]; Saualpe W Wolfsberg, Geierkogel S Klippitztörl, Gipfelbereich, 46°55′10″N / 14°40′25″E, 1910 m, GF 9054/3, 2012, *J. H.* 80652 (GZU) [m]; *ibid.*, zwischen Kienberg und Forstalpe, Kar über Schmiedbauerhütte, 46°53′30″N / 14°39′00″E, 2030 m, GF 9153/2, 2012, *J. H.* 80177 & *A. Hafellner* (GZU) [m, u]; Stubalpe NE St. Leonhard, Peterer Riegel, 47°02′10″N / 14°50′20″E, 1930 m, GF 8955/3, 2006, *J. H.* et al. 65970 (GZU) [m]; Koralpe *c.* 15 km W Deutschlandsberg, Handalpe N Weinebene, 46°50′55″N / 15°01′00″E, 1820 m, GF 9156/3, 2012, *J. H.* 79721 (GZU) [m]; *ibid.*, E Wolfsberg, Großes Kar, Bergrücken Großer Speikkogel – Steinschneider, 46°47′35″N / 14°57′55″E, 1950 m, GF 9255/2, 2012, *J. H.* 80154 et al. (GZU) [m]. *Steiermark* (*Styria*): Wölzer Tauern, Greim 11 km NW Oberwölz, Gipfelbereich, 47°14′50″N / 14°09′05″E, 2470 m, GF 8750/4, 2006, *J. H.* 67954 & *L. Muggia* (GZU) [m]; *ibid.*, Großer Rotbühel S Planneralpe, Gipfel, 47°23′35″N / 14°12′30″E, 2000 m, GF 8651/1, 2012, *J. H.* 80060 & *L. Muggia* (GZU) [m]; Triebener Tauern, Griesmoar Kogel SW Wald am Schoberpaß, 47°25′15″N / 14°36′10″E, 1950 m, GF 8553/4, 2002, *J. H.* 59157, 59161 & *J. Miadlikowska* (GZU) [m]; Seetaler Alpen, 10.5 km W Obdach, path Großer Winterleitensee – Ochsenboden – Kreiskogel, 47°05′N / 14°33′E, 2000 m, GF 8953/1, 1999, *W. Obermayer* 7777 (GZU) [m]; Gleinalpe, Roßbachalpe S Gleinalmsattel, 1586–1750 m, GF 8756, 1981, *H. Mayrhofer* 1807 & *J. Poelt* (GZU) [m].—**France:** [*Auvergne*: *Dept. Puy-de-Dôme*], Mont-Dore, 1882, *E. Lamy* (G) [m]; *ibid.*, Mont-Dore, 1879, *E. Lamy* 1169 (M) [m]; *ibid.*, Rigolet, près du Mont-Dore, 1878, *E. Lamy* (M) [m]. *Dept. Cantal*: Auvergne, Monts du Cantal, Puy Mary, gegen Puy de Peyre-Arse, 1600 m, 1980, *A. Bellemère* & *J. H.* 9492 (GZU) [m].—**Great Britain:** *Scotland*: Mid Perthshire (V. C. 88), Glen Lochay, Meall nan Subh, Grid 27(NN)/45.39, 770 m, 1991, *A. M. Fryday* 2108 (E) [m]; *ibid.*, Ben Lawers range, Meall Corranaich, Grid 27(NN)/61.40, 950 m, 1991, *A. M. Fryday* 2169 (E) [m]; *ibid.*, Ben Lawers National Nature Reserve, Creag an Lochain, Grid 27(NN)/59.41, 650 m, 1991, *A. M.*

Fryday 2082 (E) [m]; *ibid.*, Coire Odhar, Grid 27(NN)/61.40, 800 m, 1993, *A. M. Fryday* 4470 (E) [m]; *ibid.*, Breadalbane Mountains, Creag Mhòr, Coire-cheathaich, Grid 27(NN)/39.35, 600 m, 1990, *A. M. Fryday* 1067 (E) [m]. *England*: Shropshire, on Abdon Burf, highest land (1806 ft.), without date and collector = Leighton, *Lich. Brit. exs.* no. 188 (M) [m].—**Italy:** [*Lombardia*: prov. Sondrio], in termino vallis Furva (alpe Calvarána), *Anzi* = Anzi, *Lich. Rar. Langob. exs.* no. 573 (PAV).—**Norway:** *Hordaland*: Odda: Dyranut W Haukeliseter, 1100 m, 1984, *J. H.* 11613 & *A. Ochsenhofer* (GZU) [m].—**Poland:** Sudeten, *Körber* (B, as admixture in specimen of *M. griseoatra*) [m].—**Switzerland:** *Kanton Wallis*: Aletschreservat, Riederfurka, 2080 m, 193?, *E. Frey* 1343 (GZU) [m].—**U.S.A.:** *Alaska*: Southeast Alaskan Mainland near Petersburg, Deboer Lake alpine area, small valley NE Deboer Lake between Rodman and Pierce Peaks, 57.10728°N / 132.95177°W, 766 m, 2011, *K. Dillman* 2011-18 (GZU) [m]. Note: sterile specimen, therefore somewhat uncertain.

Lichenicolous fungi. Of the non-lichenized lichenicolous fungi only *Endococcus complanatae* Arnold has been seen once by us so far: **Austria:** *Kärnten* (*Carinthia*): Zentralalpen, Saualpe W Wolfsberg, Geierkogel S Klippitztörl, Gipfel, 46°55′10″N / 14°40′25″E, 1910 m, GF 9054/3, host: *M. subplumbea*, 2012, *J. H.* 80654 (GZU). The lichenicolous lichen *Rimularia furvella* (Nyl. ex Mudd) Hertel & Rambold was noticed twice on this host (on Hafellner 59157, 59161).

Discussion

Comparision of *Miriquidica* species with dark grey thallus

Re-examination of relevant type material during the present study has resulted in the re-application of several names in the genus *Miriquidica* (Table 1).

Among the *Miriquidica* species with a dark grey thallus, the morpho-anatomically closest taxa are *M. invadens* and *M. subplumbea*, both with a hyaline hypothecium. Whereas *M. invadens* exhibits a secondary thallus chemistry with miriquidic acid and stictic acid, *M. subplumbea* contains only miriquidic acid. *Miriquidica griseoatra*, also with only miriquidic acid, is easily recognized by the brown hypothecium, significantly larger ascospores and often distinctly subdivided areoles. *Miriquidica obnubila*, also with only miriquidic acid, is distinguished by sessile apothecia with a persistently prominent margin (recalling apothecia of *Farnoldia* species), but the consistency of these characters needs to be confirmed by examination of more material. Among this same subset of species, only *M. invadens* and *M. subplumbea* show a tendency to parasitism. Whereas *M. invadens* appears to be an obligate youth parasite with pronounced host specifity, *M. subplumbea* is only occasionally found lichenicolous as a facultative youth parasite without host specifity (see Rambold & Triebel 1992: 113–114, sub *M. griseoatra* auct.).

Comparision of *Miriquidica* species containing miriquidic acid and stictic acid

The chemotype miriquidic acid, stictic acid, constictic acid (+/− in traces) is not very common in *Miriquidica*. In addition to *M. invadens*, the common and widely distributed *M. garovaglii* contains this combination of lichen substances. Whereas the lichenicolous *M. invadens* has an olive-grey to dark grey thallus, that of *M. garovaglii* is glossy brown and therefore does not belong to the *M. griseoatra* group as understood here. In the morpho-anatomically very different *M. intrudens* (areoles brown with greyish margin), a chemical strain with miriquidic acid + stictic acid has been reported by Owe-Larsson & Rambold (2001) but it seems to be rare. The same chemotype was also reported for *M. pulvinatula*, but in the type specimen of that species we detected only miriquidic acid.

Comparision of lichenicolous *Miriquidica* species

Parasitic growth on other lichens is rather frequent in the genus *Miriquidica*. Facultative lichenicolous behaviour is reported by Rambold & Triebel (1992: 113–114) from *M. complanata*, *M. deusta*, *M. griseoatra* auct. (=*M. subplumbea*), *M. leucophaea* and *M. nigroleprosa*. Additionally, we quite frequently saw *M. instrata* growing on other lichens.

Among the recognized species of *Miriquidica* only two species, *M. invadens* and *M. intrudens*, are regularly recorded as lichenicolous, but their behaviour is biologically rather different. From field observations we know that *M. invadens* is rather specialized,

TABLE 1. *Re-application of species names in* Miriquidica *resulting from the present study, plus important distinguishing characters of the species treated*

Current name (Hafellner *et al.* – this publication)	Previous name (Hertel & Rambold 1987; Andreev 2004, etc.)	Thalline chemistry	Colour of hypothecium
M. griseoatra	*M. obnubila*	miriquidic acid	red-brown to dark violet-brown
M. invadens	*M. subplumbea*	miriquidic and stictic acids	hyaline
M. obnubila	–	miriquidic acid	hyaline
M. plumbea	*M. limitata*	miriquidic and protocetraric acids	hyaline
M. plumbeoatra	*M. plumbeoatra*	no substances	red-brown to violet-brown
M. subplumbea	*M. griseoatra*	miriquidic acid	hyaline

as it constantly starts its life cycle on *Sporastatia* (mostly S. *polyspora*, rarely S. *testudinea*), whereas *M. intrudens* is not host specific, growing on a wide range of crustose lichens, including *Rhizocarpon geographicum*, *Lecanora polytropa*, *Lecidea confluens*, *Lecidea lapicida*, and others (see also Owe-Larsson & Rambold 2001). On the other hand, mature specimens of *M. invadens* develop a spreading thallus and contact with the host lichen seems not to be indispensable on all sides of the thallus, thus an older thallus may well have an edge zone on one side without a *Sporastatia* thallus being the neighbour. Therefore *M. intrudens* constitutes a good example of youth parasitism. According to Owe-Larsson & Rambold (2001: 345), older thalli of *M. intrudens* may also become independent, but in our opinion *M. intrudens* is an obligately lichenicolous species; that is, it shows lichenicolous growth over its entire life cycle. The consistently small thalli of *M. intrudens* support this view.

Of the species reported as facultatively or obligately lichenicolous, only *M. invadens* and *M. subplumbea* have a medium to dark grey thallus. All the others are either brown or white to cream-coloured. It would be interesting to revise the specimens upon which the observation of lichenicolous behaviour in *M. griseoatra* is based. Rambold & Triebel (1992: 113, sub *M. griseoatra*) list *Acarospora fuscata*, *Lecanora polytropa*, *Lecidea* sp., and *Rhizocarpon* sp. as possible hosts. Interestingly, *Sporostatia polyspora* is not mentioned, although Rambold & Triebel (1992) understood *M. griseoatra* in a broad sense that included the species described here as new.

A key to the *Miriquidica* species with a grey thallus

Based on our comparative studies, a revised key to the taxa of the *M. griseoatra* group is provided.

N.B.: 'miriquidic acid' always means miriquidic acid plus the accessory substances usually present, known as the 'miriquidic acid syndrome'. Also stictic acid is commonly accompanied by related compounds in detectable amounts.

1 Thalli lichenicolous, mostly on *Sporastatia polyspora*, rarely on *S. testudinea*, grey to olive-grey to brownish grey, forming patches of various size, chem.: miriquidic acid, stictic acid, +/-constictic acid . . . . . **M. invadens**
Thalli not distinctly lichenicolous on *Sporastatia* 2

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2(1) Hypothecium red-brown to dark brown . . . 3
Hypothecium hyaline or pale . . . 5

3(2) Thallus grey to dark grey, often rusty or with brownish or ochre tinge, chem.: no lichen substances . . . **M. plumbeoatra**
Thallus grey, whithout brownish tinge, chem.: miriquidic acid . . . 4

4(3) Ascospores 4–6 µm wide, areoles subdivided, marginal areoles sometimes sublobate . . . **M. griseoatra s. str.**
Ascospores 6–8 µm wide, areoles not as above; for a detailed description see Hertel (1977: 313) . . . **M. molybdochroa** (not treated)

5(2) Thallus whitish grey to pale grey or beige . . . 6
Thallus lead grey to dark grey . . . 8

6(5) Thallus sorediate, soredia blackish, chem.: miriquidic acid (rarely replaced by lobaric acid) or psoromic acid (var. *liljenstroemii*); for a detailed description see Owe-Larsson & Rambold (2001: 346) . . . **M. nigroleprosa** (incl. var. *liljenstroemii*) (not treated)
Thallus usually fertile, without soralia . . . 7

7(6) Thallus spreading, chem.: miriquidic acid; for a detailed description see Andreev (2004: 25)! . . . **M. leucophaea** (not treated)
Thallus small, usually not exceeding 1·5 cm in diam., chem.: norstictic acid; for a detailed description see Andreev (2004: 28) . . . **M. lulensis** (not treated)

8(5) Thallus sorediate . . . 6
Thallus usually fertile, without soralia . . . 9

9(8) Medulla Pd+ orange to orange-red due to presence of protocetraric acid or stictic acid . . . 10
Medulla Pd- . . . 11

10(9) Thallus lead grey, young apothecia aspicilioid, chem.: miriquidic acid and protocetraric acid . . . **M. plumbea** (syn. *M. limitata*)
Thallus grey to olive-grey to brownish grey, young apothecia not aspicilioid, at least on one side neighboured by *Sporastatia polyspora* on which it starts as parasite (on smaller specimens the *Sporastatia* may not be present), chem.: miriquidic acid, stictic acid, +/− constictic acid . . . **M. invadens**

11(9) Hypothecium brown, at least in the lower part . . . 3
Hypothecium hyaline . . . 12

12(11) Areoles dispersed, prothallus in between distinct, apothecia sessile with persistent margin . . . **M. obnubila**
Areoles densely arranged, prothallus indistinct . . . 13

13(12) Thallus lead grey to dark grey, chem.: miriquidic acid . . . **M. subplumbea** (syn. *M. griseoatra* sensu auct.)
Thallus grey to olive-grey to brownish grey, at least on one side neighboured by *Sporastatia* (*polyspora*) on which it starts as parasite (on smaller herbarium specimens the *Sporastatia* may not be present), chem.: miriquidic acid, stictic acid, +/− constictic acid, recheck Pd-reaction of medulla . . . **M. invadens**

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