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Standard Paper

Arthonia epipolytropa and *Arthonia subclemens*, two new lichenicolous species on *Lecanora polytropa*, with a key to the microfungi known on this common species

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Abstract

Arthonia epipolytropa Hafellner & Grube and *Arthonia subclemens* Hafellner, Grube & Muggia are described as new to science. Both are specific parasites of *Lecanora polytropa* s. lat., but of differing pathogenicity and of very different appearance. Whereas the clearly parasitic *Arthonia epipolytropa* with its agglomerated ascomata is presently known with certainty from a number of localities along the arch of the Alps (Austria, Italy, Switzerland), other parts of Europe (Norway, Albania) and northern America (USA), the less harmful *A. subclemens* with its isolated sunken ascomata is currently known only from a small number of localities in the Eastern Alps (Austria, Italy) and various mountain ranges in southern Europe (Spain, North Macedonia, Greece). The species are compared with other *Arthonia* species known from *Lecanora* or one of its recently segregated genera. A key to the fungi regularly found on *Lecanora polytropa* s. lat. is presented.

Keywords: *Arthoniales*; *Ascomycota*; fungi; host-specificity; lichens

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Introduction

Lichenicolous fungi in the strict sense live exclusively on lichens (Hafellner 2018). Since they are recognizable by morphological features displayed on their host, the study of lichenicolous fungi dates back to before it was understood that lichens themselves were fungal organisms. With increasing knowledge, it became clear that most lichenicolous fungi apparently occur with high specificity on their host organisms (Lawrey & Diederich 2003; Diederich *et al.* 2018). The presence of lichenicolous fungi might therefore provide information about the relationships of the hosts, especially when molecular data provide limited resolution.

The common rim lichens in the genus *Lecanora* represent a prototype of crust-forming lichens with their apothecial ascomata, furnished in most cases by an algal-containing margin and single-celled, hyaline spores. Since the premolecular era of lichenology, studies of lichens with these characters clearly indicated that the group must be heterogenous (Hafellner 1984). A high level of polyphyly was also suggested in early studies of the family *Lecanoraceae* (Arup & Grube 1998), although the taxon sampling was limited at that time. More recently, the phylogenetic work of Zhao *et al.* (2016) provided new insights into the relationship of this morphological assemblage. Their study revealed that several genera, recognized by phenotypic features, such as *Adelolecia*, *Arctopeltis*, *Bryonora*, *Carbonea*, *Frutidella*, *Lecidella*, *Miriquidica*, *Palicella*, *Protoparmeliopsis*, *Pyrrhospora* and *Rhizoplaca*, are nested within *Lecanora* s. lat. Three well-supported monophyletic clades correlated also with phenotypic features: *Myriolecis* (including the *Lecanora dispersa* group and the monotypic *Arctopeltis* with shield-like morphology, now *Polyozosia*), *Protoparmeliopsis* (the *L. muralis* group), and *Rhizoplaca* (which includes some placodioid taxa previously classified in *Lecanora*). *Lecidella* was strongly supported as a monophyletic group while other distinct clades were not recognized at the genus level, pending further analyses of critical taxa.

One of these lineages, the *Lecanora polytropa* group, contains widespread species with usnic acid as the major compound and regularly accompanied by fatty acids. Motyka (1996) coined the name *Lecidora* for this lineage, but his work is suppressed by nomenclatural measures and thus all names and combinations are invalid according to ICN Art. 34.1 (Shenzhen Code). Interestingly, Kondratyuk *et al.* (2019) left the *Lecanora polytropa* group untouched, while accepting *Omphalodina* for related species segregated from *Rhizoplaca* and species of lobate lecanoroid lichen assigned to *Sedelnikovaea*. All of these could represent a single genus, including the *Lecanora polytropa* group. Yakovchenko *et al.* (2019) showed that the *Lecanora polytropa* group is closely related to *Lecanora* species lacking usnic acid but instead containing pulvinic acid derivates. It may remain a matter of opinion at which level in the phylogenetic reconstruction the limits of genera should be drawn in the future. Nevertheless, the diversity of lichenicolous fungi on the *Lecanora polytropa* group is remarkable. A considerable number of those are restricted to *Lecanora polytropa* s. lat. and/or related species, which indicates a certain taxonomic distance from other lecanoroid lichenized fungi.

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Arthonia is one of the genera especially rich in lichenicolous species. Diederich *et al.* (2018) propose 140, however, we traced *c.* 230 epithets of both accepted species and supposed heterotypic synonyms. Since historical times, it has been known that a considerable number of taxa are able to infest lecanoroid lichens (Almquist 1880). The first species recognized dates back to a time when all lichens were still classified in one genus, *Lichen* (i.e. *Lichen varians* Davies). In this particular case, the infection with a lichenicolous *Arthonia* has been regarded as constituting a lichen close to what is now known as the host *Lecanora* (*Glaucomaria*) *rupicola* (L.) Zahlbr., but with fruiting bodies of variable colour (Davies 1794). Although subsequently recognized as a tripartite system (Nylander 1861), only rather recently the name was finally fixed to the organism responsible for this variation, an endohymenial species of *Arthonia* (Hafellner 2013), for which the heterotypic synonym *Arthonia glaucomaria* Nyl. was in use for many decades. Some 15 *Arthonia* names are associated with lecanoroid hosts today. This, however, reflects only part of the extant diversity and here we describe two additional species developing on *Lecanora polytropa* s. lat. We compare these two species with other species on lecanoroid lichens.

Methods

For morpho-anatomical analyses, air-dried herbarium specimens from herbarium GZU were used. External morphology was studied with dissecting microscopes (WILD M3, Leica MZFl3), and anatomical studies of the thallus and ascomata were carried out using compound microscopes (Zeiss Axiophot with epifluorescence equipment, Leitz Biomed). Sectioning was performed with a freezing microtome (Leitz Kryomat; preparing sections of 12–15 mm) with squash preparations used for measurements of ascospores and conidia in particular. Preparations were mounted in water and when necessary, contrasting was performed by a pretreatment with lactic acid-cotton blue (Merck 13741). Sections and squash preparations were not pretreated with potassium hydroxide solution (K), unless otherwise stated. Measurements refer to dimensions in tap water. Only mature ascospores released from the asci were measured. Amyloidy of hymenial elements was tested by the application of iodine solution (Lugol) (Merck 9261) (I) without and with pretreatment of K. Calcofluor white (Sigma 3543) was applied as a freshly prepared 1% aqueous solution for epifluorescence microscopy.

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

Selected reference material examined. *Arthonia clemens* (Tul.) Th. Fr. hosts: *Omphalodina chrysoleuca* (Sm.) S.Y. Kondr. *et al.* (syn. *Rhizoplaca chrysoleuca* (Sm.) Zopf) (1, also host of lecto-/neotype to be designated) (apothecia), *Omphalodina opiniconensis* (Brodo) S.Y. Kondr. *et al.* (2) (apothecia). **Italy:** *Trentino-Alto Adige*: Prov. Bolzano (Südtirol), Central Alps, Ötztal Alps, Val Venosta (Vinschgau), hill S of Tárces (Tartsch) = Tartscher Bichl, NE of Glorenza (Glurns), 46°40′35″N, 10°33′40″E, elev. 1000 m, (1), 2002, *Hafellner* 61277 (GZU).—**Kazakhstan:** Vost Kazakhstanskaja, N of the road SE of Karatogay, 48°15′N, 84° 36′E, elev. 610 m, (1), 1993, *Moberg* & *Nordin* s. n. (GZU).—**Mongolia:** 10 km N von Ulan-Bator, (1), 1978, *Huneck* MVR-16a (GZU). *Umnugobi (Omnogov) Aimag*: Gobi Desert, Chanchongor Somon, Central Gurvansaikhan (Gurvan-Saichan), (1), 1988, *Huneck* MVR 88-276a (GZU).—**Russia:** *Siberia*: Chukotka, on the upper reaches of the River Milkera, (1), 1977, *Andreev* s. n. (GZU).—**Greenland:** SW Greenland, head of Søndre Strømfjord, Ravneklippen, 67°N, 50°41′W, (1), 1998, *Hansen* (GZU).—**USA**: *Colorado*: Larimer Co., 0.8 km S of Wyoming State Line, just N of Virginia Dale, 41°N, 105° 22′W, alt. 2256 m, (1), 1961, *Shushan* (GZU); Clear Creek Co., 3.8 miles E of Georgetown, 1.5 miles N of Interstate Hwy 70 near junction with Hwy 40, 39°45′30″N, 105°39′30″W, elev. 2500 m, (2), 1985, *Ryan* 20586a (GZU).

Arthonia subvarians Nyl. hosts: *Lecanora (Polyozosia/Myriolecis) dispersa* s. lat. (1, also host of type) (apothecia), *Lecanora (Polyozosia/Myriolecis) semipallida* (syn. *L. flotoviana* auct.) (2) (apothecia), *Lecanora (Polyozosia/Myriolecis) crenulata* (3) (apothecia), *Lecanora (Polyozosia/Myriolecis) perpruinosa* (4) (apothecia). **Austria:** Kärnten *(Carinthia)*: Gailtaler Alpen, Reißkofel *c.* 11 km E von Kötschach-Mauthen, am Steig von der Reißkofel-Biwakschachtel entlang des W-Grates zum Gipfel, in den Nordhängen am Fuß des Gipfelaufbaus des W Vorgipfels, 46°41′15″N, 13°08′33″E, elev. 2190 m, GF 9344/2, (2), 2009, *Hafellner* 76050 & *A. Hafellner* (GZU). *Niederösterreich (Lower Austria)*: Nördliche Kalkalpen, Schneeberg NW von Neunkirchen, Kaiserstein, knapp E unter dem Gipfel am Südrand der Abbrüche in die Breite Ries, 47°46′25″N, 15° 48′45″E, elev. 2000 m, GF 8260/2, (2), 1997, *Hafellner* 42152 (GZU). *Steiermark (Styria)*: [Nordalpen], Dachstein-Gruppe, Ramsau, Weg von der Dachsteinsüdwandhütte in Richtung Hunerscharte, unterhalb des Scheiblingsteins, elev. 1900–2000 m, GF 8547/2, (4), 1993, *Poelt* & *Grube* s. n. (GZU). Nördliche Kalkalpen, Mürzsteger Alpen, Veitsch Alpe, Großer Wildkamm, am SE-Grat ober der Gingatzwiese, 47°39′40″N, 15° 24′30″E, elev. 1850 m, GF 8358/1, (1), 1997, *Miadlikowska* & *Hafellner* 40429 (GZU). [Zentralalpen], Niedere Tauern, Wölzer Tauern, Planneralpe, am Steig vom Plannerknot zum Hochrettelstein, [47°25′00″N, 14°13′28″E], elev. 2050 m, GF 8551/3, (3), 1985, *Hafellner* 14228 (GZU). *Tirol (Tyrol)*: Osttirol, Nationalpark Hohe Tauern, Glockner-Gruppe, Teischnitztal N von Kals, untere NW-Hänge des Fiegerhorns, SW ober der Teischnitzeben, 47°02′N, 12°39′40″E, *c.* 2200 m, GF 8941/4, (1), 1997, *J. Hafellner* 47134 (GZU). *Vorarlberg*: Rätikon, Berge W über Gargellen, kurz E unter dem St. Antönier Joch, etwas SE vom kleinen namenlosen See, 46° 58′00″N, 09°52′40″E, elev. 2300 m, GF 9025/1, (1), 2008, *Hafellner* 73056 (GZU).—**Italy:** Trentino-Alto Adige: Prov. Trento, Südtiroler Dolomiten, Mte Castellazo N vom Passo di Rolle, S-Abhänge am Fuß der Schutthalden, 47°18′20″N, 11° 47′50″E, elev. 2150 m, (2), 1976, *Hafellner* 41849 (GZU).—**Switzerland:** *Kanton Graubünden*: Engadin, Ofenpass, elev. 2300 m, (2), 1954, *Schröppel* s. n. (GZU). —**USA:** *Colorado*: Jefferson Co., Rocky Mountains, near mouth of Mt Vernon Canyon, near the Interstate Hwy, 39°41′30″N, 105°12′30″W, elev. 1950 m, (3), 1977, *Anderson* & *Poelt* s. n. (GZU).

Results

Arthonia epipolytropa Hafellner & Grube sp. nov.

MycoBank No.: MB 849058

Species non lichenisata sed lichenicola. Infectio in hospiti non cecidiogena sed distincte parasitica. Ascomata humide fuscoatra ad nigra, aggregata, convexa, Ascomata ut descripta. Asci fissitunicati, octospori. Ascosporae 1-septatae, cellulis subaequalibus,

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(9–)10–12(–13) × 4–5 µm. Species habitu specie *Arthonia subvarians* similis sed ab ea differt ascomatibus in gregibus maioribus compositis et selectio hospitis. Habitat in lichene *Lecanora polytropa* (Hoffm.) Rabenh. praecipue supra hymenia, sed etiam in marginibus apotheciorum et areolis adhuc in regione holarctica.

Typus: Austria, Kärnten (= Carinthia), Ostalpen, Zentralalpen, Saualpe W von Wolfsberg, sanfte SE-exponierte Hänge zwischen Ladinger Spitz und Speikkogel, NE unterhalb der Wolfsberger Hütte, 46°50′10″N, 14°39′50″E, elev. *c.* 1750 m, GF 9153/4, Zwergstrauchheiden im Waldgrenzökoton, auf kleinen, losen Glimmerschieferplatten, auf *Lecanora polytropa* (apothecia, thallus), 24 September 2010, *Hafellner* 76280 (GZU—holotype; isotypes to be distributed in *Lichenicolous Biota* no. adhuc ined. to BR, CANB, GZU, LE, NY, UPS).

(Figs 1A, 2A, 3A)

Non-lichenized but lichenicolous. Infections causing bleaching spots and destroying the host apothecia, *c.* 0.5–1 mm diam., in dense and often agglomerated groups of *c.* 5 to more than 30 ascomata, these individual infections later sometimes merging into larger complexes. Development of ascomata usually starting on host apothecia, later spreading to thalline margins and occasionally also to sterile thalline areolae, here ascomata also remaining individually discernable. Vegetative hyphae imbedded in host plectenchyma, hard to detect, I−.

Ascomata black with slight brownish tinge (fresh material) to matt black, developing in upper part of hymenia of the host (several simultaneously), later on also in the phenocortex of thalline margins and areolae, appearing superficially cushion-like, and becoming crowded and confluent in progressive state of infections. Individual ascomata rounded, immarginate, in longitudinal section up to 300 µm diam. and 100–120 µm tall, except for hypothecial stipe. *Hymenium* 45–55 µm tall, light greyish brown, the uppermost 10–15 µm forming a brown epithecium. *Hypothecium* 50–70 µm tall (except for a central stipe), medium brown, when on the thallus then sometimes incorporating algae of the host. *Paraphysoids* branched and anastomosing, with hyphal cells 5–6 × *c.* 1 µm, becoming wider in the excipuloid margin (6–8 × 2–3 µm), paraphysal tips as part of the epithecium with indistinct caps and otherwise amorphous pigment, occasionally amorphous pigment dispersing in small granules, uppermost cells of epithecial hyphae *c.* 2 µm wide, becoming deflated and gelatinizing. *Asci* fissitunicate of *Arthonia*-type, clavate, 25–30 (–35) × 10–15 µm, 8-spored, connected to ascogenous hyphae *c.* 4 µm wide, these distinctly fluorescent with Calcofluor white. *Ascospores* obovate, remaining hyaline, (9–)10–12(–13) × 4–5 µm, 1-septate, septum more or less median, upper cell slightly or hardly wider, lower cell virtually somewhat longer, not (or very indistinctly) constricted at the septum, not distinctly halonate in LM.

Pycnidia not seen.

Reactions. Hymenial and ascal gel I_{dil}+ red, I+ red, KI+ blue, ascus with tiny KI+ blue ring basally in the tholus of the endoascus.

Etymology. The epithet is an adjective, compound of epi- (Greek = upon, over), and of the host species, on which the fungus develops.

Remarks. Concerning the apothecial characters, *A. epipolytropa* shows little variability. Among the *Arthonia* taxa invading species of *Lecanora* or one of its recently segregated genera, it is notable by being distinctly parasitic and discolouring the host in the infected areas, by having the largest agglomerations of ascomata, and finally by the capability to spread to thalline margins and areolae of the host. In this respect, it recalls infections of *Arthonia parientinaria* Hafellner & A. Fleischhacker on *Xanthoria parietina* (L.) Th. Fr. (Fleischhacker *et al.* 2016).

Judging from the protologue, *Arthonia subvarians* is not a possible name for *A. epipolytropa*, although this name has often been applied to it in the past (see below). *Arthonia subvarians* s. str. (Fig. 4A; Nylander 1868) is a species invading the apothecia of *Lecanora dispersa* (Pers.) Röhl. (in the protologue the host is named '*Lecanora galactina* var. *dispersa*'), hence a species considered to be a member of *Polyozosia* (syn. *Myriolecis*). Typical for that species is the presence of one to few merging ascomata restricted to the hymenia, not distinctly harming the host lichen except in the portions of the host apothecia where the ascomata develop. If *Arthonia apotheciorum* (A. Massal.) Almq. (type host: *Lecanora* (*Polyozosia*/*Myriolecis*) *albescens*) is proved to be a different species, *Arthonia subvarians* would be the correct name for this widely distributed species on various taxa of the *Lecanora dispersa* group (*Polyozosia*), replacing the so far repeatedly used heterotypic synonym *Arthonia galactinaria* Leight. (Leighton 1879).

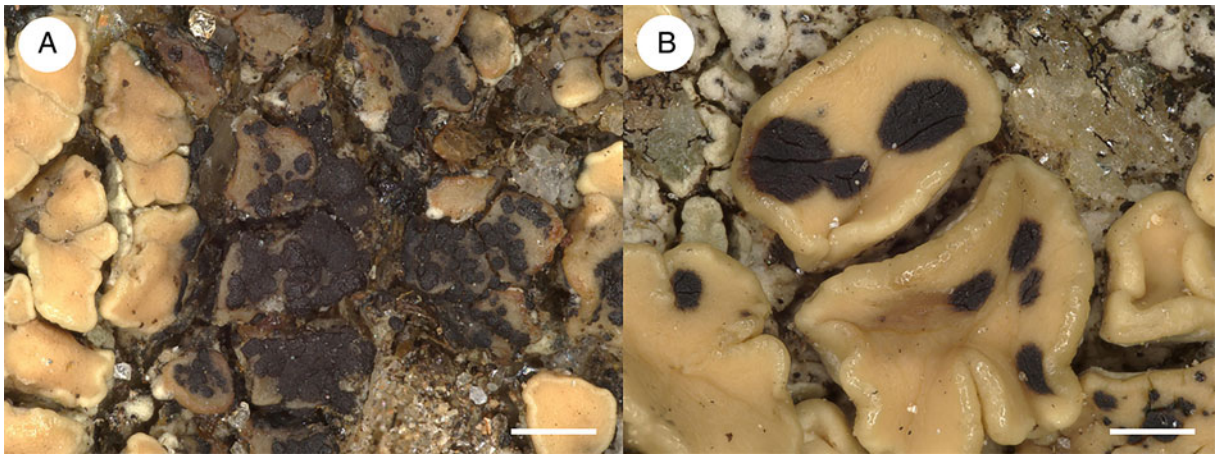

Figure 1. A, *Arthonia epipolytropa* (type material); habitus. B, *Arthonia subclemens* (type material); habitus. Scales = 0.5 mm.

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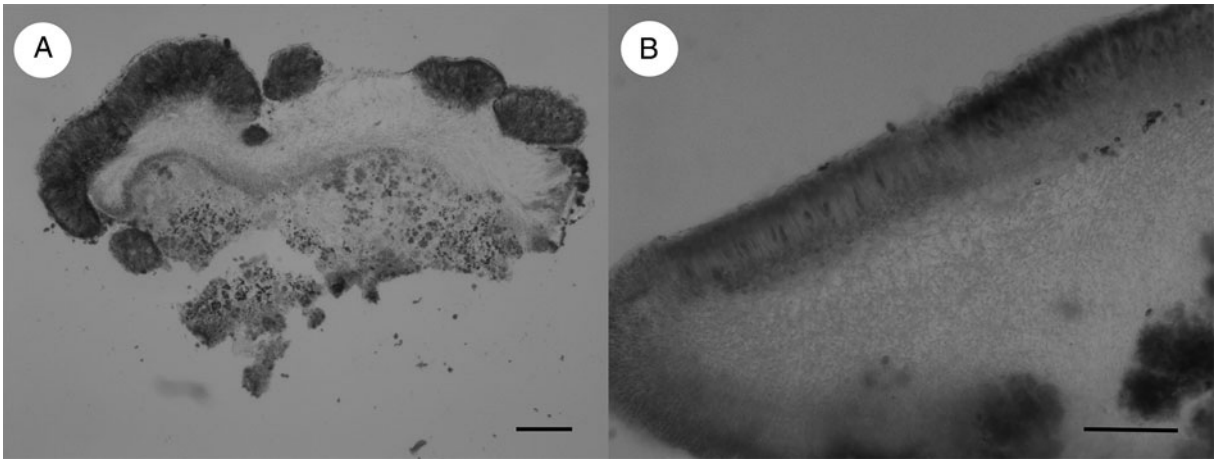

Figure 2. A, *Arthonia epipolytropa* (type); cross-section. B, *Arthonia subclemens* (type); cross-section. Scales = 100 μm.

Arthonia sherparum Grube & Matzer, a rarely collected species on *Lecanora sherparum* Poelt, differs by the distinctly convex ascomata with a dark brown hypothecium (Grube & Matzer 1997).

Host. *Lecanora polytropa* s. lat. (1) (apothecia). *Lecanora polytropa* in the wide sense applied here, includes a number of morphs for which sometimes specific or infraspecific names have been used (e.g. *Lecanora polytropa* var. *alpigena* (Ach.) Rabenh. incl. homotypic synonyms), and in other cases not. Recent split-offs, such as those introduced by Roux *et al.* (2022), have also not been distinguished.

Initially, the ascomata develop in groups on/in hymenia. In older infections, the parasite frequently spreads to apothecial margins and adjacent thalline areoles.

Distribution. The species is so far known only from Europe and North America. Most specimens have been seen from higher altitudes in Central Europe (Alps). However, we also saw material from mountains in Scandinavia (Norway) and from the Balkans (Albania), as well as from the North American Rocky Mountains (USA, Wyoming). As the host lichen, if not too narrowly circumscribed, is one of the most common lichens on siliceous rocks and reported from many additional countries on other continents, it is not unlikely that *A. epipolytropa* will prove to be also present at least in Asia.

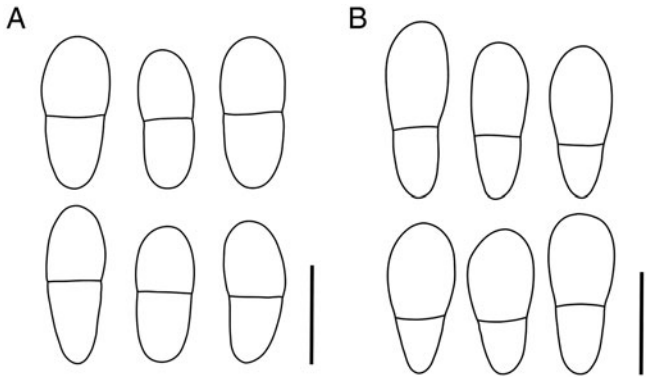

Figure 3. A, *Arthonia epipolytropa* (type material); ascospores. B, *Arthonia subclemens* (type material); ascospores. Scales = 10 μm.

Previous records. Literature records applying various names and from different parts of Europe may refer to the species described here. It is probably identical with a lichenicolous *Arthonia* growing on *Lecanora polytropa* previously recorded under various names: by Arnold (1873*a*, *b*, 1874, 1876*a*, *b*, 1878, 1879, 1893, 1896; sub *Conida subvarians sensu* auct. non *Arthonia subvarians*) from Austria and Italy, by Arnold (1891; sub *Conida apotheciorum* (A. Massal.) A. Massal.) from Germany, by Kernstock (1890, 1895; sub *Conida subvarians* (Nyl.) Arnold) from Italy, and by Lettau (1958; sub *Conida clemens* p.p.) from Austria. More recently, we traced comparable records by Triebel & Scholz (2001; sub *Arthonia subvarians* p.p.) from Germany, by Brackel (2013*a*, 2016; both sub *A. subvarians*) from Italy, by Brackel (2013*b*; sub *A. subvarians*) from Switzerland, by Brackel (2014; sub *A. subvarians*) from Germany, and by Darmostyuk (2018; sub *Arthonia subvarians*) from the Ukraine.

We are not able to decide if the record by Zhurbenko & Brackel (2013; sub *Arthonia apotheciorum* (A. Massal.) Almq.) from Svalbard belongs to one of the two species described here. This is also true for an undescribed species (*Arthonia polytropae* ad int.) mentioned by Roux *et al.* (2011) from the Pyrenees in France. As no phenotypic characters are indicated, it remains unclear to which *Arthonia* species this material belongs.

Selected additional specimens examined representing paratypes (all on Lecanora polytropa *s. lat.).* **Albania:** *Northern Albania*: Malësi e Madhe Distr., Bjeshkët e Nemuna (Prokletije) mountains, saddle N above the village Theth, somewhat E above the saddle, 42°26′40″N, 19°46′20″E, elev. 1750 m, 2007, *Hafellner* 80349, 80360 (GZU).—**Austria:** *Kärnten (Carinthia)*: Nationalpark Hohe Tauern, Ankogel Gruppe, am Westgrat des Greilkopf E ober der Hagener Hütte, elev. 2440 m, GF 8944/4, 1994, *Hafellner* 33025 (GZU). Gurktaler Alpen, Felsabbrüche am Grat zwischen dem Schoberriegel und Gruft, SE der Turracherhöhe, [46°55′25–36″N, 13°53′44–59″E], elev. *c.* 2150 m, [GF 9049], 1985, *Mayrhofer*, *Poelt* s. n. et al. (GZU) [note: with *Cercidospora epipolytropa* as admixture]. Zentralalpen, Saualpe W von Wolfsberg, Forstalpe, Forstofen (Kote 1967) am E-Rücken, 46°53′25″N, 14°40′10″E, elev. 1955 m, GF 9154/1, 2011, *Hafellner* 78147 & *Hafellner* (GZU). Steirisches Randgebirge, Koralpe, Moschkogel, kurz SW vom Gipfel NE über der Grillitschhütte, 46°49′25″N, 14°59′25″E, elev. 1800 m, GF 9155/

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4, 2007, *Hafellner* 70177 & *Muggia* (GZU, UPS). Karnische Alpen, Oisternig SW von Feistritz im Gailtal, Feistritzer Alm, silikatischer Rücken N von Maria Schnee, elev. 1750 m, GF 9447/1, 1987, *Hafellner* 17254 (GZU). *Salzburg*: Lungau, Ostalpen, Niedere Tauern, Radstädter Tauern, Speiereck N über St Michael im Lungau, im unteren Teil des E-Rückens am Steig von der Bergstation der Sonnenbahn zum Gipfel, 47°07′15″N, 13°38′30″E, elev. 2010 m, GF 8847/4, 2019, *Hafellner* 86369 (GZU). *Steiermark (Styria)*: [Nordalpen], Eisenerzer Alpen, Blaseneck N von Treglwang, kurz S unter dem E Vorgipfel, 47° 29′50″N, 14°37′15″E, elev. 1950 m, GF 8553/2, 1997, *Hafellner* 45984 & *Hafellner* (GZU). Niedere Tauern, Wölzer Tauern, Bergkette N von Lachtal *c.* 9.5 km NE von Oberwölz, Schießeck, S-Rücken zwischen dem Sattel zur Rossalm und Knappenstein, 47°14′58″N, 14°20′10″E, elev. 2120 m, GF 8752/3, 2014, *Hafellner* 83160 (GZU) [note: with *Cercidospora epipolytropa* as admixture]. Gurktaler Alpen, Kirbisch *c.* 11 km SW von Murau, oberhalb von St Lorenzen, NE-exponierte Hänge knapp unter dem Gipfel, 47°03′05″N, 14°03′05″E, elev. 2100 m, GF 8950/1, 2003, *Hafellner* 62440 (GZU). Seetaler Alpen, Fuchskogel *c.* 9 km W von Obdach, unterste NE-Hänge, 47°03′10″N, 14° 35′05″E, elev. 1930 m, GF 8953/2, 2013, *Hafellner* 82097 (GZU) [note: with *Cercidospora epipolytropa* and *Lichenoconium lecanorae* as admixture]. Steirisches Randgebirge, Stubalpe, Ameringkogel-Massiv E von Obdach, Weißenstein, S-Hänge knapp unter dem Gipfel, 47°03′55″N, 14°48′30″E, elev. 2100 m, GF 8954/2, 2005, *Hafellner* 65188 (GZU) [note: with *Cercidospora epipolytropa* as admixture]. *Tirol (Tyrol)*: Samnaun-Gruppe, Furgler W ober Serfaus, am Grat zwischen dem Furgler Joch und dem Gipfel, elev. 2800–2900 m, GF 8929, 1991, *Hafellner* 23523 (GZU). *Vorarlberg*: Silvretta-Gruppe, Kl. Lobspitze SW über der Bielerhöhe, NE-Rücken über dem Silvretta-Stausee, 46°54′45″N, 10°05′30″E, elev. 2080 m, GF 9026/4, 2008, *Hafellner* 81279 (GZU).—**Italy:** *Piemonte*: Prov. Torino, Western Alps, Alpi Cozie, mountains W of Pinerolo, north-eastern slopes and ridges of the Punta Cialáncia S above Perero Village, 44°53′00″N, 07°07′20″E, elev. 2350 m, 2001, *Hafellner* 69355 (GZU). *Trentino-Alto Adige*: Prov. Trento, Eastern Alps, Central Alps, Ortler-group (Stelvio-group), *c.* 8 km N above Cógolo, La Cascata S above Lago Lungo, summit area, 46°25′30″N, 10°41′00″E, elev. 2575 m, 2006, *Hafellner* 69336 (GZU).—**Norway:** *Oppland*: Lom, Jotunheimen, Glittertind-Massiv, frische Silikatblockhalde am Ausgang des Steinbudalen, elev. 1750 m, 1984, *Hafellner* 12212 & *Ochsenhofer* (GZU).—**Switzerland:** *Kanton Bern*: Berner Alpe, *c.* 8 km SW above Meiringen, by the road from Schwarzwaldalp to the saddle Große Scheidegg, below Alpiglen, 46°40′00″N, 08°07′10″E, elev. 1650 m, 2006, *Hafellner* 75474 (GZU). *Kanton Graubünden*: Urner Alpe, Gotthard group, Oberalppass *c.* 6 km NE of Andermatt, somewhat S above the pass, 46°39′20″N, 08°40′15″E, elev. 2100 m, 2006, *Hafellner* 77331 (GZU).—**USA:** *Wyoming*: Teton Co., Yellowstone National Park, Spruce Fir Picnic Area 7 miles SW of Bridge Bay, W shore of Yellostone Lake, 44°28′05″N, 110° 28′02″W, elev. 7750 ft, 1998, *Wetmore* 81660a (GZU).

Arthonia subclemens Hafellner, Grube & Muggia sp. nov.

MycoBank No.: MB 849059

Species non lichenisata sed lichenicola. Infectio in hospiti non cecidiogena. Ascomata nigra, plerumque singularia aut per 1–5 in hymenio hospitis immersa, haud aggregata, plana ad subconvexa, Ascomata ut descripta. Asci fissitunicati, octospori. Ascosporae 1-septatae, 12–15(–16) × 4–5(–6) µm, septis distincte basim versus excentricis ergo cellulis inaequalibus. Species habitu specie *Arthonia clemens* similis sed ab ea differt ascomatibus minus convexis et ascosporis aliquot maioribus cum septis excentricis. In hymeniis lichenis *Lecanora polytropa* vigens adhuc solum in Europa.

Typus: Italy, Trentino-Alto Adige, South Tyrol (Südtirol), Eastern Alps, Ötztal Alps, Val Venosta (Vinschgau), mountains NE above the village Silandro (Schlanders), ridge NNE above of Schönputz, 46°39′13″N, 10°48′23″E, elev. *c.* 2370 m, siliceous outcrops and boulders in treeline ecotone, on slightly inclined rock faces, on *Lecanora polytropa* s. lat. (apothecia), 28 June 2016, *Muggia* s. n. & *Ametrano* (GZU—holotype; isotypes to be distributed in *Lichenicolous Biota* no. adhuc ined. to BR, CANB, GZU, NY, TSB, UPS).

(Figs 1B, 2B, 3B)

Non-lichenized but lichenicolous. Infections not distinctly parasitic except in well-defined areas on the host apothecia. Vegetative hyphae imbedded in host apothecia, hard to detect, I −. Forming one or few ascomata per apothecium of the host.

Ascomata conspicuous, visible as pure black (somewhat paler at the margins) roundish patches 0.2–0.6(–1) mm diam. on the usually yellowish discs of the host apothecia, remaining individual, rarely 1–3 merging but not agglomerating in dense groups, entirely immersed in the hymenium of the host apothecia, flat to hardly convex; when in advanced stage or dry, often showing one to few irregular fissures indicating a shrinking of the hymenial complex (Fig. 1B). Individual ascomata rounded, immarginate, in longitudinal section up to 600(–1000) µm diam. and 100–120 µm tall. *Hymenium* 50–60 µm tall, hyaline to pale brownish, the uppermost 15–20 µm dull brown to chestnut brown forming an epithecium, epithecial hyphae conglutinated by amorphous pigments, in between with granula of unclear origin. *Hypothecium* 40–50 µm tall, hyaline to pale brownish. *Paraphysoids* branched and anastomosing, with hyphal cells 6–8 × *c.* 1 µm, with slighty enlarged terminal cells. *Asci* fissitunicate of *Arthonia*-type, clavate, 30–40 × 15–18 µm, 8-spored, connected to ascogenous hyphae *c.* 4 µm wide, distinctly fluorescent with Calcofluor white. *Ascospores* obovate, remaining hyaline, 12–15(–16) × 4–5(–6) µm, 1-septate, septum closer to the lower end, upper cell distinctly wider and longer, hardly constricted at the septum, not distinctly halonate in LM.

Pycnidia not visible from the outside but in some sections detected adhering to or even embedded in ascomatal structures, subsphaerical, with brown walls. *Pycnospores* bacilliform, 5–6 × *c.* 1 µm.

Reactions. Hymenial and ascal gel I_{dil}+ red, I+ red, KI+ blue, ascus with tiny KI+ blue ring basally in the tholus of the endoascus.

Etymology. The epithet refers to the habitually similar *Arthonia clemens*, a species restricted to *Omphalodina*.

Remarks. Concerning the apothecial characters, *A. subclemens* shows little variability. Among the *Arthonia* taxa invading species of *Lecanora* s. lat. settling on acidic rocks, it is distinctive in its relatively large, plane to hardly convex, pure black ascomata, mostly 1–3(–5) per host apothecium and in the host selection.

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Among these taxa it is most similar to *Arthonia clemens* s. str. (Fig. 4B), in terms of morphology. However, this species exhibits small but distinctly convex, cushion-like ascomata, 1-septate ascospores with less excentric septa and somewhat smaller than in *A. subclemens*, and a host selection restricted to *Omphalodina*, namely its type species *O. chrysoleuca* (Sm.) S.Y. Kondr. This follows the commonly applied concept of *Arthonia clemens*, but depends on a wise type selection for *Phacopsis clemens* Tul., namely to a specimen from the Dauphinée in France (Tulasne 1852: 125 '…in apotheciis cum *Squamariae rubinae* DC., e Delphinatus alpibus…'). This is necessary because in the protologue three different collections with three different hosts representing syntypes (but possibly belonging to three different species) are listed and the selection of a different type could destabilize the existing concepts of more than one of the lichenicolous *Arthonia* species. Similar in its habit is also *Arthonia protoparmeliopseos* Etayo & Diederich, but that species has 2–3-septate ascospores and appears to be restricted to *Protoparmeliopsis muralis* s. lat. (Etayo & Diederich 2009). More distantly related appears to be *Arthonia varians* (Davies) Nyl., the ascomata of which develop in the hymenia of *Lecanora rupicola* and its close relatives (core group of *Glaucomaria*). Ascomata of *Arthonia varians* tend to merge and finally obtect the entire discs of the host apothecia and exhibit 3-septate ascospores. *Arthonia sherparum*, a rarely collected species on *Lecanora sherparum*, differs by the distinctly convex ascomata with a dark brown hypothecium (Grube & Matzer 1997).

Distribution. The species is so far known only from some scattered localities in mountain ranges of Central and Southern Europe, but we expect it to be more widely distributed.

Previous records. Earlier literature records applying various names and from different parts of Europe are evidently few. *Arthonia subclemens* is probably identical with a lichenicolous *Arthonia* on *Lecanora polytropa* recorded from Aragon in Spain (Etayo 2010: 43 ff., sub *A. protoparmeliopseos* p. p.) for which 1-septate ascospores with a strongly excentric septum have been reported. Whether an undescribed *Arthonia* species (*Arthonia polytropae* ad int.) mentioned by Roux *et al.* (2011) from the Pyrenees in France belongs here remains unclear, as no phenotypic characters are indicated.

Additional specimens examined representing paratypes (all on Lecanora polytropa*).* **Austria:** *Kärnten (= Carinthia)*: Ostalpen, Zentralalpen, Steirisches Randgebirge, Koralpe *c.* 10 km ESE über Wolfsberg, Sprungkogel W über der Grillitschhütte, ersten Blockwerk SW vom Gipfel, 46°48′54″N, 14°58′14″E, elev. 1860 m, (1), 2012, *Fleischhacker* 12375 & *Muggia* (GZU).—**Greece:** *Epirus*: Ioannina, municipality of Konitsa, northern Pindus Range, Mt Gramos massif, N above Plikati Village, on the crest next to the border with Albania, 48° 19′10″N, 20°45′40″E, elev. 2000 m, 2014, *Muggia* s. n. (GZU, TSB).—**North Macedonia:** *SE-Macedonia*: Kožuf Mountain, Peak 92, 1.5 km NE of Kožuf summit, N surroundings of the

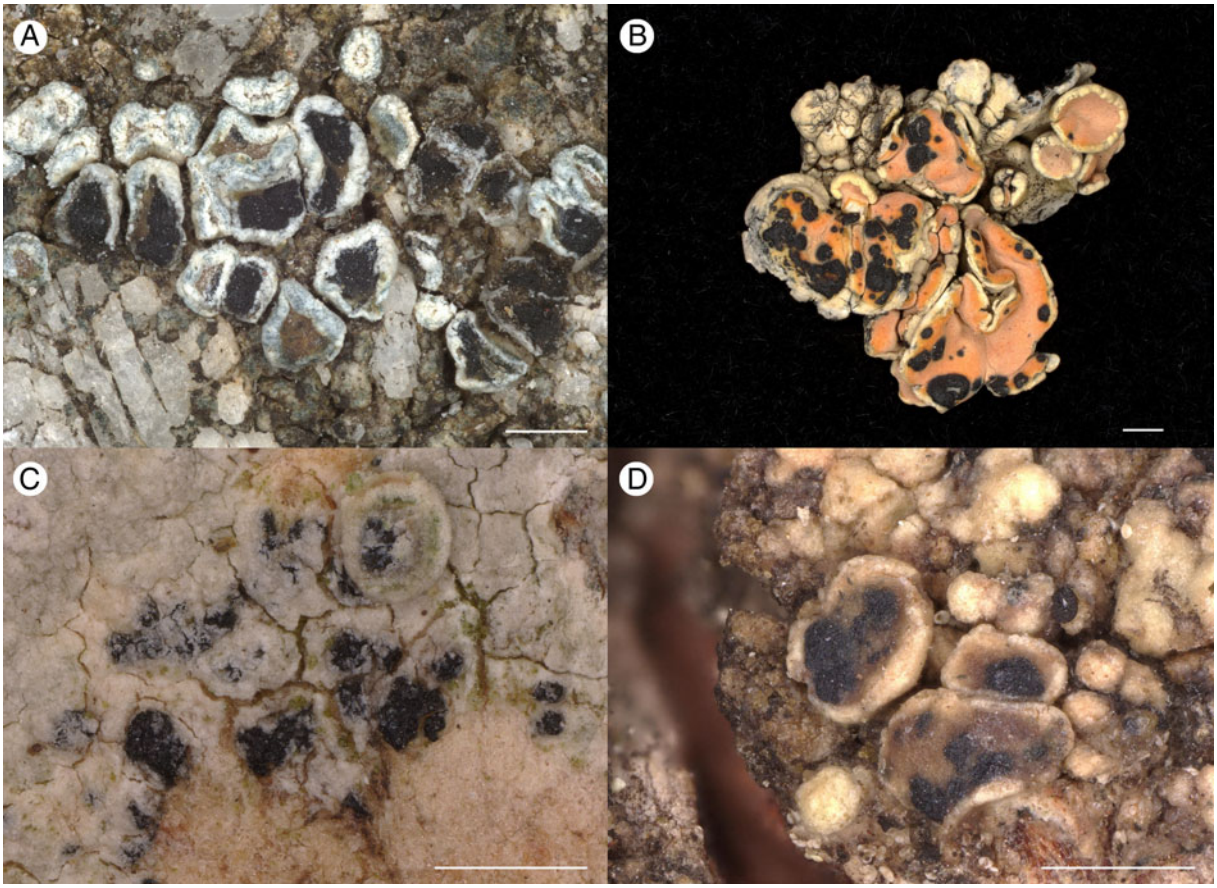

Figure 4. A, *Arthonia subvarians* (*Hafellner* 73605); habitus. B, *Arthonia clemens* (*Hafellner* 36683); habitus. C, *Arthonia subfuscicola* (*Hafellner* 78035); habitus. D, *Arthonia caerulescens* (*Mayrhofer* 641); habitus. Scales = 0.5 mm.

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meteorological station, 41°10′25″N, 22°12′59″E, elev. *c.* 2600 m, (1), 2017, *Kaltenböck* 405a (GZU).—**Spain:** *Prov. Gérona*: Pyrenäen, Nuria N von Ribas de Freser, NW-Hänge SE über der Bergstation der Zahnradbahn, elev. 2000–2100 m, (1), 1983, *Hafellner* 17632 (hb. Hafellner).

Discussion

Here we describe two new lichenicolous species of *Arthonia* occurring in the *Lecanora polytropa* group. For several reasons we refrained from using *Bryostigma* as a possible segregate name for the newly described species. First, after reanalyzing the type material of *Bryostigma leucodontis*, we confirm a relationship with *Arthonia* s. lat., as proposed by Coppins (1989), but the phenotypic characters are not sufficiently developed to confirm a relationship with other species assigned to *Bryostigma* today. Notably, Kondratyuk *et al.* (2020) recombined several species in *Bryostigma* which did not belong to a monophyletic clade in other studies (e.g. Thiyagaraja *et al.* 2020). Despite possible taxonomic consequences, we prefer to wait until the phylogenetic concepts of lichenicolous species consolidate and the status of *Bryostigma* and other species groups within a wider circumscribed genus *Arthonia* is clarified (Sundin *et al.* 2012; Frisch *et al.* 2014).

Both species on *Lecanora polytropa* s. lat. can easily be distinguished from each other by their morphological characters. The immersed ascomata of *A. subclemens* possess pale to brownish hypothecia whereas the sessile ascomata of *A. epipolytropa* have dark hypothecia and become distinctly crowded. Furthermore, ascospore shape and size easily distinguish the two species in squash preparations or sections (see descriptions or key). Both seem to reflect two distinct growth strategies of ascomata in lichenicolous *Arthonia* species. One of these, *A. epipolytropa*, is characterized by ascomata that emerge early from the surface of the host and tend to form agglomerations of more than 10 ascomata. In later stages, the ascomata also appear on the thallus. In the second type, represented by *A. subclemens*, the ascomata remain more or less immersed and tightly integrated in the host hymenia where they seem to use the host structures, for example by acting as a functional unit to maintain the lateral pressure for well-functioning ascospore release. *Arthonia varians*, occurring on part of the *Lecanora rupicola* group (*Glaucomaria*), has a similar strategy to immerse its structures in the host apothecia, but it is easily distinguished by its 3-septate ascospores (13–18 × 4–7 µm). Smaller, 2–3-septate ascospores (10–14.5 × 4–5.5 µm) are known from *Arthonia protoparmeliopseos* Etayo & Diederich, which grows preferably in the ascomata of *Protoparmeliopsis muralis* (Schreb.) M. Choisy (Etayo & Diederich 2009). An extreme outcome of this strategy has evolved by the intrahymenial parasitism of *Arthonia intexta* Almq., which occurs in the ascomata of *Lecidella* species (Hertel 1969). The parasitic structures are indistinct in external view because both fungal species develop merged black, slightly swollen ascomata complexes scarcely differing from healthy *Lecidella* fruiting bodies. Infections are usually detected in sections and are recognized under the microscope as single or few grouped asci of the parasite which are hidden and develop intermingled with hymenial elements of the host in the ascomata of the host. A closer relationship of that species with *A. varians* is probable judging from shared ascospore characters.

A reduction of its own ascomatal structures and integration in the host hymenia reflects evolutionary specialization of the parasites, and it also reflects a general evolutionary trajectory in the *Arthoniaceae*. While ascomatal excipula are present in most members of *Arthoniales*, *Arthonia* has indistinct or reduced structures to laterally delimit ascomata. Further steps to an almost complete reduction of auxiliary plectenchyma surrounding meiosporangia (asci) can be seen in the diffuse ascigerous structures in *Crypothecia* and related taxa (e.g. Santesson 1945; Thor 1997; Wolseley & Aptroot 2009; Bungartz *et al.* 2013). Many of the *c.* 140 parasitic species known so far in *Arthonia* (Diederich *et al.* 2018) emerge from the upper surface of the host thallus and have hyphal structures at the lateral delimitation of the ascomata, but it seems that lecanoroid lichens are particularly suitable hosts for evolving arthonioid parasites that colonize and specialize on hymenia.

Nevertheless, species with ascomata immersed in the hymenia do not spread to thalline structures. It is still difficult to visualize the course of the parasitic hyphae, but observations of the occasionally browning hyphae of *Arthonia diploiciae* on thalli of *Diploicia canescens* (unpublished data), indicate an affinity for the algal cells of the hosts. We can only speculate whether the hymenial specialists extend their hyphae in the host thallus or have adapted to feed either on intracellular gels or plasma of thin-walled apothecial hyphae. The loss of hypothecial pigmentation appears to be a precondition for a formation of immersed intrahymenial ascomata.

Apart from the two species newly described on *Lecanora polytropa*, the genus *Lecanora* s. lat. supports a surprising diversity of *Arthonia* species on either thalli or ascomata. Several species appear to be restricted to epiphytic species of *Lecanora* agg. *Arthonia subfuscicola* (Linds.) Triebel occurring on *Lecanora albella* (Pers.) Ach. and *L. carpinea* (L.) Vain. differs from the newly described species by its 3-septate ascospores and occurrence mostly on thalli (Fig. 4C). The presence of the ascomata on the thallus is also characteristic for *Arthonia agelastica* R. C. Harris & Lendemer, a species on *Lecanora louisiana* B. de Lesd. Its brownish ascomata occur in groups of few to many, and they have 2(–3)-septate, halonate ascospores (13–17 × 5–7.5 µm). *Arthonia caerulescens* (Almq.) R. Sant. (Fig. 4D), a species with 1-septate ascospores occurring on *Lecanora varia* (Hoffm.) Ach., is more distinctive due to the blue-green pigments in the epithecia. Moreover, Grube & Matzer (1997) observed conspicuously thick-walled ascogenous hyphae in this species. The circumscription of *Arthonia lecanorina* (Almqu.) R. Sant., a further didymosporous species on apothecia of *Lecanora albella* (Pers.) Ach. (apothecia), needs clarification.

Some other species with 1-septate spores, however, seem to be notoriously difficult to distinguish by morphological characters. From other families, we have learned that phylogenetic analyses of DNA sequences suggest sufficient genetic differences between morphologically similar species on different hosts (see Fleischhacker *et al.* 2016), which supports the host-specificity of species. More generally, there is not really evident transgression of well-circumscribed *Arthonia* species, neither between taxonomic host species groups within *Lecanora* agg. nor between the main substratum types (saxicolous vs corticolous).

Particularly problematic are species on members of *Polyozosia* (syn. *Myriolecis*), which is a segregated genus name for the *Lecanora dispersa* group. The oldest available name for an *Arthonia* on *Polyozosia* is *A. apotheciorum* (A. Massal.) Almq. with *P. albescens* (Hoffm.) S.Y. Kondr. *et al.*, a lowland species as the type host. If *A. apotheciorum* turns out to be a highly

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specialized species (which requires further study), *Arthonia subvarians* (syn. *A. galactinaria* Leight.) would be the correct name for the common species parasitizing the ascomata of various *Polyozosia* species, specifically those growing on rock in higher altitudes. Its cushion-shaped ascomata, usually 1–3 per host hymenium, have brownish olivacous pigments in the epithecium and a distinctly brownish hypothecium. However, there are also only distantly related parasites on *Polyozosia* species. For example, *Arthonia lecanoricola* Alstrup & Olech [as 'lecanoriicola'] on ascomata of *P. populicola* (DC.) S.Y. Kondr. *et al.* which has 2(–3)-septate ascospores (11–13 × 4–4.5(–5) µm, or up to 6–6.5 µm wide in the type material); or *A. oligospora* Vězda on a lowland morph of *P. crenulata* auct., non (Ach.) S.Y. Kondr. *et al.* growing close to the sea which is primarily distinguished by 4-spored asci (ascospores 10–12 × 5–6 µm) and ascomata that develop on the thallus with the infection apparently spreading to intermingled *Lecania nylanderiana* A. Massal.

Further species on silicicolous lichens include *Arthonia sherparum* on apothecia of the distinctive Himalayan species *Lecanora sherparum*, which has distinctly convex sessile ascomata with intensely brownish pigments in the epithecium and hypothecium. *Arthonia glacialis* Alstrup & E. S. Hansen occurs on *Rhizoplaca melanophthalma* (DC.) Leuckert & Poelt where it develops large, sessile and convex ascomata with pigment caps in the epithecia and brownish hypothecia (spores 11–13 × 4.5–5.5 µm). This behaviour differs clearly from *Arthonia clemens* (type of *Conida*) forming only slightly convex semi-immersed cushions on the related host *Omphalodina chrysoleuca* (former *Rhizoplaca chrysoleuca*).

Finally, we want to return to the old, yet still interesting topic of lichen parasites as indicators of host relationships (Hafellner 1990). The host spectra of lichenicolous *Arthonia* species with lecanoroid lichens as hosts is a particularly interesting case. We observe that species are fairly host-specific and specialize in representatives of different groups in *Lecanora* s. lat. (some of which are now segregated), with some difficult to clearly delineate (e.g. those occurring on *Polyozosia*). However, we also demonstrate here that some *Lecanora* species can be colonized by clearly different species, which have close relatives on more distantly related hosts, indicating potential host jumps within *Lecanoraceae*. It remains to be investigated whether such host jumps could be facilitated by required parallelisms in host morphology for infection.

Recent work shows that after decades of hesitation, phenotypically circumscribed species are carved out from the *Lecanora polytropa* group (Śliwa & Flakus 2011; Roux *et al.* 2022), and that the diversity might be massively underestimated when molecular data are considered (Zhang *et al.* 2022). As genetic diversity is high in the *Lecanora polytropa* group, and taxonomy now proceeds with segregating phenotypically characterized species, it will be interesting to examine whether lichenicolous *Arthonia* species have preferences for either certain eco-, pheno- or genotypes of their hosts.

Key to lichenicolous fungi regularly occurring on *Lecanora polytropa* s. lat.

Note: The cited references for each of the species refer to publications including full descriptions. *Stigmidium congestum* (Körb.) Triebel and *Tetramelas pulverulentus* (Anzi) A. Nordin & Tibell, which are both reported (Vouaux 1912; Alstrup & Hawksworth 1990) but unlikely to occur on *Lecanora polytropa*, have not been included.

1 Infection inducing the formation of convex brownish swellings (i.e. basidiomata) on the host apothecia, spores produced on basidia; Diederich *et al.* (2022) . . . . . **Tremella pyrenaica** Diederich et al.
Infection not gall-inducing, spores not produced on basidia 2

2(1) Fructifications (conidiomata and/or ascomata) are superficial granules entirely made of spherical yeast-like cells that easily separate in squash preparations, either with asci containing hyaline, later brown 1-septate ascospores or with brown subspherical conidia composed of *c.* 10 spherical cells; Berger & Brackel (2011), Ertz *et al.* (2014), occurrence on *L. polytropa fide* e.g. Zhurbenko & Brackel (2013) . . . . . **Lichenostigma chlaroterae** (Berger & Brackel) Ertz & Diederich
Reproductive structures different 3

3(2) Spores are pigmented or hyaline ascospores 4
Spores are pigmented conidia 21

4(3) Ascomata are apothecia or apothecioid 5
Ascomata are perithecia or perithecioid 13

5(4) Ascospores brown, septate 6
Ascospores hyaline, septate or aseptate 7

6(5) Ascospores in optical section usually with 3 trans-septa and 1–2 incomplete longisepta, 17–20 × 8–10 µm; Alstrup & Hawksworth (1990) . . . . . **Rhizocarpon destructans** Alstrup
Ascospores 1-septate, 9–10 × 5–6 µm; Müller (1872), Vouaux (1913). Note: a poorly known species, possibly a species of *Sclerococcum* (*Dactylospora*) . . . . . **'Buellia vagans'** Müll. Arg.

7(5) Ascospores septate 8
Ascospores aseptate, asci lecanoralean, with I+ intensely blue tholus and/or apical cap 10

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8(7) Ascomata deeply urceolate, in section with prominent crown of periphysoids, asci ostropalean with I− tholus, ascospores with up to 5 trans-septa, later additionally with 1–2 incomplete longisepta; Diederich *et al.* (2002) . . . . . **Sphaeropezia figulina** (Norman) Baloch & Wedin
Ascomata different, asci arthonialean, ascospores 1-septate. 9

9(8) Ascomata sessile, agglomerated, ascospores (9–)10–12(–13) × 4–5 µm with submedian septum . . . . . **Arthonia epipolytropa** Hafellner & Grube
Ascomata dispersed and sunken in hymenium of host, ascospores 12–15(–16) × 4–5(–6) µm with septum closer to the lower end, cells therefore distinctly unequal . . . . . **Arthonia subclemens** Hafellner et al.

10(7) Ascospores 14–17 × 5–7 µm, with pointed ends; Steiner (1898). Note: a poorly known species, according to Rambold & Triebel (1992) possibly a synonym of *Carbonea supersparsa* . . . . . **'Nesolechia' oxysporiza** J. Steiner
Ascospores shorter 11

11(10) Ascomata strongly convex, virtually immarginate, often agglomerated, ascospores 9.5–12 × 3–4 µm; Vouaux (1913), Cannon *et al.* (2022) . . . . . **Carbonea aggregantula** (Müll. Arg.) Diederich & Triebel
Ascomata flat, distinctly marginate 12

12(11) Epihymenium in longitudinal section bluish to blue-green, ascospores 8.5–13 × 4.5–7 µm; Vouaux (1913), Cannon *et al.* (2022) . . . . . **Carbonea supersparsa** (Nyl.) Hertel
Epihymenium sec. protologue colourless, ascospores 9–9.5 × 5–5.5 µm; Alstrup & Hawksworth (1990). Note: a poorly known species, according to Rambold & Triebel (1992) a synonym of *Carbonea supersparsa* . . . . . '**Lecidea' diexcipula** D. Hawksw. & Alstrup

13(4) Ascospores hyaline, septate 14
Ascospores pigmented, aseptate or septate 17

14(13) Ascospores with up to 5 trans-septa, later additionally with 1–2 incomplete longi-septa, the virtually perithecioid ascomata are urceolate apothecia; Diederich *et al.* (2002) . . . . . **Sphaeropezia figulina** (Norman) Baloch & Wedin
Ascospores 1-septate 15

15(14) Mature ascomata without interascal filaments, exciple in longitudinal section brown throughout; Roux & Triebel (1994) . . . . . **Stigmidium squamariae** (de Lesd.) Cl. Roux & Triebel
Ascomata with persistent interascal filaments, exciple in longitudianal section with pigment in shades of blue 16

16(15) Asci predominantly 8-spored; Calatayud *et al.* (2013) . . . . . **Cercidospora epipolytropa** (Mudd) Arnold
Asci predominantly 4-spored; Calatayud *et al.* (2013) . . . . . **Cercidospora stenotropae** Nav.-Ros. & Hafellner ad int.

17(13) Ascospores aseptate, asci 4-spored, interascal filaments persistent; Brackel (2021) . . . . **Roselliniella silvae-gabretae** Brackel
Ascospores septate 18

18(17) Ascospores 1-septate, interascal filaments in mature ascomata indistinct 19
Ascospores with more than 1 trans-septa, interascal filaments in mature ascomata distinct or indistinct 20

19(18) Asci multi-spored; Triebel (1989), occurrence on *L. polytropa fide* e.g. Triebel (1989) . . . . . **Muellerella pygmaea** (Körb.) D. Hawksw. var. **athallina** agg.
Asci with 8 spores; Triebel (1989), occurrence on *L. polytropa fide* e.g. Brackel & Wirth (2023) . . . . . **Endococcus brachysporus** (Zopf) M. Brand & Diederich agg.

20(18) Interascal filaments lacking; Pérez-Ortega & Halıcı (2008). . . . . **Lasiosphaeriopsis lecanorae** Pérez-Ortega & Halıcı
Interascal filaments persistent; Navarro-Rosinés & Roux (2008), occurrence on *L. polytropa fide* e.g. Brackel (2014) . . . . . **Pyrenidium actinellum** Nyl. agg.

21(3) Conidia developing on endohymenial conidiophores; Hawksworth (1979), occurrence on *Lecanora polytropa fide* e.g. Alstrup & Hawksworth (1990) . . . . . **Intralichen lichenicola** (M. S. Christ. & D. Hawksw.) D. Hawksw. & M. S. Cole
Conidia developing in conidiomata 22

22(21) Conidia aseptate, spherical; Hawksworth (1981) . . . . . **Lichenoconium lecanorae** (Jaap) D. Hawksw
Conidia 1-septate, basally truncate; Hawksworth (1981), occurrence on *L. polytropa fide* e.g. Brackel (2014) . . . . . **Lichenodiplis lecanorae** (Vouaux) Dyko & D. Hawksw.

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