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Arthonia parietinaria – A common but frequently misunderstood lichenicolous fungus on species of the *Xanthoria parietina*-group

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ABSTRACT

Arthonia parietinaria is described as new to science. Host of the type and at the same time the only confirmed host species is the foliose macrolichen *Xanthoria parietina*. Sequence data of nucLSU rRNA genes reveal a close relationship to *Arthonia molendoi*. *A. parietinaria* is recorded for many countries in Europe, western Asia, and northern Africa.

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Introduction

According to the traditional concepts, *Arthonia* Ach. (1806) represents one of the large genera of ascomycetes, comprising both lichenized and lichenicolous species. The number of accepted species is given with 491 in the latest edition of the ‘Dictionary of the fungi’ (Kirk et al. 2008), which seems to be a rather conservative approximation. A search in MycoBank (<http://www.mycobank.org>) reveals more than 1200 infrageneric names linked to the genus. Also the proportion of lichenicolous taxa in *Arthonia* is remarkable. The somewhat outdated, but still most comprehensive key for lichenicolous *Arthonia* species at a world wide scale (Clauzade et al. 1989)

includes 38 species, while the current version of an online-synopsis lists 115 species (Lawrey & Diederich 2015). In a private database we accumulated about 200 heterotypic names that would be relevant in connection with a generic revision (J.H., unpubl.). And the process of inventory is still going on with additional species described almost every year.

Due to high values of nitrogen deposition in European landscapes, the eutrophic conspicuous orange *Xanthoria parietina* is one of the few foliose macrolichens with populations increasing both in number and size since about the 1990s (e.g. Frahm et al. 2009), whereas even common acidophytic species like *Hypogymnia physodes* responded by decreasing thallus population numbers (e.g. Herk et al. 2003). As

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a consequence lichenicolous fungi confined to *X. parietina* as their host face a situation with much more substrate available for colonization. The fungus flora of decaying thalli of *X. parietina* has already been studied by [Etayo & Berger \(2009\)](#). It is dominated by anamorphic states of both ascomycetes and basidiomycetes. In contrast, vital thalli are colonized by a different set of species. The entire fungal flora of *X. parietina* as single host species was studied in a project resulting in the master thesis for one of us ([Fleischhacker 2011](#)).

One of the fungi we frequently came across during this survey was an *Arthonia* species, commonly determined as *Arthonia molendoi* (e.g., [Santesson et al. 2004](#)). However, a closer analysis revealed fine phenotypic differences, and here, we also confirm the distinctiveness of this lichenicolous fungus by molecular data. We therefore describe the species below as new to science and provide a discussion of apparently related species.

Material and methods

Methods for phenotype analyses

For the morpho-anatomical investigation air-dried herbarium specimens have been analysed. External morphology was studied with a dissecting microscope (WILD M3, 6.4–40×). Anatomical studies of the thallus and the ascomata were carried out under the light microscope (LEICA DMRE, 100–1000×). Sectioning was performed with a freezing microtome (LEITZ, sections of 12–15 µm) but squash preparations were also used, especially for ascus analysis. Preparations were mounted in water. When necessary, contrasting was performed by a pre-treatment with lactic acid–cotton blue (MERCK 13741). 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 and squash preparations were not pretreated with KOH unless otherwise stated, namely for the detection of hemiamyloid reactions in the hymenium. Measurements refer to dimensions in tap water. The terminology of pycnidial characters follows [Vobis & Hawksworth \(1981\)](#).

Molecular analyses

Hymenia (about 20–50 × 50–100 µm in size) of four to five ascomata of the lichenicolous species were carefully cut from the host tissue, placed in 1.5 ml microtubes using a sterilized forceps (Dupont Nr. 5), and used for a direct PCR approach ([Grube 2005](#)). Parts with either amorphous pigments (incl. melanized portions) were removed from the cuttings as far as possible as these pigments impair PCR efficiency. PCR reactions of 20 µl (DNA extractions) and 30 µl (direct PCR) were used. Each 10 µl of PCR mix contained 0.5–1 µl genomic DNA extraction (or the lichen sample), 0.4 µl of each primer (20 pmol µl⁻¹), and 5 µl HotStarTaq Plus Mastermix Kit (Qiagen). Primers LIC24R and LR7 were used for PCR amplification of nuclear ribosomal large subunit RNA gene fragments (nLSU) ([Vilgalys & Hester 1990](#); [Miadlikowska & Lutzoni 2000](#)). The PCR products were visualized in a 0.5 %

agarose gel stained with GelRed (Biotium, Hayward, California, USA) under UV light. PCR products were purified either using the QIAquick PCR Purification Kit (Qiagen) or gel extracted and purified using the QIAquick Gel Extraction Kit (Qiagen). Sequencing of the amplicons was provided by Uppsala Genome Centre (Sweden). The sequences were assembled in BioEdit v.7.1.3 ([Hall 1999](#)) and their identity checked with the Blast search in GenBank and the local Blast functionality implemented in the BioEdit v.7.1.3 package. The nLSU sequences were aligned in RNAsalsa ([Stocsits et al. 2009](#)) using the secondary structure of *Saccharomyces cerevisiae* (nLSU; [Kjer 1995](#)) as template. The final alignment comprised 676 sites and the phylogeny was reconstructed with a Maximum Likelihood (ML) approach using RAxML ([Stamatakis 2014](#)) with raxmlGUI interface (v.1.5, [Silvestro & Michalak 2012](#)). *Myriostigma candidum* was used as outgroup lineage. A GTR + GAMMA model was applied and 1000 bootstrap replicates were run. The phylogenetic tree was visualized in FigTree v.1.4.

In addition to the specimens cited below together with the treatment of *Arthonia parietinaria*, the following material was compared:

Arthonia anjutae S. Kondr. & Alstrup (on *Teloschistes spinosus* (th.))

Note: Following ICN Art. 60.12, Note 4, the gender of the epithet with the original spelling 'anjutii' is corrected because the epithet is derived from the female first name Anyuta.

Australia: South Australia, Roopera station near Whyalla, eastern fence of Extension Paddock, 1969, R. Rogers, det. J. Hafellner (herb. Hafellner 19576).

Arthonia clemens (Tul.)Th.Fr. (on *Rhizoplaca chrysoleuca* (ap.))

Europe: Italy: Prov. Sondrio, Ortler Gruppe, Pian di Cembro über dem Val di Cortena, an der Straße von San Pietro nach Trivigno, 1400–1450 m alt., 1975, H. Mayrhofer (herb. Hafellner 933 in GZU). – **Asia: Russia:** Siberia, Chukotka, on the upper reaches of the river Milkera, 1977, M. P. Andreev, det. J. Hafellner (GZU).

Arthonia epiphyscia Nyl.

Hosts: *Physcia caesia* (th.) (1, T), *Physcia dubia* (th.) (2), *Physcia phaea* (th., ap.) (3).

Europe: Austria: Burgenland, Südburgenland, in Deutsch-Kaltenbrunn, ca. 265 m, GF 8962/2, (1), 1990, J. Hafellner 26075 & W. Maurer (GZU). – Kärnten (Carinthia), Nationalpark Hohe Tauern, Glockner-Gruppe, S Hänge des Fuscherkar Kopfes, N ober der Hofmannshütte [47°05'10"N/12°44'20"E], ca. 2500 m, GF 8942/1, (3), 1988, J. Hafellner 32049, M. Walther, & A. Hafellner (GZU). – Steiermark (Styria), Niedere Tauern, Wölzer Tauern, Hochgrößen, nordöstlicher Seitengipfel, im Gratbereich [47°27'50"N/14°15'35"E], ca. 2050 m, GF 8551/2, (2), 1989, J. Hafellner 26309 (GZU). – **Norway:** Oppland, Gem. Vågå, N-Ufer des Sees Vågåvatn ca. 2 km W von Vågåmo, ca. 450 m, (2), 1984, J. Hafellner 11424 & A. Ochsenhofer (herb. Hafellner).

Arthonia molendoi (Heufl. ex Frauenf.) R. Sant. (on *Xanthoria elegans* (th., ap.))

Europe: Austria: Kärnten (Carinthia), Hohe Tauern, Kreuzeck-Gruppe, Schwarzsteinwände (Südwände des Schwarzsteins) E der Hochtristen, N der Turgger Alm [46°47'55"N/13°09'10"E], 1950–2150 m, GF 9244/2, 1978, J. Hafellner 3875 (GZU). –

Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Ennstaler Alpen, Gesäuseberge E von Admont, Gr. Buchstein, NW-Abhänge, am W-Fuß der Abbrüche der Admonter Frauenmauer, 47°36'55"N/14°35'30"E, ca. 1720 m, GF 8353/4, 2005, J. Hafellner 67595 & A. Hafellner (herb. Hafellner). – **Liechtenstein:** Eastern Alps, Rätikon, mountain ridge between Augstenberg and Nospitz, SSW above the village Malbun, S above Vaduzer Täli, 47°05'20"N/09°36'15"E, ca. 2060 m, 2008, J. Hafellner 72834 (GZU). – **Spain:** Prov. Gérona, Pyrenäen, Nuria N von Ribas de Freser, NE von der Bergstation der Zahnradbahn, 2100–2200 m, 1983, J. Hafellner 17386 (GZU). – **Africa:** **Canary Islands:** Tenerife, Las Cañadas, Montaña Guajara, auf der S-Seite knapp unter dem Gipfel, 28°13'00"N/16°36'40"W, ca. 2680 m, 1989, J. Hafellner 36202 & A. Hafellner (herb. Hafellner).

Note: The concept of *Arthonia molendoi* applied here is consistent with that of Santesson (1986) who has revised the holotype of its basionym *Tichothecium molendoi* preserved in W.

Arthonia sytnikii S. Kondr.

Hosts: *Xanthoria ligulata* (1, T) (th.), *Xanthoria* sp. (2) (th.).

Africa: **South Africa:** Cape Province, 15 km SE of Oudtshoorn, by the road above Blossoms, (2), 1998, W. L. Culberson 22493a & R. Ornduff, det. J. Hafellner, separated from Kashiwadani, Lich. Minus Cogniti Exs. 200 (GZU). – **Australasia:** **New Zealand:** North Island, Wellington, Manurewa Point W of Tora, S of Martinborough, 41°30'S/175°32'E, (1), 1992, H. Mayrhofer 13279 & E. Hierzer, det. J. Hafellner (GZU).

Results

Molecular analyses

In the nuLSU phylogeny (Fig 6) *Arthonia parietinaria* is positioned as sister species of *Arthonia molendoi*. The sequence of the Swedish *A. parietinaria* sample is identical to sequences of the three Austrian samples, and differs in few nucleotide positions. Both species belong to the well-supported *Bryostigma* clade (Frisch et al. 2014), which comprises both lichenized as well as lichenicolous species.

Taxonomy

Arthonia parietinaria Hafellner & A. Fleischhacker, **sp. nov.** (Figs 1A, 2–5).

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Species nova *Arthoniae molendoi* similis sed ab ea differt ascomatibus plus aggregatis, in gregibus ad (10–)20–30(–50), triste nigris haud atris et ascosporis aliquot minoribus, 10–12 × 4–5 µm. Species aliae xanthoriicolae different aut in chemia epithecii (*A. destruens* var. *nana* cum epithecio K+ purpurascente), aut in numero ascomatum in quaque grege (in *A. molendoi* apothecia in quaque grege solum 2–5), aut in reactione hospitis contra infectionem (*A. sytnikii* cecidiogena), aut in colore ascosporarum (*A. anjutae* ascosporis fuscis). Infectio in hospite gregis *Xanthoriae parietinae* non cecidiogena solum thallum hospitis aliquot decolorans.

Type: Austria, Steiermark (Styria), Oststeirisches Hügelland, Graz, eastern suburban area, Ragnitztal, near the rivulet

'Ragnitzbach' at lower end of Dr Hanischweg, 47°04'35"N/15°28'50"E, ca. 380 m s. m., GF 8958/2, old orchard, on canopy branches of recently felled *Juglans regia*, on *Xanthoria parietina*, 1 July 2010, J. Hafellner 77067 & W. Obermayer (GZU – holotype, BCN, BR, CANB, E, GZU, LE, M, NY, PRM, UPS – isotypes). Isotypes to be distributed in Hafellner, Lichenicolous Biota no. adhuc ined.

Etymology: parietinarius 3 (Lat.), belonging to [*Xanthoria parietina*].

Iconography: Vězda 1970: 223, Fig 1 (drawings of asci, ascospores, and paraphysoids); Giralt 1996: 365, Fig 54 A (drawing of ascospores); this paper, Fig 1A (habit), Fig 2A–C (close ups of habit), Fig 3A and B (vertical sections of ascomata), Fig 4 (young stages of ascoma development), Fig 5A, B, D, E (asci), C (ascospores), F (vertical section of conidioma).

Description: Infection not gall-inducing, not causing severe destruction of the thallus but sometimes slight discolourations can be observed. Vegetative hyphae intramatrical, inconspicuous, K/I+ blue, Cresyl-blue+ violet. Ascomata mat black, dull, often with a slight brownish tinge, up to 0.25 mm in diam., arranged in groups of up to (10–)20–30(–50), convex, immarginate, more or less roundish, distributed over the surface of the host thallus including apothecial margins and hymenia. Exciple lacking. Hymenium pale greyish, with K/I+ blue hymenial gel, 30–45 µm tall. Epithymenium dark brown (due to the pigmented paraphysoidal tips) with a bluish tinge (due to a slight pigmentation of the hymenial gel), K+ chestnut-brown. Hypothecium pale brownish with some brown agglomerations, K/I–, the hyphae directly underneath K/I+ blue. Interascal filaments paraphysoidal, septate, branched, and anastomosed, 1–1.5 µm thick, with only slightly thickened terminal cells, apically about 2–5 µm thick, with pigmented caps ('Pigmentkappen' in the sense of Kiliás 1981). Asci of *Arthonia*-type, clavate, 8-spored, with hemiamyloid (K/I+ blue) ring structure in the innermost layer of the endoascus, dehiscence fissitunicate, 26–35(–37) × (11–)12–15.5(–16.5) µm. Ascospores hyaline, K/I–, 1-septate, upper cell somewhat broader, and mostly shorter, with thin hyaline perispore (getting condensed and brownish with age; attention: perispore from deliberated spores easily squeezed off) (9–)10–12(–13.5) × (3–)4–5(–6) µm. Pycnidia subglobose to pyriform. Nonpigmented parts of the pycnidial wall K/I+ blue. Conidiophores of type I–II (Vobis & Hawksworth 1981) producing ellipsoid pycnosporos. Lichenicolous fungus growing on *Xanthoria parietina* (and possibly also on other taxa of the *X. parietina*-group).

Remarks: *Arthonia parietinaria* is not rare but in the past it has not been recognized as a distinct species. Previous records of *A. parietinaria* usually have been published under either the name *A. molendoi* (Fig 1B) or *A. epiphyscia*. Concerning the apothecial characters, *A. parietinaria* is a hardly variable species. It differs from *A. molendoi* and *A. epiphyscia* in causing larger infection spots and also by the higher mean numbers of ascomata [(10–)20–30(–50)] per infection spot (1–5(–10) in *A. molendoi* (1–)5–10 in *A. epiphyscia*). *A. parietinaria* can be distinguished from *A. molendoi* by the less intense colouration (mat black) of the ascomata (pure black in *A. molendoi*). The difference in colour recalls that between dark morphs of *Lecanora cenisia* and *Tephromela atra* at high elevations. Remnants of

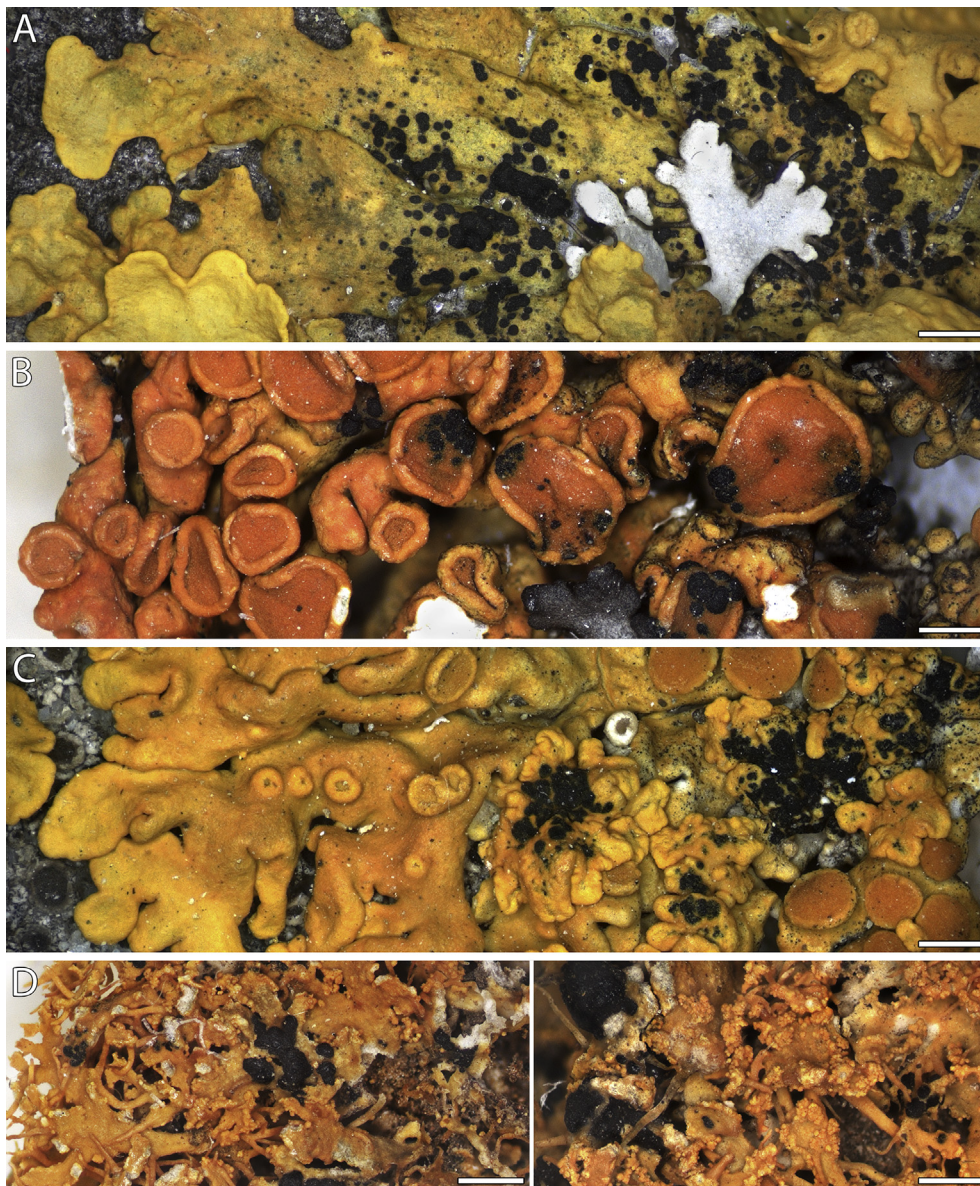


Fig 1 – *Arthonia* species on teloschistalean macrolichens. (A) *Arthonia parietinaria* on *Xanthoria parietina* (from holotype). (B) *Arthonia molendoi* on *Xanthoria elegans* (from Santesson, *Fungi Lichenicoli Exs.* 54 in GZU). (C) *Arthonia sytnikii* on *Xanthoria ligulata* (from Mayrhofer 13279). (D) *Arthonia anjutae* on *Teloschistes spinosus* (two views from Hafellner 19576). Bar = 500 μ m.

anthrachinones originating from the host may still be present in ascomata of all *Arthonia* species infesting Teloschistaceae. These remnants may cover partly the epihymenium (Fig 3B) or may even be included in the ascomata. Therefore the reaction of ascoma sections namely the epihymenium with K is sometimes misleading. Differences between *Arthonia parietinaria*, *A. molendoi*, and *A. epiphyscia* are summarized in Table 1. Several other *Arthonia* species are already known to grow on foliose or fruticose Teloschistaceae, namely *A. molendoi* (Fig 1B), *A. sytnikii* (Fig 1C), *A. anjutae* (Fig 1D), and *A. destruens* var. *nana* Grube & Hafellner. All of them infest the thallus, and some of them also develop fruiting bodies on the apothecia (hymenia) of their hosts. Selected character states of these taxa have been summarized in Table 2.

The only taxon of still unclear relationship is an infraspecific widely neglected one, *Conida destruens* f. *maculans* Rehm Rabenh. Krypt. Fl. 1(3): 423 (1891). For the species *Conida destruens* the ascospores are correctly described as becoming brownish and there is no indication that the ascospores of the form *maculans* should differ in this respect. The only difference distinguishing it from the typical form should be the aggregated ascomata (...‘schwarze Punkte, welche manchmal gehäuft beisammenstehen’). A single collection, Arnold Lich. Exs. no. 397, is cited, consequently constituting the type. However, Arnold, Lich. Exs. no. 397 is also listed among others as exsiccate of *Conida destruens* [f. *destruens*]. Arnold, on the other hand distributed no. 397 under the name *Arthonia destruens* var. *maculans* Rehm and the label data [Germany, Bavaria]:



Fig 2 – *Arthonia parietinaria* on *Xanthoria parietina*. (A) Holotype in GZU. (B) Close up of ascomata on thallus (from isotype in CANB). (C) Close up of ascomata on thallus and young apothecium (Hafellner 77067 in GZU). (D) Close up of ascomata on apothecial margin and disc (from isotype in NY). Bar = 200 μ m.

Auf der Oberseite des Thallus der *Ph.[yscia] parietina* an Feldbirnbäumen bei Sugenheim in Franken, Sommer 1868, leg. Rehm [label data from specimen in M published on the Internet: http://pictures.snsb.info/BSMlichfungicoll/web/M-0040/M-0040694_20031022_114338.jpg] as a nomen nudum. Therefore we regard it as likely that the form constitutes a heterotypic synonym of *Arthonia destruens* var. *nana* Grube & Hafellner, a taxon described from Nepal and growing there upon *Xanthomendoza fallax* (compare Grube et al. 1995) but it cannot be excluded with certainty that the taxon is identical with *Arthonia parietinaria*. Because of the confusing circumstances we decided not to consider whether the name could be used but to describe the taxon as new species founded on a recent rich collection.

Beside these arthonioid fungi the opegraphoid species *Phacothecium varium* (Tul.) Trevis (syn. *Opegrapha physciaria* (Nyl.) D. Hawksw. & Coppins) is occasionally found on *Xanthoria*. That species was treated in detail by Hafellner (2009). Furthermore, *Arthonia*-species can also colonize *Caloplaca* species with noneffigured thallus organization. This was recently shown with *Arthonia insularis* Kantvilas & Wedin, a species with ascospores becoming pale reddish brown and which causes severe infections on *Caloplaca eos* S. Kondr. & Kärnefelt in Australia (Kantvilas & Wedin 2015).

Hosts: *Xanthoria parietina* (1, T) (thallus and apothecia). Furthermore the foliose Teloschistaceae *Xanthoria parietina* var. *adpressa*, *X. mediterranea*, *X. lobulata*, *X. polycarpa*, *X. candelaria* var. *torulosa*, and *X. fallax* are recorded in the literature (see

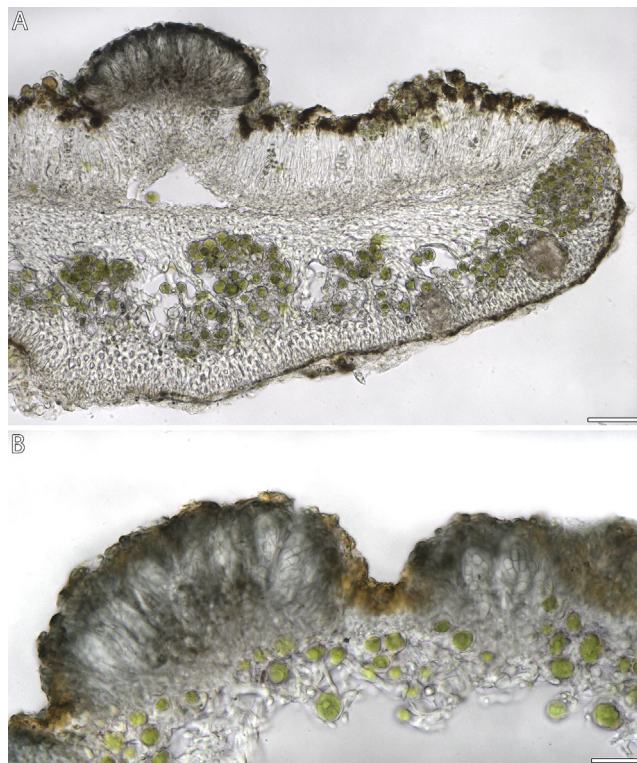


Fig 3 – *Arthonia parietinaria* on *Xanthoria parietina*. (A) Ascoma in longitudinal section upon apothecium of the host (from isotype in NY). (B) Ascoma in longitudinal section upon thallus of the host. Note the orange anthraquinone pigments originating from the host cortex still covering partly the apothecial surface of the *Arthonia* ascoma to the left (from isotype in CANB). Medium: tap water. Bar A = 50 μm , B = 20 μm .

geographic distribution). A considerable number of these records would need a critical reevaluation also under in view of the recent knowledge about phylogenetic relationships Teloschistaceae. For some of these host taxa a transfer in other genera of Teloschistaceae has been proposed but the taxonomy appears to not have yet settled. It cannot be excluded that further *Arthonia* species are hidden under these records with unusual hosts.

So far known, *Arthonia parietinaria* appears to be restricted to the *X. parietina* group. *X. parietina* is by far the most common host, but it cannot be excluded that the species will be detected also on *X. aureola* or *X. calcicola* in the future. An infection with *Arthonia parietinaria* causes no significant destruction of the host tissue outside of the infection spots. The hyphae, which according to their reactivity (K/I(Lugol)+, CrB+) belong to the inhabiting fungus, occur in the plectenchyma of the host as well as in the vicinity of living algal cells of the host thallus. The behaviour of *Arthonia parietinaria* is therefore regarded as commensalic (or ‘parasymbiotic’). However, larger groups of ascomata may cause slight discolourations on the host thallus and the fungus could be considered weakly parasitic as well. In summary, *A. parietinaria* is a nonlichenized, obligately lichenicolous, highly specialized species.

Habitats: *Arthonia parietinaria* is found together with its host lichen in various habitats ranging from solitary trees in pastures, rows of trees along roads or creeks, fruit trees in orchards but also deciduous trees at the edge or in open forests. It is not rare and has been rather frequently reported in recent years. This might correlate with the permanently increasing occurrence of the host lichen due to nitrogen pollution.

Distribution: *Arthonia parietinaria* is widely distributed. The species is so far with certainty known only from Europe, western Asia, and northwestern Africa (Canary Islands). We saw only a few specimens from outside Europe, namely from Armenia and the Canary Islands. In Central Europe specimens have been seen from lower and medium altitudes. It is not unlikely that *A. parietinaria* can also be proven to be present in further continents as well because the host lichen is extremely common and widely distributed in entire Europe and is also known from other parts of Asia, Africa, South America, and Australasia.

A larger number of earlier records of an *Arthonia* upon *Xanthoria parietina* that have been published under various names are likely to represent the species described here as new. Names used in these publications include *Arthonia molendoi*, *A. epiphyscia*, *A. destruens*, and *A. clemens* plus their homotypic synonyms namely in the genus *Conida*.

The following distribution data, of which we think that they refer to *Arthonia parietinaria*, are based on records from various *Arthonia* species always with *Xanthoria parietina* as reported host. For a compact presentation of the data we use the following abbreviations: *Arthonia molendoi* or *A. aff. molendoi* (A), *A. molendoi* p.p. or *A. aff. molendoi* p.p. (A#), *A. epiphyscia* or *A. epiphyscia* s. l. (B), *A. epiphyscia* p.p. (B#), *A. clemens* or *Conida* c. (C), *Arthonia destruens* or *Conida* d. (D), *C. destruens* f. *maculans* (E), and *Conida lecanorina* (F). As we have screened thousands of thalli of *Xanthoria parietina* and could detect only the species described above we are fairly convinced that all these records refer to the same species. The abbreviation p.p. means that the authors mentioned *Xanthoria parietina* as one of several hosts. Therefore we regard it as likely that the record refers to more than one lichenicolous taxa.

Judging from the cited hosts the species is so far known from the following European countries (records on Teloschistales other than *Xanthoria parietina* uncertain): Austria (Berger et al. 2015: 8 as (A), Keissler 1913: 386 as (F), 1930: 72 ff. as (C), Rehm 1891: 423 f. as (E)), Belgium (Ertz et al. 2008: 39 f. as (A), Santesson 2008: 10 as (A)), Denmark (Alstrup et al. 2013: 57 as (A)), Estonia (Suija et al. 2010: 105 as (A)), France (Roux et al. 2014: 85 as (A#)), Germany (Rehm 1891: 423 f. as (E), Brackel 2010: 9 as (A), 2014: 30 ff. as (A#), Cezanne & Eichler 2015: 56 as (A), Cezanne et al. 2008: 45 as (B), 2013: 189 as (A), John et al. 2011: 305 as (A), 2014: 1202 as (A), Triebel & Scholz 2001: 214 as (B)), Italy (Brackel 2011: 67 as (A#) including a record on an additional host *Caloplaca cerina*, 2015: 224 as (A)), Lithuania (Motiejūnaitė et al. 2011: 40 as (A)), Luxembourg (Cezanne & Eichler 2013: 276 as (A), 2014: 234 as (A), Van den Broeck et al. 2013: 66 as (A)), the Netherlands (Brand et al. 2013: 19 as (A#)), Norway (Santesson 1993: 17 as (A#) with additional host *Xanthoria polycarpa*), Poland (Czyżewska & Kukwa 2009: 17 f. as (A#), Kukwa 2004: 67 as (A) with short description), Portugal (Boom & Giralte 2012: 164 as (A)), Slovakia (Vězda 1970: 221

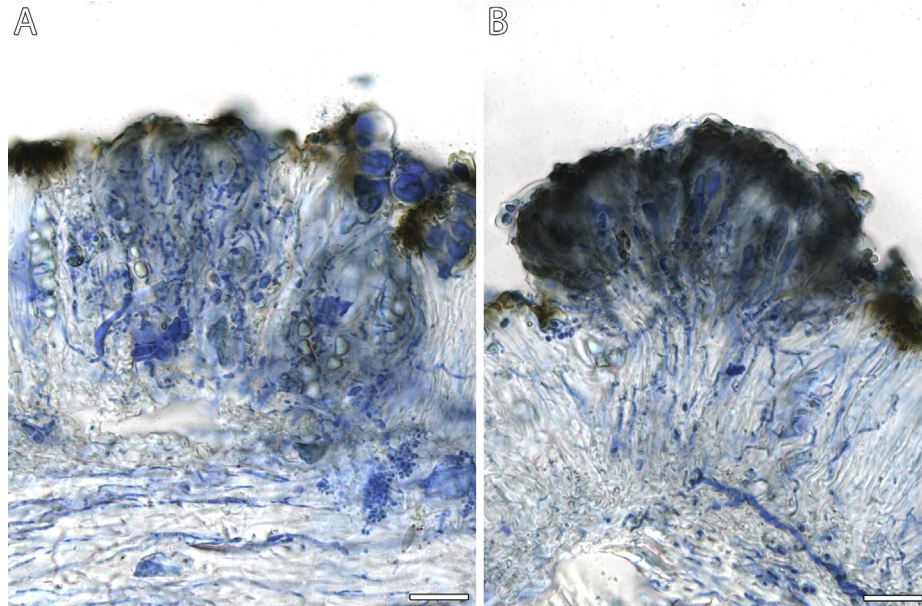


Fig 4 – *Arthonia parietinaria* on *Xanthoria parietina*. (A) Ascoma primordium developing in the hymenium of the host in longitudinal section. (B) Young ascoma in longitudinal section and vegetative hyphae penetrating the hymenium of the host (from isotype in NY). Medium tab water after treatment with Lactic acid–Cotton blue. Bar = 20 µm.

as (B) with short description), Spain (Atienza et al. 2014 as (A), Boom & Etayo 2014: 46 f. as (A), Burgaz et al. 2007: 139 as (A), Calatayud et al. 1995: 369 as (A#), Etayo 2010: 36 ff. as (A#), Giralt 1996: 364 ff. as (B) with short description, Giralt & Gomez-Bolea 1988: 195 as (B), Martínez et al. 2002: 46 as (B), Seriná et al. 2014: 39 as (B)), Sweden (Santesson 1993: 17 as (A#) with additional host *Xanthoria polycarpa*), Switzerland (Rehm 1891: 424 as *Arthonia nephromiaria* (this record remains doubtful because Stizenberger 1882: 479 to which Rehm refers to cites only *Physcia stellaris* as host under that name; other records of the species from Switzerland to which Rehm might refer to we could not trace; however, the presence in Switzerland confirmed with records cited below)), Ukraine (Kondratyuk & Khodosovtsev 1997: 589 as (C), as (D) with additional host *Xanthoria lobulata*), the British Isles (Coppins 1992: 81 as (B#), Hawksworth 1975: 186 as (B#), Hitch 2010: 120 as (A), 2012: 68 as (A), 2015: 62 as (A)). From Africa it is reported from Morocco (Werner 1932: 163 as (C), 1938: 134 as (C)) and the Canary Islands (Boom & Clerc 2015: 1 sub (A#), Boom & Ertz 2012: 73 sub (A#)). Asian reports exist for Israel (Kondratyuk et al. 2005: 106 as (A#) including an additional host *Xanthoria mediterranea*). In Australasia it has been reported from New Zealand (Kondratyuk & Galloway 1994: 26 as (B#) with additional host *Xanthoria parietina* var. *adpressa*) but the specific identity with the species we describe here should be rechecked. In America it might already be known from Chile (Etayo & Sancho Garcia 2008: 46 as (A) on *Xanthomendoza fallax*), and also the record by Werner (1937: 64 as (C) on *Xanthoria candelaria* var. *torulosa*) from Spain should be confirmed by restudying the specimens, because the hosts belong to a different clades of xanthoroid lichenized fungi. Based on specimens cited below the species is added to the mycoflora of Croatia, Greece, Slovenia, and Armenia.

Exsiccata (all on *Xanthoria parietina*): Isotypes and duplicates of three paratypes will be distributed in Hafellner, Lichenicolous Biota (for data and herbaria see below). – Santesson, Fungi Lichenicoli Exs. no. 377, sub *Arthonia molendoi* (GZU).

Further specimens examined (all on *Xanthoria parietina*):
Europe: **Austria:** Burgenland, Südburgenland, Rauchwart, Rauchwarter Berghäuser ca. 6 km SE von Stegersbach, 47°07'18"N/16°13'17"E, ca. 265 m, GF 8863/3, 2010, A. Fleischhacker 10010 & B. Fleischhacker (GZU). – Burgenland, Südburgenland, Urbersdorf, am Stausee, 47°03'36"N/16°22'04"E, 210 m, 2012, F. Berger 26201 (herb. Berger). – Kärnten (Carinthia), Sattnitz, Sabuatach ca. 13 km ESE von Klagenfurt, ca. 700 m WSW des Gehöfts Wlattinig, 46°35'19"N/14°27'57"E, ca. 580 m, GF 9452/2, 2011, F. Schlatti, det. A. Fleischhacker 11012 (GZU). – Kärnten (Carinthia), Zentralalpen, Saualpe W von Wolfsberg, ca. 1 km W von St. Michael an der Straße nach Lading, 46°50'05"N/14°47'10"E, ca. 550 m, GF 9154/4, 2010, J. Hafellner 76737 (BCN, BR, CANB, GZU, LE, NY, UPS) (duplicates distributed in Hafellner, Lichenicolous Biota no. adhuc ined.). – Niederösterreich (Lower Austria), Wienerwald, am südwestlichen Stadtrand von Mödling, am NE-Fuß des Anninger-Massivs, 48°04'35"N/16°16'50"E, ca. 275 m, GF 7963/2, 2011, J. Hafellner 78980 (GZU). – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Radmer an der Hasel ca. 9 km SW von Hieflau, S Hänge N ober dem Schloß Greifenberg, 47°31'50"N/14°42'45"E, ca. 940 m, GF 8454/3, 2006, J. Hafellner 69282 (GZU). – Steiermark (Styria), Nordalpen, Nördliche Kalkalpen, Hochschwab-Gruppe, Seetal W von Seewiesen, ca. 10 km NE von Aflenz, 47°37'15"N/15°15'20"E, ca. 930 m, GF 8357/4, 2007, J. Hafellner 69400 (GZU, herb. Hafellner). – Steiermark (Styria), Steirisches Randgebirge, Fischbacher Alpen ['Oststeirisches Hügelland' ex errore], an der Straße von Birkfeld nach Ratten, N der Abzweigung nach Strallegg,

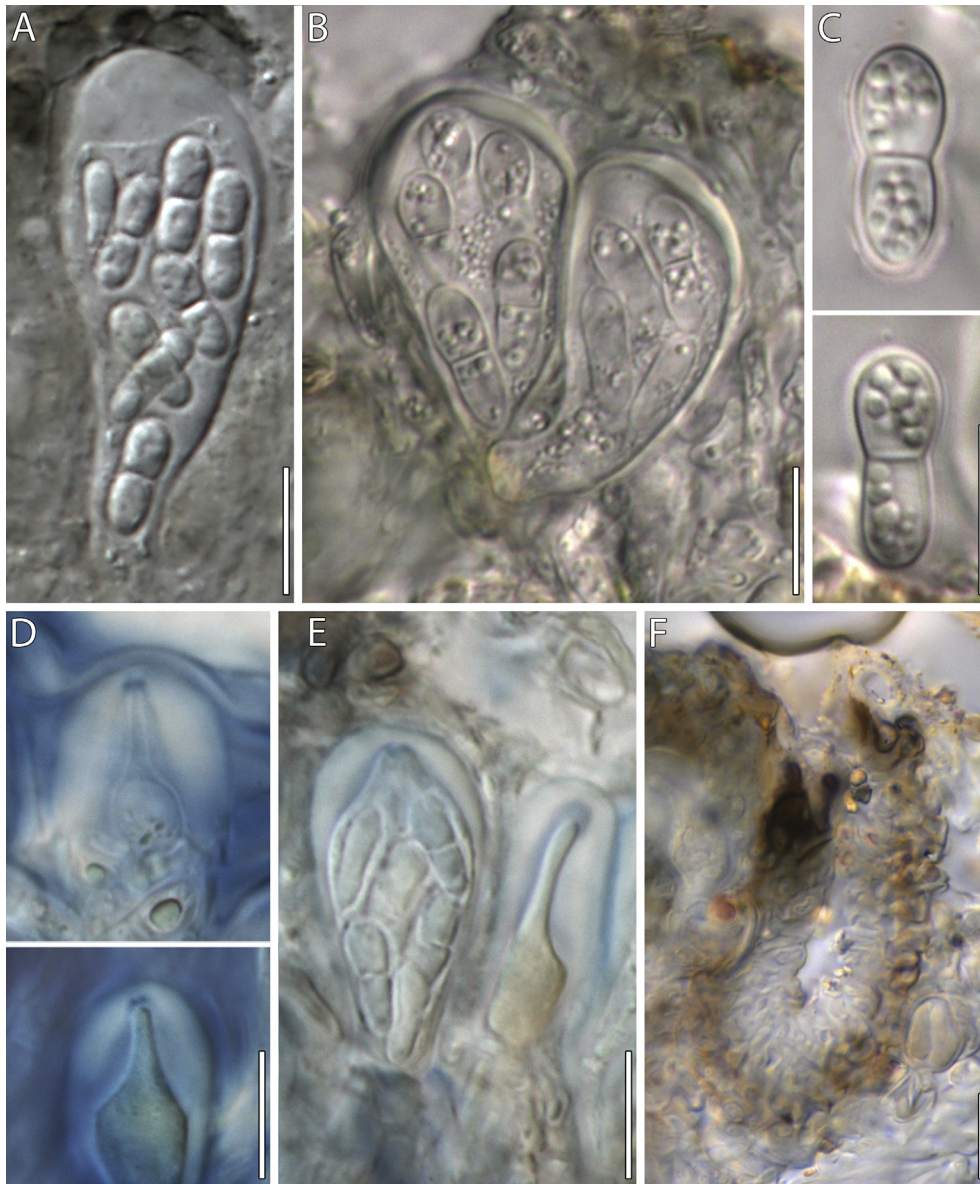


Fig 5 – *Arthonia parietinaria* on *Xanthoria parietina*. (A) Young ascus (DIC, from holotype). (B) Mature asci (DIC, from holotype). (C) Ascospores (DIC, from holotype). (D) Two ascus tips with apical ring structure in the endoascus (from holotype). (E) Two asci, one semimature, one immature (from holotype). (F) Conidioma in longitudinal section (from holotype). Medium: A, B, C, F tap water; D, E I(Lugol) after pretreatment with K. Bar = 10 µm.

47°25'05"N/15°41'40"E, ca. 645 m, GF 8560/3, 1989, J. Hafellner 22193 & A. Hafellner (GZU). – Steiermark (Styria), Steirisches Randgebirge, Grazer Bergland, Bergrücken NE vom Hörgasgraben, ca. 2.8 km N von Stift Rein, beim SE Ende des Kaschlsteiges, 47°09'40"N/15°17'20"E, ca. 620 m, GF 8857/2, 2013, J. Hafellner & A. Hafellner (GZU). – Steiermark (Styria): Steirisches Randgebirge, Grazer Bergland, Weizbach Graben, an der Straße vom Dorf Schmied in der Weiz auf den Sattel Brandlucken, ca. 0.8 km NE des Ghf. Granitzer, Waldstreifen zwischen Bach und Straße, 47°20'10"N/15°35'15"E, ca. 940 m, GF 8659/4, 2011, J. Hafellner 78997 (GZU). – Steiermark (Styria), Sausal, Kitzeck ca. 9 km W von Leibnitz, am NW Ortsrand, 46°47'35"N/15°26'00"E, ca. 480 m, GF 9258/2, 2011, J. Hafellner 77054 (GZU). – Steiermark (Styria), Oststeirisches Hügelland,

Loimeth ca. 8 km NW von Fürstenfeld, 47°06'52"N/16°01'56"E, ca. 335 m, GF 8862/3, 2010, A. Fleischhacker 10001 (GZU). – Steiermark (Styria), Oststeirisches Riedelland, 7 km NE of the centre of Graz, along the road from Stifting to Schaftal, close to the junction to Schillingsdorf, 47°06'09"N/15°30'42"E, ca. 435 m, GF 8859/3, 2010, W. Obermayer 11931 (BR, CANB, E, GZU, M, NY, UPS) (duplicates distributed in Hafellner, Lichenicolous Biota no. adhuc ined.). – Steiermark (=Styria), Oststeirisches Riedelland, 6.5 km E of the centre of Graz, 380 m SSE of Eichenhof, 47°04'40"N/15°31'12"E, 440 m s. m., GF 8959/1, mixed forest, on branches of trees lying on ground, 30 May 2012, W. Obermayer 12467, det. J. Hafellner (GZU). – Belgium: De Panne, Westhoek, NE border of nature reserve. 51°05'N/02°34'E. Grid: IFBL, C056, 2008, P. Diederich (n.

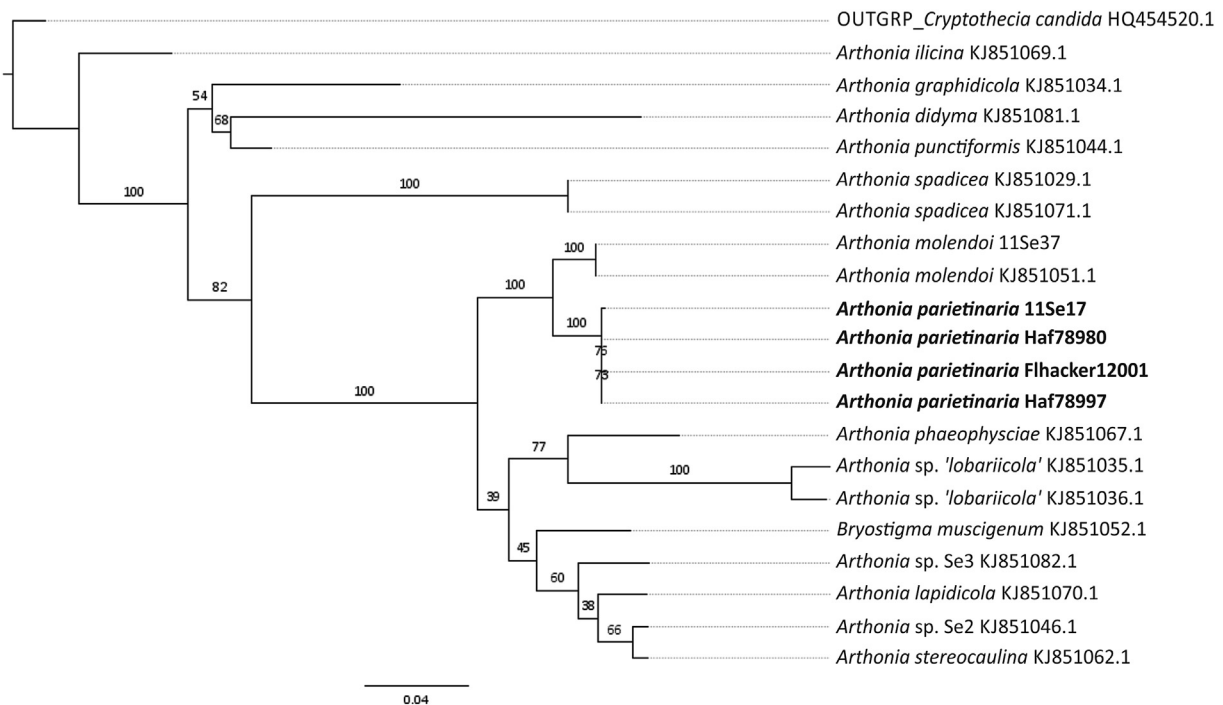


Fig 6 – Phylogenetic position of *Arthonia parietinaria* (in bold) according to partial nuLSU rRNA gene sequences. Maximum likelihood tree, with bootstrap support values from 1000 replication above branches.

Table 1 – Selected character states of <i>Arthonia parietinaria</i> and the often confused <i>Arthonia</i> species (data for <i>Arthonia destruens</i> from Grube et al. 1995).				
	<i>A. parietinaria</i>	<i>A. molendoi</i>	<i>A. epiphyscia</i>	<i>A. destruens</i> (incl. var. <i>nana</i>)
Number of ascomata per infection spot	(10–)20–30(–50)	1–5(–10)	(1–)5–10	2–10
Colour of ascoma in surface view	Dull black	Pure black	Pure black	Dull black
Colour of hymenium	Pale greyish bluish	Pale brownish	Pale brownish	Yellowish
Pigmentation of epihymenium	Dark brown with bluish tinge	Blackish brown with dark olive tinge	Brown with dark olive tinge	Brownish with yellowish tinge
Chemical reactions of epihymenium	K+ chestnut-brown	K–	K–	K+ purplish violet then dissolving
Colour of hypothecium	Brownish with some brown agglomerations	Pale yellowish to medium brown	Olive brown	Brown with yellowish tinge
Colour of ascospores	Hyaline	Hyaline	Hyaline	Soon brown, verrucose
Size of ascospores	10–12 × 4–5 µm	10–13 × 4–6 µm	10–13 × 3.5–5 µm	14–17 × 5–7 µm (v. <i>destruens</i>) 10.5–13 × 5–7 µm (v. <i>nana</i>)

16731) = Santesson, Fungi Lichenicoli Exs. 377 (GZU). – **Croatia:** Dalmatien, Insel Korčula, nahe der Stadt Korčula, 47°57'20"N/17°07'55"E, ca. 70 m, 2004, N. Cernic (herb. Hafellner 41734). – **France:** Rhône-Alpes, Haute-Savoie, Western Alps, Bornes Massif (Le Massif des Bornes), Burzier NW above Sallanches, SE below the parking area at Route de Doran, 45°57'22"N/6°36'42"E, ca. 935 m, 2011, J. Hafellner 82562 (GZU). – **Germany:** Bayern (Bavaria), Unterfranken, Kreis Kitzingen, Schwanberg-Südhang SW Kirchberglein, ca. 300 m, MTB 6227/4, 2010, W. v. Brackel 5307 (herb. Brackel). – Bayern (Bavaria), Allgäu, Bayerniederhofen NE vom Bannwaldsee, ca. 10 km NE von Füssen, am SE Ortsrand, 47°37'25"N/10°48'15"E, ca. 800 m, 2004, J.

Hafellner 77194 (GZU). – **Greece:** Western Macedonia, Kozani distr., Mt. Vourinon, on slopes exposed to the E, 1956, K. H. Rechinger, det. J. Hafellner (GZU). – **Italy:** Sardinien [Prov. Nuoro], Gennarentu, Monte Tonneri, Funt na Pauli, 39°54'38"N/9°23'42"E, 650 m, 2011, F. Berger 25439 (herb. Berger) as admixture in specimen of *Xanthoriicola physciae*. – **Liechtenstein:** Eastern Alps, Rätikon, W below the village Triesenberg by the road to Vaduz, 47°06'45"N/09°32'30"E, ca. 750 m, 2008, J. Hafellner 83053 (GZU). – **Luxembourg:** distr. Lorrain, Lorentzweiler, Roude Bam., alt. 225 m., IFBL: L8.46.31, UTM: KA.90, 2010, P. Diederich 16909 (herb. Diederich). – distr. Lorrain, Entre Dudelange et Kayl, Haardt, IFBL: M8.54.23, UTM: KV.88,

Table 2 – Selected character states of *Arthonia parietinaria* and other *Arthonia* species on teloschistalean macrolichens (data from Kondratyuk 1996 and own observations).

	<i>A. parietinaria</i>	<i>A. molendoi</i>	<i>A. syntniki</i>	<i>A. arnjutae</i>	<i>A. destruens</i> v. <i>nana</i>
Type host; further hosts	<i>Xanthonia parietina</i> ; <i>X. parietina</i> group	<i>Xanthonia elegans</i> ; <i>X. elegans</i> group, <i>Caloplaca saxicola</i> group	<i>Xanthonia ligulata</i> ; <i>Xanthonia</i> spec.	<i>Teloschistes velifer</i> f. <i>nodulosus</i> ; <i>Teloschistes spinosus</i>	<i>Xanthonia fallax</i>
Fungus gall inducing	No	No	Yes	No	No
Number of ascospores per infection spot	(10–)20–30(–50)	1–5(–10)	ca. 5–10	5–20, fusing	2–10
Colour of ascospores in surface view	Dull black	Pure black	Pure black	Pure black	Dull black
Pigmentation of epiphymenium	Dark brown with bluish tinge	Blackish brown with dark olive tinge	Brown with dark olive tinge	Dark brown	Brownish with yellowish tinge
Reactions of epiphymenium	K+ chestnut-brown	K–	K– or greenish	K– or olive greenish	K+ purplish violet then dissolving
Colour of hypothecium	Brownish with some brown agglomerations	Pale yellowish to medium brown	Hyaline	Dark brown	Brown with yellowish tinge
Colour of ascospores	Hyaline with thin perispore, slightly pigmented with age	Hyaline with thin perispore, slightly pigmented with age	Hyaline	Pigmented in early stage, finally dark brown	Soon brown, verrucose
Size of ascospores	10–12 × 4–5 µm	10–13 × 4–6 µm	10–13 × 3–5 µm	12–15 × 5–7 µm	10.5–13 × 5–7 µm
Phytogeography	Widespread in Holarctic, in the temperate zone at lower altitudes	Bipolar, in the temperate zone at higher altitudes	Australasia, S. Africa, coastal	Australasia	Himalaya

together with *Xanthonicola physciae*, 2011, P. Diederich 17158 (herb. Diederich). – **Slovenia**: Central Alps, Kobansko, Koralpe, Bistrica (Feistritz) valley ca. 9 km NW of Muta (Hohenmauthen), close to the border to Austria, surroundings of former border station on E (= orographically left) river bank, 46°39'15"N/15°07'10"E, ca. 460 m, 2008, J. Hafellner 77110 & L. Muggia (GZU). – Southern Alps, Julian Alps, Cezsoča S of Bovec, SE above the village, 46°19'10"N/13°33'20"E, ca. 380 m, 2003, J. Hafellner 77510 (BR, CANB, E, GZU, NY, PRM, UPS) (duplicates distributed in Hafellner, Lichenicolous Biota no. adhuc ined.). – **Switzerland**: Kanton Bern, Berner Alps, by the road from Meiringen to Rosenlaui, S above Meiringen near the inn Zwirgi, 46°42'45"N/08°10'55"E, ca. 980 m, 2006, J. Hafellner 77458 (GZU). – Kanton Graubünden, Engadiner Alps, Sesvenna group, San Niclà ca. 12 km NE of Scuol, N of the church close to the right river bank of the Inn, 46°51'30"N/10°25'35"E, ca. 1080 m, 2006, J. Hafellner 77196 (GZU). – **Asia**: **Armenia**: Syunik province, road from Dilijan to Ijevan; SW of Ijevan along the river Aghstev, 40°49'08"N/45°06'26"E, ca. 600 m, slopes along the road, 2005, S. Harutyunyan 33-30b, det. J. Hafellner (GZU). – **Africa**: **Canary Islands**: El Hierro, Mirador de las Playas NE ober dem Ort Taibique, am Rand der SE-exponierten Abbrüche, 27°44'N/17°58'W, ca. 1060 m, 1995, J. Hafellner 48238 (herb. Hafellner).

Discussion

As shown in the phylogenetic tree of a restricted set of related *Arthonia* species (14 taxa, Fig 6), *Arthonia parietinaria* apparently represents a sister species of *Arthonia molendoi*, both occurring on members of Teloschistaceae as hosts. However, we are not sure that this will be confirmed when the study is based on a more representative set of lichenicolous arthonioid taxa. Judging from morpho-anatomy we would not be surprised when other lichenicolous *Arthonia* species are closer related to *A. parietinaria* than *A. molendoi* (e.g. *Arthonia diploiciae* Calat. & Diederich, *Arthonia peltigerina* (Almq.) H. Olivier), but this is just a guess.

Arthonia molendoi was also included in a thorough phylogenetic reconstruction of arthonioid fungi, both comprising lichenized and nonlichenized species (Frisch et al. 2014). In the present analysis, *A. molendoi* forms a lineage together with lichenized *Arthonia muscigena* Th.Fr., a species to which *Bryostigma leucodontis* Poelt & Döbberler is regarded to represent a younger heterotypic synonym (Sundin et al. 2012). As this clade has a basal position to the majority of other arthonioid fungi and is strongly supported in a Bayesian consensus tree it was called 'Bryostigma clade'. Judging from the sister position of *A. parietinaria* and *A. molendoi* in our phylogenetic reconstruction we can expect that *A. parietinaria*, once included in a reanalysis of a larger set of species, will also belong to the 'Bryostigma clade'. However, due to the limited number of molecular data for many other *Arthonia* species we still refrain from accepting *Bryostigma* taxonomically at the level of genus.

The taxonomy of the group of hosts here in focus, the Teloschistaceae, is strongly debated in recent years (e.g. Gaya et al. 2008, 2012; Arup et al., 2013; Kondratyuk et al. 2014). A consistent taxonomic implementation of molecular data gained by

various working groups is still not in sight, but questions about the interrelationship of selected xanthorioid and caloplacoid species groups can well be addressed with the published phylogenetic trees. These relationships are relevant in connection with the observed host spectra of selected lichenicolous *Arthonia*-species. Both *A. parietinaria* and *A. molendoi* have their hosts nesting in the Xanthorioideae-clade (Gaya et al. 2012). The *Xanthoria parietina* clade (including type host of *A. parietinaria*) has a more distant relationship to the *Xanthoria elegans* clade (including type host of *A. molendoi*) than the latter to the lineage comprising *Caloplaca decipiens* and *Caloplaca arnoldii* which includes the effigurate *Caloplaca* species that are often observed as additional hosts of *A. molendoi*. Thus, the lichenicolous fungus taxonomy reflects ‘cum grano salis’ the taxonomy of the host species, an often observed phenomenon in parasitic fungi (see e.g. Savile 1979; Hijwegen 1979).

The anamorph briefly described above clearly belongs to *A. parietinaria* and is the state that produces the microconidia (spermatia) for the fertilization of ascogons. As we saw them only tightly attached to or in between ascogonia we do not expect that they can appear also alone and outside of infection spots of *A. parietinaria* and in greater distance to its ascogonia. Formally the pycnidia are *Phoma*-like except that they are smaller and that they produce conidia distinctly smaller than what is regarded to represent vegetative diaspores. Two *Phoma*-like fungi are known to grow on *X. parietina*, both with distinctly larger conidia and both now classified in *Didymocyrtis* (Ertz et al. 2015). One constitutes an anamorphic state of the *Didymocyrtis slaptioniensis* (D. Hawksw.) Hafellner & Ertz, an ascomycete obviously restricted to *X. parietina*, the other with a broader host spectrum was named *Didymocyrtis epiphyscia* Ertz & Diederich and is only known in its anamorphic state.

Acknowledgements

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