Two new species of lichenicolous Arthonia (Arthoniaceae) from southeastern North America highlight the need for comparative studies of lichen parasites and their hosts

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ABSTRACT. Arthonia frostiicola and A. galligena are described as new to science based on collections from mountainous regions of southeastern North America. Arthonia frostiicola infects the saxicolous lichen Dirinaria frostii, producing emarginate black apothecia which erupt from within the host thallus. It is characterized by a dark hypothecium and 1-septate, obovoid ascospores which turn brownish and verruculose in age. It is known from five collections made in the southern Appalachian Mountains and Ozark Mountains in southeastern North America. Arthonia galligena produces galls in the thallus and apothecia of the corticolous lichens Lecanora masana and L. rugosella, and is apparently endemic to the high elevations of the southern Appalachian Mountains. It is characterized by a variably pigmented, pale to red-brown hypothecium and 2-septate, macrocephalic ascospores which turn brownish and verruculose in age. Keys to the species of Arthonia on Caliciales and Lecanoraceae are provided.

KEYWORDS. New taxa, biodiversity, endemism, host-parasite relationships, lichenicolous fungi, taxonomy

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Lichenicolous fungi are a diverse group of organisms living on or within lichens (Clauzade et al. 1989; Diederich 1996; Diederich et al. 2018). Unlike endolichenic fungi, which live entirely within the thalli of their hosts and do not produce readily visible infections, lichenicolous fungi produce visible external reproductive structures, often causing discolorations, necrosis or galls in the hosts (Richardson 1999; U'Ren et al. 2012). Over 2,300 species of lichenicolous fungi have been recognized worldwide to date, which is only a third to half of the estimated total number of species (Diederich et al. 2018; Zhurbenko 2008). Despite being speciesrich and having a highly distinctive lifestyle that involves parasitizing hosts that are widely regarded as charismatic and ecologically important, fine scale documentation of rarity, geographic distribution, ecology and biology is lacking for most lichenicolous fungi (Ihlen & Wedin 2008; Lawrey & Diederich 2003; Zhurbenko 2012), making completion of conservation assessments and development of management strategies for these fungi challenging

(Woods & Coppins 2012). Conservation of lichenicolous fungi is further complicated by the fact that parasites historically have been considered unimportant, or even detrimental, based on the widespread perception that they detract from ecosystem health and that high parasite abundance and diversity indicates a disturbed or stressed ecosystem (G´omez & Nichols 2013). To the contrary, increasing evidence suggests that parasites play critical roles in healthy ecosystems (Hudson et al. 2006). Moreover, diversity of parasites has been found to be correlated with overall diversity and quality of habitats, making them valuable bioindicators (Palm & R¨uckert 2009; Poulin 2014; Sasal et al. 2007).

Many lichenicolous fungi are restricted to a single host genus or even host species, while others appear to be generalists across a wide array of host taxa (e.g., Diederich et al. 2022a,b; Matzer 1996; Matzer & Hafellner 1990). Although the latter should be interpreted in light of detailed studies with deep sampling and use of molecular data that have repeatedly demonstrated taxa with presumed broad host selection to instead be complexes of superficially similar, host-specific species (e.g., Diederich et al. 2022b; Fleischhacker et al. 2016; Suija et al. 2015, 2018). Much like how perspectives of host specificity in lichenicolous fungi have evolved over time, the perception that geographic distributions of lichenicolous fungi uniformly mirror those of their hosts (e.g., Grube 2007) has shifted to a nuanced recognition that some lichenicolous fungi are rarer and more geographically restricted than their hosts (e.g., Hollinger & Lendemer 2021; Lendemer et al. 2016). Nonetheless, understanding of the ecological and biological factors that drive lichenicolous fungus species richness and distribution is also limited, although studies have implicated biotic interactions as well as microhabitat and microclimate (Lawrey & Diederich 2003; Łubek et al. 2019), a situation similar to fungal parasites of herbaceous plants (e.g., Majewski 1971).

Among the many fungal lineages that have evolved to parasitize lichens, the genus Arthonia Ach. is notable for being a particularly species-rich genus that, in a taxonomically broad sense, includes more than 500 species worldwide whose morphologies and nutrition modes span a full spectrum from lichens, with highly organized thalli, to non-lichenized, evidently saprobic fungi, and everything in between, including non-lichenized parasites on lichens (Frisch et al. 2014a; Grube 1998; Grube & Matzer 1997; Sundin 1999; Sundin & Tehler 1998; Sundin et al. 2012). More than 140 species belong to the latter category and are obligate parasites on lichens, almost all of which are restricted to a single host species or genus (Diederich et al. 2018; Supplementary Table S1). One should note, however, that Diederich et al. (2018) frequently include only the primary or typical hosts, and that one can find reports of many lichenicolous species on atypical hosts in the literature (e.g., Brackel (2015) reports Arthonia coronata Etayo on Cladonia spp.). Such reports may reflect the presence of undescribed cryptic species, differing significantly from related congeners only in host selection, or they may indicate that lichenicolous species have broader host tolerances than previously thought. Lichenicolous Arthonia typically produce infections on the host lichens that are readily detected in the field with a hand lens (Grube & Matzer 1997). Despite being relatively conspicuous, previously overlooked lichenicolous Arthonia are routinely reported and described from even well-studied areas such as Europe (e.g., Fleischhacker et al. 2016). The same is true in North America, where for two decades there has been a steady stream of newly documented and described lichenicolous Arthonia (Hafellner et al. 2002; Houde et al. 2007; Ihlen et al. 2004; Knudsen & Lendemer 2007; Kocourkova´ & Knudsen 2015; Lendemer & Harris 2012; Lendemer et al. 2016; Zhurbenko 2013). Surprisingly, no lichenicolous Arthonia species have been previously reported from the southern Appalachian Mountains, a biodiversity hotspot for many organisms (Stein et al. 2000), including lichens (Dey 1978; Lendemer et al. 2013). As was discussed by Hollinger & Lendemer (2021), while southern Appalachian lichens are well-studied relative to many other regions globally, there have been remarkably few reports of lichenicolous fungi given the high diversity of rare species and the large quantity of high-quality, natural habitats. Here we describe two new species of lichenicolous Arthonia found during fieldwork in the southern Appalachian Mountains, both of which appear to be rare and more narrowly restricted than their host lichens. We provide identification keys for the lichenicolous Arthonia growing on hosts in the Caliciales and

Lecanoraceae and contextualize the description of the new species within a broader discussion of hostparasite distribution patterns in lichenicolous fungi.

Methods

This study was based on specimens collected by the authors and deposited in the herbarium of the New York Botanical Garden (NY). Georeferenced voucher data for all NY specimens examined can be accessed via the C.V. Virtual Herbarium at NY (http://sweetgum.nybg.org/science/vh/). Specimens were studied using standard laboratory techniques, with hand-cut sections mounted in water, 10% KOH (K), 10% HNO_3 (N) and 10% Lugol's solution (I). The absence of crystals in the apothecia was confirmed using polarizing (POL) filters. Measurements were made of structures mounted in water from digital photographs taken with an OMAX model A3RDF50 camera inserted into the ocular tube of a microscope and calibrated with a reference micrometer slide. Measurements are presented as follows: (minimum)5th percentile–[mean]–95th percentile(maximum), where the extreme values are in parentheses, and 5th–95th percentile is the range within which 90% of individual measurements fall. The L/W ratio is the length divided by width, calculated individually for each spore, then the statistics are calculated as usual.

Taxonomy

Arthonia frostiicola Hollinger & Lendemer, sp. nov Fig. 1

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Parasitic species, occurring in the thallus of Dirinaria frostii (Tuck.) Hale & W.L.Culb., similar to Arthonia phaeophysciae Grube & Matzer in having erumpent black apothecia and 1-septate ascospores, but the hypothecium is dark brown (vs. hyaline to pale brown in A. phaeophysciae), and the ascospores have a submedian septum and turn brown and verruculose in age (vs. septum occurring at or above the middle and the ascospores remaining hyaline and smooth in age in A. phaeophysciae).

Type: U.S.A. Tennessee: Blount Co., Great Smoky Mountains National Park, Shop Creek, 35831$_0$53.4$_{00}$N 83859$_0$27.2$_{00}$W, 280 m, on Dirinaria frostii (thallus) on overhanging siliceous rock at top of outcrop at mouth of creek, overlooking lake, 11 May 2022, J.P. Hollinger 27058 (NY!, holotype; H!, isotype).

Description. Habit lichenicolous, weakly to moderately pathogenic, often causing discolorations in host thallus. Vegetative hyphae indistinct, I– and K/I–. Apothecia dispersed but becoming confluent with adjacent apothecia creating irregular compound apothecia, erumpent, becoming moderately to strongly convex very early, rounded, black, epruinose but usually retaining remnants of the host cortex over most of the surface, (0.09)0.15–[0.27]–0.50(0.56) mm (n¼119 from 3 specimens) in diam., margin indistinct, sometimes surrounded by a distinct round, blackened or bleached necrotic zone; epihymenium red-brown, Kþolive-brown, N– or a slightly brighter, redder brown, POL–; hymenium 25–50 lm high, hyaline, not inspersed with oil or crystals, Iþ red, K/Iþ blue; hypothecium 25–50 lm thick, red-brown, Kþ olive-brown and N– as in the epihymenium, K/Iþ blue; paraphyses indistinct, branched and anastomosing, some tips browncapped, 2.5–4.5 lm wide; asci 8-spored, broadly clavate, more elongate in age, with a 5–7 lm long foot, tip much thickened, lacking a K/Iþ blue ring structure, (17)23–[29]–41(42) 3 (11)13–[16]–20(21) lm (n¼52 from 5 specimens); ascospores hyaline, becoming brown and verruculose in age, 1-septate, narrowly obovoid, not constricted in middle, septum generally submedian resulting in upper cell being both wider and longer than lower cell, (8.8)10.1–[12.0]–13.9(15.6) 3 (2.7)3.7–[4.4]–5.8(6.4) lm, L/W ratio ¼ (2.0)2.2–[2.8]–3.5(4.5) (n¼164 from 5 specimens), wall and septum 0.5–0.7 lm thick; perispore thin and not easily seen, ca. 0.5 lm thick, collapsing in age, I– and K/I–. Anamorph not seen.

Etymology. The epithet ‘‘frostiicola’’ refers to the host lichen, Dirinaria frostii.

Ecology and distribution. Arthonia frostiicola is so far known only from thalli of Dirinaria frostii, a common species of sheltered and protected microhabitats on non-calcareous rock outcrops with a distribution that extends throughout temperate eastern North America southward across northern Mexico into Baja California Sur (Awasthi 1975; Harris & Ladd 2005; Kalb 2004; Tripp & Lendemer 2020; Fig. 2A herein). In contrast to the range of D. frostii, the new species is known from only four locations in the southern Appalachian and Ozark

Mountains of southeastern North America (Fig. 2B).

Given the conspicuous visibility of the infection caused by Arthonia frostiicola, namely large, darkened spots on the host thallus, the small number of known occurrences may reflect rarity of the lichenicolous fungus rather than collection bias and under detection. Indeed, the host is often locally abundant in sheltered siliceous rock overhangs and faces and widely distributed across a large area of North America and northern Mexico. Subsequent to our initial discoveries of A. frostiicola in 2010 and 2020, we searched both the holdings of D. frostii at NY and many populations of D. frostii in situ in the southern Appalachian Mountains. These attempts to locate additional occurrences of the new species led to the discovery of only two additional locations.

Discussion. Arthonia frostiicola is characterized by small, black, erumpent apothecia in the thallus of Dirinaria frostii. In the field it causes the host thallus to appear dirty or necrotic, and only close inspection reveals that the dark spots are actually erumpent apothecia of the lichenicolous fungus. While the apothecia may be difficult to see without a hand lens, the discoloration of the host is readily observed in the field with the naked eye and the coloration of infected thalli contrasts strongly with that of adjacent healthy thalli.

Compared to other foliose lichen genera, relatively few lichenicolous fungi have been reported from Dirinaria and we were only able to locate seven such taxa in the literature, none of which also occur on D. frostii. Buelliella dirinariae Diederich & Aptroot, described from D. picta (Sw.) Clem. & Shear, differs from A. frostiicola in producing marginate, red-brown apothecia (vs. emarginate black apothecia) (Aptroot et al. 1997). Plectocarpon dirinariae Ertz & van den Boom, described from D. applanata (F´ee) D.D.Awasthi, has hyaline, 3-septate ascospores (vs. 1-septate and turning brown in A. frostiicola) and its apothecia are immersed in stroma (the apothecia of A. frostiicola are scattered within typical host thalline tissue) (Ertz & van den Boom 2012). Stictographa dirinariicola Diederich & Ertz, also described from D. picta, forms irregular, black, erumpent apothecia that superficially resemble A. frostiicola, but the exciple is well-developed in S. dirinariicola (vs. essentially absent in A. frostiicola) (Diederich et al. 2017). Tephromela cerasina

(M¨ull.Arg.) Rambold & Triebel (” Nesolechia cerasina M¨ull.Arg.) produces black, marginate apothecia (vs. emarginate in A. frostiicola), has simple, hyaline ascospores (vs. 1-septate and turning brown in A. frostiicola) and has been reported from D. picta and D. confusa var. saxicola (R¨as¨anen) D.D.Awasthi (Hafellner et al. 2002; Rambold & Triebel 1992). Tremella dirinariae Diederich, Millanes & Wedin is a basidiomycete that forms black warts on thalli of D. aegialita (Afz.) B.J.Moore and has basidia instead of asci (Ariyawansa et al. 2015). Tremella purpurascentis Diederich, Common & Millanes is another basidiomycete, this one forming brown, resupinate patches on thalli of Dirinaria purpurascens (Vainio) B.J.Moore (Diederich et al. 2022b). Lastly, Xenonectriella dirinariae Etayo & van den Boom produces striking, erumpent, orange perithecia on an unidentified Dirinaria sp. (Etayo & van den Boom 2013).

Fifteen parasitic species of Arthonia have 1-septate ascospores which darken and become verruculose in age. Interestingly, all but A. cohabitans Coppins lack a K/Iþblue ring structure in the ascus, and most are reported to have a perispore (Frisch et al. 2014b; Grube & Matzer 1997; Grube et al. 1995; Kantvilas & Wedin 2015; Kondratyuk 1996; Lendemer et al. 2016; Wedin & Hafellner 1998). Four of these fifteen species differ from A. frostiicola in having Kþ purple pigments in the apothecia: A. cohabitans, A. destruens Rabenh., A. physidiicola Frisch & G.Thor and A. pseudocyphellariae Wedin (Frisch et al. 2014b; Grube et al. 1995). The rest have a brown pigment in the upper hymenium which either does not react or, like A. frostiicola, reacts Kþ olive or green (Brackel 2010; Coppins & Aptroot 2009; Grube & Matzer 1997; Kantvilas & Wedin 2015; Kondratyuk 1996; Lendemer et al. 2016; Wedin & Hafellner 1998). Five of the species that lack Kþ purple pigments differ from A. frostiicola in having been reported to have amyloid instead of hemiamyloid hymenia: A. badia Wedin & Hafellner, A. coriifoliae Wedin & Hafellner, A. flavicantis Wedin & Hafellner, A. plectocarpoides (S.Y.Kondr. & D.J.Galloway) Wedin & S.Y.Kondr. and A. punctella Nyl. All of those taxa except A. punctella occur on species of Pseudocyphellaria (Coppins & Aptroot 2009; Wedin & Hafellner 1998).

Of the six remaining species, Arthonia anjutae

S.Y.Kondr. & Alstrup induces galls in the host thallus (A. frostiicola only discolors the host) and parasitizes a different host genus, Teloschistes (Kondratyuk 1996). Arthonia coniocraeae Brackel and A. maculiformis Wedin & Hafellner both have a hyaline to pale brownish hypothecium (vs. dark brown in A. frostiicola). Additionally, A. coniocraea grows on Cladonia and has a taller hymenium (60–80 lm fide Brackel 2010 vs. 25–50 lm in A. frostiicola), while A. maculiformis grows on Pseudocyphellaria and has somewhat larger ascospores (13–16.535.0–6.5 lm fide Wedin & Hafellner (1998) vs. 10.1–13.9 3 3.7–5.8 lm in A. frostiicola). Arthonia colombiana Etayo has an orange hypothecium (vs. red-brown in A. frostiicola) and ascospores that turn gray in age (vs. brown in A. frostiicola) (Etayo 2002). Arthonia insularis Kantvilas & Wedin and A. japewiae Grube & Holien are very similar to A. frostiicola and, except for occurring on other host taxa, they have only slightly larger ascospores (12–17 35.0–8.5 lm in A. insularis and 10–1635.0–6.0 lm in A. japewiae, vs. 10.1–13.9 3 3.7–5.8 lm in A. frostiicola) (Grube & Matzer 1997; Kantvilas & Wedin 2015). Among all the lichenicolous Arthonia with 1-septate ascospores, A. stevensoniana R.C.Harris & Lendemer appears to be the most morphologically similar to the new species. It occurs on a very different host (Haematomma accolens) that is allopatric with the host of A. frostiicola and infects the hymenium of the apothecia rather than the thallus (Lendemer et al. 2016). A key to the lichenicolous Arthonia reported from host lichens classified in the Caliciales, the order to which Dirinaria belongs, is provided in the keys section at the end of this paper.

Additional specimens examined (all on Dirinaria frostii). U.S.A. Arkansas: Perry Co., Ouachita National Forest, vicinity of Goat Bluff along N side of South Fourche LaFave River, E of AR7, ca. 1.2 mi NE of Hollis, on sandstone, 6 Oct. 2010, J.C. Lendemer et al. 26084 (NY). North Carolina: Haywood Co., Pisgah National Forest, Dicks Trail, ridge and outcrops above mouth of Cataloochee Creek, on quartzite on ground in cave mouth, 21 Mar. 2021, J.P. Hollinger 25445a (NY); Swain Co., Great Smoky Mountains National Park, Twentymile Creek, ca. 1 km E of jct. of Twentymile and Wolf Ridge Trails, above trail, on shaded siliceous outcrop, 10 May 2022, J.P. Hollinger 27009 (NY). Tennessee: Blount Co., same location as the type, on siliceous rock overhang, 10 Dec. 2020, J.P. Hollinger et al. 24445a (NY).

Arthonia galligena Hollinger, Lendemer & P.A.Scott, sp. nov. Fig. 3

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Similar to Arthonia agelastica R.C.Harris & Lendemer in occurring on species of the Lecanora subfusca group, having clustered apothecia immersed in the host thallus, a hemiamyloid hymenium and 2-septate, macrocephalic ascospores that turn brown and verruculose in age, but differing in host (L. masana Lendemer & R.C.Harris and L. rugosella Zahlbr. vs. L. louisianae de Lesd. in A. agelastica), in inducing galls in the host (vs. not inducing galls in A. agelastica), and producing smaller ascospores (9.6–13.1 3 4.7–6.4 lm vs. 13.0–16.7 3 5.2–7.5 lm in A. agelastica).

Type: U.S.A. Tennessee: Sevier Co., Great Smoky Mountains National Park, Mount LeConte, Nfacing slopes above Trillium Gap Trail, 0.4 mi N of jct w/ Rainbow Falls Trail/Boulevard Trail at LeConte Lodge, 35839031.700N 83826016.400W, 1923 m, 24 Oct. 2018, on Lecanora masana (thallus and apothecia) on Sorbus americana branch, J.C. Lendemer 57121 (NY!, holotype).

Description. Habit lichenicolous, pathogenic, inducing formation of galls in host thallus, and sometimes completely taking over and blackening host apothecia. Vegetative hyphae penetrating the host thallus and apothecia, Iþ red and K/Iþ violet contrasting sharply with nonamyloid tissue of the host. Apothecia dispersed, or more commonly strongly aggregated and then inducing the formation of wart-like galls; individual apothecia immersed in the thallus and apothecia of the host; disk flat, flush with the surface of the host, black, epruinose, rounded, (0.04)0.05–[0.09]–0.14(0.16) mm in diam. (n¼114 from 5 specimens); epihymenium red-brown, Kþ olive-brown, Nþ bright orange-brown, POL–; hymenium hyaline, not inspersed with oil or crystals, Iþred, K/Iþblue, 40–60 lm high; hypothecium brownish in places, same pigment as epihymenium, Iþ red, K/Iþ blue, POL–, 15–25 lm thick; paraphyses abundant, branched and anastomosing, irregularly 1–3 lm thick, upper parts brown-walled and sometimes granular, tips swollen to 2.5–5.5 lm; asci 8-spored, broadly clavate, tip thick, lacking a K/Iþ blue ring structure, endoascus Iþ red and K/Iþ red, (26)30–[36]–43(49) 3(13)14–[18]–23(23) lm (n¼36 from 6 specimens); ascospores hyaline, turning brown and verruculose in age, obovoid, ends broadly rounded, 2-septate (rarely 1 or 3) becoming constricted at septa, upper cell the widest and longest, middle cell the shortest, and lower cell the narrowest, (8.5)9.6–[11.4]–13.1(14.3) 3 (3.6)4.7–[5.4]–6.4(6.8) lm, L/W ratio (1.7)1.8–[2.1]–2.5(2.9) (n¼213 from 7 specimens), walls and septa 0.5–1.0 lm thick; perispore present while spores hyaline, 1.0–1.5 lm thick, K/Iþ faintly bluish. Pycnidia immersed in gall between apothecia, globose, 30 lm in diam. (only seen once in Lendemer 57121); conidia hyaline, ellipsoid-oblong, 3.4–3.8 3 1.4–1.6 lm.

Etymology. The epithet ‘‘galligena’’ refers to the characteristic wart-like galls this species induces in the thallus of its host.

Ecology and distribution. The new species appears to be endemic to the southern Appalachian Mountains of eastern North America where it has only been found on two host lichen species (Lecanora masana and L. rugosella) that are restricted to high elevation habitats (Fig. 4C). Lecanora masana is narrowly endemic to the high elevations of the southern Appalachians where it grows in a wide array of habitat types ranging from northern hardwood forests to shrub balds and spruce-fir forests (Lendemer et al. 2013; Tripp & Lendemer 2020; Fig. 4B). It has been assessed as Vulnerable for the IUCN Red List in light of the threats to high elevation southern Appalachian ecosystems (Allen & Lendemer 2016; Allen et al. 2021). Lecanora rugosella was originally described from Europe and the European population is currently treated as conspecific with L. charlotera Nyl. (Mal´ıˇcek 2014). However, the North American population treated as L. rugosella by Brodo (1984) may represent a distinct species from L. charlotera (see Brodo 1984: 155) and is widespread in the Appalachian Mountains and Great Lakes regions of eastern North America (Brodo 1984; Tripp & Lendemer 2020). In the southern Appalachians it is common throughout high elevation habitats, much like L. masana, and it occurs in similar habitats northward into the central Appalachians and mountain ranges of New England (Lendemer unpublished data; Fig. 4A). As is the case with many members of high elevation Appalachian lichen communities, L. rugosella is also common in lower elevation forests throughout New England and the Canadian Maritime Provinces, especially in coastal habitats and the Great Lakes region (Dey 1976, 1984; Tripp & Lendemer 2019). Both L. masana and L. rugosella occur on a wide array of woody substrates, including the branches and boles of both conifers and hardwoods, subcanopy shrubs or trees (especially Ilex montana) and ericaceous shrubs (especially Gaylussacia, Rhododendron and Vaccinium) (Tripp & Lendemer 2020; Lendemer unpublished data).

Given the frequency and abundance of both host species in the southern Appalachians, and the widespread distribution of Lecanora rugosella outside of that region (Fig. 4A), it seems odd that the new species would occur in only a subset of the combined range of the two host species. It is unlikely that this Arthonia, which is so readily visible in the field, has been overlooked in the broad range of Lecanora rugosella given that lichenicolous Arthonia have received much attention in recent decades (e.g, Etayo 2002, 2017; Fleischhacker et al. 2016; Frisch & Holien 2018; Grube et al. 1995; Hafellner 2018; Kantvilas & Wedin 2015), that there have been intensive, albeit sporadic, studies of lichenicolous fungi in northeastern North America where L. rugosella is common (e.g., Driscoll et al. 2016; Seaward et al. 2017). The situation may be similar to that of Capronia harrisiana Hollinger & Lendemer, another apparent southern Appalachian endemic lichenicolous fungus that occurs on the otherwise widely distributed foliose lichen Crocodia aurata (Ach.) Link (Hollinger & Lendemer 2021).

On the other hand, it is also plausible that the primary host of A. galligena is L. masana, and that careful searching will discover A. galligena to be found throughout this limited range of the host, and that it is only within this small area that A. galligena is also able to grow on the closely related L. rugosella. Alternatively, A. galligena might grow equally well on both hosts, but be limited by the same factors that have resulted in the narrow distribution of L. masana. Since A. galligena has been found only in relatively mature, little-disturbed forest stands located within large tracts of intact natural habitat, we hypothesize that the species may be tied to high habitat quality and prolonged continuity of the natural landscape.

Discussion. This species is readily recognizable in the field by its distinctively clustered, black apothecia which are immersed in small wart-like galls in the host thallus, often additionally blackening the apothecia of the host. At least a dozen species of Arthonia are known to grow on hosts in Lecanora or related genera (Diederich et al. 2018) and a key to these is provided at the end of this paper. Of these, A. agelastica is closest to the new species in that it has 2-septate, macrocephalic ascospores which become brown and verruculose with age. Arthonia agelastica grows on L. louisianae, which like L. masana and L. rugosella, is a member of the Lecanora subfusca group (see Brodo 1984; Zhao et al. 2016). However, A. agelastica does not induce the formation of galls in the thallus of its host and has larger ascospores (13.0–16.7 3 5.2–7.5 lm fide Lendemer et al. (2016), vs. 9.6–13.1 3 4.7–6.4 lm in A. galligena). The host species of A. galligena are also entirely allopatric with that of A. agelastica (Figs. 4A, B vs. Fig. 5A), as L. louisianae is widespread in the Coastal Plain of southeastern North America with a distribution that extends into the low elevations of the Southern Appalachians while L. masana and L. rugosella are restricted to middle and high elevations of the Appalachians in southeastern North America (Allen & Lendemer 2016; Brodo 1984; Lendemer & Noell 2018; Lendemer et al. 2013, 2016). In both cases the lichenicolous fungus is known from only a narrow subset of sites from where the host occurs, this despite extensive searching of existing herbarium vouchers of the host species (see Lendemer et al. 2016; compare Figs. 4 and 5 herein).

Other species of Arthonia that occur on species of Lecanora s.l. differ from A. galligena in one of two primary ways. One set of species differs in having 1-septate, persistently hyaline ascospores: the A. apotheciorum-lecanorina group, A. caerulescens (Almq.) R.Sant., A. clemens (Tul.) Th.Fr., A. glacialis Alstrup & E.S.Hansen, A. oligospora Vˇezda and A. sherparum Grube & Matzer (Alstrup & Hansen 2001; Brackel 2015; Candan & Halıcı 2008; Coppins & Aptroot 2009; Darmostuk 2018; Foucard 2001; Grube 2007; Grube & Matzer 1997; Ihlen & Wedin 2008). The other set of species has 2–3-septate ascospores, but these differ from the ascospores of

A. galligena in having equally sized cells (i.e., isolocular) rather than the uppermost cell enlarged (i.e., macrocephalic): A. lecanoricola Alstrup & Olech, A. protoparmeliopsidis[1] Etayo & Diederich, A. subfuscicola (Linds.) Triebel and A. varians (Davies) Nyl. (Etayo & Diederich 2009; Foucard 2001; Grube 2007).

In addition to the species listed above, approximately 40 lichenicolous Arthonia have multi-septate ascospores, but only eleven of these have 2-septate, macrocephalic ascospores that turn brown and verruculose in age. Distinguishing characteristics of one of these eleven species, A. agelastica are presented above. The other ten species can easily be separated from A. galligena as follows: Arthonia amandineicola van den Boom & Ertz, A. polia Etayo & R.Sant. and A. tetraspora S.Y.Kondr. & K¨arnefelt have 4-spored asci, do not induce the formation of galls in the host thallus, and occur on unrelated genera (A. amandineicola on Amandinea efflorescens (M¨ull.Arg.) Marbach, A. polia on Diploicia canescens (Dickson) A.Massal. and A. tetraspora on Caloplaca chilensis S.Y.Kondr., K¨arnefelt, Fr¨od´en & Arup) (Etayo 2010; K¨arnefelt et al. 2002; van den Boom et al. 2017). While A. arthoniicola Diederich & Aptroot, A. graphidicola Coppins, A. ingaderiae Follmann and A. prominens Follmann all have 8-spored asci, they have longer ascospores (average length _15 lm), do not induce galls, and occur on different hosts (A. catenulata Nyl., Graphis scripta (L.) Ach., Ingaderia spp., and Pentagenella gracillima (Kremp.) Ertz & Tehler, respectively) (Aptroot et al. 1995; Coppins 1989; Follmann & Werner 2003). Arthonia invadens Coppins and A. subgraphidicola Ertz, Common & Diederich both have 8-spored asci and similarly sized ascospores to A. galligena, however they differ in not inducing galls, having an amyloid hymenium (Iþ persistently blue instead of rapidly turning red as in A. galligena) and a minute K/Iþblue ring structure in the ascus (lacking in A. galligena), and in occurring on unrelated hosts (Schismatomma and Graphis, respectively) (Coppins 1989; Diederich et al. 2019). Lastly, A. brussei Egea & Torrente has very similar ascospores to A. galligena, but differs in not inducing galls in the host, producing much larger ascomata (0.2–0.7 mm in diam. vs. 0.05–0.14 mm) and occurring on an unrelated host genus, Lecanographa (Egea & Torrente 1996).

Not surprisingly, there are many (ca. 100) species of lichenicolous fungi outside of Arthonia which have been reported on hosts in Lecanora and related genera (Diederich et al. 2018). Many are generalist parasites which are also known from other, often unrelated, genera (e.g., Epithamnolia xanthoriae (Brackel) Diederich & Suija, Lichenoconium lecanorae (Jaap) D.Hawksw., Lichenodiplis lecanorae (Vouaux) Dyko & D.Hawksw. and Muellerella lichenicola (Sommerf.) D.Hawksw.; Diederich et al. 2018). Most, however, are restricted to one or more species within a single ''group'' of Lecanora species, and a few groups stand out as having particularly diverse lichenicolous species—the L. subfusca group has the most (14 species), followed by the L. dispersa and L. rupicola groups (eight species each) and the L. polytropa group (five species) (Diederich et al. 2018). However, none of these species shares the characteristics of A. galligena, namely the apothecioid ascomata without seta, 8-spored asci and 2-septate, macrocephalic ascospores which turn verruculose and brown in age. The closest is Opegrapha lamyi (Nyl.) Triebel, reported from various corticolous Lecanora, however it has much longer (16.5–20.035.5–7.0 lm vs. 9.6–13.1 3 4.7–6.4 lm in A. galligena), 3-septate ascospores (vs. 2-septate in A. galligena) (Ertz et al. 2021).

The color of the region below the hymenium—called ''subhymenium'' by some authors (e.g., Grube 2007), ''hypothecium'' by others (e.g., Lendemer et al. 2016), and ''hypothecioid layer'' by yet others (e.g., Follmann & Werner 2003)—has been used as a taxonomic character in Arthonia. However, in some cases, such as A. galligena, it can be variable, often within a single specimen or even a single apothecium, with some areas hyaline and others pale to dark brown. This variability initially led us to believe that A. galligena consisted of two species, each specific to one of the two host Lecanora species. However, we came to realize this was not the case after further study of the material led to the discovery of apothecia with variably colored hypothecia on both host species. Our observations suggest that in species with this kind of variable pigmentation, the hypothecium may darken with age or perhaps because of interaction with the host. In addition to the hypothecial pigment produced by the parasite, specimens of A. galligena often have additional brown pigmented areas below the hypothecium which are apparently produced by the host. That this pigment is not produced by the Arthonia is supported by the fact that the hyphae are not amyloid and the pigment is K– whereas the reproductive and vegetative hyphae of the parasite are strongly amyloid or hemiamyloid and the pigment produced by the parasite is Kþ olive (Fig. 3H).

Another morphological character that has been widely used to distinguish species of Arthonia involves whether the ascospores turn grayish or brownish with age (Grube & Matzer 1997). Some authors have described the stage at which ascospores turn color variously as ''old'' (e.g., Grube 2007), ''mature'' (e.g., Aptroot et al. 1997) or ''postmature'' (e.g., Diederich et al. 2019). When the change in pigmentation is accompanied by distorted shape, enlargement or collapse, it may indeed be appropriate to consider them postmature, comparable to the usage of the term in Pyrenula (e.g., Harris 1989, 1995). In some other groups such as Diploschistes (Lumbsch et al. 1997), Trypetheliaceae (Sweetwood et al. 2012) and Rinodina (Mayrhofer et al. 2001), the color shift occurs during development before the ascospores fully mature. In A. galligena, the ascospores turn brown and lose their perispore near the end of their development, often while still in the ascus, and do not appear to be deformed. In A. frostiicola, on the other hand, most pigmented ascospores were deformed, hence should probably be considered postmature. Therefore, we excluded pigmented ascospores from our measurements for A. frostiicola but not A. galligena.

Based on our review of the literature, differences in interpretation of the color of the hypothecium and ascospores may have contributed to confusion among several species of lichenicolous Arthonia which occur on Lecanora s.l. One group, comprising A. apotheciorum, A. galactinaria, A. lecanorina and A. subvarians, is badly in need of critical revision and delimitations vary between authors. For example, these names have been applied to material from host taxa belonging to different groups of Lecanora s.l. which are now regarded as corresponding to different genera (Zhao et al. 2016); however, opinions differ as to which names apply to material on each host genus, something which presents an issue in a group of fungi considered to be highly host specific.

First, consider Arthonia apotheciorum and A. lecanorina. Most authors treat A. apotheciorum as occurring on Myriolecis albescens (” L. albescens (Hoffm.) Flörke, a member of the L. dispersa group; Zhao et al. 2016) and A. lecanorina as occurring on Lecanora albella (a member of the L. subcarnea group; Zhao et al. 2016) and distinguish them by hypothecium color (paler in A. apotheciorum, darker in A. lecanorina; e.g., Foucard 2001; Ihlen & Wedin 2008; Nimis 2022). Zhurbenko & Brackel (2013) reported A. apotheciorum from Svalbard on L. polytropa (a member of the L. polytropa group; Zhao et al. 2016), while Darmostuk (2018) used the name A. subvarians for Ukrainian material on L. polytropa, however the latter gave much smaller ascospore measurements than the former. Grube (2007) applied A. apotheciorum to material on L. varia (a member of the L. varia group; Zhao et al. 2016) and A. lecanorina to material on the L. dispersa group, distinguishing the two species by the presence of thick-walled ascogenous hyphae in A. apotheciorum.

The status of Arthonia galactinaria is similarly unclear at present. Foucard (2001) distinguished it from A. apotheciorum by host: A. apotheciorum on Myriolecis albescens and A. galactinaria on M. semipallida (as L. flotowiana). Ihlen & Wedin (2008) did the same but considered A. galactinaria to occur on M. dispersa instead of M. semipallida, and included additional subtle differences in ascospore size, epihymenium and hypothecium color. Nimis (2022) also distinguished the two by host: A. apotheciorum on M. albescens and A. galactinaria on various other Myriolecis species. The ascospores of A. galactinaria have also been reported to turn subhyaline (Brackel 2015) or brownish (Foucard 2001), the latter apparently agreeing with the protologue (Kocourková 2000). Hafellner (2018) and Diederich et al. (2018) tentatively synonymized A. apotheciorum, A. galactinaria and A. subvarians.

Another pair of species in need of revision is Arthonia glaucomaria and A. varians, both growing on the Lecanora rupicola group. Arthonia glaucomaria was described as having a brown hypothecium and (red)brown ascospores by Foucard (2001) while A. varians was reported to have a hyaline hypothecium and hyaline ascospores by Grube (2007). Grube (2007) listed A. glaucomaria as a synonym of A. varians but Diederich et al. (2018) did not accept this synonymy.

Additional specimens examined. U.S.A. NORTH CAROLINA: Haywood Co., Pisgah National Forest, Balsam Mountains, Middle Prong Wilderness, Eslopes of Fork Ridge, ~0.5 mi N of jct of Green Mountain Trail & Mountains to Sea Trail, ~0.3 mi S of Green Knob, on Lecanora rugosella on Rhododendron catawbiense, 26 Jun. 2019, J.C. Lendemer et al. 60717 (NY), on L. rugosella on Picea, J.C. Lendemer et al. 60744 (NY); Swain Co., Great Smoky Mountains National Park, Mount Sequoyah, on L. masana on Betula alleghaniensis, 5 Oct. 2022, P.A. Scott 8399 & J.P. Hollinger (NY) , on L. masana on Prunus pennsylvanica, J.P. Hollinger 27411 & P.A. Scott (NY), on L. masana on Viburnum lantanoides, P.A. Scott 8406a & J.P. Hollinger (NY), J.P. Hollinger 27414 & P.A. Scott (NY); Watauga Co., Grandfather Mountain State Park, Grandfather Mountain, S slopes of Calloway Peak, on Lecanora masana on Sorbus, 13 Jul. 2020, J.C. Lendemer et al. 66625 (NY). TENNESSEE: Sevier Co., Great Smoky Mountains National Park, Mount Guyot, on Lecanora rugosella on Vaccinium, 6 Oct. 2022, J.P. Hollinger 27433 & P.A. Scott (NY).

DISCUSSION

Climatic factors have been implicated as main drivers of species richness and biodiversity patterns for macroscopic organisms such as vascular plants and vertebrates (Currie 1991; Gaston 2000; Hawkins et al. 2003; Jetz & Fine 2012; McCain 2007). Biotic factors, or interactions between organisms, have long also been thought to be major drivers of these patterns, but are little studied due to the intractability of studying the large number of possible interactions across an entire system (Maynard et al. 2017; McCain & Grytnes 2010; Schemske et al. 2009). As obligate symbioses, lichens are a highly diverse and ecologically important group of evolutionary cohorts whose diversity and distributions appear to be strongly driven by a combination of biotic factors that are both internal (e.g., physiological constraints and environmental specificity of the photobionts; e.g., Dal Grande et al. 2018; Haughiana et al. 2019; Hurtado et al. 2020; Jüriado et al. 2019; Leavitt et al. 2013; McCune et al. 2022; Medeiros et al. 2021; Ortiz-Álvarez et al. 2015) and external (e.g., overall woody plant species richness, as well as specific chemical and structural characteristics of phorophytes for epiphytic lichens; Barkman 1958; Ca´ceres et al. 2007; Esseen 1981; Loppi & Frati 2004; McDonald et al. 2017; Rose 1976; Watson et al. 1988; Wigle et al. 2021). While lichen biodiversity drivers are the subject of increasing study, the factors that underpin patterns of species richness, abundance and community assembly in the fungi that parasitize lichens remain largely unknown. This is despite a call for study and presentation of an explicit hypothesis driven framework two decades ago (Lawrey & Diederich 2003). Presumably this is due in large part to insufficient large-scale, systematically gathered, primary occurrence data that can be linked to hosts, phorophytes and ecological variables collected both in the field and extrapolated from GIS data (see e.g., Lendemer 2021; Lendemer et al. 2019).

Studies across other host-parasite systems have strongly implicated biotic interactions as major drivers of parasite diversity and distribution (Arneberg 2002; Poulin 2004; Press & Phoenix 2005; Schwelm et al. 2021; Thieltges et al. 2008), which is logical for organisms that require living hosts to complete at least some, if not all, stages of their life cycles. However, rather than being strictly uniform, the correlation between occurrence, abundance and diversity of hosts, and that of their corresponding parasites, often reflects an interplay of multiple abiotic and biotic factors (Aalto et al. 2015; Budria 2017; Dallas et al. 2020; McNew et al. 2021; Poulin & Mouritsen 2003). This is almost certainly the case for lichenicolous fungi, although it has yet to be empirically tested.

Among lichenicolous fungi there are four primary gradients along which a given species can be placed: degree of host specificity, degree of concordance between host and parasite distribution, degree of concordance between host and parasite frequency, and degree of concordance between host and parasite abundance. Quantitative placement of a broad sampling of lichenicolous fungi along each of these gradients requires high quality, granular occurrence data across small and large spatial scales for both the parasites and their lichen hosts. Assembly of such a dataset could facilitate transformative insights into the biology of these organisms, particularly if placed in an evolutionary context.

The new species described here illustrate how intensive and geographically broad study of both lichenicolous fungi and their hosts informs development of questions about what drives their patterns of species richness and community assembly. Arthonia frostiicola is a rare species whose range appears to be highly restricted to a subset of locations within the much larger range of the host Dirinaria frostii, a lichen that itself is restricted to a relatively narrow set of saxicolous microhabitats. In contrast, A. galligena occurs on two closely related hosts: Lecanora masana which is frequent and abundant but geographically restricted to high elevation southern Appalachian Mountain ecosystems, and L. rugosella which is frequent and abundant in the same habitats but also has a distribution that extends much further northward into northeastern North America and the Great Lakes. What accounts for the fact that both new species appear to be geographically restricted, infrequent and less abundant than their hosts, regardless of the frequency and abundance of the hosts themselves? The answers to this and other questions are critical to effective conservation of lichenicolous fungi, a topic which has been generally neglected for parasitic organisms until recently, despite their ecological importance (e.g., Dougherty et al. 2016; Dunn et al. 2009). We assert that concerted and systematic study of lichenicolous fungi, nested within frameworks of existing largescale studies of lichen biodiversity is urgently needed.

KEYS

The following keys were compiled from the literature, primarily emphasizing ascospore characters. Size ranges are the typical ranges given by the cited sources, not the extreme ranges. Additional information not required for complementarity in a couplet, such as host preference, is included in square brackets. Sources used for each taxon are cited after the name at each terminal node. A spreadsheet summarizing the main taxonomic characters reported for all known lichenicolous Arthonia is included in the Supplementary Table S1.

KEY TO SPECIES OF ARTHONIA PARASITIC ON CALICIALES

1. Ascospores turning brown and often verruculose in age 2

1. Ascospores remaining hyaline and smooth [all with Iþ red hymenium].. 9

2. Ascospores 1–2-septate 3

2. Ascospores 1-septate.. 4

3. Hymenium Iþ blue; hypothecium dark; ascospores 2-septate, macrocephalic, verruculose, 13–16 3 5.5–7.0 lm; on Diploicia canescens .... Arthonia polia Etayo & R.Sant. (Etayo 2010)

3. Hymenium Iþ red; hypothecium pale; ascospores 1–2-septate, macrocephalic, verruculose, 11–14 3 4–5 lm; on Amandinea efflorescens.. .... Arthonia amandineicola van den Boom & Ertz (van den Boom et al. 2017)

4. Hymenium with yellowish, Kþ purple pigment [hymenium Iþ blue; ascospores verruculose, 10.5–17.0 3 5–7 lm; on Physcia spp.] .... Arthonia destruens Rabenh. var. destruens (Brackel 2015; Grube et al. 1995)

4. Hymenium without yellowish pigment, K– or Kþ greenish 5

5. Ascospores becoming verruculose in age....................................... 6

5. Ascospores remaining smooth 7

6. Hymenium Iþred; ascospores 10–1433.5–6.0 lm; on Dirinaria frostii .... Arthonia frostiicola Hollinger & Lendemer (this paper)

6. Hymenium Iþ blue; ascospores 12–17 3 5.0–6.5 lm; on Diplotomma spp.. .... Arthonia punctella Nyl. (Coppins & Aptroot 2009; Etayo 2002; Nimis 2022)

7. Ascospores 17–21 3 6–8 lm [hymenium Iþ red, hypothecium hyaline, on Heterodermia] .... Arthonia heterodermiae Etayo (Etayo 2017)

7. Ascospores 9–13 3 3.5–5.5 lm... 8

8. Hymenium I–; ascospores 10–13 3 4.5–5.5 lm; on Rinodina oleae... .... Arthonia rinodinicola Candan & Halıcı (Candan & Halıcı 2009)

8. Hymenium Iþ blue or red; ascospores 9–11 3 3.5–4.0 lm; on Amandinea punctata... .... Arthonia vorsoeensis Alstrup (Alstrup 1993; Alstrup et al. 2004)

9. On hosts in the Physciaceae, all foliose lichens (except Diploicia) 10

9. On hosts in the Caliciaceae, all crustose lichens.......................... 14

10. Asci 4-spored [ascospores 8–13 3 3.5–5.0 lm; on Diploicia canescens] .... Arthonia diploiciae Calat. & Diederich (Calatayud et al. 1995; Grube 2007; Nimis 2022)

10. Asci 8-spored 11

11. Inducing formation of dark, tuberculate galls in host that resemble the stromatic ascomata of Plectocarpon [hypothecium pale; ascospores 10–12 3 3.0–4.0 lm; on Heterodermia spp.] .... Arthonia tremelloides Etayo (Etayo 2002; Grube 2007)

11. Not inducing formation of galls in host...................................... 12

12. Ascospores narrow, 11–12 3 2.5–2.8 lm [hypothecium pale; on Heterodermia leucomela] .... Arthonia leucomelodis F. Berger & E. Zimm. (Berger & Zimmermann 2016)

12. Ascospores .3.0 lm wide... 13

13. Ascomata erumpent; hypothecium pale; ascospores 12–1434–6 lm; on Phaeophyscia spp... .... Arthonia phaeophysciae Grube & Matzer (Grube 2007; Nimis 2022)

13. Ascomata superficial; hypothecium dark; ascospores 9–1433.5–5.0 lm; on Physcia spp.. .... Arthonia epiphysciae Nyl. (Grube 2007; Nimis 2022)

14. Ascospores .15 lm long 15

14. Ascospores ,14 lm long 16

15. Ascospores 15–18 3 5.5–7.0 lm; on Amandinea petermannii .... Arthonia rakusae Alstrup & Olech (Alstrup et al. 2018)

15. Ascospores 16–21 3 9.0–11.0 lm; on Diplotomma hedenii.......... ..... Arthonia rubescens (Arnold) Clauzade, Diederich & Cl.Roux, comb. inval., ” Conida rubescens Arnold (Clauzade et al. 1989; Nimis 2022)

16. Ascomata reaching over 0.4 mm in diam 17

16. Ascomata 0.1–0.4 mm in diam... 18

17. Northern hemisphere [ascospores 9.0–13.0 3 3.5–4.5 lm; on Amandinea punctata] ....

.... Arthonia epimela (Almq.) Minks (Alstrup 1993; Clauzade
et al. 1989; Kantvilas & Wedin 2015)
17. Southern hemisphere [ascospores 9.5–14.0 3 3.5–5.0 lm; on
Amandinea and Buellia spp.] ....
.... Arthonia subantarctica Øvstedal (Alstrup 2002)
18. Epihymenium K–; hymenium hyaline, 50–65 lm high; ascospores
11.5–14.0 3 4.0–5.5 lm; on Dimelaena spp.......................
.... Arthonia hawksworthii Halıcı (Halıcı 2008)
18. Epihymenium Kþgreen; hymenium diffusely olive-brown, 30–55
lm high; ascospores 10–1334.0–5.0 lm; on Calicium tricolor...
.... Arthonia calicii Kantvilas & Wedin (Kantvilas & Wedin 2015)

KEY TO SPECIES OF ARTHONIA PARASITIC ON LECANORACEAE

1. Ascospores 1-septate... 2
1. Ascospores 2–3-septate [all with Iþ red hymenium] 9
2. Asci 4-spored [epihymenium and hypothecium dark brown, K–;
hymenium Iþ red; ascospores 10–16 3 5–7 lm; on Myriolecis
spp.] ....
.... Arthonia oligospora Vˇezda (Candan & Halıcı 2008; Hora´kova´
1994; Nimis 2022)
2. Asci 8-spored 3
3. Epihymenium blue-green; hymenium Iþ blue [hypothecium pale;
ascospores 10–12 3 4–6 lm; on Lecanora varia] ....
.... Arthonia caerulescens (Almq.) Arnold (Foucard 2001;
Nimis 2022)
3. Epihymenium brown to olive-brown; hymenium Iþ red 4
4. On apothecia and occasionally thallus of Rhizoplaca spp............. 5
4. On apothecia or thallus of species of Lecanora or Myriolecis 6
5. Apothecia 6plane; hypothecium hyaline; ascospores 10–14 3 4–7
lm........................... Arthonia clemens (Tul.) Th.Fr. (Grube 2007)
5. Apothecia convex; hypothecium brownish; ascospores 11–1334.5–
5.5 lm..
.... Arthonia glacialis Alstrup & E.S.Hansen (Alstrup &
Hansen 2001)
6. Hypothecium hyaline to pale brown... 7
6. Hypothecium medium to dark brown.. 8
7. Ascospores 11–15 3 4–6 lm; on Myriolecis albescens ....
.... Arthonia apotheciorum (A. Massal.) Almq. (Coppins &
Aptroot 2009; Nimis 2022)
7. Ascospores 9–13 3 4–5 lm; on Myriolecis spp.................................
.... Arthonia galactinaria Leight., (Brackel 2015; Grube &
Matzer 1997; Ihlen & Wedin 2008; Nimis 2022)
8. On Lecanora albella; ascospores 9–14 3 4–6 lm..............................
.... Arthonia lecanorina (Almq.) R.Sant. (Foucard 2001; Grube
2007; Grube & Matzer 1997; Ihlen & Wedin 2008)
8. On Lecanora polytropa; ascospores 8.5–10 3 3.5–4.5 lm.................
.... Arthonia subvarians Nyl. (Darmostuk 2018)
8. On Lecanora sherparum; ascospores 9–13 3 4–5 lm........................
.... Arthonia sherparum Grube & Matzer (Grube & Matzer 1997)
9. Ascospores macrocephalic, turning brown and verruculose in age
[ascospores 2-septate] 10
9. Ascospores isolocular, remaining hyaline and smooth in age (except
A. subfuscicola possibly turning pale brown) 11
10. Inducing formation of wart-like galls in the host thallus; ascospores
9.5–13.0 3 4.5–6.5 lm long; on Lecanora masana and ....
L. rugosella.................. Arthonia galligena Hollinger, Lendemer &
P.A. Scott (this paper)
10. Not inducing galls in the host thallus; ascospores 13.0–16.5 3 5.0–
7.5 lm long; on Lecanora louisianae..
.... Arthonia agelastica R.C. Harris & Lendemer (Lendemer et al.
2016)
11. Ascospores 10–14.5 lm long (average ,14 lm)......................... 12
11. Ascospores 13–20 lm long (average .15 lm)........................... 13
12. Paraphyses tips uniformly dark pigmented; ascospores 2–3-septate,
10–14.5 3 4.0–5.5 lm wide; on Protoparmeliopsis muralis...........
.... Arthonia protoparmeliopsidis Etayo & Diederich (Etayo &
Diederich 2009)
12. Paraphyses tips with conspicuous dark pigment caps; ascospores 2-

septate, 11–12.5 3 6.0–6.5 lm wide; on *Myriolecis populicola*..... *Arthonia lecanoricola* Alstrup & Olech (Etayo & Diederich 2009)

13. Ascomata nearly invisible, extremely reduced, producing only asci within host apothecia; ascospores 2–3-septate, 13–20 3 3.5–6.0 lm; on *Lecidella* spp .... *Arthonia intexta* Almq. (Triebel 1989)

13. Ascomata conspicuously visible as blackened spots overtaking host apothecia; ascospores 2–3-septate, 13–1834–7 lm; on *Lecanora* spp.. 14

14. On corticolous species (*Lecanora albella*, *L. carpinea*, *L. chlarotera*) .... *Arthonia subfuscicola* (Linds.) Triebel (Coppins & Aptroot 2009; Foucard 2001; Grube 2007; Nimis 2022)

14. On saxicolous species (*Lecanora rupicola* group) .... *Arthonia varians* (Davies) Nyl. (¼? *A. glaucomaria* (Nyl.) Nyl.) (Foucard 2001; Grube 2007; Ihlen & Wedin 2008; Nimis 2022)

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LITERATURE CITED

Aalto, S. L., E. Decaestecker & K. Pulkkinen. 2015. A three-way perspective of stoichiometric changes on host-parasite interactions. Trends in Parasitology 31: 333–340. [doi:10.1016/j.pt.2015.04.005]

Allen, J. L. & J. C. Lendemer. 2016. Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. Biodiversity and Conservation 25(3): 555–568. [doi:10.1007/s10531-016-1071-4]

Allen, J. L., J. C. Lendemer & T. McMullin. 2021. *Lecanora masana*. The IUCN Red List of Threatened Species 2021: e.T80702914A80702917. [doi:10.2305/IUCN.UK.2021-2.RLTS.T80702914A80702917.en]

Alstrup, V. 1993. News on lichens and lichenicolous fungi from the Nordic countries. Graphis Scripta 5(2): 96–104.

Alstrup, V. 2002. Revisions of some lichens and lichenicolous fungi from Antarctica. Folia Cryptogamica Estonica 39: 1–2.

Alstrup, V. & E. S. Hansen. 2001. New lichens and lichenicolous fungi from Greenland. Graphis Scripta 12(2): 41–50.

Alstrup, V., M. Olech, P. Wietrzyk-Pełka & M. H. We¸ grzyn. 2018. The lichenicolous fungi of the South Shetland Islands, Antarctica: Species diversity and identification guide. Acta Societatis Botanicorum Poloniae 87(4): 3607. [doi:10.5586/asbp.3607]

Alstrup, V., S. Svane & U. Søchting. 2004. Additions to the lichen flora of Denmark VI. Graphis Scripta 15: 45–50.

Aptroot, A., P. Diederich, E. S´erusiaux & H. J. M. Sipman. 1995. Lichens and lichenicolous fungi of Laing Island (Papua New Guinea). Bibliotheca Lichenologica, No. 57, J. Cramer, Berlin-Stuttgart, pp. 19–48.

Aptroot, A., P. Diederich, E. S´erusiaux & H. J. M. Sipman. 1997. Lichens and Lichenicolous Fungi from New Guinea. Bibliotheca Lichenologica, No. 64, J. Cramer, Berlin-Stuttgart, 220 pp.

Ariyawansa, H. A., K. D. Hyde, S. C. Jayasiri, B. Buyck, K. W. T. Chethana, D. Q. Dai, Y. C. Dai, D. A. Daranagama, R. S. Jayawardena, R. L¨ucking, M. Ghobad-Nejhad, T. Niskanen, K. M. Thambugala, K. Voigt, R. L. Zhao, J.-J. Li, M. Doilom, S. Boonmee, Z. L. Yang, Q. Cai, Y. Y. Cui, A. H. Bahkali, J. Chen, B. K. Cui, J. J. Chen, M. C. Dayarathne, A. J. Dissanayake, A. H. Ekanayaka, A. Hashimoto, S. Hongsanan, E. B. G. Jones, E. Larsson, W. J. Q.-R, Li, J. K. Liu, Z. L. Luo, S. S. N. Maharachchikumbura, A. Mapook, E. H. C. McKenzie, C.

Norphanphoun, S. Konta, K. L. Pang, R. H. Perera, R. Phookamsak, C. Phukhamsakda, U. Pinruan, E. Randrianjohany, C. Singtripop, K. Tanaka, C. M. Tian, S. Tibpromma, M. A. Abdel-Wahab, D. N. Wanasinghe, N. N. Wijayawardene, J.-F. Zhang, H. Zhang, F. A. Abdel-Aziz, M. Wedin, M. Westberg, J. F. Ammirati, T. S. Bulgakov, D. X. Lima, T. M. Callaghan, P. Callac, C.-H. Chang, L. F. Coca, M. Dal-Forno, V. Dollhofer, K. Fliegerova´ , K. Greiner, G. W. Griffith, H.-M. Ho, V. Hofstetter, R. Jeewon, J. C. Kang, T.-C. Wen, P. M. Kirk, I. Kyt¨ovuori, J. D. Lawrey, J. Xing, H. Li, Z. Y. Liu, X. Z. Liu, K. Liimatainen, H. T. Lumbsch, M. Matsumura, B. Moncada, S. Nuankaew, S. Parnmen, A. L. C. M. de Azevedo SantiagoLi, S. Sommai, Y. Song, C. A. F. de Souza, C. M. de Souza-Motta, H. Y. Su, S. Suetrong, Y. Wang, S.-F. Wei, T. C. Wen, H. S. Yuan, L. W. Zhou, M. R´eblova´ , J. Fournier, E. Camporesi, J. J. Luangsa-ard, K. Tasanathai, A. Khonsanit, D. Thanakitpipattana, S. Somrithipol, P. Diederich, A. M. Millanes, R. S. Common, M. Stadler, J. Y. Yan, X. Li, H. W. Lee, T. T. T. Nguyen, H. B. Lee, E. Battistin, O. Marsico, A. Vizzini, J. Vila, E. Ercole, U. Eberhardt, G. Simonini, H.-A. Wen & X.-H. Chen. 2015. Fungal diversity notes 111–252 – taxonomic and phylogenetic contributions to fungal taxa. Fungal Diversity 75(1): 27–274. [doi:10.1007/s13225-015-0346-5]

Arneberg, P. 2002. Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. Ecography 25: 88–94. [doi:10.1034/j.1600-0587.2002.250110.x]

Awasthi, D. D. 1975. A Monograph of the Lichen Genus Dirinaria. Bibliotheca Lichenologica, No. 2, J. Cramer, Berlin-Stuttgart, 108 pp.

Barkman, J. J. 1958. Phytosociology and ecology of cryptogamic epiphytes including a taxonomic survey and a description of their vegetation units in Europe. Van Gorcum, Assen. xiii, 628 pp.

Berger, F. & E. Zimmermann. 2016. Addition to the lichen flora of Madeira with special focus on lichenicolous fungi. Herzogia 29(2): 235–276. [doi:10.13158/heia.29.2.2016.235]

Brackel, W. v. 2015. Lichenicolous fungi from Central Italy with notes on some remarkable hepaticolous, algicolous and lichenized fungi. Herzogia 28(1) 212–281. [doi:10.13158/heia.28.1.2015.212]

Brackel, W. v. 2010. Weitere Funde von flechtenbewohnenden Pilzen in Bayern – Beitrag zu einer Checkliste V. Berichte der Bayerischen Botanischen Gesellschaft 80: 5–32.

Brodo, I. M. 1984. The North American species of the Lecanora subfusca group. Pages 63–185. In: H. Hertel & F. Oberwinkler (eds.): Beitrage zur Lichenologie. Festscrift J. Poelt. Beiheft zur Nova Hedwigia 79. J. Cramer, Vaduz.

Budria, A. 2017. Beyond troubled waters: the influence of eutrophication on host-parasite interactions. Functional Ecology 31: 1348–1358. [doi:10.1111/1365-2435.12880]

Ca´ceres, M. E. S., R. L¨ucking & G. Rambold. 2007. Phorophyte specificity and environmental parameters versus stochasticity as determinants for species composition of corticolous crustose lichen communities in the Atlantic rain forest of northeastern Brazil. Mycological Progress 6(3): 117–136. [doi:0.1007/s11557-007-0532-2]

Calatayud, V., V. Atienza & E. Barreno. 1995. Lichenicolous fungi from the Iberian Peninsula and the Canary Islands. Mycotaxon 55: 363–382.

Candan, M. & M. Halıcı. 2008. Seven new records of lichenicolous fungi from Turkey. Mycotaxon 104: 241–246.

Candan, M. & M. Halıcı. 2009. Two new lichenicolous Arthonia species from Turkey. Mycotaxon 107: 209–213.

Clauzade, G., P. Diederich & C. Roux. 1989. Nelikenigˆintaj fungoj likenlogˆ aj: ilustrita determinlibro. Bulletin de la Soci ´et ´e linn´eenne de Provence, Num´ero sp´ecial 1: 1–142.

Coppins, B. J. & A. Aptroot. 2009. *Arthonia*. Pages 153–171. In: C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley (eds.). The Lichens of Great Britain and Ireland. The British Lichen Society, London.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. The American Naturalist 137: 27–49.

Dal Grande, F., G. Rolshausen, P. K. Divakar, A. Crespo, J. Otto, M. Schleuning & I. Schmitt. 2018. Environment and host identity structure communities of green algal symbionts in lichens. New Phytologist 217(1): 277–289. [doi:10.1111/nph.14770]

Dallas, T., L. A. Holian & G. Foster. 2020. What determines parasite species richness across host species? Journal of Animal Ecology 89: 1750–1753. [doi:10.1111/1365-2656.13276]

Darmostuk, V. V. 2018. The new records of lichenicolous fungi from Ukrainian Carpathians. Chornomorskiy Botanichniy Zhurnal 14(2): 173–179. [doi:10.14255/2308-9628/18.142/7]

Dey, J. P. 1976. Phytogeographic relationships of the fruticose and foliose lichens of the southern Appalachian Mountains. Pages 398–416. In: B. C. Parker & M. K. Roane (eds.). The Distributional History of the Biota of the Southern Appalachians. Part IV. Algae and Fungi. Biogeography, Systematics, and Ecology. University of Virginia Press, Charlottesville.

Dey, J. P. 1978. Fruticose and foliose lichens of the high-mountain areas of the southern Appalachians. The Bryologist 81: 1–93.

Dey, J. P. 1984. Lichens of the southern Appalachian mountain spruce-fir zone and some unanswered ecological questions. Pages 139–150. In: P. S. White (ed.), The Southern Appalachian Spruce-Fir Ecosystem: Its Biology and Threats. Research/Resources Management Report SER-71. U.S. Department of the Interior, National Park Service.

Diederich, P. 1996. The lichenicolous heterobasidiomycetes. Bibliotheca Lichenologica, No. 61, J. Cramer, Berlin-Stuttgart, 198 pp.

Diederich, P., R. S. Common, U. Braun, B. Heuchert, A. Millanes, A. Suija & D. Ertz. 2019. Lichenicolous fungi from Florida growing on Graphidales. Plant and Fungal Systematics 64(2): 249–282. [doi:10.2478/pfs-2019-0021]

Diederich, P., J. D. Lawrey & D. Ertz. 2018. The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. The Bryologist 121(3): 340–425. [doi:10.1639/0007-2745-121.3.340]

Diederich, P., R. L¨ucking, A. Aptroot, H. J. M. Sipman, U. Braun, T. Ahti & D. Ertz. 2017. New species and new records of lichens and lichenicolous fungi from the Seychelles. Herzogia 30(1): 182–236. [doi:10.13158/heia.30.1.2017.182]

Diederich, P., A. M. Millanes, J. Etayo, P. P. G. van den Boom & M. Wedin. 2022a. Finding the needle in the haystack: A revision of *Crittendenia*, a surprisingly diverse lichenicolous genus of Agaricostilbomycetes, Pucciniomycotina. The Bryologist 125(2): 248–293.

Diederich, P., A. M. Millanes, M. Wedin & J. D. Lawrey. 2022b. Flora of Lichenicolous Fungi, Volume 1, Basidiomycota. National Museum of Natural History, Luxembourg. 351 pp.

Dougherty, E. R., C. J. Carlson, V. M. Bueno, K. R. Burgio, C. A. Cizauskas, C. F. Clements, D. P. Seidel & N. C. Harris. 2016. Paradigms for parasite conservation. Conservation Biology 30(4): 724–733. [doi:10.1111/cobi.12634]

Driscoll, K. E., S. R. Clayden & R. C. Harris. 2016. *Lecanora insignis* (Lecanoraceae) and its lichenicolous fungi in North America, including a new species of *Skyttea* (Helotiales). The Bryologist

119(1): 39–51. [doi:10.1639/0007-2745-119.1.039]

Dunn, R. R., N. C. Harris, R. K. Colwell, L. P. Koh & N. S. Sodhi. 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proceedings of the Royal Society B: Biological Sciences 276: 3037–3045. [doi:10.1098/rspb.2009.0413]

Egea, J. M. & P. Torrente. 1996. Tres nuevas especies de hongos liquenizados de la Provincia del Cabo (Suda´frica). Cryptogamie, Bryologie-Lich´enologie 17(4): 295–312.

Ertz, D., K. E. Driscoll & S. R. Clayden. 2021. Two new lichenicolous species of Opegrapha (Arthoniales) from Canada. The Bryologist 124(1): 39–51. [doi:10.1639/0007-2745-124.1.039]

Ertz, D. & P. P. G. van den Boom. 2012. Plectocarpon frostiicola (Arthoniales), a new lichenicolous species from Cape Verde. Lichenologist 44(5): 591–593. [doi:10.1017/S0024282912000345]

Esseen, P. A. 1981. Host specificity and ecology of epiphytic macrolichens in some central Swedish spruce forests. Wahlenbergia 7: 73–80.

Etayo, J. 2002. Aportaci ´on al Conocimiento de los Hongos Liquen´ıcolas de Colombia. Bibliotheca Lichenologica, No. 84, J. Cramer, Berlin-Stuttgart, 154 pp.

Etayo, J. 2010. Hongos liquen´ıcolas de Per ´ u: Homenaje a Rolf Santesson. Bulletin de la Soci´et´e linn´eenne de Provence 61: 83–128.

Etayo, J. 2017. Hongos liquen´ıcolas de Ecuador. Opera Lilloana 50: 1–535.

Etayo, J. & P. Diederich. 2009. Arthonia protoparmeliopseos, a new lichenicolous fungus on Protoparmeliopsis muralis from Spain and Luxembourg. Bulletin de la Soci ´et´e des Naturalistes Luxembourgeois 110: 93–96.

Etayo, J. & P. P. G. van den Boom. 2013. A first checklist of lichenicolous fungi from the Dominican Republic, including the description of a new species of Xenonectriella. Opuscula Philolichenum 12(1): 142–150.

Fleischhacker, A., M. Grube, A. Frisch, W. Obermayer & J. Hafellner. 2016. Arthonia parietinaria – A common but frequently misunderstood lichenicolous fungus on species of the Xanthoria parietina-group. Fungal Biology 120(11): 1341–1353. [doi:10.1016/j.funbio.2016.06.009]

Follmann, G. & B. C. Werner. 2003. Lichenicolous fungi occurring on Roccellaceae (Arthoniales). I. New Species from South America. Journal Hattori Botanical Laboratory 94: 261–292.

Foucard, T. 2001. Svenska Skorplavar. Interpublishing, Stockholm. 39 pp.

Frisch, A. & H. Holien. 2018. Arthonia toensbergii, a new lichenicolous fungus on Mycoblastus affinis from the boreal rainforests in Norway. Graphis Scripta 30(6): 34–43.

Frisch, A., G. Thor, D. Ertz & M. Grube. 2014a. The Arthonialean challenge: restructuring Arthoniaceae. Taxon 63(4): 727–744.

Frisch, A., G. Thor & D. Sheil. 2014b. Four new Arthoniomycetes from Bwindi Impenetrable National Park, Uganda – supported by molecular data. Nova Hedwigia 98(3–4): 295–312. [doi:10.1127/0029-5035/2013/0155]

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

G´ omez, A. & E. Nichols. 2013. Neglected wild life: Parasitic biodiversity as a conservation target. International Journal for Parasitology: Parasites and Wildlife 2: 222–227. [doi:10.1016/j.ijppaw.2013.07.002]

Grube, M. 1998. Classification and phylogeny in the Arthoniales (lichenized Ascomycetes). The Bryologist 101(3): 377–391.

Grube, M. 2007. Arthonia. Pages 39–61. In: T. H. Nash, III, C. Gries

& F. Bungartz (eds.), Lichen Flora of the Greater Sonoran Desert Region. Volume 3. Lichens Unlimited, Arizona State University, Tempe.

Grube, M. & M. Matzer. 1997. Taxonomic concepts of lichenicolous Arthonia species. Pages 1–17. In: R. T¨urk & R. Zorer (eds.), Progress and Problems in Lichenology in the Nineties. Bibliotheca Lichenologica, No. 68, J. Cramer, Berlin-Stuttgart.

Grube, M., M. Matzer & J. Hafellner. 1995. A preliminary account of the lichenicolous Arthonia species with reddish, Kþ reactive pigments. Lichenologist 27(1): 25–42.

Hafellner, J. 2018. Noteworthy records of lichenicolous fungi from various countries on the Balkan Peninsula [Nennenswerte Funde von lichenicolen Pilzen von verschiedenen L¨anderen auf der Balkanhalbinsel]. Herzogia 31(1): 476–493. [doi:10.13158/heia.31.1.2018.476]

Hafellner, J., D. Triebel, B. D. Ryan & T. Nash, III. 2002. On lichenicolous fungi from North America. II. Mycotaxon 84: 293–329.

Halıcı, M. 2008. Arthonia hawksworthii sp. nov. (Ascomycota, Arthoniaceae) on Dimelaena oreina from Turkey. Mycotaxon 105: 89–93.

Halıcı, M. G. & M. Candan. 2011. Arthonia anatolica sp. nov. (Arthoniaceae) on Aspicilia contorta subsp. hoffmanniana, a new lichenicolous species from Turkey. Mycotaxon 116: 335–339. [doi:10.5248/116.335]

Harris, R. C. 1989. A sketch of the family Pyrenulaceae (Melanommatales) in eastern North America. Memoirs of the New York Botanical Garden 49: 74–107.

Harris, R. C. 1995. More Florida Lichens. Including the 10ø Tour of the Pyrenolichens. Published by the author, Bronx, N.Y. 192 pp.

Harris, R. C. & D. Ladd. 2005. Preliminary Draft: Ozark Lichens, enumerating the lichens of the Ozark Highlands of Arkansas, Illinois, Kansas, Missouri, and Oklahoma. Published by the authors. 249 pp.

Haughiana, S. R., S. R. Clayden & R. Cameron. 2019. On the distribution and habitat of Fuscopannaria leucosticta in New Brunswick, Canada. Ecoscience 26(2): 999–112. [doi:10.1080/11956860.2018.1526997]

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Gu´egan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter & J. R. G. Turner 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84: 3105–3117.

Hollinger, J. P. & J. C. Lendemer. 2021. Capronia harrisiana (Ascomycota, Chaetothyriales), a new lichenicolous species on Crocodia aurata from the southern Appalachian Mountains of southeastern North America. The Bryologist 124(4): 522–532. [doi:10.1639/0007-2745-124.4.522]

Hora´kova´ , J. 1994. Arthonia pragensis spec. nov. (Ascomycetes, Arthoniales), a new lichenicolous fungus from the Czech Republic. Czech Mycology 47: 139–143.

Houde, I., S. Leech, F. L. Bunnell, T. Spribille & C. Bj¨ork. 2007. Old forest remnants contribute to sustaining biodiversity: the case of the Albert River valley. BC Journal of Ecosystems and Management 8(3): 43–52.

Hudson, P. J., A. P. Dobson & K. D. Lafferty. 2006. Is a healthy ecosystem one that is rich in parasites? Trends in Ecology and Evolution 21(7): 381–385. [doi::10.1016/j.tree.2006.04.007]

Hurtado, P., M. Prieto, F. de Bello, G. Arag ´ on, J. L´ opez-Angulo, P. Giorandi, E. M. D´ıaz-Pe˜na, R. Vicente, S. Merinero, A. Koˇsuthova´, R. Benesperi, E. Bianchi, H. Mayrhofer, J. Nascimbene, M. Grube, M. Wedin, M. Westberg & I. Martinez. 2020. Contrasting environmental drivers determine biodiversity patterns in epiphytic lichen communities along a European gradient . Microorganisms 8: 1913. [doi :10.3390/microorganisms8121913]

Ihlen, P. G., B. Owe-Larsson & T. Tønsberg. 2004. *Arthonia biatoricola* sp. nov. from north-western Europe and northern
//TITAN
Pacific North America. Symbolae Botanicae Upsalienses 34(1): 107–111.

Ihlen, P. G. & M. Wedin. 2008. An annotated key to the lichenicolous Ascomycota (including mitosporic morphs) of Sweden. Nova Hedwigia 86(3–4): 275–365. [doi:10.1127/0029-5035/2008/0086-0275]

Jetz, W. & P. V. A. Fine. 2012. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. PLoS Biology 10: e1001292.

Joshi, S., D. K. Upreti & S. Nayaka. 2013. A new lichenicolous *Arthonia* species (Arthoniaceae) on *Diorygma* from India. Lichenologist 45(3): 323–327. [doi:10.1017/S0024282913000042]

J ¨uriado, I., U. Kaasalainen, M. Jylh¨a & J. Rikkinen. 2019. Relationships between mycobiont identity, photobiont specificity and ecological preferences in the lichen genus *Peltigera* (Ascomycota) in Estonia (northeastern Europe). Fungal Ecology 39: 45–54. [doi:/10.1016/j.funeco.2018.11.005]

Kalb, K. 2004. *Dirinaria*. Pages. 98–103. In: T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz (eds.), Lichen Flora of the Greater Sonoran Desert Region, Vol. 2. Lichens Unlimited, Arizona State University, Tempe.

Kantvilas, G. & M. Wedin. 2015. Lichenicolous species of the Ascomycete genus *Arthonia* Ach. from Kangaroo Island. Journal of the Adelaide Botanic Gardens 29: 1–6.

K¨arnefelt, I., S. Kondratyuk, U. Søchting, P. Fr¨od´en & U. Arup. 2002. Two new species of *Caloplaca* (Teloschistaceae) from the Southern Hemisphere. The Bryologist 105(3): 301–309.

Knudsen, K. & J. C. Lendemer. 2007. Studies in lichens and lichenicolous fungi: notes on some North American taxa. Mycotaxon 101: 81–87.

Kocourkova´ , J. 2000. Lichenicolous fungi of the Czech Republic, the first commented checklist. Acta Musei Nationalis Pragae, Series S, Historia Naturalis, 55(3–4): 59–169.

Kocourkova´ , J. & K. Knudsen. 2015. Notes on the California lichen flora 7: more new records. Opuscula Philolichenum 14: 118–120.

Lawrey, J. D. & P. Diederich. 2003. Lichenicolous fungi: Interactions, evolution, and biodiversity. The Bryologist 106(1): 80–120.

Leavitt, S. D., M. P. Nelsen, H. T. Lumbsch, L. A. Johnson & L. L. St. Clair. 2013. Symbiont flexibility in subalpine rock shield lichen communities in the Southwestern USA. The Bryologist 116(2): 149–161. [doi:10.1639/0007-2745-116.2.149]

Lendemer, J. C. 2021. Proposed best practices for taxonomic innovations in lichen and allied Fungi: A framework derived from analysis of more than 1,000 new taxa and new combinations. The Bryologist 124(1): 90–99. [doi:10.1639/0007-2745-124.1.090]

Lendemer, J. C. & R. C. Harris. 2012. Studies in lichens and lichenicolous fungi – no. 16. Opuscula Philolichenum 11: 313–321.

Lendemer, J. C., R. C. Harris & A. M. Ruiz. 2016. A review of the lichens of the Dare Regional Biodiversity Hotspot in the Mid-Atlantic Coastal Plain of North Carolina, eastern North America. Castanea 81(1): 1–77. [doi:10.2179/15-073R2]

Lendemer, J. C., R. C. Harris & E. A. Tripp. 2013. The lichens and allied fungi of Great Smoky Mountains National Park: an annotated checklist with comprehensive keys. Memoirs of the

New York Botanical Garden 104: 1–152.

Lendemer, J. C. & N. Noell. 2018. Delmarva lichens: An illustrated manual. Memoirs of the Torrey Botanical Society 28: 1–386.

Lendemer, J. C., B. Thiers, A. H. Monfils, J. Zaspel, E. R. Ellwood, A. Bentley, K. Levan, J. Bates, D. Jennings, D. Contreras, L. Lagomarsino, P. Mabee, L. S. Ford, R. Guralnick, R. E. Gropp, M. Revelez, N. Cobb, K. Seltmann & M. C. Aime. 2019. The Extended Specimen Network: A strategy to enhance US biodiversity, collections, promote research and education. BioScience 70(1): 23–30. [effectively published online 22 November 2019] [doi:10.1093/biosci/biz140].

Loppi, S. & L. Frati. 2004. Influence of tree substrate on the diversity of epiphytic lichens: comparison between Tilia platyphyllos and Quercus ilex (Central Italy). The Bryologist 107(3): 340–344. [doi :10.1639/0007-2745(2004)107[0340:IOTSOT]2.0.CO;2]

Łubek, A., M. Kukwa, P. Czortek & B. Jaroszewicz. 2019. Lichenicolous fungi are more specialized than their lichen hosts in primeval forest ecosystems, Białowieza Forest, northeast Poland. Fungal Ecology 42: 1–10. [doi:10.1016/j.funeco.2019.100866]

Lumbsch, H. T., R. Guderley & G. B. Feige. 1997. Ascospore septation in Diploschistes (Thelotremataceae, lichenized Ascomycota) and the taxonomic significance of macro- and microcephalic ascospore types. Plant Systematics and Evolution 205: 179–184.

Majewski, T. 1971. Parasitic fungi of the Białowieza National Park against the background of the mycoflora of Poland (Peronosporales, Erysiphaceae, Uredinales, Ustilaginales). Acta Mycologica 7: 299–388.

Mal´ıˇcek, J. 2014. A revision of the epiphytic species of the Lecanora subfusca group (Lecanoraceae, Ascomycota) in the Czech Republic. The Lichenologist 46(4): 489–513. [doi:10.1017/S0024282914000139]

Matzer, M. 1996. Lichenicolous Ascomycetes with Fissitunicate Asci on Foliicolous Lichens. Mycological Papers 171, CAB International, Wallingford. x þ 202 pp.

Matzer, M. & J. Hafellner. 1990. Eine Revision der lichenicolen Arten der Sammelgattung Rosellinia (Ascomycetes). Bibliotheca Lichenologica, No. 37, J. Cramer, Berlin-Stuttgart, pp. 1–138.

Maynard, D. S., M. A. Bradford, D. L. Lindner, L. T. A. van Diepen, S. D. Frey, J. A. Glaeser, & T. W. Crowther. 2017. Diversity begets diversity in competition for space. Nature Ecology & Evolution 1: 0156.

Mayrhofer, H., J. W. Sheard, M. C. Grassler & J. A. Elix. 2001. Rinodina intermedia (Physciaceae, lichenized Ascomycetes): a well-characterized species with submuriform ascospores. The Bryologist 104(3): 456–463.

McCain, C. M. 2007. Could temperature and water availability drive elevational species richness? A global case study for bats. Global Ecology and Biogeography 16: 1–13. [doi:10.1111/j.1466-822x.2006.00263.x]

McCain, C. M. & J. A. Grytnes. 2010. Elevational gradients in species richness, Encyclopedia of Life Sciences. John Wiley & Sons, Ltd.

McCune, B., S. Yang, S. Jovan & H. T. Root. 2022. Climate and epiphytic macrolichen communities in the Four Corners region of the U.S.A. The Bryologist 125(1): 70–90. [doi:10.1639/0007-2745-125.1.070]

McDonald, L., M. Van Woudenberg, B. Dorin, A. M. Adcock, R. T. McMullin & K. Cottenie. 2017. The effects of bark quality on corticolous macro-lichen community composition in urban parks in Guelph, Ontario. Botany 95(12): 1141–1149. [doi:10.1139/cjb-2017-0113]

McNew, S. M., L. N. Barrow, J. L. Williamson, S. C. Galen, H. R.

Skeen, S. G. DuBay, A. M. Gaffney, A. B. Johnson, E. Bautista,
//
P. Ordo˜nez, C. J. Schmitt, A. Smiley, T. Valqui, J. M. Bates, S. J. Hackett & C. C. Witt. 2021. Contrasting drivers of diversity in hosts and parasites across the tropical Andes. Proceedings of the National Academy of Sciences U.S.A. 118(12): e2010714118. [doi:10.1073/pnas.2010714118]

Medeiros, I. D., E. Mazur, J. Miadlikowska, A. Flakus, P. C. J. Pardo-De la HozRodriguez-Flakus, E. Cies´lak, L. ´Sliwa & F. Lutzoni. 2021. Turnover of Lecanoroid mycobionts and their Trebouxia photobionts along an elevation gradient in Bolivia Highlights the role of environment in structuring the lichen symbiosis. Frontiers in Microbiology 12: 774839. [doi:10.3389/fmicb.2021.774839]

Nimis, P. L. 2022. ITALIC - The Information System on Italian Lichens. Version 7.0. University of Trieste, Dept. of Biology, (https://dryades.units.it/italic), accessed 18 Dec. 2022.

Ortiz-A´ lvarez, R., A. De Los R´ıos, F. Ferna´ndez-Mendoza, A. Torralba-Burrial & S. P´erez-Ortega. 2015. Ecological specialization of two photobiont-specific maritime cyanolichen species of the genus Lichina. PLoS ONE 10(7): e0132718. [doi:10.1371/journal.pone.0132718]

Palm, H. W. & S. R¨uckert. 2009. A new approach to visualize ecosystem health by using parasites. Parasitology Research 105: 539–553. [doi:10.1007/s00436-009-1423-z]

Poulin, R. 2004. Macroecological patterns of species richness in parasite assemblages. Basic and Applied Ecology 5: 423–434. [doi:10.1016/j.baae.2004.08.003]

Poulin, R. 2014. Parasite biodiversity revisited: frontiers and constraints. International Journal for Parasitology 44: 581–589. [doi:10.1016/j.ijpara.2014.02.003]

Poulin, R. & K. N. Mouritsen. 2003. Large-scale determinants of trematode infections in intertidal gastropods. Marine Ecology Progress Series 254: 187–198.

Press, M. C. & G. K. Phoenix. 2005. Impacts of parasitic plants on natural communities. New Phytologist 166(3): 737–751. [doi:10.1111/j.1469-8137.2005.01358.x]

Rambold, G. & D. Triebel. 1992. The Inter-lecanoralean Associations. Bibliotheca Lichenologica, No. 48, J. Cramer, Berlin-Stuttgart, 201 pp.

Richardson, D. H. S. 1999. War in the world of lichens: parasitism and symbiosis as exemplified by lichens and lichenicolous fungi. Mycological Research 103(6): 641–650.

Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. Pages 279–307. In: D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), Lichenology: Progress and Problems. Academic Press, London.

Sasal, P., D. Mouillot, R. Fichez, S. Chifflet & M. Kulbicki. 2007. The use of fish parasites as biological indicators of anthropogenic influences in coral-reef lagoons: a case study of Apogonidae parasites in New-Caledonia. Marine Pollution Bulletin 54: 1697–1706. [doi:10.1016/j.marpolbul.2007.06.014]

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel & K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40: 245–269.

Schwelm J., C. Selbach, J. Kremers & B. Sures. 2021. Rare inventory of trematode diversity in a protected natural reserve. Scientific Reports 11(1): 22066. [doi:10.1038/s41598-021-01457-2]

Seaward, M. R. D., D. H. S. Richardson, I. M. Brodo, R. C. Harris & D. L. Hawksworth. 2017. Checklist of lichen-forming, lichenicolous and allied fungi of Eagle Hill and its vicinity, Maine. Northeastern Naturalist 24(3): 349–379. [doi:10.1656/045.024.0305]

Stein, B. A., L. S. Kutner & J. S. Adams (eds.). 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, Oxford.

Suija, A., D. L. Hawksworth & S. P´erez-Ortega. 2018. The generic name Abrothallus (Abrothallales, Dothideomycetes), and names proposed in the genus by Giuseppe De Notaris, Søren Christian Sommerfelt, and Ignaz TaxonKotte. 67(6): 1169–1179. [doi:10.12705/676.13]

Suija, A., A. de los R´ıos & S. P´erez-Ortega. 2015. A molecular reappraisal of Abrothallus species growing on lichens of the order Peltigerales. Phytotaxa 195(3): 201–226. [doi:10.11646/phytotaxa.195.3.1]

Sundin, R. 1999. [Dissertation] Phylogenetic and taxonomic studies within Arthonia Ach. (Ascomycetes, Arthoniales). Stockholm University, Stockholm. 162 pp., not continuously paginated pp.

Sundin, R. & A. Tehler. 1998. Phylogenetic studies of the genus Arthonia. Lichenologist 30(4–5): 381–413.

Sundin, R., G. Thor & A. Frisch. 2012. A literature review of Arthonia s. lat. Bibliotheca Lichenologica, No. 108, J. Cramer, Berlin-Stuttgart, pp. 257–290.

Sweetwood, G., R. L¨ucking, M. P. Nelsen & A. Aptroot. 2012. Ascospore ontogeny and discharge in megalosporous Trypetheliaceae and Graphidaceae (Ascomycota: Dothideomycetes and Lecanoromycetes) suggest phylogenetic relationships and ecological constraints. Lichenologist 44(2): 277–296.

Thieltges D. W., K. T. Jensen & R. Poulin. 2008. The role of biotic factors in the transmission of free-living endohelminth stages. Parasitology 135(4): 407–426. [doi:10.1017/S0031182007000248]

Triebel, D. 1989. Lecideicole Ascomyceten. Eine Revision der obligat lichenicolen Ascomyceten auf lecideoiden Flechten. Bibliotheca Lichenologica, No. 35. J. Cramer, Berlin-Stuttgart, 278 pp.

Tripp, E. A. & J. C. Lendemer. 2019. Highlights from 10þ years of lichenological research in Great Smoky Mountains National Park: Celebrating the United States National Park Service Centennial. Systematic Botany 44(4): 943–980. [doi:10.1600/036364419X15710776741332]

Tripp, E. A. & J. C. Lendemer. 2020. Field Guide to the Lichens of Great Smoky Mountains National Park. University of Tennessee Press, Knoxville. 572 pp.

U'Ren, J. M., F. Lutzoni, J. Miadlikowska, A. D. Laetsch, & A. E. Arnold. 2012. Host- and geographic structure of endophytic and endolichenic fungi at a continental scale. American Journal of Botany 99: 898–914.

van den Boom, P. P. G. & M. H. Moniri. 2018. Notes on the lichen genus Lecania (Ramalinaceae) in Iran, with the description of a new Arthonia species (Arthoniaceae). Nova Hedwigia 107(3-4): 407–421. [doi:10.1127/nova_hedwigia/2018/0479]

van den Boom, P. P. G., H. J. M. Sipman, P. K. Divakar & D. Ertz. 2017. New or interesting records of lichens and lichenicolous fungi from Panama, with descriptions of ten new species. Sydowia 69: 47–72. [doi:10.12905/0380.sydowia69-2017-0047]

Watson, M. F., D. L. Hawksworth & F. Rose. 1988. Lichens on elms in the British Isles and the effect of Dutch Elm Disease on their status. Lichenologist 20(4): 327–352.

Wedin, M. & J. Hafellner. 1998. Lichenicolous species of Arthonia on Lobariaceae with notes on excluded taxa. Lichenologist 30(1): 59–91.

Wigle, R., Y. Wiersma, A. Arsenault & R. T. McMullin. 2021. Drivers of arboreal lichen community structure and diversity on Abies balsamea and Betula alleghaniensis in the Avalon Forest Ecoregion, Newfoundland. Botany 99: 43–54. [doi:10.1139/cjb-2020-0061]

Woods, R. G. & B. J. Coppins. 2012. A Conservation Evaluation of

British Lichens and Lichenicolous Fungi. Species Status 13. Joint Nature Conservation Committee, Peterborough.

Zhao, X., S. D. Leavitt, Z. T. Zhao, L. L. Zhang, U. Arup, M. Grube, S. P´erez-Ortega, C. Printzen, L. ´ Sliwa, E. Kraichak, P. K. Divakar, A. Crespo & H. T. Lumbsch. 2016. Towards a revised generic classification of lecanoroid lichens (Lecanoraceae, Ascomycota) based on molecular, morphological and chemical evidence. Fungal Diversity 78(1): 293–304.

Zhurbenko, M. P. 2008. Lichenicolous lichen species in Russian flora. Botanicheskii Zhurnal 93(9): 1329–1353.

Zhurbenko, M. P. 2012. Lichenicolous mycobiota of the Russian Arctic: taxonomic analysis. Mikologiya i fitopatologiya 45(5): 387–396.

Zhurbenko, M. P. 2013. Lichenicolous fungi and some allied lichens from the Canadian Arctic. Opuscula Philolichenum 12(1): 180–197.

Zhurbenko, M. P. & W. von Brackel. 2013. Checklist of lichenicolous fungi and lichenicolous lichens of Svalbard, including new species, new records and revisions. Herzogia 26(2): 323–359.

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Supplementary document online:
Supplementary Table S1. Taxonomic characters of the lichenicolous Arthonia.