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Atronectria thelotrematis (*Sordariomycetes*), a remarkable new pyrenomycete on *Thelotrema lepadinum* from Chile, with a key to the lichenicolous fungi growing on *Thelotrema*

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Abstract. *Atronectria thelotrematis*, a lichenicolous pyrenomycete growing on *Thelotrema lepadinum*, is described as new to science from Chile. The species is characterized by black perithecioid ascomata; a brown, not changing color in K and lactic acid, N+ reddish orange exciple resembling textura angularis or textura epidermoidea; 0–4-septate periphyses; a I−, K/I− hymenium with rather rare lipid droplets; the absence of distinct interascal filaments; inoperculate, unitunicate, cylindrical, 8-spored, I−, K/I− asci; and hyaline to occasionally light brown, smooth to mostly finely verruculose, 1-septate, homopolar ascospores, uniseriate in the ascus. A key to ten species of lichenicolous fungi known to occur on *Thelotrema* is provided.

Key words: lichen parasites, South America, taxonomy

Introduction

This paper continues the publication of the results of a revision of the collection of lichenicolous fungi curated by the late Rolf Santesson and preserved in the Herbarium of the Museum of Evolution at Uppsala University (see Zhurbenko 2021, 2022a, b). This collection contains, among others, a pyrenomycete growing on *Thelotrema lepadinum*, annotated '*Zwackhiomyces*?'. Subsequent examination of this specimen revealed that it represents a species of *Sordariomycetes* unknown to science.

The genus *Thelotrema* includes about 100 species of lichens mainly growing on bark and wood, distributed all over the globe, but particularly abundant in tropical forests (James & Hawksworth 2009). This host genus, on which ten species of lichenicolous fungi have been observed (see key below), is relatively poor in associated lichenicolous mycobiota, compared with lichen genera such as *Cladonia* and *Peltigera* supporting no less than 93 and 79 species of these fungi respectively (Diederich et al. 2018).

The aims of this paper are to (1) describe a new species of *Sordariomycetes* and (2) present a key to lichenicolous fungi growing on *Thelotrema* worldwide.

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Material and methods

Microscopy was carried out, and photographs were taken, using a Zeiss Axio Zoom.V16 stereomicroscope fitted with an AxioCam 712 color digital camera and a Zeiss Axio Imager.A1 compound microscope equipped with Nomarski differential interference contrast optics and fitted with an AxioCam 506 color digital camera. Microscopic characters were studied using sections hand-cut with a razor blade and mounted in water, 10% potassium hydroxide (K), Lugol's iodine directly (I) or after a K pretreatment (K/I), concentrated nitric acid (N) or lactic acid. Measurements were taken from water mounts and rounded to the nearest 0.5 µm. The length, width and length/width ratio (l/w) of the ascospores are given as (min–)($\bar{x}$−SD)–($\bar{x}$+SD)(–max), where 'min' and 'max' are the extreme values observed, $\bar{x}$ the arithmetic mean and SD the corresponding standard deviation. Colors were named according to Kornerup & Wanscher (1978). Voucher specimen is kept in UPS.

Taxonomy

Atronectria thelotrematis Zhurb., sp. nov. (Fig. 1)

MycoBank MB 845998

Diagnosis: Differs from *Atronectria magellanica* mainly by a K− vs K+ greenish black exciple and broader ascospores, 4.5–6.5 µm vs 2.5–3.5 µm wide.

Type: Chile, Prov. Chiloé, Isla Grande de Chiloé, Ancud, ~41°52′S, 73°50′W, on *Thelotrema lepadinum* (thallus) growing

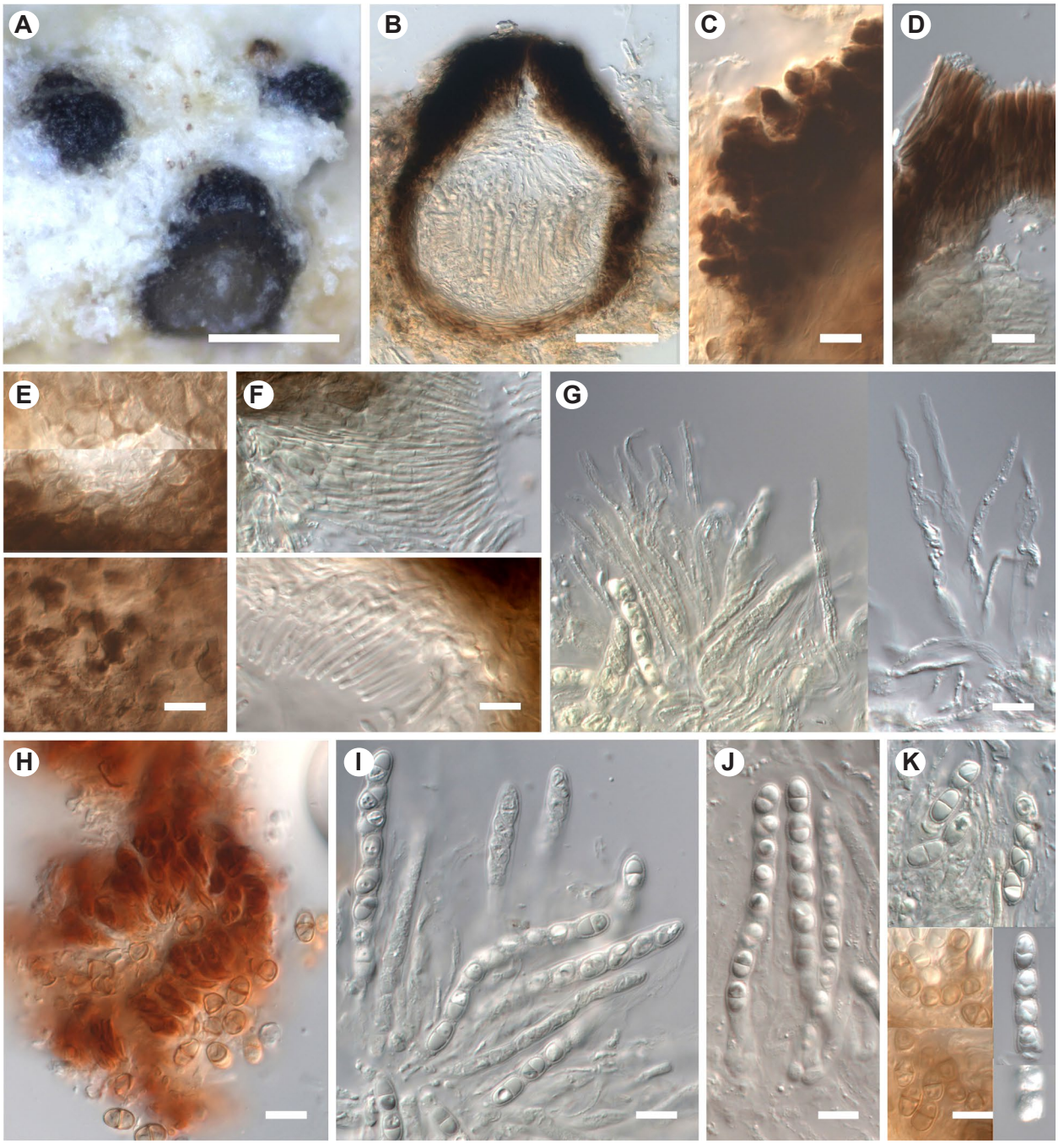

Figure 1. *Atronectria thelotrematis* (holotype). A – ascomata on the host lichen thallus, the one in the foreground is sectioned; B – ascoma in cross section, in water; C – outgrowths/papillae at the top outside of the exciple, in K; D – acuminate, aseptate hyphae framing the ostiole, in I; E – exciple in surface view resembling textura angularis (above, in I) or textura epidermoidea (below, in K/I); F – periphyses, in I (above) and K (below); G – filaments of unclear origin between the asci, in I; H – exciple and pigmented ascospores, in N; I – asci with spores, in N; J – asci with spores, in K; K – ascospores, in water. Scales: A = 100 µm, B = 50 µm, C–K = 10 µm.

on stem of *Rhaphithamnus* at the edge of the forest, 30 Oct. 1940, Rolf Santesson 6918a (UPS F-892080 – holotype!).

Description. Vegetative hyphae not observed. Stroma absent. Ascomata perithecioid, black, with a delicately roughened surface of the exposed parts, subglobose to ovoid or narrowly ampulliform (with an indistinct papilla), 80–160 µm diam. (n = 12), with ostiole up to 20 µm diam., mostly immersed with only ostiolar area protruding, sometimes semi-immersed or rarely almost superficial, arising singly or sometimes in groups of 2–8. Exciple dark brown around ostiole, medium to light brown below, pigmentation amorphous, uneven, K−, N+ reddish orange, coloration is unaffected by lactic acid; in surface view resembling textura angularis or textura epidermoidea, composed of cells up to 13 µm in greatest dimension, with walls 0.5–2.5 µm thick; in cross section 30–35 µm thick near the ostiole, 15–20 µm thick at the base, composed of 4–8 layers of tangentially elongated cells, outer region composed of pigmented, ellipsoid cells with walls 0.5–1 µm thick, inner region composed of almost colorless, strongly elongated cells with a very narrow lumen, with walls ~0.5 µm thick; at the top outside with dark brown outgrowths/papillae 5–15 × 4–7 µm; the ostiole is

framed by coherent, medium to dark brown, acuminate, aseptate hyphae, 10–25 × 2–4 µm. Periphyses abundant, hyaline, subcylindrical to slightly acuminate, 15–40 × 1.5–2.5 µm, 0–4-septate, often formed in two on the basal cells. Hymenium with rather rare lipid droplets, I−, K/I−. Interascal filaments indistinct, however delicate, inspersed, aseptate, cytoplasmic strands of unclear origin, 1.5–4.5 µm wide, with thin walls, without branching or anastomoses are sometimes observed between the asci (best seen in I). Asci inoperculate, unitunicate, cylindrical, with rounded apex and rather short pedicel, with non-thickened apical wall, without ocular chamber or apical ring, 60–75 × 7–8.5 µm (n = 9), 8-spored, I−, K/I−. Ascospores hyaline or occasionally becoming light brown (probably when old) and then N+ reddish orange, smooth to mostly finely verruculose, with verrucae up to 0.5 µm diam., ellipsoid to oblong, (7.5–)8–9.5(–10.5) × (4.5–)5–6(–6.5) µm, l/w = (1.3–)1.4–1.8(–2.0) (n = 81), 1-septate, not constricted at the septum, with equal cells, often with 1–3 conspicuous guttules in each cell, wall 0.5–1 µm wide, without halo, uniseriate, sometimes obliquely so, in the ascus. Conidiomata not observed.

Etymology. The epithet refers to the host lichen genus.

Distribution and ecology. The new species is known from the type locality in Chiloé Archipelago located in southern Chile. It was collected on the crustose lichen *Thelotrema lepadinum* (*Graphidaceae*, *Lecanoromycetes*) growing on *Rhaphithamnus* bark in the forest. This lichen is a widespread, probably cosmopolitan species that lives on the bark of deciduous trees, rarely on siliceous rocks, and is an indicator of ancient woodland conditions (James & Hawksworth 2009). The parasite fruiting bodies mainly grow on the well-developed parts of the lichen thallus, out of contact with the phorophyte bark, but are also sometimes found on its poorly developed parts, possibly in contact with the bark. Harmful effects on *Thelotrema lepadinum* are not visible.

Notes. Due to its perithecioid ascomata and inoperculate unitunicate asci, the new species clearly belongs to *Sordariomycetes*. A search in Maharachchikumbura et al. (2016), Hyde et al. (2020) and other relevant literature revealed that, within this class of ascomycetes, it most closely resembles some species of *Nectriaceae* and *Niessliaceae* (both in *Hypocreales*) with blackish ascomata atypical for this order and some species of *Phyllachoraceae* (*Phyllachorales*), but does not exactly fit any genus of these families.

Within *Nectriaceae* the new species is most reminiscent of the bark-inhabiting *Geejayessia atrofusca* (Schw.) Schroers & Gräfenhan, characterized by initially dark purple-red, finally almost black ascomata, and an exciple not changing color in K and lactic acid (Samuels & Rogerson 1984; Schroers et al. 2011). However, the latter species differs in its ascomata arising from a stroma, an ascal apex with a small ring, consistently hyaline and smooth ascospores and a different life style. The only rather suitable genus of *Niessliaceae* is *Atronectria* previously including two species known from South America, the type species *A. magellanica* Etayo growing on lichen genera *Nephroma* and *Pseudocyphellaria* (Etayo & Sancho 2008) and *A. lobariellae* Etayo & Flakus growing on lichen genus *Lobariella* (Flakus et al. 2019). The species of this genus share most characters with the examined fungus, but are distinct in a K+ greenish black or slightly purplish exciple, and consistently hyaline ascospores. Additionally, 1) asci of *A. magellanica* are ±truncate, with a small apical ring, 2) brown hyphae framing the ostiole of the new species have not been previously reported in this genus.

Within *Phyllachoraceae* the examined fungus fits in most respects the broad concept of the lichenicolous genus *Lichenochora* (Hafellner 1989). Although the ascospores of species of this genus are usually hyaline and smooth, they can also be finally light to dark brown (for example in *L. aipoliae* Etayo, Nav.-Ros. & Coppins, *L. arctica* Zhurb., *L. atrans* Halici, K. Knudsen & Candan, *L. galligena* R. Sant. & Hafellner, and *L. thorii* Zhurb.) and ornamented (for example in *L. aipoliae*) (Hafellner 1989; Hafellner & Navarro-Rosinés 2004; Etayo & Navarro-Rosines 2008; Zhurbenko 2008, 2013; Halici et al. 2009). It is noteworthy that similar brown filaments framing the ostiole have been reported in this genus (Zhurbenko 2013; Zhurbenko & Brackel 2013). However, *Lichenochora* species differ in having abundant lipid droplets in all parts of ascomata, an exciple composed in surface view of uniformly colored, larger cells with thinner walls, and the presence of interascal filaments, noticeable at least in young ascomata (Hafellner & Navarro-Rosinés 2004).

The genus *Zwackhiomyces* Grube & Hafellner (*Collemopsidiomycetes*) is also characterized by perithecioid ascomata, cylindrical asci, and 1-septate, verruculose ascospores, but is obviously distinct by the absence of periphyses, the presence of branched and anastomosed interascal filaments, and bitunicate asci (Grube & Hafellner 1990; Hoffmann & Hafellner 2000).

As the fungus studied is morphologically distinctive and evidently represents an unknown species of *Sordariomycetes*, I tentatively describe it here in the genus *Atronectria* pending further phylogenetic analyses based on fresh material.

A key to the species of lichenicolous fungi growing on *Thelotrema*

This key is based on the literature cited below under 'Lit.' Lichenicolous fungi on *Thelotrema glaucopallens* and *T. petractoides* that have recently been combined in *Wirthiotrema glaucopallens* (Rivas Plata et al. 2010) and *Crutarndina petractoides* (Parnmen et al. 2012), respectively, are also included and given in square brackets. *Nectria byssophila* Rossman, occasionally growing on '*Thelotrema*? *clathroporina*', is not included as it also grows on mosses and is probably not lichenicolous (Rossman 1983). *Bergerella atrofusca* Diederich & Lawrey, a virulent pathogen on *Physcia* species once collected on *Thelotrema lepadinum*, is omitted because its presence on this host is probably accidental, as explained in Diederich et al. (2022: 55). Nomenclature of the species follows MycoBank (2022), Etayo & Aptroot (2006) and the present paper.

1 Spores produced in asci 2
Spores produced on conidiogenous cells 9

2(1) Ascospores 6–10-septatae, 40–60 × 6–9 µm; on *Thelotrema* sp. Lit.: Stirton (1879). Note: this is a poorly known species; the host taxon probably also needs revision . . . . . ***Opegrapha tenuior***

Ascospores with at most 3 septa, up to 24 µm long . . . 3

3(2) Ascomata perithecioid; on *Thelotrema lepadinum*. Lit.: present paper . . . . . ***Atronectria thelotrematis***

Ascomata apothecioid 4

4(3) Ascomata urceolate; ascospores persistently hyaline, 0–1-septate 5

Ascomata not urceolate; ascospores becoming brown, 2–3-septate 6

5(4) Ascomata dark brownish; exciple with K+ bright aeruginose green and K+ purplish violet pigments; ascospores (0–)1-septate; on *Thelotrema lepadinum*. Lit.: Sherwood et al. (1981), Diederich & Etayo (2000) . . . . . ***Skyttea nitschkei***

Ascomata dark greenish to blackish; with a K+ violet pigment; ascospores 0-septate; on *Thelotrema lepadinum*. Lit.: Diederich & Etayo (2000) . . . . . ***Skyttea thelotrematis***

6(4) Lateral exciple indistinct, ascospores 11–14 × 4.5–5 µm; on *Thelotrema lepadinum*. Lit.: Coppins (1989) . . . . . ***Arthonia thelotrematis***

Lateral exciple well-developed, ascospores longer 7

7(6) Exciple K−; asci without an amyloid apical ring; ascospores 17–24 µm long; on *Wirthiotrema glaucopallens* (≡ *Thelotrema glaucopallens*). Lit.: Etayo & Aptroot (2006) . . . . . **[*Opegrapha pigozziana*]**

Exciple K+ greenish; asci with an amyloid apical ring; ascospores up to 18 µm long 8

8(7) Ascomata soon becoming elliptical or disciform, with widely expanded disc; asci 4-spored; on *Crutarndina petractoides* (≡ *Thelotrema petractoides*). Lit.: Coppins (1987), Cannon et al. (2021) . . . . . **[*Opegrapha brevis*]**

Ascomata persistently lirellate, with a slit-like disc; asci 6–8-spored; on *Thelotrema lepadinum*, *T. macrosporum* and *T. weberi*. Lit.: Coppins (1987), Hafellner & Mayrhofer (2007), Cannon et al. (2021) . . . . . ***Opegrapha thelotrematis***

9(1) Conidiomata ±subspherical, stromatic, entirely composed of globose cells multiplying by budding; conidiophores absent; conidia composed of 4–22 cells; on *Thelotrema lepadinum*. Lit.: Alstrup et al. (2004), Ertz et al. (2014). Note: this species mostly grows on *Lepra*, *Ochrolechia* and *Varicellaria*, but was also reported from many other lichen genera . . . . . ***Lichenostigma* cf. *alpinum***

Hyphomycetous fungi, conidiophores present, conidia composed of 1–4 cells 10

10(9) Conidiophores aggregated in well-developed sporodochia; conidia 5–8 µm broad, with conspicuously thickened and darkened, distinctly multilayered septa; on *Thelotrema weberi*. Lit.: Heuchert et al. (2018) . . . . . ***Taeniolella weberi***

Conidiophores not aggregated in well-developed sporodochia; conidia 3–7 µm broad, conidial septa different 11

11(10) Conidiophores 1–9-septate, up to 65 µm long, usually branched; conidial chains not toruloid, easily disarticulating; on *Thelotrema lepadinum* and *Thelotrema* sp. Lit.: Heuchert et al. (2018) . . . . . ***Taeniolella thelotrematis***

Conidiophores 0–5-septate, up to 34 µm long, usually unbranched; conidial chains toruloid, not easily disarticulating; on *Thelotrema antoninii* and *T. lepadinum*. Lit.: Heuchert et al. (2018) . . . . . ***Taeniolella toruloides***

Table 1. Comparison of the proportion of lichenicolous fungi species described as new to science in recent studies of their diversity in South America and some other regions of the world.

Region	Countries	Total number of species identified	Percentage of species described as new to science	Reference
South America	Argentina and Chile (Tierra del Fuego)	189	32%	Etayo & Sancho 2008
	Columbia	104	38%	Etayo 2002
	Ecuador	352	21%	Etayo 2017
	Peru	97	18%	Etayo 2010a
Extratropical Asia	Japan and South Korea	74	5%	Zhurbenko et al. 2015
	Mongolia	102	5%	Zhurbenko et al. 2019
	Russia (Kamchatka Territory)	51	6%	Zhurbenko et al. 2012
	Russia (Trans-Baikal Territory)	37	3%	Zhurbenko & Yakovchenko 2014
Europe	Germany (Bavaria)	120	3%	Brackel 2009
		56	5%	Brackel 2019
	Iceland	53	2%	Brackel 2010
	Italy (central part)	161	2%	Brackel 2015
	Norway (Svalbard)	136	3%	Zhurbenko & Brackel 2013
	Portugal (Azores)	49	2%	Etayo 2018
	Spain (Aragón)	246	5%	Etayo 2010b
	Ukraine	220	5%	Darmostuk & Khodosovtsev 2017
Extratropical North America	Canada, Mexico, USA	142	4%	Diederich 2003
	USA (Alaska)	96	5%	Spribille et al. 2020
		98	1%	Spribille et al. 2010
	USA (Greater Sonoran Desert Region)	~150	6%	Nash III et al. 2007

Note. Only regions with a similar level of knowledge of lichenicolous mycobiota are included in the comparison.

Degree of taxonomic novelty of current research on lichenicolous mycobiota in South America and some other regions of the world

South America remains a promising region for discovering new species of lichenicolous fungi. The proportion of these species described as new to science in local studies of their diversity is still much higher in South America than in comparable studied regions of the world, such as Europe and extratropical parts of Asia and North America (Table 1).

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