

Lichenicolous fungi growing on *Thamnolia*, mainly from the Holarctic, with a worldwide key to the known species

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Abstract: Twenty species of lichenicolous fungi are reported on *Thamnolia* species and discussed. *Epithamnolia karatyginii* gen. et sp. nov., *Capronia thamnoliae* sp. nov., *Cercidospora epithamnolia* sp. nov., *C. thamnogalloides* sp. nov., *C. thamnoliae* sp. nov., and *Sphaerellothecium thamnoliae* sp. nov. (var. *thamnoliae*, var. *taimyricum*) are described from *Thamnolia*. *Dacampia thamnoliicola* and *Phoma thamnoliae* are introduced *ad interim*. *Cercidospora lecidomae* is reduced to synonymy with *C. punctillata*. *Polycoccum vermicularium* is new to Asia, *Odontotrema santessonii* and *O. thamnoliae* are new to North America, *Cladosporium licheniphilum* is new to the Arctic, *Thamnogalla crombiei* is new to Greenland and Svalbard, *Stigmidium frigidum* is new to Mongolia and confirmed in the USA, *Lichenopeltella thamnoliae* is new to Bolivia. *Cladosporium licheniphilum* and *Phaeospora arctica* are newly documented on *Thamnolia* and *Lichenopeltella thamnoliae* on *Thamnolia papelillo* var. *subsolida*. *Thamnolia vermicularis*, supporting 23 species of lichenicolous fungi, is shown to be the 15th most hospitable lichen species in the world. A worldwide key to 23 species of fungi known to occur on *Thamnolia* is provided.

Key words: lichen, new records, new taxa, thamnoliicolous fungi

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Introduction

Within the last eight years, the number of known lichenicolous fungal species has risen by about one quarter, roughly from 1300 to 1700 [Lawrey & Diederich 2003; author's database, derived from Culberson *et al.* (2011)], which corresponds to a long-established opinion that the diversity of this hostal group of fungi is yet to be revealed. However, specific estimates of their species richness vary from 2000 (Hawksworth 1991) to 5000–7000 (Lawrey & Diederich 2003). Taking into consideration that 1) the value of the Lichenicolous Index (ratio of species of lichenicolous fungi per species of lichens within an area) for the best known mycobiotas of the world is about 0.2 (Zhurbenko 2007), 2) the known and estimated numbers of lichen species in the world vary from

17 500 to 28 000 (Feuerer & Hawksworth 2007; Lücking 2008), 3500 to 5500 species of lichenicolous fungi could be expected worldwide, which means that approximately 30–50% of them are presently described. This corresponds with the results of studies of fungi inhabiting particular lichen genera, such as *Pilophorus*, *Stereocaulon*, *Tephromela* or *Thamnolia*, where about 15–35% of the species occurring are new to science (Zhurbenko & Triebel 2005; Hafellner 2007; Zhurbenko 2010a; present study). Such studies are also optimal to show various aspects of 'host-parasite' relationships, for instance, how many fungi can invade one lichen species. The world record in that respect seems to belong to *Peltigera rufescens* (Weiss) Humb., supporting 54 species of lichenicolous fungi (author's database).

The oroarctic lichen genus *Thamnolia* consists of three species: a widely distributed, cosmopolitan *T. vermicularis* (Sw.) Schaer., *T. papelillo* R. Sant., known from South America, and *T. juncea* R. Sant., known from Papua New Guinea (Santesson 2004). Until

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now, 13 species of lichenicolous fungi were known to occur on *Thamnolia*, four of which were specifically treated in Norway (Ihlen 1995). The results of the revision of fungi found on *Thamnolia vermicularis* within the Holarctic (with one find on *T. papelillo* from the Neotropics) are presented here. They nearly double the number of thamnoliicolous fungi species now reaching 23, including eight (35%) described herewith. A new anamorphic lichenicolous fungal genus and a synonym within *Cercidospora* are introduced. Since no key to fungi growing on *Thamnolia* has been published previously, one is provided here, along with notes on their taxonomy, hosts, and geography.

Materials and Methods

The study is based on 190 samples of lichenicolous fungi on *Thamnolia vermicularis*, obtained from no less than 1500–2000 host specimens examined from the Holarctic, and one sample on *T. papelillo* from South America. Furthermore, 37 LE herbarium specimens were revised. The material was examined and photographed using Zeiss microscopes Stemi 2000–CS and Axio Imager A1 equipped with Nomarski differential interference contrast optics. Microscopical examination was carried out on material mounted in water, 10% KOH (K), Lugol's iodine, directly (I) or after a KOH pre-treatment (K/I), or Brilliant Cresyl blue (BCr). The length, breadth, and length/breadth ratio (l/b) of asci and ascospores are given (where possible) as: $(\min-)\{\bar{x} -SD\} - \{\bar{x} +SD\} (-\max)$, where min and max are the extreme values, \bar{x} the arithmetic mean, and SD the corresponding standard deviation. Measurements of the ascus sizes were rounded to the nearest 1 μm , those of the ascospores and conidia to the nearest 0.5 μm . The *Ascomycota* classification follows Lumbsch & Huhndorf (2007). Terms for simple plane shapes, used for describing asci and ascospores, mostly follow Stearn (1992: 539). The estimation of total diversity of thamnoliicolous fungi in the Holarctic was based on a simple estimator proposed by Turing (Chao & Shen 2003), based on the proportion of single occurrences (singletons) in the sample $C = 1 - \frac{f}{S} \times 100\%$, where f is the number of singletons and S is the number of known species. All examined specimens are housed in the mycological herbarium of the V. L. Komarov Botanical Institute in St. Petersburg (LE).

The following specimens have been examined and compared with the species studied: *Cercidospora lecidomae* Zhurb. & Triebel: LE 207636 (paratype), LE 260308, LE 260555. *Cercidospora parva* Hafellner & Ihlen: LE 260155, LE 260054, LE 233214. *Cercidospora punctillata* (Nyl.) R. Sant.: LE 206999, LE 207003, LE 207007, LE 207012, LE 207779, LE 233253, LE

260095, LE 260166, LE 260177, LE 260245, LE 260276, LE 260296.

The Taxa

Capronia thamnoliae Zhurb. sp. nov.

Mycobank no.: MB 563049

Fungus lichenicola in thallis lichenum generis *Thamnolia* crescens. Similis speciei *Capronia normandinae*, sed differt praecipue ascosporis minoribus, $(11-13-18(-29) \times (5-6-8(-8.5) \mu\text{m})$, et hospite diverso.

Typus: USA, Alaska, Great Kobuk Sand Dunes, 67°05' N, 159°00' W, 45 m elev., *Dryas*-lichen-moss vegetation among sparse *Picea glauca*, on moribund bases of *Thamnolia vermicularis* var. *subuliformis* thalli, 13 August 2000, M. Zhurbenko 003 (LE 260400—holotypus).

(Fig. 1)

Vegetative hyphae pale brown, cylindrical to torulose, 2–3 μm wide, septate, with cells 4–15 μm long, scarcely branched, originating from the base of ascomata, mostly superficial.

Ascomata perithecioid, black, subglobose to occasionally pyriform, (70–)90–160 μm diam., with an ostiole c. 15 μm diam., usually densely setose throughout, semi-immersed to mostly sessile, arising singly, dispersed. *Setae* dark brown, subulate, the tips rounded, 15–75 μm tall, 2–3 μm wide, base swollen 6–9 μm wide, thick-walled, the edges smooth or occasionally crenate, non-septate or rarely with 1(–2 ?) septa, unbranched. *Exciple* medium brown, in surface view composed of angular pseudoparenchymatous cells (*textura angularis*) 4–13 μm across, K+ acquiring a vague grey shade. *Hymenial gel* I+ coral to rose, K/I+ blue. *Hamathecium* not observed. *Asci* clavate to subcylindrical, with strongly thickened apical wall, often penetrated by an internal apical beak (best developed in immature asci), $(56-60-72(-76) \times (13-14-18(-21) \mu\text{m})$ ($n = 29$), 8-spored, I–, K/I–. *Ascospores* initially hyaline, then pale to medium grey (septa sometimes with a brown shade), mostly elliptic to narrowly elliptic, occasionally very narrowly elliptic, broadly elliptic, rotund, narrowly ovate, or narrowly obovate, the apices attenuated or occasionally rounded, $(11-13.5-18.0(-29) \times (5-6-$

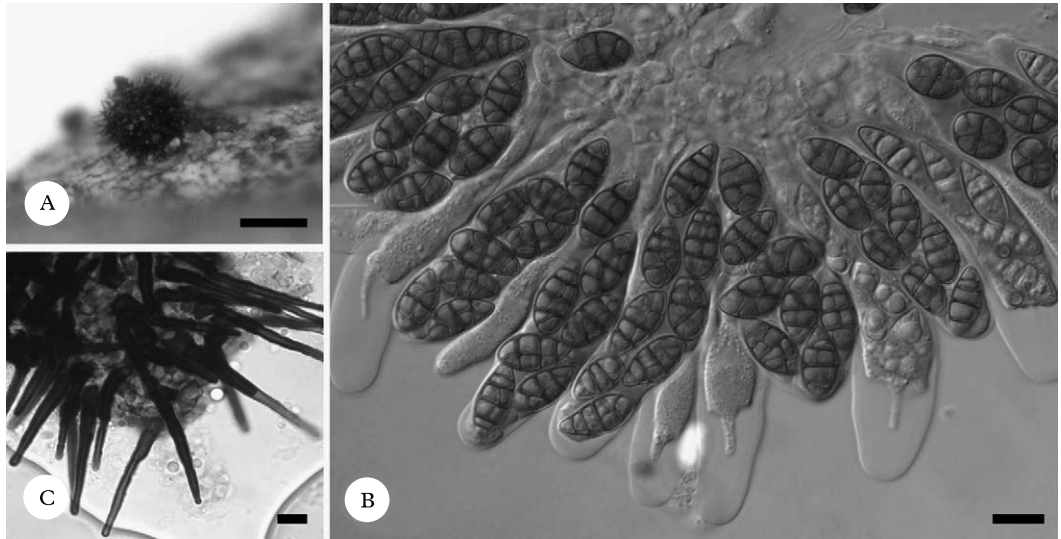


FIG. 1. *Capronia thamnoliae*. A, ascoma (holotype); B, asci with spores in K/I (LE 260410); C, setae in K/I (holotype). Scales: A = 100 μm ; B & C = 10 μm .

8(–12) μm , l/b = (1.3–)1.8–2.8(–5.8) ($n = 154$), mostly submuriform, with (0–)3–5(–7) transverse septa and as a rule with longitudinal or oblique septa in 1–3(–4) segments (very rare, probably when immature, non-septate), not or rarely constricted at the septa (when overmature), smooth-walled, non-halonate, often guttulate, arranged biseriate to partly overlapping and uniseriate in the ascus.

Anamorph not observed.

Notes. Thirteen of c. 60 previously known species of *Capronia* Sacc. (*Herpotrichiellaceae*, *Chaetothyriales*) grow on lichens (Untereiner 2000; Lawrey & Diederich 2011) [*Capronia triseptata* (Diederich) Etayo does not belong to *Capronia* (P. Diederich, pers. comm., 2011)], all being exclusively lichenicolous. Nearly all of them are restricted to a particular lichen host genus [with the exception of *Capronia hypotrachynae* Etayo & Diederich known on *Hypotrachyna* and *Menegazzia* (Etayo & Diederich 1998; von Brackel 2010b) and perhaps *C. epilobarina* S. Y. Kondr. & D. J. Galloway, which was described from *Lobaria* and was reported (with ‘cf.’) also on *Erioderma* (Etayo 2002)]; none has been found on *Thamnolia* yet. Ascospore

colour, size, and septation are among the most reliable morphological characters for the species delimitation within the genus. Seven lichenicolous *Capronia* species also have submuriform (or muriform) ascospores, characteristic of *Capronia thamnoliae*. Of these, *Capronia epilobarina* differs from the latter in its greyish brown, narrower ascospores up to 7 μm wide (Kondratyuk & Galloway 1995; Etayo & Diederich 1996b); *C. guatemalense* Etayo & van den Boom has larger ascospores (22–27 \times 9.0–11.5 μm), which are brownish from the beginning and have more septa (Etayo & van den Boom 2006); *C. hypotrachynae* has slightly narrower ascospores (12–19 \times 5.5–7.5 μm) and aseptate and much shorter setae, measuring 5–35 \times 3–4 μm , often less than 10 μm long (Etayo & Diederich 1998); *C. leopoldiana* Etayo has longer and narrower ascospores [(15–)17–22(–24) \times 4–5.5 μm], shorter setae (15–40 \times 3–4 μm), and smaller ascomata (70–100 μm diam.) (Etayo & Sancho 2008); *C. magellanica* Etayo differs in its shorter and narrower ascospores [(11–)13–16(–17.5) \times 4–6 μm], which only occasionally have 1 longitudinal septum in some cells, shorter setae (20–45 \times 4–5 μm), and the I–, K/I– reaction of the hymenial gel

(Etayo & Sancho 2008); *C. normandinae* R. Sant. & D. Hawksw. has pale olivaceous brown, slightly larger ascospores [(13–)15–21(–27) × 7.5–9.0 μm], tending to appear densely dictyosporous due to guttules and putative distosepta, and non-septate setae, mostly developing around the ostiole (Hawksworth 1990); *C. pseudonormandinae* Diederich has pale brown, smaller and less septate ascospores (12.5–16 × 6–7.5 μm), and non-septate, shorter setae, measuring 10–30 × 2.5–4 μm (Aptroot *et al.* 1997).

Distribution and host. Circumpolarly known in the Holarctic from arctic and alpine tundras and northern boreal forests. Saprotrophic or commensalistic on old or moribund portions of *Thamnomia vermicularis* thalli.

Additional specimens examined [all on *Thamnomia vermicularis* var. *subuliformis* (Ehrh.) Schaer.]. **Canada:** Canadian Arctic Archipelago: Axel Heiberg Island, Bunde Fjord, 80°30' N, 94°36' W, 30 m, 1999, *N. Marveeva* (LE 260410).—**Norway:** Troms County: Skibotndalen Valley, 69°15' N, 20°23' E, 950 m, 2003, *M. Zhurbenko* (LE 260458).—**Russia:** Taimyr Peninsula: Byrranga Mts., Levinson-Lessinga Lake, 74°30–33' N, 98°26–33' E, 120–300 m, 1994, *M. Zhurbenko* (LE 207477c); *ibid.*, 1995, *M. Zhurbenko* (LE 260390, LE 260598).

***Cercidospora epithamnomia* Zhurb. sp. nov.**

MycoBank no.: MB 563050

Fungus lichenicola in thallis lichenum generis *Thamnomia* crescens. Similis speciei *Cercidospora solearispora*, sed differt praecipue ascosporis minoribus, (12–)13–16(–19) × (3–)3.5–4.5(–5) μm, et hospite diverso.

Typus: Russia, Severnaya Zemlya, Bolshevik Island, W coast of Mikoyana Bay, 79°18' N, 101°55' E, 10 m elev., polar desert, on thalli of *Thamnomia vermicularis* var. *subuliformis*, 21 July 1996, *M. Zhurbenko* 96908 (LE 232954—holotypus).

(Fig. 2A, B, D & F)

Vegetative hyphae indistinct.

Ascomata perithecioid, black, often with a greenish or bluish grey shade when slightly shielded by host tissues, smooth, subglobose, 90–120 μm diam., with an ostiole of 10–25 μm diam., immersed to slightly protruding in the ostiolar area, arising singly or occasionally contiguous, aggregated into

groups of up to 100 or more. *Exciple* dark bluish green with a grey shade above, hyaline below, in surface view resembling *textura angularis* (cells mostly 3–5 μm across), K–. *Hymenial gel* I–, K/I–. *Hamathecium* of sparse or sometimes indistinct paraphysoids, non-capitate, *c.* 1.5 μm wide, septate, scarcely branched. *Asci* subcylindrical or moderately thickened in lower part, wall 1–2 μm thick apically and 0.5–1.5 μm laterally, sometimes with a small ocular chamber, with an indistinct or short stalk, (40–)44–60(–63) × 10–13(–14) μm (*n* = 12; in K elongated up to 76 μm), 8-spored, I–, K/I–. *Ascospores* hyaline, strongly heteropolar, narrowly soleiform or skittle-shaped with narrower to attenuated lower part and rounded ends, (12–)13–16(–19) × (3–)3.5–4.5(–5) μm, l/b = (2.9–)3.1–4.1(–5.0) (*n* = 40), with (0–)1 central septum, constricted at the septum only in K, smooth-walled, halo not observed, sometimes with a few conspicuous guttules per cell, arranged irregularly biserially in the ascus.

Anamorph not observed.

Notes. Sixteen of 27 *Cercidospora* Körb. species previously described have exclusively or mainly 1-septate ascospores. Of these, the following five species are most similar to *C. epithamnomia* by colour of exciple and mainly 8-spored asci: *C. caudata* Kernst. s. lat. (grows on *Caloplaca* and *Xanthopeltis*), *C. epipolytropa* (Mudd) Arnold (on *Lecanora*), *C. parva* (on *Baeomyces*), *C. solearispora* Calat., Nav.-Ros. & Hafellner (on *Aspicilia* and *Circinaria*) and *C. verrucosaria* (Linds.) Arnold (on *Megaspora*) (Ihlen 1998; Navarro-Rosinés *et al.* 2004, 2009; specimens of *Cercidospora parva* were examined for comparison). *Cercidospora caudata* is distinguished from *C. epithamnomia* by its larger ascospores [(14–)16–24(–30) × (3–)4–6(–7) μm], which are usually strongly heteropolar, with the lower cells curved and attenuated as a tail; *C. epipolytropa* has larger ascospores [(14–)15–19(–22) × (4.5–)5–6(–7) μm]; *C. parva* has a more green exciple, 4–8-spored asci and is a weak parasite; *C. solearispora* differs in its larger ascospores [(15–)17–21(–22) × (4.5–)5–6(–7) μm] with much shorter

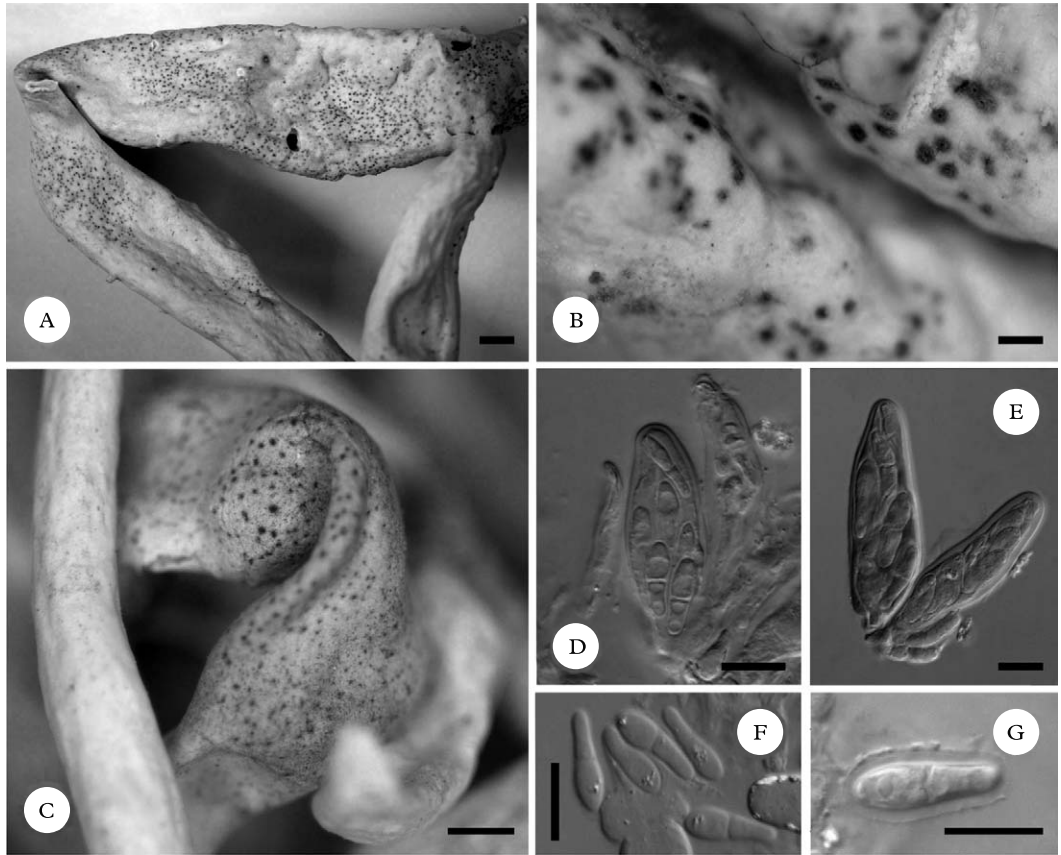


FIG. 2. *Cercidospora epithamnolia* A, B, D & F; A, infection habitus (LE 260574); B, ascomata (LE 233044) D, ascus in water (LE 260590); F, ascospores in K (LE 260590). *Cercidospora thamnogalloides* (holotype) C, E & G; C, infection habitus, note gall; E, asci in I; G, ascospore in water, note halo. Scales: A = 1 mm; B = 200 µm; C = 500 µm; D–G = 10 µm.

and narrower lower cells; *C. verrucosaria* has a more brown exciple and larger ascospores, measuring $(14.5\text{--}15.5\text{--}19.5(-23) \times (4.5\text{--}5\text{--}6(-7)) \mu\text{m}$. Moreover, all of them grow on different host genera (most *Cercidospora* species are restricted to a particular host genus) and have better developed paraphysoids. Comparison with *C. thamnogalloides* Zhurb., which also has 1-septate ascospores, is provided in Table 1. Though scarce interascal filaments are not typical for *Cercidospora*, they have been reported for *C. cladoniicola* Alstrup, *C. macrospora* (Uloth) Hafellner & Nav.-Ros. (type species of the genus) and *C. thamnoliicola* Ihlen (Ihlen

1995; Alstrup 1997; Navarro-Rosinés *et al.* 2004).

Distribution and host. Known from polar desert and arctic tundra of Asia. Commensalistically growing throughout healthy-looking thalli of *Thamnolia vermicularis*.

Additional specimens examined (all on *Thamnolia vermicularis* var. *subuliformis*). **Russia:** *Severnaya Zemlya*: Bolshevik Island, Akhmatova Bay, 79°04' N, 102°45' E, 10 m, 1996, M. Zhurbenko (LE 260574); *ibid.*, Shokalskogo Strait, 79°18' N, 101°40' E, 20 m, 1996, M. Zhurbenko (LE 233044). *Taimyr Peninsula*: Byrranga Mts., Levinson-Lessing Lake, 74°33' N, 98°26' E, 100 m, 1995, M. Zhurbenko (LE 260490). *Wrangel Island*: Naskhok River, 71°25' N, 178°20' W, 10 m, 1998, S. Kholod (LE 260590, LE 260530).

TABLE 1. Distinguishing characteristics of *Cercidospora* species growing on *Thamnolia* (based on the author's own data).

Character	<i>C. epithamnolia</i>	<i>C. thamnogalloides</i>	<i>C. thamnoliae</i>	<i>C. thammollicola</i>
Ascomata	aggregated	aggregated	scattered	aggregated
Paraphysoids	sparse to indistinct	sparse to indistinct	abundant	sparse to indistinct
Exciple	bluish green	bluish grey	bluish green	olive-brown
Spores per ascus	8	8	(4-)8	(2-)4(-6)
Ascospores				
length (µm)	(12-)13-16(-19)	(12-)14-17(-19)	(12.5-)16.5-21.0 (-27.5)	(11-)14.0-17.5(-21)
breadth (µm)	(3-)3.5-4.5(-5)	(3.5-)4-5(-5.5)	(4-)4.5-5.5(-8)	(4.0-)4.5-5.5(-6.5)
l/b ratio	(2.9-)3.1-4.1(-5.0)	(2.7-)3.0-3.8(-4.1)	(2.5-)3.2-4.2(-5.4)	(2.2-)2.6-3.4(-4.2)
septa	(0-)1	1	(1-)3(-4)	(1-)2-3
halo	absent	always present	occasionally present	absent or indistinct
Pathogenicity	commensal	gall-inducer, mild pathogen	mild pathogen or saprotroph	mild pathogen

***Cercidospora thamnogalloides* Zhurb. sp. nov.**

Mycobank no.: MB 563051

Fungus lichenicola in thallis lichenum generis *Thamnolia* crescens. Similis speciei *Cercidospora galligena*, sed differt praecipue ascomatibus minoribus, 80–120 µm diam., ascosporis angustioribus, (12-)14–17(-19) × (3.5-)4-5(-5.5) µm, et hospite diverso.

Typus: Russia, Komi Republic, Northern Ural, Pechora-Ilych State Reserve, headwaters of Pechora River, Yanyupuner Range, Mt. "981", 62°05' N, 59°06' E, 800 m elev., dwarf shrub alpine tundra, on thalli of *Thamnolia vermicularis* var. *subuliformis*, 30 June 1997, M. Zhurbenko 97394 (LE 260510—holotypus).

(Fig. 2C, E & G)

Vegetative hyphae indistinct.

Ascomata perithecioid, black, smooth, subglobose, 80–120 µm diam., with an ostiole mostly of 10–20 µm diam., immersed to slightly protruding in the ostiolar area, arising singly, aggregated in groups of up to 100 or more. *Exciple* dark bluish grey and 15–20 µm thick above, hyaline and 10–15 µm thick below, in surface view resembling *textura angularis* (cells 5–12 µm across), K-. *Hymenial gel* I-, K/I-. *Hamathecium* of sparse or sometimes indistinct paraphysoids, non-capitate, 1.5–2.0 µm wide, septate, scarcely branched. *Asci* obclavate to narrowly elliptic, occasionally subcylindrical, apical wall strongly thickened only in immature asci, rarely with an indistinct ocular chamber, with an indistinct or short stalk, (41–

46–60(-72) × (10-)12–16(-18) µm ($n = 34$; in K elongated up to 85 µm), 8-spored, I-, K/I-. *Ascospores* hyaline, distinctly heteropolar, narrowly soleiform, skittle-shaped, or narrowly oblanceolate, lower cell narrower than the upper one, usually with rounded ends, (12-)14–17(-19) × (3.5-)4-5(-5.5) µm, l/b = (2.7-)3.0-3.8(-4.1) ($n = 57$), with 1 central septum, not constricted at the septum, smooth-walled, with distinct halo 1.5–2.0 µm thick, usually with a few conspicuous guttules per cell best seen in K, arranged biseriate to partly diagonally uniseriate in the ascus.

Anamorph not observed.

Etymology. The specific epithet reflects external similarity of the new species to *Thamnogalla crombiei* (Mudd) D. Hawksw.

Notes. Just two previously known species of *Cercidospora* regularly induce galls: *C. cecidiiformans* Grube & Hafellner (on *Rhizocarpon*) and *C. galligena* Hafellner & Nav.-Ros. (on *Aspicilia* and *Circinaria*). However, occasional production of cecidia was also observed in *C. macrospora* [on the *Lecanora muralis* (Schreb.) Rabenh. group], *C. solearispora*, and *C. stereocaulorum* (Arnold) Hafellner (on *Stereocaulon*) (Hafellner 1993; Navarro-Rosinés *et al.* 2004, 2009; Zhurbenko 2010a). *Cercidospora cecidiiformans* differs from *C. thamnogalloides* in its larger ascomata (130–150 µm diam.),

olive-brown exciple, wider ascospores (13–19 × 5–8 µm), and the I+ red, K/I+ blue reaction of the hymenial gel; *C. galligena* has larger ascomata (mainly 120–190 µm diam.), a brown to violet-black exciple, (4–)6–8-spored asci, and occasionally simple, somewhat wider ascospores [(13·5–)14–19 × 5–6(–7) µm], being only slightly heteropolar; *C. macrospora* has larger ascomata (150–250 µm diam.), 4(–8)-spored asci, and longer, rarely slightly heteropolar, ascospores [(19–)20–25(–30) × 4–6(–7) µm]; *C. solearispora* differs in its larger ascomata (160–230 µm diam.) and larger ascospores [(15–)17–21(–22) × (4·5–)5·0–6·0(–7·0) µm] with a very different shape and size of lower and upper cells; *C. stereocaulorum* has larger, sometimes superficial ascomata [100–200(–300) µm diam.], (2–)4(–8)-spored asci, and (1–)3(–6)-septate, larger ascospores, measuring (13–)18·5–25·5(–30) × (4–)5–7(–8) µm. Moreover, all these species grow on different hosts and all, except *C. macrospora*, have abundant paraphysoids. Galls induced by the new species strongly resemble those caused by *Thamnogalla crombiei*. Curiously, the latter species was also found in the type collection.

Distribution and host. Known from alpine tundra in the type locality in the Northern Ural at the boundary between Europe and Asia. The species induces gall-like swellings on healthy-looking thalli of *Thamnolia vermicularis*. The swellings are concolorous with the host thalli or pale brownish vinaceous. Host thalli are sometimes contorted under infection.

Additional specimen examined. **Russia:** Northern Ural: headwaters of Pechora River, Yanyupuner Range, 62°05' N, 59°06' E, 800 m, on *Thamnolia vermicularis* var. *subuliformis*, 1997, M. Zhurbenko (LE 260560).

***Cercidospora thamnoliae* Zhurb. sp. nov.**

Mycobank no.: MB 563052

Fungus lichenicola in thallis lichenum generis *Thamnolia* crescens. Similis speciei *Cercidospora ochrolechia*, sed differt praecipue ascosporis (1–)3(–4)-septatis, et hospite diverso.

Typus: Russia, Taimyr Peninsula, Byrranga Mts., N of Levinson-Lessinga Lake, 74°33' N, 98°26' E, 180 m

elev., arctic tundra, on thalli of *Thamnolia vermicularis* var. *subuliformis*, 26 August 1995, M. Zhurbenko 95571 (LE 260533—holotypus).

(Fig. 3A–D)

Vegetative hyphae indistinct.

Ascomata perithecioid, black, smooth, subglobose, (60–)90–130(–200) µm diam. (ascomata of more than 150 µm diam. were observed only in LE 260528), with an ostiole of 15–30 µm diam., almost always immersed, rarely slightly protruding in the ostiolar area or exceptionally 1/3 exposed (only in LE 260528), arising singly, dispersed. *Exciple* dark bluish green often with a grey shade and 30–40 µm thick above, hyaline below, in surface view resembling *textura epidermoidea* or *textura angularis* (cells 3–10 µm across), K–. *Hymenial gel* I–, K/I–. *Hamathecium* of abundant paraphysoids, non-capitate, 1·5–2·0 µm wide, septate with individual cells 6–15 µm long, rather frequently branched and anastomosed. *Asci* subcylindrical or usually moderately thickened in lower or sometimes central part, wall 1·5–5·0 µm thick apically and 0·5–1·5 µm laterally, often with a small ocular chamber, with an indistinct or short stalk, (41–)53–69(–80) × (10–)11–15(–18) µm (*n* = 100; in K elongated up to 112 µm), (4–)8-spored, I–, K/I–. *Ascospores* hyaline, usually distinctly heteropolar, narrowly soleiform with a narrower to attenuated lower part, rarely almost narrowly elliptic, upper or both ends often rather acute, (12·5–)16·5–21·0(–27·5) × (4–)4·5–5·5(–8) µm, l/b = (2·5–)3·2–4·2(–5·4) (*n* = 308), with (1–)3(–4) septa (4-septate spores occurred only in LE 260528), usually not or only slightly constricted at the septa (markedly constricted only when overmature or in K), smooth walled, with many small guttules best seen in K, arranged irregularly (often diagonally) uni- or more commonly biseriolate in the ascus; a halo, 1·0–1·5 µm thick, was sometimes observed around spores within the asci.

Anamorph not observed.

Notes. The following eight previously described *Cercidospora* species regularly have

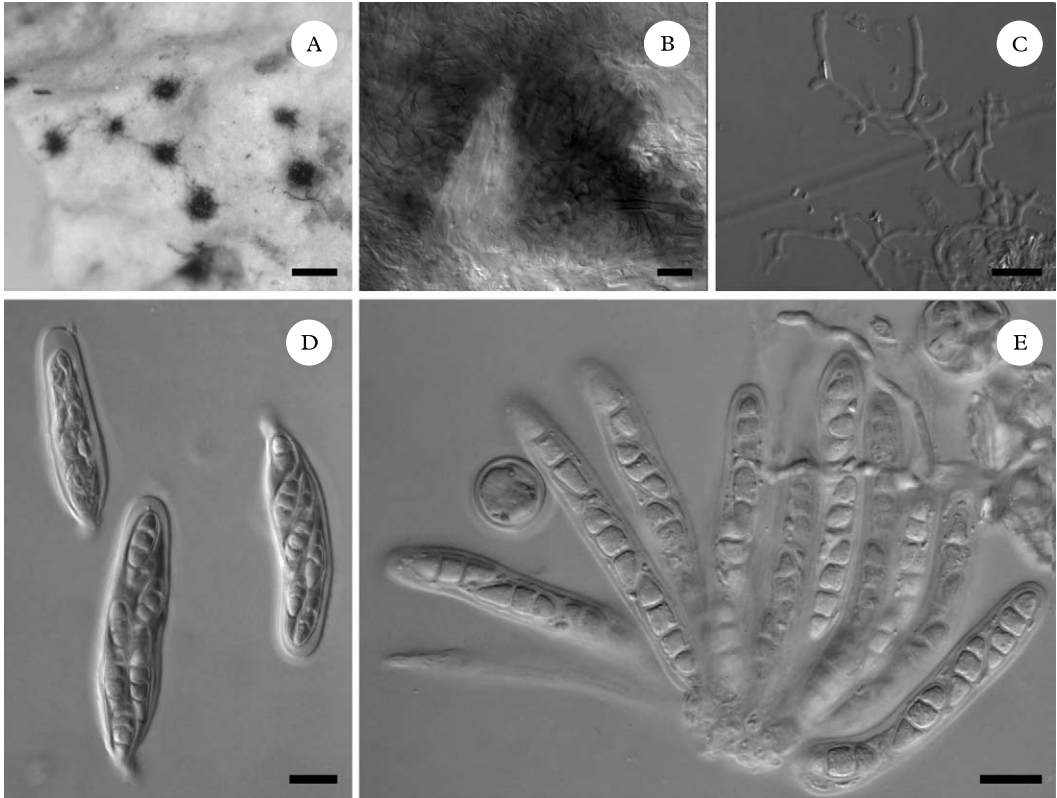


FIG. 3. *Cercidospora thamnoliae* A–D; A, ascomata (LE 260570); B, exciple in surface view in K (LE 260600); C, interascal filaments in K/I (LE 260600); D, asci with spores in I (LE 232882). *Cercidospora thamnoliicola* E, asci with spores in water (LE 260420). Scales: A = 100 μm ; B–E = 10 μm .

ascospores with three or more septa: *C. alpina* Ihlen & Wedin (on *Stereocaulon*), *C. cladoniicola* (on *Cladonia*), *C. decolorella* (Nyl.) O. E. Erikss. & J. Z. Yue (on terricolous algal films, *Mycobilimbia*, *Peltigera*, *Protopannaria*, and *Solorina*), *C. ochrolechia* Zhurb. (on *Ochrolechia* and *Pertusaria*), *C. pluriseptata* (Nyl.) Zopf (on *Lecanora*), *C. punctillata* (on *Biatora*, *Buellia*, *Cladonia*, *Lecanora*, *Micarea*, *Mycobilimbia*, *Peltigera*, *Phaeorrhiza*, *Pilophorus*, *Protopannaria*, *Pso-roma*, *Solorina*, and *Sphaerophorus*), *C. soror* Obermayer & Triebel (on *Arthrurhaphis*), and *C. stereocaulorum* (on *Stereocaulon*) (Nylander 1866; Alstrup *et al.* 1994; Hafellner & Obermayer 1995; Zhurbenko *et al.* 1995; Zhurbenko & Santesson 1996; Alstrup 1997; Zhurbenko 2002, 2008, 2009a, b, 2010b; Zhurbenko & Alstrup 2004; Zhurbenko &

Triebel 2005; Ihlen & Wedin 2007; von Brackel 2010a; specimens of *Cercidospora punctillata* examined for comparison). *Cercidospora alpina* differs from *C. thamnoliae* in its much larger (200–350 μm diam.), semi-immersed ascomata and longer ascospores [(18–)19.5–33(–43) \times (4–)4.5–6.5(–7) μm] with up to 7 septa; *C. decolorella* has somewhat larger ascomata (100–250 μm diam.) and ascospores often with 4–5 septa; *C. cladoniicola* readily differs in its olive-brown exciple; *C. ochrolechia* is most similar to the new species, differing from the latter mainly in the occasional presence of 5-septate ascospores; *C. pluriseptata* has a brown exciple and ascospores with up to 7 septa; *C. punctillata* differs in its somewhat larger and markedly erumpent ascomata, larger ascospores [(14–)18.5–25.0(–33) \times (4–)4.5–6.5(–9) μm]

with (1–)3–5(–6) septa, and distinct pathogenicity; *C. soror* is clearly distinguished by its (2–)4-spored asci; *C. stereocaulorum* has larger, sometimes almost superficial ascospores [100–200(–300) μm diam.], (2–)4(–8)-spored asci, and larger ascospores [(13–)18.5–25.5(–30) \times (4–)5–7(–8) μm] with up to 6 septa. Additionally, all these species grow on different host genera. The comparison with *C. thamnoliicola*, which also has many 3-septate ascospores, is provided in Table 1.

Features such as markedly exposed ascospores of more than 150 μm diam., the occurrence of 4-septate ascospores, and the clear bleaching of host tissues were observed only in LE 260528, the inclusion of which significantly broadened the new species concept. That deviating sample resembles some specimens of *Cercidospora punctillata* agg., which thus might be the fifth *Cercidospora* species growing on *Thamnolia*. However, the latter species is the only one in the genus with an extremely wide host range, which suggests that it might be heterogenous. It is noteworthy in this connection that 20 of 27 *Cercidospora* species are confined to one host genus, the exceptions being, apart from *C. punctillata* [syn. *C. decolorella* var. *lichenicola* (Zopf) O. E. Erikss. & J. Z. Yue], *C. decolorella* (actually indistinguishable from the latter), *C. caudata*, *C. galligena*, *C. ochrolechia*, *C. solearispora*, and *C. wernerii* Nav.-Ros., Calat. & Hafellner. Another consideration is that in LE 260528 *Cercidospora thamnoliae* occurred on an abnormally robust host thallus, which might be the reason for developing comparatively large and exposed ascospores. Further material is needed to confirm the suggested broad species concept or make it narrower.

Specimens examined of *Cercidospora thamnoliae* also fit the protologue of *C. lecidomae* Zhurb. & Triebel, the species distinguished from the earlier described *C. punctillata* (Nyl.) R. Sant. mainly by its smaller and less septate ascospores (Zhurbenko & Triebel 2003). However, careful comparison of additional material of *Cercidospora lecidomae* and *C. punctillata* revealed that ascospores of both species are (1–)3–5(–6)-septate and almost indistinguishable in size: (15.0–)

18.5–27.0(–35.5) \times (4.5–)5.0–6.5(–8.0) μm ($n = 92$) vs. (14–)18.5–25.0(–33) \times (4–)4.5–6.5(–9) μm ($n = 479$). No additional discriminating characters between the two species were found. As a consequence, *Cercidospora lecidomae* Zhurb. & Triebel [*Bibliotheca Lichenologica* **86**: 206 (2003)] is reduced here to synonymy (syn. nov.) with *Cercidospora punctillata* (Nyl.) Sant. [*Lichen forming and Lichenicolous fungi of Fennoscandia* 83 (2004); basionym: *Verrucaria punctillata* Nyl. *Flora* **67**: 223 (1884)]. *Cercidospora lecidomae* has been reported on *Thamnolia vermicularis* by Kukwa & Flakus (2009). Although I did not examine this material, it is likely to belong to *Cercidospora thamnoliae*.

Distribution and host. Known from polar deserts and arctic tundra of the American and Russian Arctic. Mostly found on old or decaying thalli of *Thamnolia vermicularis*, sometimes possibly causing local bleaching of host tissues (their distinct discoloration was observed only in LE 260528).

Additional specimens examined [on *Thamnolia vermicularis* var. *subuliformis* (15), var. *vermicularis* (Sw.) Schaer. (2)]. **Canada:** *Canadian Arctic Archipelago:* Ellef Ringnes Island, Isachsen Bay, 78°47' N, 103°33' W, 40 m, 2005, N. Matveeva (LE 260316, LE 260526).—**Russia:** *Nenets Region:* Malozemel'skaya Tundra, Seduiyakh River, 68°23' N, 53°15' E, 1998, O. Lavrinenko (LE 232884). *Sverdrupa Island in Kara Sea:* 74°33' N, 79°25' E, 10 m, 1992, Yu. Kozhevnikov (LE 260483). *Severnaya Zemlya:* Bolshevik Island, Mikoyana Bay, 79°18' N, 101°55' E, 10 m, 1996, M. Zhurbenko [LE 210306, erroneously reported as *Cercidospora thamnoliicola* in Zhurbenko (2008); LE 260573]; *ibid.*, Shokalskogo Strait, 79°16' N, 101°40' E, 20 m, 1996, M. Zhurbenko (LE 233034, LE 232844, LE 232813, LE 260583, LE 260528); Sedova Archipelago, 79°25' N, 91°40' E, 1930, V. Savicz [LE 207056, erroneously reported as *C. thamnoliicola* in Zhurbenko & Santesson (1996)]. *Novosibirskie Islands:* Zhokhova Island, 76°08' N, 152°45' E, 1989, M. Samarskii [LE 207223, erroneously reported as *C. thamnoliicola* in Karatygin *et al.* (1999)]. *Wrangel Island:* Klark River, 71°07' N, 178°14' W, 100 m, 1998, S. Kholod (LE 232882); Naskhok River, 71°24' N, 178°08' W, 5 m, 1998, S. Kholod (LE 260570, LE 260600); Neozhidannaya River, 71°02' N, 179°10' E, 110 m, 1992, S. Kholod (LE 260374a).

Cercidospora thamnoliicola Ihlen

Graphis Scripta 7(1): 18 (1995); type: Norway, Nordland, on *Thamnolia vermicularis* var. *subuliformis*, Norman (O—holotype, n. v.).

Notes. Considering that the newly examined specimens reveal some discrepancies with the protologue of this insufficiently known species (Ihlen 1995), its full description is provided here.

Vegetative hyphae indistinct.

Ascomata perithecioid, black, smooth, subglobose to broadly ovate, 50–125 µm diam., with an ostiole of 15–20(–40) µm diam., immersed to slightly protruding in the ostiolar area, arising singly or sometimes contiguous, aggregated in groups of up to 100 or more at the apices or central parts of the host thalli. *Exciple* medium to dark olive-brown to olivaceous buff and 17–25 µm thick above, hyaline and 8–12 µm thick below, in surface view resembling *textura epidermoidea* or *textura angularis* (cells 3–8 µm across), K+ yellowish brown. *Hymenial gel* I–, K/I–. *Hamathecium* of sparse or sometimes indistinct, non-capitate, *c.* 1.5 µm wide, septate, scarcely branched paraphysoids. *Asci* cylindrical or slightly thickened in the central or lower part, wall 1–3 µm thick apically and 0.5–1.5 µm laterally, ocular chamber not observed (with shallow ocular chamber from the protologue), (35–)46–62(–65) × (7–)8–10 µm (*n* = 46; in K elongated up to 76 µm), (2–)4(–6)-spored (almost always with 4 well-developed spores, very rare with 2–3 normal and 1–2 abortive spores or with 4 normal and 2 abortive spores) [37–41 × 6–8(–12) µm, 4(–6)-spored taken from the protologue], I–, K/I– (Fig. 3E). *Ascospores* hyaline, usually distinctly heteropolar, narrowly elliptic, mostly with narrower to attenuated lower or occasionally upper part and often with rather acute ends, (11–)14.0–17.5(–21) × (4.0–)4.5–5.5(–6.5) µm, l/b = (2.2–)2.6–3.4(–4.2) (*n* = 158), with (1–)2–3 septa (3-septate according to the protologue), not or sometimes slightly constricted at the septa, smooth-walled, distinct halo not observed (halonate in the protologue), often with a few conspicuous guttules per cell best seen in K, uniseriate or diagonally arranged in the ascus.

Anamorph not observed. Infected host parts usually are slightly greyish and ‘scurfy’, sometimes also somewhat curved or swollen.

Poorly developed paraphysoids (also stressed in the protologue), asci with an indistinct ocular chamber, and K+ reaction of the exciple are not typical for *Cercidospora*. This evidently rare species has been confused with the more frequent *C. thamnoliae* (see above under the latter species) and thus was in fact formerly known only from two finds in the Norwegian mountains (Ihlen 1995). Here it is confirmed for this type region and also reported new to the Asian Arctic.

The occurrence of four *Cercidospora* species on one host species (Table 1) is remarkable for lichenicolous fungi in general, but not for this particular lichenicolous fungal genus, where almost half of the host lichen genera support more than one *Cercidospora* species. For instance, three *Cercidospora* species are known on *Aspicilia* and *Circinaria* (*C. galligena*, *C. solearispora* and *C. wernerii*) and another three on *Caloplaca* [*C. caudata*, *C. epicallospisma* Arnold and *C. epicarphinea* (Nyl.) Grube & Hafellner] (Navarro-Rosinés *et al.* 2004, 2009). It may also reflect the high heterogeneity of *Thamnolia vermicularis* populations (Nelsen & Gargas 2009a, b). It is also possible that three *Cercidospora* species with indistinct paraphysoids, treated above (Table 1), might be better disposed in another genus.

Specimens examined [all in arctic or alpine tundras on *Thamnolia vermicularis* var. *subuliformis* (2), var. *vermicularis* (1)]. **Norway:** Troms County: Skibotndalen Valley, 69°16' N, 20°23' E, 950 m, 2003, M. Zhurbenko (LE 260460).—**Russia:** Taimyr Peninsula: Byrranga Mts., Levinson-Lessinga Lake, 74°24' N, 98°38' E, 150 m, 1995, M. Zhurbenko (LE 260420). Chukchi Peninsula: Provideniya, 64°27' N, 173°11' W, 100 m, 2001, M. Zhurbenko (LE 260440).

Cladosporium licheniphilum Heuchert & U. Braun

Herzogia 19: 12 (2006); type: Russia, Altai, on *Pertusaria alpina* Hepp ex H. E. Ahles, 1999, Davydov (LE—holotype!).

Notes. New to the Arctic. *Thamnolia* is a new host genus.

Specimen examined. **Russia:** Taimyr Peninsula: Byrranga Mts., Levinson-Lessinga Lake, 74°32' N, 98°33' E, 250 m, arctic tundra, on damaged portions of

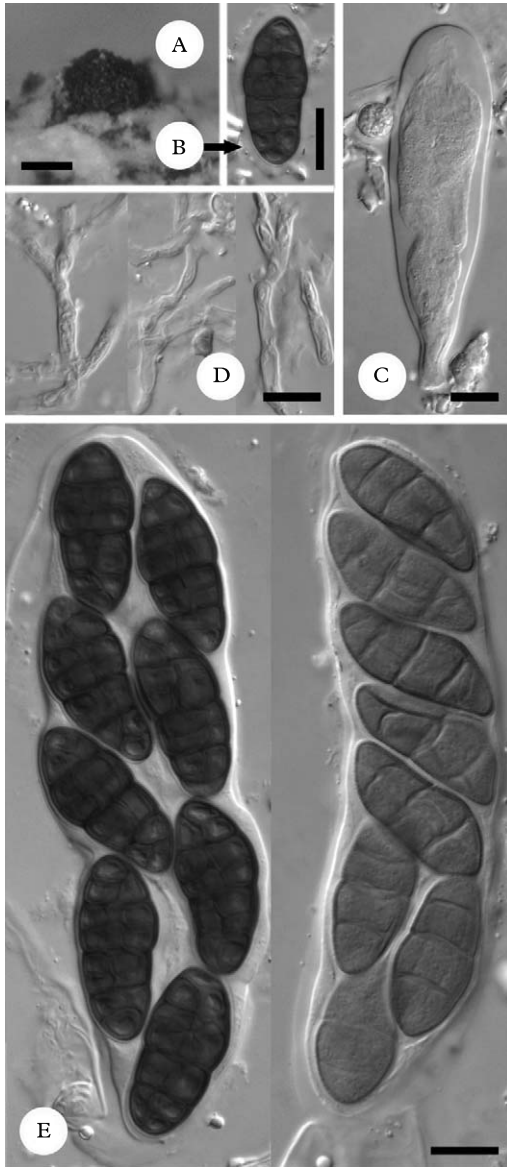


FIG. 4. *Dacampia thamnoliicola* (LE 207531b). A, ascomata; B, ascospore in water, note halo; C, immature ascus in water; D, interascal filaments in water; E, asci with spores in water. Scales: A = 100 μ m; B–E = 10 μ m.

Thamnolia vermicularis var. *subuliformis* thalli, 1995, M. Zhurbenko (LE 260309, HAL 2444 F; det. U. Braun).

***Dacampia thamnoliicola* Zhurb. ad int.**

(Fig. 4)

Ascomata perithecioid, black, subglobose, 100–200 μ m diam., ostiolate, erumpent to sessile. Exciple brown, in surface view similar to *textura angularis*, composed of thick-walled, angular, pseudoparenchymatous cells. Hamathecium formed by well-developed interascal filaments, which are 1.5–3.5 μ m wide, septate, and branched. Asci fissitunicate, clavate, with a distinct foot, 70–100 \times 22–24 μ m ($n = 5$), 8-spored. Ascospores initially pale, then dark brown, elliptic, with rounded or rather acute ends, (23–)25–29(–31.5) \times (10.5–)11–13(–14) μ m, l/b = (1.8–)2.1–2.5(–2.7) ($n = 45$), muriform when mature with 5–7 transverse septa and a longitudinal or oblique septum in central cells, slightly constricted at the septa, wall ornamented ($\times 1000$), with halo 1.5–2.5 μ m thick, guttules not observed, arranged diagonally uniseriate to biseriate in the ascus. On \pm decaying podetia of the host.

Notes. As noted by Halici & Hawksworth (2008), the lichenicolous species in the *Dacampiaceae*, with the exception of *Pyrenidium actinellum* Nyl., are almost always host-specific. None of the 13 previously known *Dacampia* A. Massal. species has been found on *Thamnolia*. Among them, ascospores with up to 7 trans-septa were known in *D. cyrtellae* Brackel (on *Lecania*), *D. lecaniae* Kocourk. & K. Knudsen (on *Lecania*), *D. leptogiicola* (D. Hawksw.) D. Hawksw. (on *Collema*, *Leptogium*, and *Pannaria*), and *D. muralicola* Halici & D. Hawksw. (on *Protoparmeliopsis*) (Hawksworth 1975; Etayo & Breuss 1996; Halici & Hawksworth 2008; Lopez de Silanes *et al.* 2009; von Brackel 2010b; Kocourková & Knudsen 2010). *Dacampia cyrtellae* differs from *D. thamnoliicola* in its smaller ascomata (110–160 μ m diam.) and smaller ascospores [(19.5–)21.2–24.9(–26.0) \times (6.5–)6.8–8.3(–9) μ m]; *D. lecaniae* seems to be the closest to this presumably new species, including the presence of a conspicuous gelatinous sheath, but has somewhat smaller ascospores, measuring (21–)22.8–26.5(–28) \times (8–)9.5–12.0 μ m; *D. leptogiicola* has smaller ascospores (21–25 \times 5.0–6.5 μ m); and *D. muralicola* has somewhat smaller ascospores [21–26(–31.5) \times

(7.0–)9.0–12.5(–14.5) μm] and smaller ascocmata (95–120 μm diam.). Ascospores of *Dacampia thammoliicola* are not that typical for the genus in being halonate and ornamented; the first feature also shared by *D. lecaniae* and *D. rubra* Halici, Candan & Calat. and the second one by *D. rhizocarpicola* D. Hawksw., *D. rubra*, and *D. xanthomendozae* Etayo & Halici (Halici & Hawksworth 2008; Halici *et al.* 2009a, b).

Specimen examined. **Russia:** *Severnaya Zemlya*: Sedova Archipelago, 79°25' N, 91°40' E, on *Thamnolia vermicularis* var. *vermicularis*, 1930, *V. Savicz* 2017b (LE 207531b).

Epithamnolia Zhurb. gen. nov.

Mycobank no.: MB 563053

Genus lichenicola ad Coelomycetes pertinens. Conidiomata plus minusve nigra, subglobosa ad cupuliformia, cum muris textura globulosa vel porrecta, subimmersa ad superficialia, singularia, dispersa. Conidiophora desunt. Cellulae conidiogenae enteroblasticae, phialidicae, non prolifericae, hyalinae, lagenulatae vel anguste ellipticae. Conidia acrogena, hyalina, cylindrica, (0–)1(–2?) septata, laevia.

Typus: *Epithamnolia karatyginii* Zhurb.

Genus lichenicolous, belonging to the Coelomycetes.

Conidiomata pycnidial, blackish, rugose, irregularly subglobose, but becoming cupuliform with age, initially almost closed, then with an irregular opening, subimmersed in thalli of *Thamnolia* species to finally superficial, arising singly, dispersed. *Exciple* in cross-section dark to medium brown throughout, in surface view resembling *textura angularis/globulosa* or *textura porrecta*, K–. *Conidiophores* absent. *Conidiogenous cells* lining the pycnidial cavity, enteroblastic, phialidic, with indistinct collarette and periclinal thickening, not proliferating, hyaline, lageniform to narrowly elliptic, smooth-walled. *Conidia* acrogenous, arising singly, not catenate, hyaline, cylindrical, with obtuse to sometimes slightly truncated ends, \pm straight, (0–)1(–2?) septate, not constricted at the septum, smooth-walled, sometimes with sparse inconspicuous guttules.

Notes. Amongst the non-lichenicolous pycnidial fungal genera, the new genus mainly

recalls *Ascochyta* Lib. agg., *Clypeopycnis* Petr., *Didymochaeta* Sacc. & Ellis, *Gelatinopycnis* Dyko & B. Sutton, *Pocillopycnis* Dyko & B. Sutton emend. DiCosmo, *Pseudocenangium* P. Karst., and *Septopatella* Petr. (Dyko & Sutton 1979; DiCosmo 1980; Sutton 1980; Mel'nik 2000). However, there are significant differences. In *Ascochyta* agg. the conidiomata are non-cupulate; in *Clypeopycnis* the conidiomata are non-cupulate, and conidiophores are present; in *Didymochaeta* Sacc. & Ellis the conidiomata are non-cupulate, and the conidiogenous cells have a distinct collarette and a periclinal thickening; in *Gelatinopycnis* the conidiomata are closed and have a complex wall, and conidiophores are present; in *Pocillopycnis* conidiophores are present, the conidiogenous cells are sympodially proliferating, and the conidia are holoblastic, lunate to sigmoid, 3–10-septate; in *Pseudocenangium* conidiophores are present and the conidiogenous cells are annelidic; in *Septopatella* conidiophores are present, and the conidiogenous cells are sympodially proliferating. Considering the coelomycetes known to occur on lichens, *Epithamnolia karatyginii*, the type species of this monotypic genus, resembles species of *Hainesia* Ellis & Sacc. in having finally cupulate conidiomata and hyaline, cylindrical, septate conidia (Etayo & Diederich 1996a; von Brackel 2009). However, the latter are easily distinguished from the new species by their branched conidiophores (Punithalingam & Spooner 1997). *Epithamnolia karatyginii* may also resemble the lichenized *Woessia fusarioides* D. Hawksw., Poelt & Tsch.-Woess., which differs from the former in having white, shallow cupuliform to disc-like conidiomata, falcate, non-septate conidia and in the lignicolous life habit (Hawksworth & Poelt 1986).

Epithamnolia karatyginii Zhurb. sp. nov.

Mycobank no.: MB 563054

Fungus lichenicola in thallis lichenum generis *Thamnolia* crescens. Conidiomata 110–220 μm diam. Cellulae conidiogenae (5–)6.5–9(–10) \times (1.5–)2–3 μm . Conidia (14–)18.5–27(–32) \times (1–)1.5–2(–2.5) μm .

Typus: Canada, British Columbia, Wells Gray Provincial Park, Mt. Raft, 51°44' N, 119°50' W, 2100 m

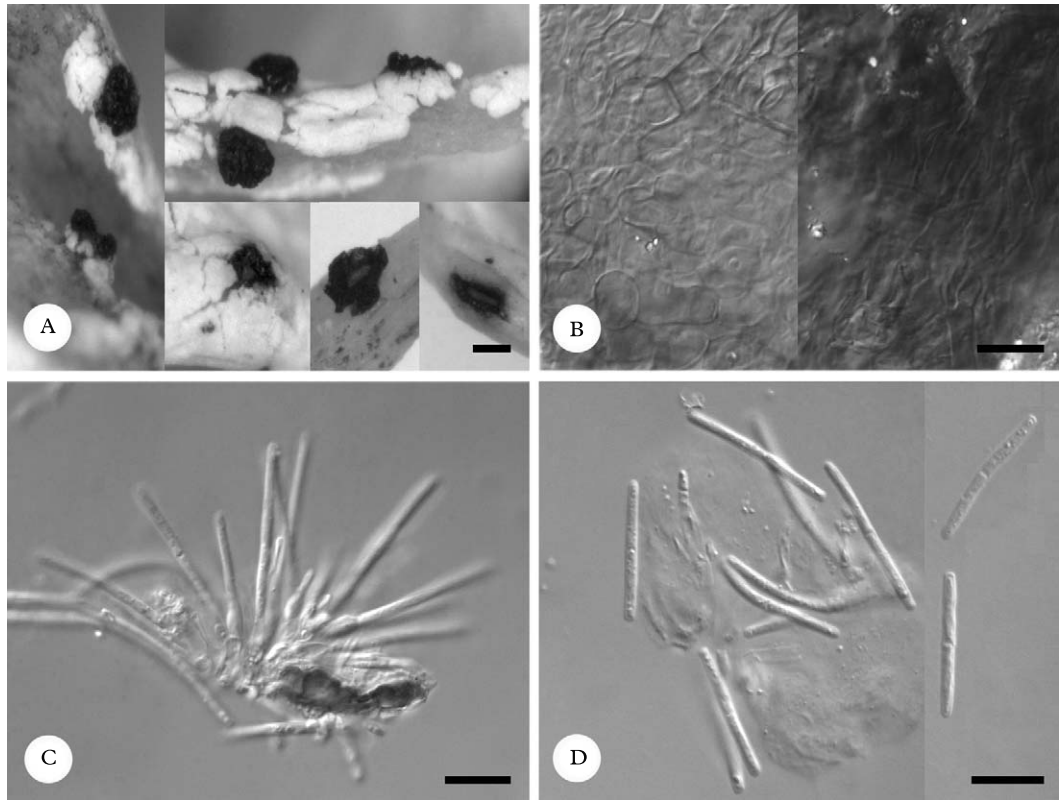


FIG. 5. *Epithamnolia karatyginii* (holotype). A, conidiomata; B, exciple in water; C, conidiogenous cells and conidia in water; D, conidia in water. Scales: A = 100 μm ; B–D = 10 μm .

elev., alpine tundra with sparse *Picea engelmannii*, on moribund thalli of *Thamnolia vermicularis* var. *subuliformis*, 3 August 2002, M. Zhurbenko 02343 (LE 260498—holotypus).

(Fig. 5)

Vegetative hyphae pale brown, somewhat flexuose, 2.5–5.0 μm wide, scarcely septate, constricted at the septa, immersed.

Conidiomata pycnidial, blackish, glossy, rugose, irregularly subglobose at first, becoming cupuliform with age, 110–220 μm diam., initially almost closed, then with an irregular opening (20–)40–60(–100) μm across, exposing the pale brown interior, sub-immersed to finally superficial, arising singly, dispersed. *Exciple* in cross-section dark to medium brown throughout, basally of 3–5 cell layers, in surface view resembling *textura angularis/globulosa* (cells 3.5–10.0 μm across)

or *textura porrecta*, K–. *Conidiophores* absent. *Conidiogenous cells* lining the pycnidial cavity, enteroblastic, phyalidic, with indistinct collarette and periclinal thickening, not proliferating, hyaline, lageniform to narrowly elliptic, (5–)6.5–9.0(–10) \times (1.5–)2–3 μm ($n = 39$), smooth-walled. *Conidia* abundant, acrogenous, arising singly, not catenate, hyaline, cylindrical, with obtuse to sometimes slightly truncated ends, \pm straight, (14–)18.5–27.0(–32) \times (1.0–)1.5–2.0(–2.5) μm , $l/b = (6.0–)9.8–17.4(–21.3)$ ($n = 122$), (0–)1(–2?)–septate, not constricted at the septum, smooth-walled, sometimes with sparse inconspicuous guttules.

Etymology. The species is named after the eminent Russian mycologist Dr Igor V. Karatygin, the main author of the first

catalogue of the Russian Arctic fungi (Karatygin *et al.* 1999).

Distribution and host. Known from polar deserts, arctic and alpine tundras of North America and Eurasia. On \pm damaged basal or apical parts of *Thamnolia vermicularis* thalli, sometimes intermixed with *Sphaerellothecium thamnoliae* Zhurb. or *Stigmidium frigidum* (Th. Fr. ex Sacc.) Alstrup & D. Hawksw.

Additional specimens examined [on *Thamnolia vermicularis* var. *subuliformis* (5), var. *vermicularis* (1)]. **Russia:** *Severnaya Zemlya:* Bolshevik Island, Shokalskogo Strait, 79°16' N, 101°40' E, 20 m, 1996, *M. Zhurbenko* (LE 232933). *Northern Ural:* headwaters of Pechora River, Yanypupuner Range, 62°05' N, 59°06' E, 800 m, 1997, *M. Zhurbenko* (LE 260538a, intermixed with *Sphaerellothecium thamnoliae* var. *thamnoliae*). *Kola Peninsula:* Barents Sea coast, Voron'ya River mouth, 69°09' N, 35°50' E, 20 m, 1997, *M. Zhurbenko* (LE 260448). *Taimyr Peninsula:* Byrranga Mts., Bolshaya Bootankaga River, 74°30' N, 97°40' E, 350 m, 1995, *M. Zhurbenko* (LE 232994b, intermixed with *Stigmidium frigidum*). *Yakutiya:* Laptev Sea coast, Tiksi, 71°40' N, 128°40' E, 50 m, 1998, *M. Zhurbenko* (LE 260444b, intermixed with *Stigmidium frigidum*).

Geltingia associata (Th. Fr.) Alstrup & D. Hawksw.

Meddel. Grønland, Biosc. 31: 33 (1990); type: Spitsbergen, Danskøen, 1861, *Malmgren* (UPS—lectotype, n. v.).

Note. This fungus mostly grows on *Ochrolechia* spp., but has also been recorded from *Thamnolia* (Walker 1970; Zhurbenko & Santesson 1996; Diederich *et al.* 2010).

Specimen examined. **Russia:** *Taimyr Peninsula:* Byrranga Mts., Levinson-Lessinga Lake, 74°31' N, 98°36' E, 250 m, arctic tundra, on moribund thalli of *Thamnolia vermicularis* var. *subuliformis*, 1995, *M. Zhurbenko* (LE 260468).

Lichenoconium usneae (Anzi) D. Hawksw.

Persoonia 9(2): 185 (1977); type: Italy, on *Usnea filipendula* Stirt. agg. (K—isotype, n. v.).

Note. This common coelomycete has been recorded from no less than 29 lichen genera, including one previous record on *Thamnolia* (Hafellner & Türk 1995).

Specimens examined. **Russia:** *Taimyr Peninsula:* Byrranga Mts., Levinson-Lessinga Lake, 74°32–33' N, 98°26–33' E, 180–300 m, arctic tundra, on partly mori-

bund thalli of *Thamnolia vermicularis* var. *subuliformis*, 1994, *M. Zhurbenko* (LE 207532c); *ibid.*, 1995, *M. Zhurbenko* (LE 260544).

Lichenopeltella thamnoliae R. Sant.

Thunbergia 28: 7 (1998); type: Colombia, Boyacá, on *Thamnolia vermicularis* var. *vermicularis*, 1972, *Cleef* (UPS—holotype, n. v.).

Notes. Previously known from Colombia, Venezuela, Ecuador, and Peru (Santesson 1998; Etayo 2010). New to Bolivia. *Thamnolia papelillo* var. *subsolida* (M. Sató) R. Sant. is a new host variety.

Specimen examined. **Bolivia:** 25 km S of Sorata, 1 km NE of Laguna Ajuyani, 15°53' S, 68°39' W, 4250 m, on *Thamnolia papelillo* var. *subsolida*, 2000, *A. Elvebakk* (LE).

Merismatium thamnoliicola Alstrup & E. S. Hansen

Graphis Scripta 12: 43 (2001); type: Greenland, Thule District, on *Thamnolia vermicularis*, 1992, *Alstrup* (C—holotype, n. v.).

Vegetative hyphae pale to medium brown, 1.5–2.5 μ m wide.

Ascomata perithecioid, black, subglobose, often with a small papilla, 100–150 μ m diam., 1/4–3/4 protruding (superficial according to the protologue). **Hymenial gel** I+ brownish orange, K/I+ blue. **Ascospores** initially hyaline, then pale to medium olivaceous buff, snuff brown, or greyish brown, at maturity with contrasting darker septa, elliptic to oblanceolate (Fig. 6), constricted lower ends noted in the protologue were observed only in some overmature spores and are evidently the result of spore destruction, (14–)16.5–24.0(–34) \times (6–)6.5–8.5(–9) μ m, l/b = (1.6–)2.1–3.3(–4.3) ($n = 89$) (22–30 \times 8.5–9.5 μ m according to the protologue), with (3–)5–7(–8) transverse septa and a longitudinal or oblique septum in central or all cells, smooth-walled.

Notes. Mostly found on moribund bases of host thalli, pathogenicity not observed. The species was described and known previously from two collections in Greenland (Alstrup & Hansen 2001) and thus is new to Eurasia. Examination of new material revealed some

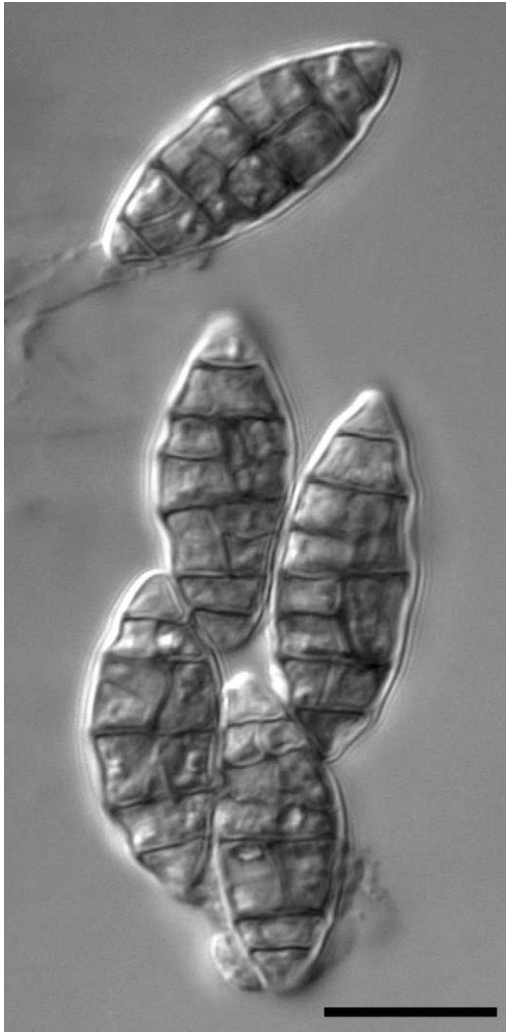


FIG. 6. *Merismatium thamnolicola*, old ascospores in I (LE 260554). Scale = 10 μ m.

discrepancies with its protologue, described above.

Specimens examined (all in polar desert, arctic or alpine tundras on *Thamnolia vermicularis* var. *subuliformis*). **Russia:** *Severnaya Zemlya:* Bolshevik Island, Akhmatova Bay, 79°04' N, 102°45' E, 10 m, 1996, M. Zhurbenko (LE 260554); Sedova Archipelago, 79°25' N, 91°40' E, 1930, V. Savicz (LE 260430, LE 260450). *Taimyr Peninsula:* Byrranga Mts., Bolshaya Bootankaga River, 74°20' N, 98°05' E, 400 m, 1991, V. Kuvaev (LE 260473). *Eastern Sayan Mts.:* Kryzhina Range,

headwaters of Belyi Kitat River, 53°59' N, 95°32' E, 1500 m, 2009, M. Zhurbenko (LE 260373).

Odontotrema santessonii Zhurb., Etayo & Diederich

Lichenologist 34: 495; type: Russia, Chukchi Peninsula, on *Thamnolia vermicularis* var. *subuliformis*, 1971, Yurtsev (LE 207696—holotype!; hb. Diederich—iso-type!).

Notes. *Ascomata* up to 450 μ m diam., finally sometimes almost sessile. *Hymenium* I+ brownish red to coral throughout. *Ascospores* hyaline, narrowly oblanceolate, (15–)18–23(–25) \times (3–)3.5–4.5(–5) μ m, l/b = (3.8–)4.7–5.9(–6.6) ($n = 39$), with (3–)7–8 transverse septa and often a few longitudinal or oblique septa in central cells, arranged \pm in two 4-spored fascicles in the ascus. Pathogenicity not observed. New to North America.

Specimens examined [all in polar desert or arctic tundra on *Thamnolia vermicularis* var. *subuliformis* (5), var. *vermicularis* (4)]. **Canada:** *Canadian Arctic Archipelago:* Axel Heiberg Island, Bunde Fjord, 80°30' N, 94°36' W, 30 m, 1999, N. Marveeva (LE 260543).—**Russia:** *Severnaya Zemlya:* Bolshevik Island, Akhmatova Bay, 79°04' N, 102°45' E, 10 m, 1996, M. Zhurbenko (LE 232853). *Taimyr Peninsula:* Byrranga Mts., Bolshaya Bootankaga River, 74°30' N, 97°40' E, 200 m, 1995, M. Zhurbenko 95309 (LE 232814). *Yakutiya:* Laptev Sea coast, Tiksi, 71°39–40' N, 128°40–45' E, 50 m, 1998, M. Zhurbenko (LE 232854, LE 260524, LE 260324); Lena River delta, Stolb Island, 72°24' N, 126°40' E, 50 m, 1998, M. Zhurbenko (LE 260364). *Wrangel Island:* Neizvestnaya River, 71°11' N, 179°15' W, 170 m, 1987, S. Kholod (LE 232962). *Chukotka:* Gil'mymlineiveem River, 65°48' N, 173°15' W, 1977, I. Makarova (LE 233094).

Odontotrema thamnoliae Zhurb., Diederich & Etayo

Lichenologist 34: 497; type: Russia, Chukchi Peninsula, on *Thamnolia vermicularis* var. *vermicularis*, 1971, Makarova (LE 207695—holotype!).

Notes. *Hymenium* I+ orange except the uppermost part, which is I+ blue. *Ascal wall* I+ blue at the apex, I– below. Sometimes slightly bleaching the host tissues. New to North America.

Specimens examined [all in arctic or alpine tundras on *Thamnolia vermicularis* var. *subuliformis* (3), var. *vermicularis* (3)]. **USA:** *Alaska:* Seward Peninsula, 7 km NE of Nome, 64°33' N, 165°21' W, 220 m, 2001, M. Zhurbenko (LE 260376).—**Russia:** *Kola Peninsula:* Barents

Sea coast, Voron'ya River mouth, 69°09' N, 35°50' E, 20 m, 1997, *M. Zhurbenko* (LE 260464). *Western Sayan Mts.*: Kulumys Range, 52°51' N, 93°17' E, 1700 m, 2010, *M. Zhurbenko* (LE 260588). *Taimyr Peninsula*: Byrranga Mts., Levinson-Lessinga Lake, 74°24' N, 98°38' E, 150 m, 1995, *M. Zhurbenko* (LE 260597). *Yakutiya*: Laptev Sea coast, Tiksi, 71°37' N, 128°54' E, 70 m, 1998, *M. Zhurbenko* (LE 233074). *Chukotka*: Kolyuchinskaya Bay, Yuniveem River mouth, 66°40' N, 173°54' W, 20 m, 1980, *A. Katenin* & *M. Zhurbenko* (LE 232864).

Phaeospora arctica Horáková & Alstrup

Graphis Scripta 6: 61 (1994); type: Greenland, Disco Island, on *Arctocetraria andreievii* (Oxner) Kärnefelt & A. Thell, 1983, *Poelt* (PRM 842918—holotype, n. v.).

Ascomata black, subglobose, *c.* 120 µm diam., semi-immersed. *Hymenial gel* appears I+ pale red. *Hamathecium* not observed. *Asci* subcylindrical to obclavate, with a long internal apical beak, *c.* 55–60 × 11–14 µm, 6–8-spored, I–. *Ascospores* hyaline to pale cinnamon-brown, narrowly elliptic (mostly) to elliptic and often slightly narrower below, (10–)15·5–20·5(–22) × (4·5–)5–6(–8·0) µm, *l/b* = (1·7–)2·7–3·9(–4·7) (*n* = 51), (1–)3-septate, not constricted at the septa, smooth-walled, without halo, guttulate, biseriate in the ascus. Growing on the bleached, possibly moribund base of the host's podetia.

Notes. The specimen fits well the species concept of *Phaeospora arctica*, except staining of the hymenial gel with I, not reported before (Horáková & Alstrup 1994; Zhurbenko & Santesson 1996). The species was formerly known on *Allocetraria*, *Arctocetraria*, and *Arctoparmelia*, thus *Thamnolia* being a new host genus.

Specimen examined. **USA:** *Alaska*: Great Kobuk Sand Dunes, 67°05' N, 158°58' W, 50 m, on *Thamnolia vermicularis* var. *subuliformis*, 2000, *M. Zhurbenko* (LE 260359).

Phoma thamnoliae Zhurb. ad int.

(Fig. 7)

Vegetative hyphae pale brown, 3–5(–7) µm diam., septate, constricted at the septa.

Conidiomata pycnidial, black, subglobose, indistinctly papillate, 75–110 µm diam., with

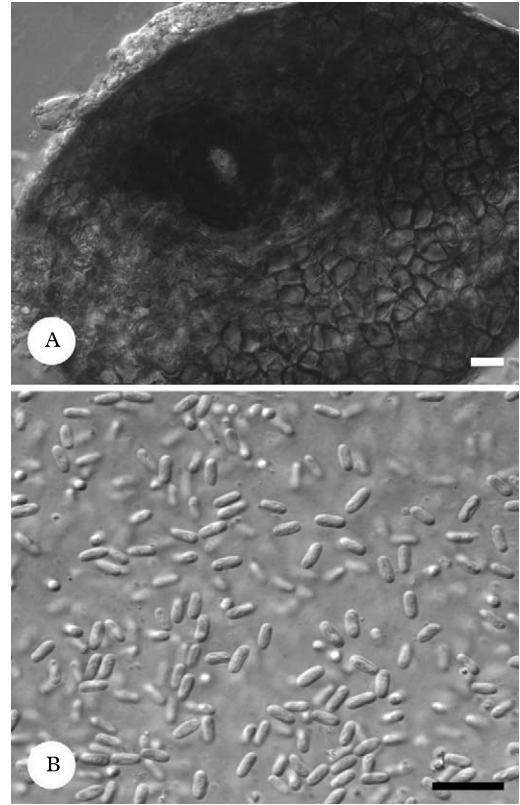


FIG. 7. *Phoma thamnoliae* (LE 260349). A, squashed peridium in water; B, conidia in water. Scales: A & B = 10 µm.

an ostiole of *c.* 10 µm diam., subimmersed to almost sessile. *Pycnidial wall* brown, darker around the ostiole, in surface view composed of angular pseudoparenchymatous cells (*textura angularis*) 4–10 µm across, K–. *Pycnidial gel* I–, K/I–. *Conidiogenous cells* not observed clearly, probably ampulliform, *c.* 5 × 2 µm. *Conidia* hyaline, oblong to occasionally elliptic, with rounded ends, (3·5–)4–5(–5·5) × (1·5–)2·0(–2·5) µm, *l/b* = (1·6–)2·0–2·6(–2·8) (*n* = 135), non-septate, smooth-walled, with 2–3 conspicuous, usually apical, guttules, abundant, arising singly. Infected parts of the host thalli are bleached or pale red.

Notes. The rather scant material does not permit a formal description of this evidently new *Phoma* Sacc. species. Most (*c.* 70%) of

the 22 currently recognized lichenicolous species of *Phoma* are restricted to a single host genus, and none of them has been reported on *Thamnolia* (*Icmadophilaceae*, *Pertusariales*). The only other *Phoma* species hosted by a *Pertusariales* genus (*Dibaeis*) is *P. maculiformans* Ihlen (Ihlen 1998), which readily differs from *P. thamnoliae* in its larger pycnidia (120–200 µm diam.) and non-guttulate, longer conidia, measuring 5–6 (–7) × 2.0–2.5 µm. The shape and size of the conidia are among the most important diagnostic morphological characters in *Phoma* taxonomy. Of the other lichenicolous species referred to the genus, *Phoma thamnoliae* is most similar in these characters to *P. aggregata* Calat. & Etayo, *P. cladoniicola* Diederich, Kocourk. & Etayo, *P. grumantiana* Zhurb. & Diederich, *P. lecanorina* Diederich, *P. melanohaleicola* D. Hawksw. & Earland-Benn., *P. peltigerae* (P. Karst.) D. Hawksw., and *P. rozziana* Etayo (Hawksworth 1981; Diederich 1986; Etayo 1996; Calatayud & Etayo 2001; Hawksworth & Cole 2004; Earland-Bennett *et al.* 2006; Diederich *et al.* 2007; Etayo & Sancho 2008). However, *Phoma aggregata* (on *Diploschistes*) is clearly separated from the new species by the minute pycnidia (30–50 µm diam.), aggregated in dense groups of up to 200; *P. cladoniicola* (on *Cladonia*) has larger conidia [(4–)4.5–6.0 (–7.5) × (2–)2.5–3.0(–3.5) µm]; *P. grumantiana* is very similar to the studied material in the sizes of pycnidia (50–100 µm diam.) and conidia [(3–)4–5(–6) × 1.5–2.0(–3) µm], but could be distinguished by its host selection (*Cladonia*, *Lecanorales*); *P. lecanorina* (on *Lecanora* and *Flavoparmelia*) differs in its smaller pycnidia (15–60 µm diam.), the peridium, being dark green above and subhyaline below, and narrower conidia (3.2–5.0 × 1.2–1.6 µm); *P. melanohaleicola* (on *Melanohalea*) has slightly longer conidia (5–5.5 × 2–2.5 µm); *P. peltigerae* (on *Peltigera*) has larger pycnidia (up to 200 µm diam.) and conidia [(4–)4.5–6.0(–7) × 2.0–2.5(–3) µm]; and *P. rozziana* (on *Pseudocyphellaria*) has smaller pycnidia, measuring 50–80 µm diam. *Phoma thamnoliae* might also be compared with *Briancoppinsia cytospora* (Vouaux) Diederich, Ertz, Lawrey & van den

Boom [syn. *Phoma cytospora* (Vouaux) D. Hawksw.], growing on a wide range of different host genera (Diederich *et al.* 2012). However, that species differs in its smaller pycnidia (40–80 µm diam.), the peridium reacting K+ dark olivaceous, pycnidial gel reacting I+ and K/I+ red, and basally truncate, slightly curved, longer conidia, measuring 5–7 × 1.5–2 µm.

Specimens examined (both on upper parts of podetia of *Thamnolia vermicularis* var. *subuliformis*). **USA:** Alaska: Great Kobuk Sand Dunes, 67°05' N, 158°58'–159°00' W, 50 m, *Dryas*-lichen-moss vegetation among sparse *Picea glauca*, 2000, M. Zhurbenko 00226, 00468 (LE 260369, LE 260349).

***Polycoccum vermicularium* (Linds.) D. Hawksw.**

Bull. Br. Mus. nat. Hist., Bot. 14(2): 172 (1985); type: Falkland Isles, on *Thamnolia vermicularis*, 1842, Hooker (E—holotype, n. v.).

Rich material now available of this species permits us to improve or complete its previous descriptions (Hawksworth 1985; Hawksworth & Diederich 1988; Ihlen 1995).

Ascomata perithecioid, black, subglobose, 50–120 µm diam., ostiolate, initially completely immersed (sometimes in few layers), then mostly protruding in the ostiolar area, arising singly, sometimes adjacent or a few confluent, aggregated in dense groups. *Hamathecium* of well-developed interascal filaments, which are 1.5–3.5 µm wide, septate, branched, composed of individual cells 4–12 µm long. *Asci* elongate-clavate, often with a distinct ocular chamber, with a short foot, (55–)61–75(–80) × 20–26(–30) µm ($n = 30$), 8-spored, I– (except plasma becoming red-brown). *Ascospores* long hyaline, then olive and finally dark brown, walls and septum of young pale olive spores markedly darker than lumina, narrowly obovate to elliptic, upper cell usually wider than lower one, sometimes equally-celled, (13–)15.5–20.0(–28) × (6–)7–9(–12) µm, $l/b = (1.5–)1.9–2.5(–3.3)$ ($n = 165$), (0–)1-septate, not to markedly constricted at the septum, wall smooth, not verruculose as stated in Hawksworth (1985), occasionally with halo 1–2 µm thick (mostly around young hyaline

spores), often with one big guttule in each cell, arranged irregularly biseriate in the ascus.

Conidiogenous cells ± pyriform, 6–8 × 2–3 µm. *Conidia* hyaline, ± oblong, straight to slightly bent, (3–)4–6(–7.5) × (1–)1.5 µm ($n = 63$), non-septate.

Notes. Infected host tissues become grey, then black, sometimes exhibit brown gall-like swellings up to 2 mm diam., or disintegrate. Macroscopically the infections are similar to those of *Stigmidium frigidum*. New to Asia (Russia and Mongolia).

Specimens examined [all in polar desert, arctic or alpine tundras, or northern boreal forest on *Thamnomia vermicularis* var. *subuliformis* (22), var. *vermicularis* (7)]. **USA:** Alaska: Great Kobuk Sand Dunes, 67°05' N, 158°58' W, 50 m, 2000, *M. Zhurbenko* (LE 260339).—**Norway:** Troms County: Skibotndalen Valley, 69°16' N, 20°23' E, 950 m, 2003, *M. Zhurbenko* (LE 260306).—**Russia:** Kola Peninsula: Barents Sea coast, Voron'ya River mouth, 69°09' N, 35°50' E, 20 m, 1997, *M. Zhurbenko* (LE 260414). Nenets Region: Bolshoi Tsinkovyi Island, 70°27' N, 58°40' E, 1997, *V. Shevchenko* (LE 232924). Altai Mts.: Ukok Tableland, 49°19' N, 87°36' E, 2500 m, 1996, *T. Lunke* (LE 260453). Western Sayan Mts.: Chernoe Lake, 52°49' N, 94°07' E, 1570 m, 2010, *M. Zhurbenko* (LE 260320); Kulumys Range, 52°51'–52' N, 93°15'–17' E, 1700 m, 2010, *M. Zhurbenko* (LE 260326, LE 260360); Oiskii Range, headwaters of Olen'ya River, 52°48' N, 93°15' E, 1650 m, 2010, *M. Zhurbenko* (LE 260380a). Eastern Sayan Mts.: Kryzhina Range, headwaters of Belyi Kitat River, 53°59'–54°01' N, 95°27'–95°33' E, 1800 m, 2009, *M. Zhurbenko* (LE 260403b, LE 260393). Taimyr Peninsula: Byrranga Mts., Levinson-Lessinga Lake, 74°34'–37' N, 98°33'–47' E, 150–250 m, 1995, *M. Zhurbenko* (LE 233054, LE 260424); *ibid.*, Bolshaya Bootankaga River, 74°30' N, 97°40' E, 350 m, 1995, *M. Zhurbenko* (LE 260593); *ibid.*, Krasnaya River, 74°35' N, 98°08' E, 200 m, 1994, *M. Zhurbenko* (LE 232803, LE 260563 – anamorph); Mt. “217” near junction of Pravaya Uboinaya and Uboinaya Rivers, 73°25' N, 82°51' E, 150 m, *M. Zhurbenko* (LE 260363). Yakutiya: Laptev Sea coast, Tiksi, 71°37'–39' N, 128°45'–54' E, 70 m, 1998, *M. Zhurbenko* (LE 232833, LE 260344a, LE 260348); Lena River delta, 3 km E of Cape Krest-Tumsa, 72°22' N, 126°42' E, 50 m, 1998, *M. Zhurbenko* (LE 232914). Wrangel Island: Nashkok River, 71°24' N, 178°08' W, 5 m, 1998, *S. Kholod* (LE 260580); Neizvestnaya River, 71°20' N, 179°29' W, 1986, *A. Dobrysh* (LE 260397 – anamorph). Komandorskie Islands: Bering Island, Nikolskoe, 55°12' N, 165°57' E, 1980, *A. Dombrovskaya* (KPABG, LE 232804). Chukotka: Baranikha, 68°30' N, 168°16' E, 1971, *A. Galanin* (LE 260553); *ibid.*, 1971, *I. Makarova* (LE 260319 – anamorph); Chaplinskii hot

springs, 64°25' N, 172°30' W, 1957, *V. Gavrilyuk & P. Gagarin* (LE 232934); Inchoun, 66°15' N, 170°20' W, 1975, *I. Makarova* (LE 232874).—**Mongolia:** Bayan-Khongor Region: N of Khukh-Nur Lake, 47°31' N, 98°33' E, 3000 m, 1972, *L. Biazrov* 5804 (LE 260474). Dzabkhan Region: Tarbagatai Range, Solongotuin-Daba Pass, 48°15' N, 98°54' E, 2650 m, 1973, *L. Biazrov* 2134 (LE 260494).

Sphaerellothecium thamnoliae Zhurb. sp. nov.

MycoBank no.: MB 563055

Fungus lichenicola in thallis lichenum generis *Thamnomia* crescens. Similis speciei *Stigmidium frigidum*, sed differt hyphis semper copiosis, bene visibilibus, ascomatibus minoribus, (30–)50(–80) µm diam., sessilibus vel semi-immersis, dispersis, ascosporis interdum 2–3-septatis et halonatis.

Typus: USA, Alaska, Kobuk Valley Wilderness, junction of Kobuk River and Kavet Creek, 67°07' N, 159°03' W, 50 m elev., *Dryas*-lichen-moss vegetation among sparse *Picea glauca*, on thalli of *Thamnomia vermicularis* var. *subuliformis*, 13 August 2000, *M. Zhurbenko* 00212 (LE 260567—holotypus).

(Fig. 8)

Vegetative hyphae medium brown, with sculptured surface, composed of elongate cells 3.5–9.0 µm wide, septate, markedly constricted at the septa, branched (often more or less rectangularly) and anastomosed, BCr+ blue-green, I–, mostly superficial, abundant, forming a conspicuous dense reticulum.

Ascomata perithecioid, black, subglobose to somewhat conical above, (30–)50(–80) µm diam., with an ostiole of 5–15 µm diam., without appendices or projections, sessile to semi-immersed, dispersed. *Exciple* in surface view brown throughout, sculptured, similar to *textura angularis*, composed of a few layers of angular, pseudoparenchymatous cells (3–)5–8(–12) µm across, BCr+ blue-green, K–. *Hymenial gel* I–, K/I–. *Hamathecium* not observed. *Asci* elliptic to pyriform, occasionally with a short foot, endoascus thickened above, distinct ocular chamber not observed, size significantly differing in the two varieties described below, 8-spored, BCr–, I–, K/I– (except plasma reacting BCr+ blue, I+, and K/I+ yellow to orange). *Ascospores* colourless and smooth-walled or rarely (when over-mature ?) pale to medium brown and with a

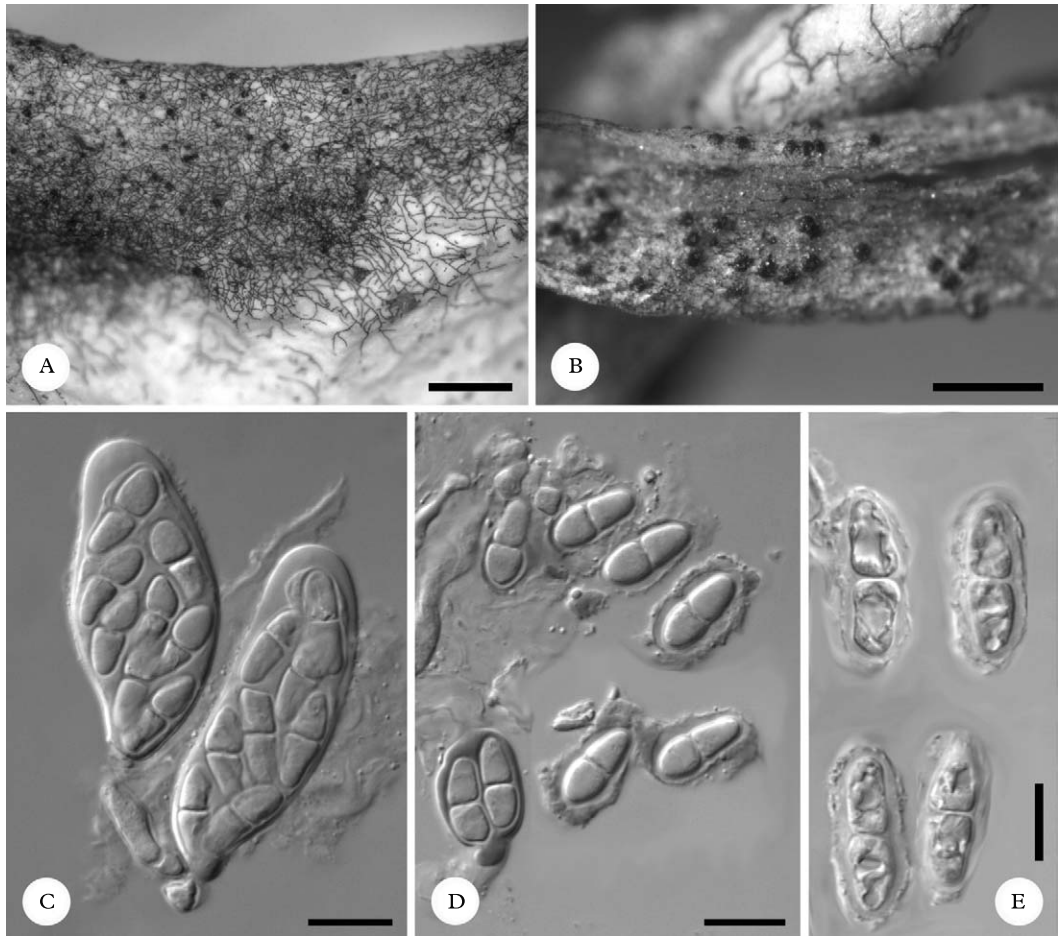


FIG. 8. *Sphaerellothecium thamnoliae*. A, C & D, var. *thamnoliae*; A, infection habitus (holotype); C, asci in water (LE 260558); D, ascospores in I, note halo (holotype); B & E, var. *taimyricum*; B, infection habitus (LE 232894); E, ascospores in water, note halo (holotype). Scales: A & B = 500 μ m; C–E = 10 μ m.

rough wall, obskittle-shaped to narrowly obovate, usually with a wider and sometimes shorter upper cell, occasionally located upside down in the ascus, size significantly differing in the two varieties described below, almost always 1-septate, but non-septate hyaline and 2–3-septate brown spores were also observed, mostly constricted at the septa, sometimes with halo 0.5–2.0 μ m thick, usually with a few big guttules in each cell, irregularly arranged in 2–3 rows in the ascus, wall and septum BCr–, plasma BCr+ blue.

Conidiomata pycnidial. *Conidia* hyaline, bacilliform, 2.0–4.5 \times 0.5 μ m.

Notes. The material examined (42 specimens) exhibits significant variability in the development of vegetative hyphae, size of the ascomata, degree of their immersion in the host thalli, and size of asci and ascospores. The species is typified on the specimen representing the group with abundantly developed superficial hyphae, comparatively small, mostly sessile ascomata, and small ascospores. It can be opposed to the group distinguished by the larger asci and ascospores. However, there is no sharp delimitation between the two groups (Table 2), which are therefore recognized here as varieties.

TABLE 2. Distinguishing characteristics of *Sphaerellothecium* and *Stigmidium* taxa growing on *Thamnolia* (based on the author's own data).

Characters	<i>Sphaerellothecium thamnoliae</i>	
	var. <i>thamnoliae</i>	var. <i>tainyricum</i>
	<i>Stigmidium frigidum</i>	
Vegetative hyphae	usually immersed and inconspicuous	superficial, conspicuous
Ascospores	(30-)50-80(-120)	(30-)50(-80)
immersion in the host thalli	mostly protruding only in the ostiolar area	sessile to semi-immersed
dispersion on the host thalli	aggregated in groups	dispersed
location on the host thalli	mostly on tops	mostly on bases
Size of asci (µm)	(33-)40-52(-60) × (13-)15-21(-33)	47-64(-85) × (14-)17-27(-33)
Ascospores size (µm)	(11-)13.5-16.5(-20) × (4.0-)5.0-6.5(-7.5)	(12.5-)14.0-19.5(-24.0) × (4.5-)5-8(-9.0)
septa	1	(0-)1(-3)
halo	absent	sometimes present
Malformations of host thalli	sometimes present	absent

In spite of the absence of visible interascal filaments, the species is disposed within *Sphaerellothecium* Zopf vs. *Stigmidium* Trevis. due to its brown, thick-walled, sculptured, comparatively thick and short-celled vegetative hyphae with swollen individual cells, forming a conspicuous superficial reticulum, and non-pseudotetrablastic ascospores (generic delimitation according to: Triebel 1989; Roux & Triebel 1994; Calatayud & Triebel 1999, 2001). Up to now, no *Sphaerellothecium* species have been reported from *Thamnolia*. Together with *Sphaerellothecium araneosum* (Arnold) Zopf, *S. icmadophilae* (R. Sant.) Zhurb. and *S. stereocaulorum* Zhurb. & Triebel, the new species belongs to the group with 1(-3)-septate, hyaline ascospores, occasionally becoming brown with age (Santesson 1984; Roux & Triebel 1994; Zhurbenko & Triebel 2008). *Sphaerellothecium araneosum* differs from both varieties of *S. thamnoliae* in its sometimes distinct interascal and ostiolar filaments and different sizes of asci (34-45 × 14-16 µm) and ascospores [(12.5-) 13.5-17.0 (-22.0) × (3.5-) 5-7 (-7.5) µm], *S. icmadophilae* has non-halonate ascospores of intermediate size (14-19 × 4.5-5.5 µm), and *S. stereocaulorum* has slightly smaller ascospores (20-50 µm diam.), smaller asci [(23-)25-34(-38) × (10-)11-16(-19) µm], non-halonate, smaller ascospores [(9-)10-13(-16) × 3.0-4.5(-6.0) µm] and grows in the epinecral layer of the host thallus. Characters distinguishing *Sphaerellothecium thamnoliae* from *Stigmidium frigidum* are summarized in Table 2.

Distribution and host. Circumpolarly known in the Holarctic from polar deserts, arctic and alpine tundras. Mainly growing on bases of *Thamnolia vermicularis* thalli; occasionally throughout whole thallus, particularly when they are prostrate. Also found on galls induced in the host by *Thamnogalla crombiei*. Evidently pathogenic as infected host parts are bleached.

***Sphaerellothecium thamnoliae* var. *thamnoliae* Zhurb.**

(Fig. 8A, C & D)

Notes. The type variety of the species is mainly characterized by comparatively small asci, measuring (26–)31–41(–55) × (10–)14–20(–21) μm ($n = 129$) and ascospores, measuring (8.5–)11.0–13.5(–16.0) × (3.5–)4.5–5.5(–6.5) μm, $l/b = (1.8–)2.3–2.9(–3.9)$ ($n = 502$; including free over-mature spores).

Specimens of Sphaerellothecium thamnoliae var. thamnoliae examined [all in arctic or alpine tundras or northern boreal forest on *Thamnolia vermicularis var. subuliformis* (16), *var. vermicularis* (5)]. **USA:** *Alaska:* Great Kobuk Sand Dunes, 67°02–06' N, 158°50'–159°01' W, 50 m, 2000, *M. Zhurbenko* (LE 260518, LE 260318, LE 260338, LE 260387).—**Canada:** *Canadian Arctic Archipelago:* Prince Patrick Island, Mould Bay, 76°14' N, 119°18' W, 2004, *D. Walker* (LE 260388).—**Greenland:** *Mellem Land:* Skovfjorden, Qinnua River mouth, 61°15' N, 45°30' W, 150 m, 2005, *M. Zhurbenko* (LE 260368).—**Svalbard:** *Dickson Land:* W coast of Billefjorden, 78°37' N, 16°20' E, 200 m, 2003, *M. Zhurbenko* (LE 260577).—**Norway:** *Troms County:* Skibotndalen Valley, 69°15' N, 20°23' E, 950 m, 2003, *M. Zhurbenko* (LE 260478).—**Russia:** *Kola Peninsula:* Barents Sea coast, Voron'ya River mouth, 69°09' N, 35°50' E, 20 m, 1997, *M. Zhurbenko* (LE 260398). *Northern Ural:* headwaters of Pechora River, Yanypun-ner Range, 62°05' N, 59°06' E, 800 m, 1997, *M. Zhurbenko* (LE 260538b). *Taimyr Peninsula:* Byrranga Mts., Levinson-Lessinga Lake, 74°30–32' N, 98°30–33' E, 120–300 m, 1994, *M. Zhurbenko* (LE 207477a); *ibid.*, 1995, *M. Zhurbenko* (LE 260428); Enisei Gulf, Sibiryakova Island, 72°55' N, 79°00' E, 10 m, 1989, *V. Kuvaev* (LE 260558). *Yakutiya:* Laptev Sea coast, Tiksi, 71°37' N, 128°54' E, 70 m, 1998, *M. Zhurbenko* (LE 232964, LE 260344b); Lena River delta, Stolb Island, 72°24' N, 126°40' E, 50 m, 1998, *M. Zhurbenko* (LE 260378). *Wrangel Island:* Klark River, 71°05' N, 178°16' E, 110 m, 1998, *S. Kholod* (LE 260508); Neizvestnaya River, 71°14' N, 179°23' W, 130 m, 1987, *S. Kholod* (LE 260548). *Chukotka:* Baranikha, 68°30' N, 168°16' E, 1971, *I. Makarova* (232944b, LE 260599); Yanrakynnot, 64°53' N, 172°30' E, 1976, *A. Sytin* (LE 260408).

Additional specimens examined of Sphaerellothecium thamnoliae var. thamnoliae, formerly published as Stigmidium frigidum (Zhurbenko & Santesson 1996; Zhurbenko & Pospelova 2001; Zhurbenko 2008): LE 210405, LE 207538, LE 207540, LE 207541, LE 207543, LE 207544.

Sphaerellothecium thamnoliae var. taimyricum Zhurb. var. nov.

Mycobank no.: MB 563057

Differt ab varietate *Sphaerellothecium thamnoliae var. thamnoliae* ascis et ascosporis majoribus.

Typus: Russia, Taimyr Peninsula, Byrranga Mts., N of Levinson-Lessinga Lake, 74°34' N, 98°47' E, 250 m elev., arctic tundra, on thalli of *Thamnolia vermicularis var. subuliformis*, 20 August 1995, *M. Zhurbenko* 95586 (LE 260438—holotypus).

(Fig. 8B & E)

Etymology. The specific epithet refers to Taimyr Peninsula in Siberia, where the holotype was found.

Notes. This variety is mainly distinguished from the type variety by its larger asci, measuring 47–64(–85) × (14–)17–27(–33) μm ($n = 15$), and ascospores, measuring (12.5–)14.0–19.5(–24.0) × (4.5–)5.8(–9.0) μm, $l/b = (1.7–)2.2–3.0(–3.8)$ ($n = 159$). Furthermore, the variety *taimyricum* seems to differ from the variety *thamnolia* in having a more immersed mycelium, mostly semi-immersed and slightly larger ascomata, and a better developed halo around the ascospores. It is so far also known only from the Arctic.

Specimens of Sphaerellothecium thamnoliae var. taimyricum examined (all in polar desert or arctic tundra on *Thamnolia vermicularis var. subuliformis*). **Russia:** *Severnaya Zemlya:* Bolshevik Island, Akhmatova Bay, 79°01' N, 102°43' E, 60 m, 1996, *M. Zhurbenko* (LE 232894); Oktyabr'skoi Revolutsii Island, Cape Nekrasova, 80°02' N, 99°19' E, 2007, *M. Gavrilov* (LE 260418). *Taimyr Peninsula:* Byrranga Mts., Levinson-Lessinga Lake, 74°24–31' N, 98°36–46' E, 150–300 m, 1995, *M. Zhurbenko* (LE 260328, LE 260568); Uboinaya River mouth, 73°39' N, 82°22' E, 20 m, 1990, *M. Zhurbenko* (LE 260503). *Novosibirskie Islands:* Zhokhova Island, 76°08' N, 152°45' E, 50 m, 1989, *M. Samarskii* (LE 232974). *Wrangel Island:* Neozhidannaya River, 71°01' N, 179°09' E, 100 m, 1992, *S. Kholod* (LE 260488). *Chukotka:* Iskaten' Pass near km 32 Egvekinot–Iul'tin Highway, 66°35' N, 179°10' W, 1971, *I. Makarova* (LE 260578).

Additional specimens examined of Sphaerellothecium thamnoliae var. taimyricum, formerly published as Stigmidium frigidum (Zhurbenko & Santesson 1996; Karatygin et al. 1999): LE 207531a, LE 207534, LE 207535, LE 207536, LE 207542, LE 207545, LE 207546.

Stigmidium frigidum (Th. Fr. ex Sacc.) Alstrup & D. Hawksw.

Meddel. Grönl., Biosc. 31: 67 (1990); type: Canada, British Columbia, Rocky Mountains, Hector, c. 51°25' N, 116°21' W (I. Brodo, pers. comm.), on *Thamnolia*

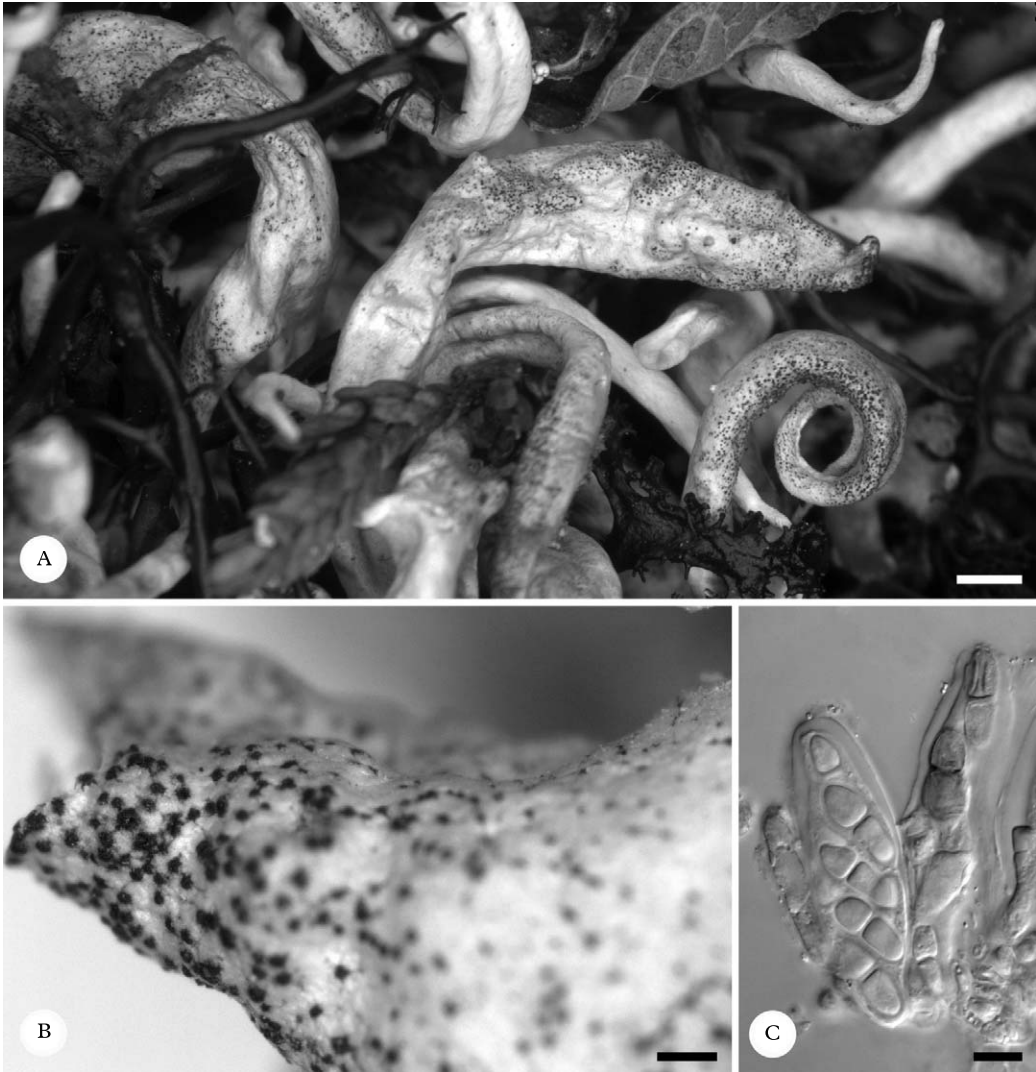


FIG. 9. *Stigmidium frigidum*. A, infection habitus (LE 260444); B, ascomata (LE 232994); C, asci with spores in water, note dark over-mature ascospores (LE 260354). Scales: A = 1 mm; B = 200 µm; C = 10 µm.

vermicularis var. *subuliformis*, 27 July 1885, J. Macoun (E—neotype, photographs examined).

(Fig. 9A & B)

Vegetative hyphae pale to medium brown, composed of elongate cells 2.5–7.0 µm wide, septate, constricted at the septa, scarcely branched, BCr+ blue-green, I–, immersed to

occasionally superficial, rather sparse, usually inconspicuous.

Ascomata perithecioid, black, subglobose, (30–)50–80(–120) µm diam., sometimes with an indistinct papilla, with an ostiole of 10–20 µm diam., initially completely immersed (sometimes in a few layers), then mostly protruding in the ostiolar area or

occasionally up to half erumpent, arising singly or sometimes adjacent or a few confluent, aggregated in groups of up to 500. *Exciple* in surface view brown, smooth, similar to *textura angularis*, composed of a few layers of thick-walled, angular, pseudoparenchymatous cells (3–)5–8(–12) μm across, BCr+ blue-green, K+ olive. *Hymenial gel* I–, K/I–. *Hamathecium* not observed. *Asci* elliptic to pyriform, endoascus thickened above, sometimes with a small ocular chamber, foot not observed, (33–)40–52(–60) \times (13–)15–21(–33) μm ($n = 62$), 8-spored, BCr–, I–, K/I– (except plasma reacting BCr+ blue, I+ and K/I+ yellow to orange). *Ascospores* colourless or occasionally pale to medium brown (when over-mature?) (Fig. 9C), obskittle-shaped to narrowly obovate, usually with a wider and shorter upper cell, occasionally located upside down in the ascus, (11–)13.5–16.5(–20) \times (4.0–)5.0–6.5(–7.5) μm , l/b = (1.7–)2.3–2.9(–4.1) ($n = 214$), 1-septate, usually constricted at the septum, smooth-walled, halo not observed, usually with a few big guttules in each cell, irregularly diagonally arranged in 2–3 rows in the ascus, wall and septum BCr–, plasma BCr+ blue.

Anamorph not observed.

Notes. The species was originally described from Greenland as “*Sphaeria* n. 10” by Fries (1879: 370) and later formally introduced as “*Epicymatia frigida* Sacc. ex Fr. Hedw. 1881, p. 60 (*Sphaeria* n. 10)” (Saccardo 1882: 572). According to this description, the type specimen had dark torulose superficial hyphae and ascospores of 15–18 \times 5–7 μm , and thus may well represent *Sphaerellothecium thamnoliae* var. *taimyricum*. According to Alstrup & Hawksworth (1990: 67), this original material was lost and the authors neotypified the species on John Macoun’s “Canadian Lichens” no. 180 (E—neotype) and combined it into *Stigmidium*. The locality on the neotype label (“Hector, B.C.”) is indistinctly handwritten, which was evidently the reason for erroneously referring it to Alaska (Hawksworth 1980: 180). The examination of the neotype by R. Yahr (pers. comm.), together with the notes of Hawksworth (*op. cit.*), leave little doubt that

it fits the species concept presented here (see below). This concept also corresponds to the description of *Stigmidium frigidum* in Ihlen (1995). The only deviating character of the species reported by the latter author is the 4(–6)-spored asci, not typical for *Stigmidium* in general and not observed in the examined material.

Usually growing on the upper parts or even tips of *Thamnolia vermicularis* thalli, but occasionally observed on their middle or basal parts. Evidently pathogenic, as causing bleaching or even destruction of the host tissues; heavy infections also induce various malformations of the host thalli which, for example, become bent, twisted and/or somewhat swollen (Fig. 9A). Superficially the infections are similar to those of *Polycoccum vermicularium*.

Typical *Stigmidium frigidum* can be readily distinguished from *Sphaerellothecium thamnoliae*, even with a dissecting microscope, by its numerous, more or less immersed ascomata, crowded at the tips of the host thalli, and the absence of a visible mycelium; malformations of the host thalli are also diagnostic (Table 2). Confusion can be caused by the occasional development of superficial vegetative hyphae. However, in well-developed specimens it is clearly seen that such hyphae are associated only with some groups of ascomata and not forming a reticulum.

New to Mongolia; a first verified report from the USA.

Specimens examined [all in polar deserts, arctic or alpine tundras on *Thamnolia vermicularis* var. *subuliformis* (13), var. *vermicularis* (8)]. **USA:** Alaska: Brooks Range, headwaters of Atigun River near mile 248 Dalton Highway, 68°07' N, 149°28' W, 1400 m, 2001, *M. Zhurbenko* (LE 260356); Kotzebue, 66°53' N, 162°31' W, 30 m, 2000, *M. Zhurbenko* (LE 260406).—**Russia:** *Severnaya Zemlya*: Bolshevik Island, Mikoyana Bay, 79°18' N, 101°55' E, 10 m, 1996, *M. Zhurbenko* (LE 232943). *Taimyr Peninsula*: Byrranga Mts., Bolshaya Bootankaga River, 74°30' N, 97°40' E, 350 m, 1995, *M. Zhurbenko* (LE 232994a); *ibid.*, Levinson-Lessinga Lake, 74°24–34' N, 98°26–47' E, 60–300 m, 1994, *M. Zhurbenko* (LE 207612); *ibid.*, 1995, *M. Zhurbenko* (LE 232984, LE 232923, LE 232823, LE 232863, LE 260523, LE 260334, LE 260564, LE 260354); Dikson Island, 73°30' N, 80°20' E, 30 m, 1990, *M. Zhurbenko* (LE 260353); Ragozinka River mouth, 72°48' N, 80°53' E, 30 m, 1990, *M. Zhurbenko* (LE 260413). *Yakutiya*: 60 km E of Cherskii, Belaya Strelka Mts.,

68°40' N, 162°40' E, 400 m, 1975, *A. Egorova* (LE 260454); Laptev Sea coast, Tiksi, 71°39–40' N, 128°40–45' E, 50–70 m, 1998, *M. Zhurbenko* (LE 260484, LE 260444a). *Chukotka*: Baranikha, 68°30' N, 168°16' E, 1971, *I. Makarova* (LE 233084); Gil'mymliveem River, 65°48' N, 173°15' W, 1977, *I. Makarova* (LE 232953).—**Mongolia**: *Dzabkhan Region*: Mt. Otgon-Tenger, 47°35' N, 97°32' E, 3250 m, 1976, *L. Biazrov* 7513 (LE 260384).

Additional examined specimens of Stigmidium frigidum published in Zhurbenko & Santesson (1996): LE 207533, LE 207537, LE 207539.

Thamnogalla crombiei (Mudd) D. Hawksw.

Notes Roy. Bot. Gard. Edinburgh **38**(1): 178 (1980); type: Scotland, Ben Lawers, on *Thamnolia vermicularis*, 1864, *Crombie* (BM—lectotype, n. v.).

Notes. Ascomata perithecioid, 75–125 µm diam., immersed or rarely erumpent. *Exciple* in cross-section orange-brown throughout, K+ becoming more intensively red-orange. *Hamathecium* of filiform, non-capitate, c. 1 µm wide, septate, scarcely branched interascal filaments. *Asci* cylindrical, with a long foot, (50–)70–90 × 5–6 µm (*n* = 17), 8-spored. *Ascospores* hyaline, mostly narrowly elliptic to narrowly oblong, with rounded ends, (7–)8–11.5(–15) × (2–)2.5–3.0(–4) µm, l/b = (2.1–)2.8–4.0(–5.2) (*n* = 113) [(7–)9.6(–12) × (2.5–)3.7(–5.0) µm, l/b = 2.6 according to Hoffmann & Hafellner (2000)], non-septate, smooth-walled, non-halonate, often with a few guttules, arranged uniseriate and overlapping to biseriate in the ascus. Inducing concolorous or pale coloured (cinnamon, pinkish buff, peach, flesh pink, or grey), finally bullate and basally constricted galls throughout the host thalli. Otherwise pathogenicity not observed.

This is a frequent and cosmopolitan thamnolicolous fungus yet is reported here for the first time from Greenland and Svalbard.

Specimens examined [all in polar deserts, arctic or alpine tundras, or northern boreal forest on *Thamnolia vermicularis* var. *subuliformis* (26), var. *vermicularis* (14)]. **USA**: *Alaska*: Kotzebue, 66°53' N, 162°31' W, 30 m, 2000, *M. Zhurbenko* (LE 260386, LE 260493); *ibid.*, 1961, *B. Neiland* (LE 260466); Great Kobuk Sand Dunes, 67°06' N, 159°01' W, 50 m, 2000, *M. Zhurbenko* (LE 260336); Seward Peninsula, Bering

Land Bridge National Preserve, 65°50' N, 164°32' W, 612 m, 2002, *J. Roth* (LE 260423); *ibid.*, 66°17' N, 165°19' W, 22 m, 2002, *J. Roth* (LE 260383, LE 260433).—**Canada**: *British Columbia*: Wells Gray Provincial Park, Mt. Raft, 51°44' N, 119°50' W, 2100 m, 2002, *M. Zhurbenko* (LE 260456).—**Greenland**: Mellem Land, Skovfjorden, Qinnua River mouth, 61°15' N, 45°30' W, 150 m, 2005, *M. Zhurbenko* (LE 260370); Tugtugtoq Island SW of Narssaq, 2 km SW of Blue Moon Lake, 60°51' N, 46°25' W, 15 m, 2005, *M. Zhurbenko* (LE 260340, LE 260330).—**Svalbard**: *Bünsow Land*: Norddammen Lake, 78°38' N, 16°44' E, 10 m, 2003, *M. Zhurbenko* (LE 260350).—**Norway**: *Troms County*: Skibotndalen Valley, 69°13–19' N, 20°21–29' E, 70–650 m, 2003, *M. Zhurbenko* (LE 260416, LE 260366).—**Russia**: *Kola Peninsula*: Barents Sea coast, Voron'ya River mouth, 69°09' N, 35°50' E, 20 m, 1997, *M. Zhurbenko* (LE 260534); *ibid.*, 4 km SSE of Dal'nie Zelyentsy, 69°05' N, 36°07' E, 100 m, 1997, *M. Zhurbenko* (LE 260594); *ibid.*, 17 km N of Tumannyi, 69°01' N, 35°48' E, 100 m, 1997, *M. Zhurbenko* (LE 260584); Khibiny Mts., headwaters of Kaskasnyunjok Creek, 67°46' N, 33°49' E, 2007, *M. Zhurbenko* (LE 233042). *Nenets Region*: Dolgii Island, 69°18' N, 58°52' E, 1998, *V. Shevchenko* (LE 232824). *Northern Ural*: headwaters of Pechora River, Yanyupuner Range, Mt. "981", 62°05' N, 59°06' E, 800 m, 1997, *M. Zhurbenko* (LE 260404, LE 260504). *Western Sayan Mts.*: Kulumys Range, 52°51' N, 93°17' E, 1700 m, 2010, *M. Zhurbenko* (LE 260310); Oiskii Range, headwaters of Olen'ya River, 52°48' N, 93°15' E, 1650 m, 2010, *M. Zhurbenko* (LE 260380b). *Eastern Sayan Mts.*: Kryzhina Range, headwaters of Belyi Kitat River, 54°01' N, 95°27' E, 1800 m, 2009, *M. Zhurbenko* (LE 260403a). *Severnaya Zemlya*: Bolshevik Island, Akhmatova Bay, 79°04' N, 102°45' E, 10–20 m, 1996, *M. Zhurbenko* (LE 233064, LE 260314, LE 260514); *ibid.*, Mikoyana Bay, 79°18' N, 101°55' E, 10 m, 1996, *M. Zhurbenko* (LE 232904); *ibid.*, Shokalskogo Strait, 79°18' N, 101°40' E, 20 m, 1996, *M. Zhurbenko* (LE 232834). *Taimyr Peninsula*: Byranga Mts., Levinson-Lessinga Lake, 74°33' N, 98°43' E, 100 m, 1995, *M. Zhurbenko* (LE 260434); Ragozinka River mouth, 72°48' N, 80°53' E, 25 m, 1990, *M. Zhurbenko* (LE 260513); Uboinaya River mouth, 73°36' N, 82°22' E, 10 m, 1990, *M. Zhurbenko* (LE 260463). *Yakutiya*: Lena River delta, 3 km E of Cape Krest-Tumsa, 72°22' N, 126°42' E, 50 m, 1998, *M. Zhurbenko* (LE 233014). *Magadan Region*: Magadan, Mt. Nagaevskaya, 59°34' N, 150°45' E, 400 m, 2003, *N. Sazanova* (LE 260443). *Wrangel Island*: Gusinaya River, 71°08' N, 179°10' E, 1991, *V. Shtrik* (LE 232982); Naskhok River, 71°24' N, 178°08' W, 5 m, 1998, *S. Kholod* (LE 232932); Neozhidannaya River, 71°02' N, 179°10' E, 110 m, 1992, *S. Kholod* (LE 260374b); Tundrovaya River, 71°30' N, 179°45' W, 1996, *S. Kholod* (LE 233004). *Chukotka*: Baranikha, 68°30' N, 168°16' E, 1971, *I. Makarova* (LE 232944a); Chaplinskii hot springs, 64°25' N, 172°30' W, 1957, *V. Gavrilyuk & P. Gagarin* (LE 232843).

Discussion

To date, 23 species representing 18 genera of lichenicolous fungi are known on *Thamnolia* worldwide, of which 18 species (see key below; c. 80%) and two genera (*Epithamnolia* and *Thamnogalla* D. Hawksw.; c. 10%) have been reported only from this host genus. All these species inhabit *Thamnolia vermicularis*, six of them (*Endococcus thamnoliae*, *Lichenopeltella thamnoliae*, *Odontotrema santessonii*, *Polycoccum vermicularium*, *Stigmidium frigidum*, and *Thamnogalla crombiei*) are also known on *T. papelillo* (Etayo 2010), and none has yet been found on *T. juncea*. Of the 190 newly studied fungal specimens growing on *Thamnolia vermicularis*, 144 (76%) were found on its var. *subuliformis* and 46 (24%) on var. *vermicularis*. This disproportion might merely reflect the fact that the former variety is more abundant in the Northern Hemisphere than the latter (Thomson 1984).

The genus *Thamnolia* has no species of lichenicolous fungi in common with the other genera of the lichen family *Icmadophilaceae* and is much more 'hospitable' compared to other genera in the family: *Dibaeis* (hosts 5 species of lichenicolous fungi), *Icmadophila* (5), *Pseudobaeomyces* (0), *Siphula* (1 ?), *Siphulella* (0) (author's database).

In the richness of lichenicolous mycobiota which it supports, *Thamnolia vermicularis* ranks 15th worldwide after *Peltigera rufescens* (hosts 54 species of lichenicolous fungi), *Cladonia pyxidata* (L.) Hoffm. (35), *Xanthoria parietina* (L.) Th. Fr. (34), *Peltigera didactyla* (With.) J.R. Laundon (32), *P. canina* (L.) Willd. (30), *P. praetextata* (Flörke ex Sommerf.) Zopf (29), *Lobaria pulmonaria* (L.) Hoffm. (28), *Parmelia saxatilis* (L.) Ach. (28), *P. sulcata* Taylor (27), *Cladonia pocillum* (Ach.) Grognot (26), *Peltigera polydactylon* (Necker) Hoffm. (26), *P. aphthosa* (L.) Willd. (25), *Physcia stellaris* (L.) Nyl. (25), and *Circinaria calcarea* (L.) A. Nordin, S. Savić & Tibell (24) (author's database). It is noteworthy that 14 of these 15 most hospitable lichen species of the world occur in the Arctic, and at least 11 of them thrive there (Kristinsson *et al.* 2010).

The following taxa of *Thamnolia*-inhabiting fungi were the most common in the Holarctic: *Thamnogalla crombiei* (21% of 190 specimens examined), *Polycoccum vermicularium* (15%), *Sphaerellothecium thamnoliae* var. *thamnoliae* (12%), *Stigmidium frigidum* (11%), *Cercidospora thamnoliae* (9%), and *Odontotrema santessonii* (5%).

The study ends in formally describing six, and introducing another two, new species of thamnoliicolous fungi, which is about 35% of their known total number. However, some of their specimens still remain unnamed. Among these are a *Lasiosphaeriopsis*-like pyrenomycete with brown, 4–6-septate ascospores, c. 33–38 × 10–13 µm (1996, *M. Zhurbenko* 96910); a fungus with a closed fruit body containing filiform, hyaline, 4–5-septate diaspores, c. 58–69 × 1.5–2 µm (1998, *S. Kholod*); a gall-inducing hyphomycete (1989, *A. Katenin*); and a rather common fungus with thick dark superficial hyphal strands and conspicuous black discoid sterile fruit-like structures, resembling species of *Lichenostigma* Hafellner subgenus *Lichenogramma* Nav.-Ros. & Hafellner. One more unidentified coelomycete on *Thamnolia* with pleurogenous conidiogenous cells was mentioned by Hawksworth (1980: 180). Four of 21 named *Thamnolia*-dwelling fungal species found in the Holarctic were represented by single finds. According to a Turing estimator, this suggests that about 80% of these fungi were detected during the survey, or that their real diversity in the Holarctic is no less than 26 species.

Three of the 23 fungal species that have been reported from *Thamnolia* were not found in the Holarctic lichen collections examined: *Cornutispora intermedia* Punith. & D. Hawksw., *Endococcus thamnoliae* Etayo & R. Sant., and *Odontotrema intermedium* Diederich, Zhurb. & Etayo (Diederich *et al.* 2002; Etayo 2010); all are known only from a single or a few finds, which makes it futile to speculate about their geography. On the other hand a fourth, *Lichenopeltella thamnoliae*, seems to be rather common in South America (Etayo 2010) and thus its absence in the Holarctic might not be accidental. More observations from the

extra-holarctic regions are needed to answer questions about the distribution patterns of thamnollicolous fungi and their infrageneric preferences within *Thamnolia*.

Key to the lichenicolous fungi growing on *Thamnolia*

Based on data in Hawksworth (1977), Santesson (1998), Diederich *et al.* (2002, 2010), Punithalingam (2003), Heuchert & Braun (2006), Etayo (2010), and the present publication. Species of lichenicolous fungi not specific to *Thamnolia* are given in parentheses.

- 1 Anamorphic fungus 2
Teleomorphic fungus 8
- 2(1) Hyphomycete, conidiophores usually with divergent terminal branches, conidigenous cells integrated, mostly terminal, with a single or few distant enteroblastic-percurrent proliferations, conidia pale brown or yellowish brown, usually in branched acropetal chains, subglobose or limoniform to ellipsoid-subcylindrical, aseptate ($3.5\text{--}8.0 \times 3\text{--}5 \mu\text{m}$) or 1-septate ($7\text{--}13 \times 5\text{--}7 \mu\text{m}$)
. (**Cladosporium licheniphilum**)
Coelomycete 3
- 3(2) Conidia dark brown, subglobose, aseptate, ($2.5\text{--}3.0\text{--}4.0\text{--}5.0$) μm diam., ornamented ($\times 1000$), pycnidia ($40\text{--}50\text{--}80\text{--}110$) μm diam.
. (**Lichenocodium usneae**)
Conidia hyaline 4
- 4(3) Conidia with (1)–3(–4) divergent arms (**Cornutispora intermedia**)
Conidia without arms 5
- 5(4) Conidia (0)–1(–2?)–septate, cylindrical, ($14\text{--}18.5\text{--}27.0\text{--}32$) \times ($1.0\text{--}1.5\text{--}2.0\text{--}2.5$) μm **Epithamnolia karatyginii**
Conidia aseptate 6
- 6(5) Conidia $2.0\text{--}4.5 \times 0.5 \mu\text{m}$, bacilliform
. anamorph of **Sphaerellothecium thamnoliae**
Conidia over $0.5 \mu\text{m}$ wide 7
- 7(6) Conidia ($3.0\text{--}4\text{--}6\text{--}7.5$) \times ($1\text{--}1.5$) μm , oblong
. anamorph of **Polycoccum vermicularium**
Conidia ($3.5\text{--}4\text{--}5\text{--}5.5$) \times ($1.5\text{--}2.0\text{--}2.5$) μm , oblong to occasionally elliptic
. **Phoma thamnoliae ad int.**
- 8(1) Hymenium at least partly exposed at maturity, ascospores hyaline 9
Hymenium not exposed at maturity. 12
- 9(8) Ascospores aseptate, subglobose to shortly ellipsoid, $6\text{--}10 \times 5.0\text{--}7.5 \mu\text{m}$
. (**Geltingia associata**)
Ascospores septate, ascomata urceolate 10
- 10(9) Ascospores with (3)–6–8(–9) transverse septa and often a few longitudinal or oblique septa in central cells, ($12.5\text{--}18\text{--}23\text{--}25.0$) \times ($3\text{--}3.5\text{--}4.5\text{--}5$) μm
. **Odontotrema santessonii**
Ascospores with less septa, never submuriform. 11

- 11(10) Ascospores 1(–2)-septate, (9–)11–15(–18) × 2.5–3.0(–3.5) μm
 **Odontotrema thamnoliae**
 Ascospores 3-septate, (10.0–)10.5–12.5(–13.5) × (3–)3.5–4.0(–4.5) μm
 **Odontotrema intermedium**
- 12(8) Ascomata catathecia, non-setose, asci 4-spored, ascospores hyaline, 1-septate, 11.5–
 16 × 2.5–5 μm, without setulae. **Lichenopeltella thamnoliae**
 Ascomata perithecioid, ascospores hyaline or pigmented. 13
- 13(12) Ascomata setose, ascospores initially hyaline, then pale to medium grey, with (0–)3–
 5(–7) transverse septa and usually longitudinal or oblique septa in central cells,
 (11–)13.5–18.0(–29) × (5–)6–8(–12) μm **Capronia thamnoliae**
 Ascomata without setae 14
- 14(13) Ascospores pigmented, at least when mature 15
 Ascospores not or only occasionally pigmented. 19
- 15(14) Ascospores muriform 16
 Ascospores only transversely septate 17
- 16(15) Interascal filaments present, ascospores ornamented (×1000), (23–)25–29
 (–31.5) × (10.5–)11–13(–14) μm **Dacampia thamnoliicola ad int.**
 Interascal filaments absent, ascospores smooth-walled, (14–)16.5–24.0(–34) × (6–)
 6.5–8.5(–9) μm **Merismatium thamnoliicola**
- 17(15) Ascospores (1–)3-septate, hyaline to pale cinnamon-brown, (10–)15.5–20.5(–22)
 × (4.5–)5–6(–8.0) μm (**Phaeospora arctica**)
 Ascospores (0–)1-septate 18
- 18(17) Interascal filaments absent, ascospores 9.0–12.5 × 3.5–5.0 μm
 **Endococcus thamnoliae**
 Interascal filaments well developed, ascospores (13–)15.5–20.5(–28) × (6–)7–9
 (–12) μm **Polycoccus vermicularium**
- 19(14) Ascomata immersed in distinct bullate galls 20
 Ascomata not associated with bullate galls 21
- 20(19) Exciple orange-brown throughout, interascal filaments well developed, ascospores
 aseptate, (7–)8.0–11.5(–15) × (2–)2.5–3.0(–4) μm, without halo
 **Thamnogalla crombiei**
 Exciple bluish grey, interascal filaments sparse to indistinct, ascospores 1-septate,
 (12–)14–17(–19) × (3.5–)4–5(–5.5) μm, halonate
 **Cercidospora thamnogalloides**
- 21(19) Exciple bluish green or olive-brown above, hyaline below, vegetative hyphae incon-
 spicuous, ascomata subimmersed, interascal filaments indistinct or abundant . 22
 Exciple brown throughout, vegetative hyphae conspicuous or not, ascomata sub-
 immersed to sessile, interascal filaments absent 24
- 22(21) Exciple olive-brown above, asci mainly 4-spored, interascal filaments sparse to
 indistinct, ascospores (11–)14.0–17.5(–21) × (4.0–)4.5–5.5(–6.5) μm, (1–)2–3-
 septate, without halo **Cercidospora thamnoliicola**
 Exciple bluish green above, asci only/mainly 8-spored 23

- 23(22) Interascal filaments abundant, ascospores (1–)3(–4)–septate, (12·5–)16·5–21·0 (–27·5) × (4–)4·5–5·5(–8) μm, occasionally halonate **Cercidospora thamnoliae**
 Interascal filaments sparse to indistinct, ascospores (0–)1–septate, (12–)13–16 (–19) × (3–)3·5–4·5(–5) μm, without halo **Cercidospora epithamnolia**
- 24(21) Ascospores (1–)3–septate, hyaline to pale cinnamon-brown, (10–)15·5–20·5 (–22) × (4·5–)5·0–6·0(–8·0) μm (**Phaeospora arctica**)
 Ascospores only or mainly 1-septate 25
- 25(24) Vegetative hyphae usually inconspicuous, ascomata (30–)50–80(–120) μm diam., mostly subimmersed and aggregated on tips of host thalli, ascospores 1-septate, (11–)13·5–16·5(–20) × (4·0–)5·0–6·5(–7·5) μm, without halo **Stigmidium frigidum**
 Vegetative hyphae forming a conspicuous dark reticulum, ascomata (30–)50(–80) μm diam., semi-immersed to sessile, dispersed, usually on bases of host thalli, ascospores (0–)1(–3)–septate, sometimes halonate 26
- 26(25) Asci (26–)31–41(–55) × (10–)14–20(–21) μm, ascospores (8·5–)11·0–13·5(–16·0) × (3·5–)4·5–5·5(–6·5) μm **Sphaerellothecium thamnoliae var. thamnoliae**
 Asci 47–64(–85) × (14–)17–27(–33) μm, ascospores (12·5–)14·0–19·5(–24·0) × (4·5–)5–8(–9) μm . . **Sphaerellothecium thamnoliae var. taimyricum**

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