

## Lichenicolous ascomycetes on *Siphula*-like lichens, with a key to the species

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**Abstract:** Sixteen species of lichenicolous fungi are documented from *Siphula*-like lichens. Two new genera based on new species are introduced. *Amylogalla* Suija, Motiej. & Kantvilas, characterized by I+ blue, K/I+ violet vegetative hyphae and ascomatal wall, immersed, cleistohymenial, yellowish to orange ascomata, unitunicate, non-amyloid, 8-spored asci and hyaline, ellipsoid, aseptate ascospores, is described from *Parasiphula* in Tasmania. *Saania* Zhurb., characterized by superficial, stromatic, multilocular ascomata, non-amyloid hymenial gel, persistent periphysoids, bitunicate, non-amyloid, 4(–8)-spored asci and narrowly obovate to ellipsoid, 1(–3)-septate, initially hyaline and smooth-walled, later sometimes brown and verruculose ascospores, is described from *Siphula* in South Africa. Four additional species are described as new: two from *Siphula* (*Cercidospora santessonii* Motiej., Zhurb., Suija & Kantvilas and *Stigmidium kashiwadani* Zhurb.) and two from *Parasiphula* (*Endococcus hafellnerianus* Motiej., Suija & Kantvilas and *Pyrenidium macrosporum* Motiej., Zhurb., Suija & Kantvilas). Additional hosts and/or expanded geographical ranges are reported for *Aabaarnia siphulicola*, *Epigloea soleiformis*, *Plectocarpon gayanum* and *Pyrenidium actinellum*. The Southern Hemisphere is the centre of species richness for siphulicolous fungi, with 12 species restricted to this region. Taxa recorded for the Northern Hemisphere are *Sphaerellothecium siphulae* (arctic and boreal) and the subcosmopolitan *Epigloea soleiformis* and *Pyrenidium actinellum*, both of which are also known from various lichen hosts. The distribution of siphulicolous fungi strongly underpins the current generic classification of *Siphula*-like lichens, with five species being confined exclusively to *Parasiphula* and nine to *Siphula*. A key to the taxa occurring on *Siphula* and *Parasiphula* is provided.

**Key words:** new records, new taxa, *Parasiphula*, siphulicolous fungi, Southern Hemisphere

Accepted for publication 19 September 2018

### Introduction

The lichen genus *Siphula* Fr. s.l. was long considered a challenge for taxonomists, principally because it was never observed with ascomata. Thus without the benefit of characters such as apothecial anatomy, morphology and ontogeny, ascus structure and ascospore morphology, inferences regarding its systematic position were at best

speculative. Authors, such as Hafellner (1988), regarded the genus as *incertae sedis* although Poelt (1973) recognized the family *Siphulaceae* Reichenb., containing the genera *Endocaena* Cromb., *Siphula* and *Thamnolia* Ach. ex Schaer., and placed it close to the *Cladoniaceae* on account of its chemistry. The advent of molecular methods offered great insights into the relationships of *Siphula* and its relatives. *Thamnolia* and some species of *Siphula* were shown to be members of, or at least close to, the *Icmadophilaceae* (Stenroos & DePriest 1998; Platt & Spatafora 2000; Stenroos *et al.* 2002). Subsequently Grube & Kantvilas (2006), studying a broader sample of taxa, found that *Siphula* was heterogeneous and comprised two unrelated groups with remarkable morphological convergence. The core of *Siphula* was confirmed to lie within the *Icmadophilaceae* but a complex of strictly austral species was found to be

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unrelated to *Siphula* and transferred to a new genus, *Parasiphula* Kantvilas & Grube within the *Coccotremataceae*. More recently, molecular work by Ludwig *et al.* (2016) has suggested that a further subdivision of *Siphula* might be warranted with the erection of a separate genus for the *S. decumbens* Nyl. group, although these results are yet to be formally published. These authors (*loc. cit.*) also reported the discovery of ascomata in *S. decumbens* and its relative, *S. fastigiata* (Nyl.) Nyl., which confirmed their close relationship to the *Icmadophilaceae*.

Species of *Siphula* s.l. are frequently hosts for lichenicolous fungi and, historically, some early reports or observations of supposed fruiting bodies were based on fungal parasymbionts (e.g. Nylander 1888) or on fungus-induced galls. For example, Hue (1914) erected the genus *Nylanderella* Hue for *Siphula decumbens*, but what he thought to be ascomata were the fruiting bodies of a lichenicolous fungus from the genus *Cercidospora* Körb. (R. Santesson, *in litt.*). Lichenicolous fungi, especially those that are commensalistic (Fleischhacker *et al.* 2015), are known to have potentially very selective host relationships and the possibility that they might help clarify *Siphula* taxonomy was already alluded to by Kantvilas (2002).

Even though the lichens ascribed to *Siphula* s.l. are widespread and diverse, and lichenicolous species have been observed on them for a long time, knowledge of the fungi inhabiting these lichens was surprisingly scant until recently. The first siphulicolous species, *Plectocarpon gayanum* Etayo, growing on an unidentified species of *Siphula*, was described only a decade ago (Etayo & Sancho 2008). Subsequently three further species were described: *Aabaarnia siphulicola* Diederich (Diederich 2014) and *Pyrenidium coccineum* Aptroot (Aptroot 2014), both on *Siphula decumbens* Nyl., and *Sphaerellothecium siphulae* Zhurb., together with an unidentified species of *Epithamnolia* Zhurb. (reported as *Hainesia* sp.), on *S. ceratites* (Wahlenb.) Fr. (Zhurbenko 2015).

The origins of the present study lie in a preliminary unpublished survey by JM and GK of lichenicolous fungi occurring in

Tasmania, a centre of speciation for *Siphula*-like lichens. The study was subsequently expanded to include collections of *Siphula* s.l. (*Siphula* and *Parasiphula*) from other regions, enabling a broader overview of the fungi occurring on these hosts. In the present paper, two new genera and seven new species of lichenicolous fungi growing on *Siphula* s.l. are described, new data on the geographical distribution and the host range of siphulicolous fungi are presented, and a key to all taxa studied is provided.

## Material and Methods

The study is based on 135 specimens of fungi found on *Siphula* s.l. deposited in the following herbaria: BILAS (1 specimen), H (25), HO (49), O (8), TNS (10), TU (4) and UPS (38). Microscopy and microimaging were undertaken using light and stereo microscopes; for some anatomical features, Nomarski interference contrast was employed. Microscopic characters were studied using hand-cut sections or squash preparations mounted in tap water, a 10% aqueous solution of potassium hydroxide (KOH; K), Lugol's Iodine solution, directly (I) and after KOH pretreatment (K/I), Brilliant Cresyl Blue (BCr), a 50% aqueous solution of nitric acid (N), phloxine and Congo red. Measurements were made in water. When > 10 measurements are summarized in the text, they are presented in the following format: (minimum–) (– SD) – ( $\bar{x}$  + SD) (–maximum) (*n*), where  $\bar{x}$  is the arithmetic mean, SD the standard deviation and *n* the number of measurements. Where ≤ 10 measurements are available, only extreme values are given. The length/width ratios of ascospores and conidia are indicated as 'l/w' and presented in the same way.

## The Species

### *Aabaarnia siphulicola* Diederich

*Bull. Soc. Nat. Luxemb.* 115: 144 (2014); type: New Zealand, Auckland Islands, Rose Island, Observation Point, on *Siphula decumbens*, 1963, *James* 992/1 (UPS—holotype).

*Notes.* This fungus is characterized by pale, immersed, gall-inducing, cleistohymenial, hyaline ascomata, 100–200 µm diam., a K/I+ blue hymenium, subcylindrical, 4–6-spored, K/I– asci with a massive apical cap, and oval to shortly cylindrical, 3-septate ascospores, 23–29 × 7–8.5 µm (Diederich 2014). Our specimens correspond well with the protologue, although we observed a wider

variation of gall forms. Galls on *S. decumbens* and *S. dissoluta* were identical to those described by Diederich (2014); that is, laminal, strongly basally constricted and often slightly more pinkish than the host thallus. However, galls on *S. fastigiata* were marginal, causing only slight thickening and no discoloration of the host thallus.

**Ecology and distribution.** *Abaarnia siphulicola* was first described from *Siphula decumbens* (Diederich 2014) and is here documented as occurring also on *S. dissoluta* and *S. fastigiata*. All host taxa have wide ecological amplitudes, from growing as epiphytes in wet forests to being terricolous in treeless vegetation. A wide range of specimens representing all habitats was examined but *A. siphulicola* was found only on terricolous host lichens, mainly from alpine areas. Similar trends have been observed by other workers. For example, Ihlen (1998) showed that different lichenicolous species may inhabit the same host (*Baeomyces rufus* (Huds.) Rebert.) at different altitudes. Furthermore, Muggia & Grube (2018) showed that the lineages of lichenicolous fungi differ considerably between sheltered, temperate, boreal environments and exposed arctic and high-altitude environments. On *Siphula fastigiata*, *A. siphulicola* was found together with *Sphaerellothecium* sp., whereas on *Siphula decumbens* it was accompanied by *Cercidospora santessonii* and *Plectocarpon gyanum*.

**Specimens examined.** **Australia:** *Tasmania:* Mount Anne, 42°55'57.3"S, 146°26'25"E, 1090 m, on *Siphula decumbens*, 2016, *Kantvilas* 71/16 (HO 583062); Mount King William I, 42°14'S, 146°08'E, 1300 m, on *S. fastigiata*, 1984, *Kantvilas* 108/84 (HO 319763); Lawson Range, 42°58'S, 145°41'E, 480 m, on *S. fastigiata*, 1986, *Moscal* 11954 (HO 114215); Mount Norold, 41°15'S, 146°15'E, 950 m, on *S. decumbens*, 1994, *Kantvilas* 31/94A (HO 585488); tarn above Lake Oberon, 43°09'S, 146°16'E, 880 m, on *S. decumbens*, 2002, *Felton* (HO 520187); Wylids Craig, 42°28'S, 146°23'E, 1250 m, on *S. fastigiata*, 1998, *Kantvilas* 272/98 (HO 0232).—**New Zealand:** *South Island:* Arthur's Pass, 1006 m, on *S. fastigiata*, 1962, *James* 1902 (UPS); *ibid.*, 975–1036 m, on *S. dissoluta*, 1962, *James* 1907a (UPS); Rock and Pillars, Taieri County, Museum Rock, 1260 m, on *S. dissoluta*, 1972, *Imshaug* 56044 (HO 309723). *Auckland Island:* saddle between Meggs Hill and Mount Eden, on *S. decumbens*, 1963, *James* 865/1 (UPS); Port Ross, above Erebus Cove, on *S. decumbens*, 1927, *G. E. Du Rietz* 2283:1

(UPS L-860156a, UPS L-860157); *ibid.*, on *S. dissoluta*, 1927, *G. E. Du Rietz* 2283:1 (UPS L-860150a).

**Amylogalla fava Suija, Motiej. & Kantvilas gen. et sp. nov.**

MycoBank No.: MB 827417 (genus) and MB 827434 (species)

Gall-inducing lichenicolous fungus. Ascomata cleistohymenial, immersed in the host thallus, yellowish to orange. Vegetative structures covered with a granulose, I+ blue, K/I+ violet pigment. Asci unitunicate, non-amyloid, with eight, aseptate, hyaline ascospores.

Type: Australia, Tasmania, South West National Park, Mount Scorpio, 43°10'S, 146°21'E, 1020 m, alpine heathland, on thallus of *Parasiphula georginae*, growing on soil in rock crevices, 16 December 1984, *G. Kantvilas* 720/84 (HO 132436—holotype).

(Fig. 1)

Lichenicolous ascomycete inducing galls on the host thallus; galls mostly distinct, becoming rounded, not constricted at the base, with numerous immersed ascomata, sometimes indistinct and simply forming breaks through the cortex of the host thallus and leaving a characteristic honeycomb pattern when the fungus dies. *Vegetative hyphae* extending between the mycobiont hyphae and photobiont cells of the host, reaching to the medullary layer of the lichen, colourless, irregularly branched, *c.* 3 µm wide, I+ blue, K/I+ violet, walls covered with minute I+ dark blue granules.

*Ascomata* cleistohymenial, hemioangiocarpic (closed when young and developing within the medullary layer of the lichen, hymenial layer opening at maturity when emerging through breaks in the lichen cortex); mature ascomata aggregated, immersed, 90–185 µm diam. (*n* = 7), concave, irregular in shape when viewed from above, globose to subglobose in section, orange to red to dark red. *Exciple* yellowish to orange in the upper part, 10–30 µm wide, K–, I+ blue, K/I+ violet, composed of rectangular cells (*textura angularis*) 5–8 × 3–6 µm, without excipular hairs; layer below the exciple composed of interwoven hyphae (*textura intricata*), *c.* 30 µm wide, K–, I+ blue, K/I+ violet. *Hymenium* 90–110 µm thick, orange in the upper part, colourless in the lower part; hymenial gel I–,



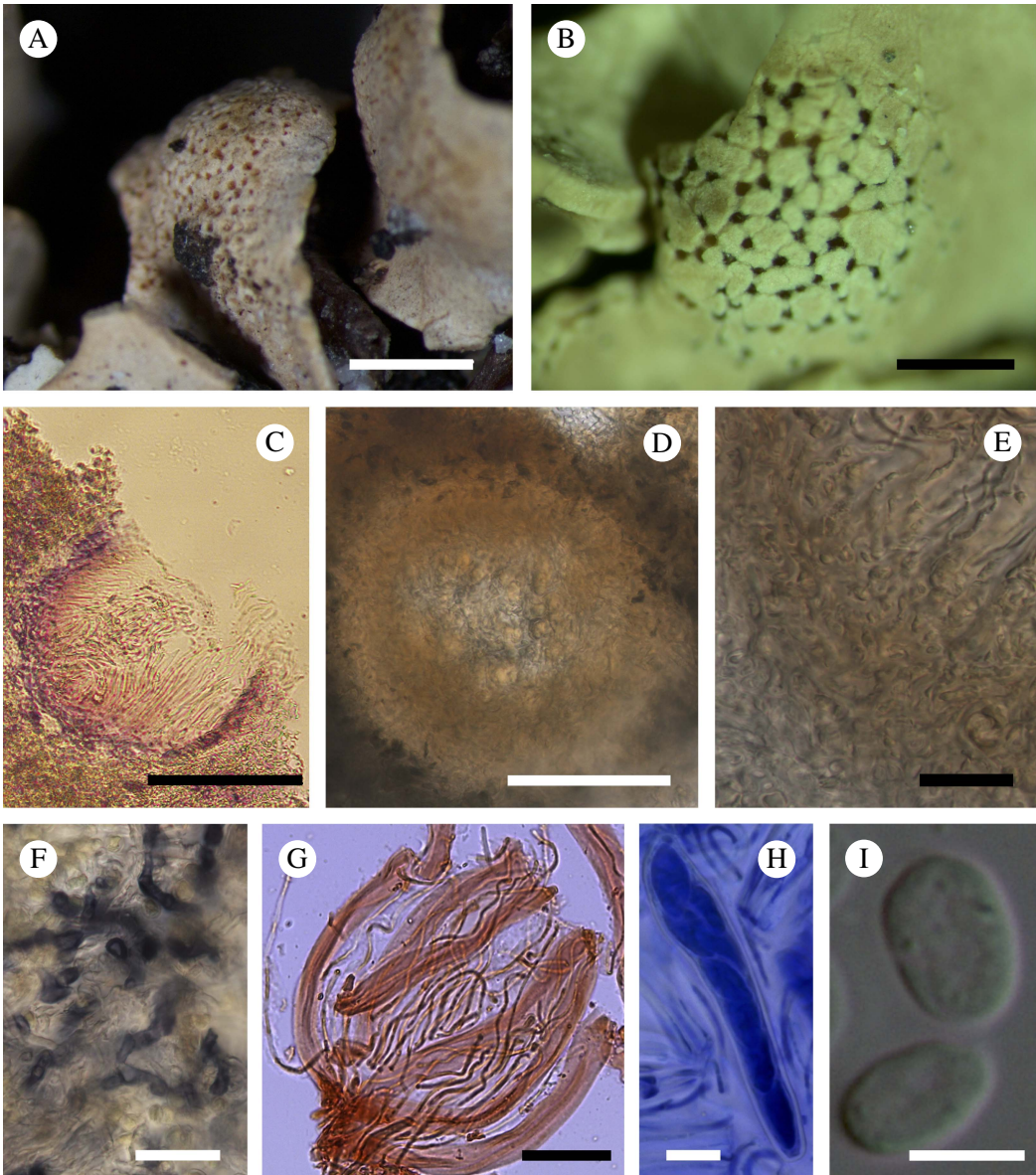


FIG. 1. *Amylogalla fava*. A, host thallus with honeycomb traces of former infection of the fungus (Jarman, HO 113707); B, galls with sunken ascomata (holotype); C, vertical section through an ascoma showing I+ violet reaction of the exciple (Kantvilas, HO 520227); D, vertical section through an immature ascoma (mounted in water); E, lower part of an ascoma showing the structure of the ascomatal wall (in water); F, vegetative hyphae after treatment with Lugol's solution; G, asci and paraphyses (in Congo red); H, ascus with ascospores (in BCr); I, ascospores (D–I, Kantvilas, HO 585552). Scales: A & B = 1 mm; C = 100  $\mu$ m; D = 50  $\mu$ m; E, F, H & I = 10  $\mu$ m; G = 20  $\mu$ m. In colour online.

K/I–; subhymenium colourless, composed of interwoven hyphae (*textura intricata*). *Paraphyses* mostly simple, dichotomously branched only at the base, separating easily in squash preparations, distantly septate, 1.5–2.0 µm wide, not or slightly swollen to 2.0–3.0 µm in upper part and covered with an orange gel (some gel-covered paraphyses up to 3 µm wide); gel patchily I+ blue, K/I–; contents of paraphyses Congo red+ reddish, BCr+ dark blue. *Asci* unitunicate, inoperculate, clavate to subcylindrical, 65–81 × 10–16 µm ( $n=7$ ), 8-spored, thin-walled, non-stipitate, without apical apparatus, I–; croziers not observed. *Ascospores* (11.0–) 11.7–14.3(–15.0) × ( 5.0–)5.7–7.3(–7.5) µm, l/w = 1.7–2.4 ( $n=16$ ), aseptate, hyaline, ellipsoid, with rounded apices, irregularly biseriolate in the asci; contents BCr+ blue; wall smooth, <1 µm wide, BCr–. *Asexual morph* not observed.

*Etymology.* The generic name refers to the unique amyloid reaction of the fungal structures and to the induction of galls, whereas the specific epithet 'fava' alludes to the characteristic 'honeycomb' pattern of the gall surface.

*Notes.* In the absence of molecular data, the relationships of this monotypic genus remain unclear. At first glance, the new fungus is reminiscent of *Thamnogalla crombiei* (Mudd) D. Hawksw. (*Cordieritiaceae*, *Helotiales*) in having ascomata immersed in galls, aseptate ascospores and non-amyloid asci (Hoffmann & Hafellner 2000). *Abaarnia siphulicola* is likewise characterized by cleistohymenial ascomata, non-amyloid asci and the formation of galls but differs in having 3-septate ascospores (Diederich 2014). The most conspicuous difference between these two species and *Amylogalla fava* is the granular pigment on vegetative structures of *Amylogalla* which reacts persistently blue in I and violet in K/I. Such strong and persistent hemiamyloidy is quite uncommon in ascomycetes. A similar reaction was recorded in a few species of *Patellariales* (Kutorga & Hawksworth 1997), whereas in *Trypetheliaceae* and *Graphidaceae*

the hymenial gel or ascospores may sometimes react I+ violet to purple (Hawksworth 1985; Staiger 2002). In some species of lichenized genera, for example *Bellemerea* Hafellner & Cl. Roux, *Immersaria* Rambold & Pietschm. and *Lecidea* Ach., the hyphae of the mycobiont are also I+ violet (Calatayud & Rambold 1998; Purvis & Gilbert 2009; Ruprecht *et al.* 2010; Knudsen & Kocourková 2014). On the other hand, the hyphae surrounding the exciple in *Halospora deminuta* (Arnold) Tomas. & Cif. are reported to occasionally react I+ violet but this character is not constant (Orange 2009). Likewise *Polycoccum stictaria* (Linds.) D. J. Galloway is reported to have asci that turn I+ deep violet (Galloway 2004). In *Helotiales*, a faint hemiamyloid reaction (I+ rose, K/I+ pale violet) was reported in the ectal exciple of several species of *Lachnellula* P. Karst., *Proliferodiscus* J. H. Haines & Dumont and *Perrotia* Boud. by Baral (1987, 2008), who noted that this feature is important taxonomically and illustrates the relationships between these genera. The structure and composition of fungal polysaccharides, responsible for different reactions with iodine solutions, are acknowledged as important characters in fungal taxonomy (Ruiz-Herrera & Ortiz-Castellanos 2010), albeit mostly above the rank of genus.

*Ecology and distribution.* This species is known only from Tasmania where it grows on the thalli of *Parasiphula complanata*, *P. elixii*, *P. fragilis* and *P. georginae*. Although extensive herbarium collections were available for study, it was not found on other species of *Parasiphula* (*P. comata*, *P. foliacea*, *P. jamesii*) even though these occur sympatrically with the infected taxa, often in close proximity. Species of *Parasiphula* are chiefly alpine and occur on peaty soil in a variety of microhabitats, ranging from exposed situations in rock crevices, on the ground in gaps in heathland, or seasonally submerged in puddles and around the fringes of tarns. Host thalli infected with *A. fava* occurred within the entire range of such habitats. Microscopic examination revealed no obvious damage to either the mycobiont or the photobiont; thallus colour remains

unchanged at the locus of infection, although the fungus usually induces galls on the host thallus.

On *Parasiphula complanata*, *A. fava* was found associated with *Endococcus hafellnerianus* and an unidentified species of *Sphaerellothecium*, whereas on *Parasiphula fragilis* it was associated with *Pyrenidium macrosporum* and an undetermined agent inducing galls on the host thallus.

*Additional specimens examined. Australia: Tasmania:* Mount Algonkian, 42°24'S, 146°03'E, 1010 m, on *Parasiphula fragilis*, 1990, *Kantvilas* 79/90 (HO 122448); Mount Bobs, 43°18'S, 146°36'E, 1080 m, on *P. fragilis*, 1987, *Jarman* (HO 113707); Mount Campbell, NE of Lake Dove, 41°39'S, 145°59'E, on *P. fragilis*, 1972, *Bratt* 72/1224 (HO 45778); *ibid.*, on *P. complanata*, 1972, *Bratt* 72/1223 (HO 45777); Clear Hill, 42°41'S, 146°16'E, 1190 m, on *P. elixii*, 1996, *Kantvilas* 30/96 (HO 316441); Crest Range, 43°17'31"S, 146°30'26"E, 960 m, on *P. fragilis*, 2016, *Kantvilas* 167/16A (HO 585552); Dove Lake, 41°39'S, 145°58'E, 950 m, on *P. fragilis*, 1984, *Kantvilas* & *James* 320/84 (HO 124471); Mount Ironstone, 41°43'S, 146°28'E, 1440 m, on *P. complanata*, 2005, *Kantvilas* 327/05 (HO 534844); Travellers Rest Lake, 42°03'S, 146°14'E, 950 m, on *P. complanata*, 2003, *Kantvilas* 2/03 (HO 520227); Mount Tyndall, 41°56'S, 145°34'E, 1060 m, on *P. georginae*, 1989, *Kantvilas* 253/89 (HO 129677), 254/89 (HO-544736).

***Cercidospora santessonii* Motiej., Zhurb., Suija & Kantvilas sp. nov.**

Mycobank No.: MB 827416

Lichenicolous fungus similar to *Cercidospora epipolytropia* (Mudd) Arnold but distinguished mainly by host selection (*Siphula* s.s. instead of *Lecanora*), richly branched and anastomosed pseudoparaphyses, 1.5–2 µm thick, and consistently 8-spored asci, with the ascospores (0–) 1-septate, 14.4–20.8 × 4.4–7.5 µm.

Type: Australia, Tasmania, Walls of Jerusalem National Park, c. 0.5 km NE of Twin Spires, 41°53'S, 146°07'E, 1250 m, alpine heathland, on thallus of *Siphula fastigiata*, 20 March 1999, *G. Kantvilas* 73/99 (HO 442924—holotype).

(Fig. 2)

*Vegetative hyphae* not observed. *Ascomata* perithecioid, subglobose in section, 120–270 µm diam. ( $n=9$ ), immersed in the host thallus, with only the ostiolar region breaking through the surface of the host; ostiole indistinct. *Exciple* 30–40 µm thick, in the

upper half bluish green around the ostiole to ± greenish brown at 1/3 of the peridium, or blue-green inside and olive-grey outside, in the lower half hyaline, composed of cells that are rectangular to somewhat elongate at the base, green coloration enhanced in K or K–. *Pseudoparaphyses* abundant, septate, richly branched and anastomosing, 1.5–2.0 µm wide, not swollen at the apices. *Asci* 8-spored, clavate to subcylindrical, (54–) 56–77(–85) × (10–)10.5–14.5(–15) µm ( $n=13$ ), I–, KI–, with a short, indistinct ocular chamber and a short stalk. *Ascospores* (0–)1-septate, (14.4–)15.8–19.3(–20.8) × (4.4–)4.7–6.4(–7.5) µm, l/w = (2.3–)2.7–3.8(–4.3) ( $n=43$ ), hyaline, ovate-ellipsoid to slightly fusiform, with a median septum and cells somewhat heteropolar, the lower cell slightly longer and narrower than the upper one, occasionally with a halo 0.5–1 µm thick, biseriate to diagonally uniseriate in the ascus.

*Asexual morph* pycnidia, 80–100 µm diam., intermixed with ascomata, immersed in the host thallus, globose, with the upper part of the pycnidial wall bluish green, and the lower part colourless or slightly greyish, consisting of 3–4 rows of rectangular cells c. 10 µm wide. *Conidiophores* absent. *Conidiogenous cells* lining the pycnidial wall, colourless, elongate, 15 × 1 µm. *Conidia* borne apically, 3.0–6.0 × 1.0 µm ( $n=10$ ), bacilliform, aseptate, hyaline.

*Etymology.* This species is named after the eminent Swedish lichenologist, the late Rolf Santesson, in acknowledgement of his enormous contribution to the study of lichenicolous fungi, including those on *Siphula*.

*Nomenclatural note.* The specimen UPS L-860064 was previously examined by Rolf Santesson, whose handwritten note on the label indicates that he intended to propose a new combination "*Cercidospora medioxima*" based on *Nylanderella medioxima* (Nyl.) Hue (Hue 1914), which itself is based on *Siphula medioxima* Nyl. This new combination was never published and the name *Nylanderella medioxima* (Nyl.) Hue has since been synonymized with *Siphula decumbens* (Kantvilas 1998).



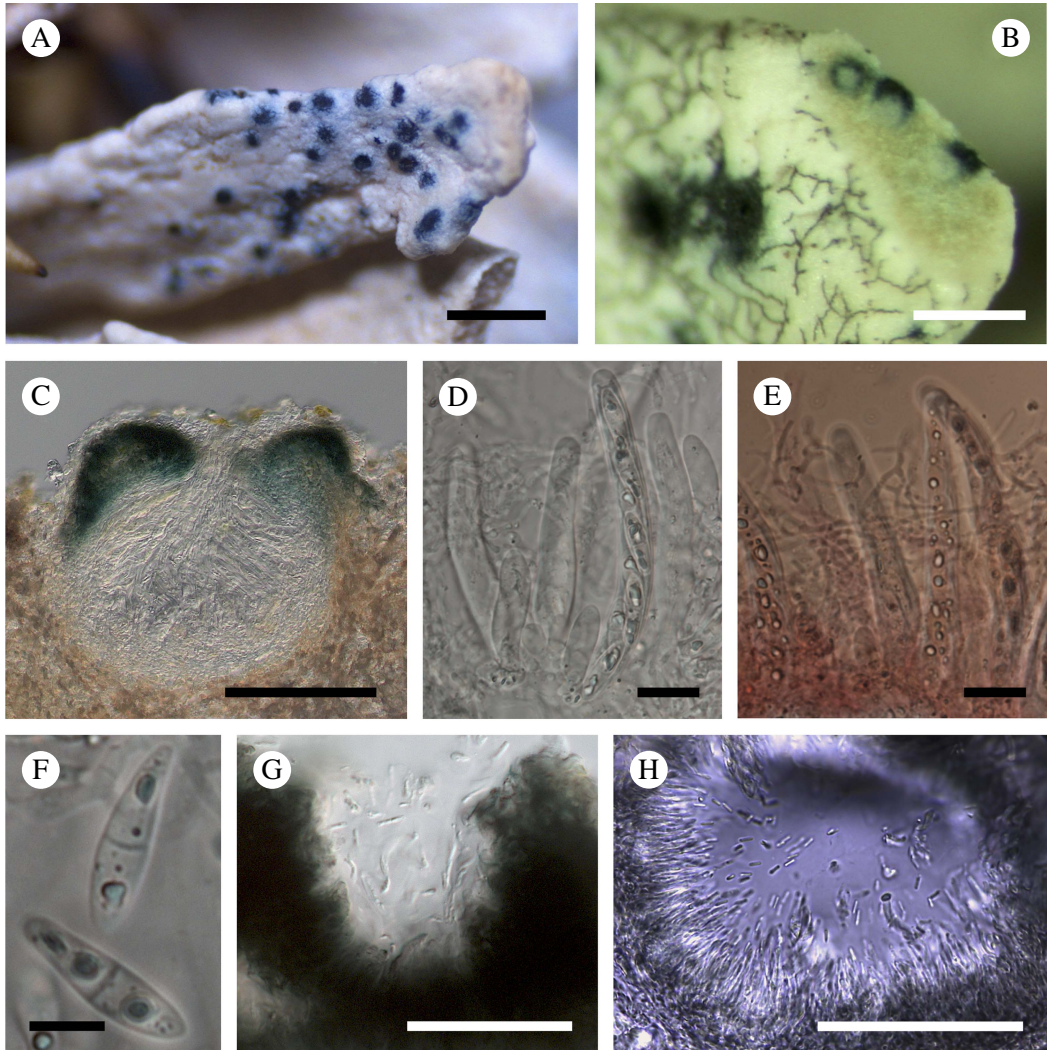


FIG. 2. *Cercidospora santessonii*. A, ascomata on the host thallus (holotype); B, ascomata of *C. santessonii* intermixed with hyphae of *Sphaerellothecium* sp. (Felton, HO 520187); C, vertical section through an ascoma (in water) (Malcolm & Vězda, H); D, asci with ascospores and pseudoparaphyses (in water); E, asci with ascospores and pseudoparaphyses (in Congo red); F, ascospores (in water; D–F, Felton, HO 520187); G, pycnidia with conidia (Du Rietz & Du Rietz, UPS L-860067c); H, pycnidia, conidiogenous cells and conidia (in water) (Felton, HO 520187). Scales: A = 1 mm; B, G & H = 500  $\mu$ m; C = 100  $\mu$ m; D & E = 20  $\mu$ m; F = 5  $\mu$ m. In colour online.

*Notes.* According to Navarro-Rosinés *et al.* (2009), the colour of the peridial pigment, the number of ascospores per ascus, ascospore shape and septation, the dimensions of all parts of the ascomata, and host selection are the main characters for distinguishing species of *Cercidospora* Körb. Of *c.* 30

*Cercidospora* species (Lawrey & Diederich 2018), seven are superficially similar to *C. santessonii*, with an exciple that is bluish green above and hyaline below, exclusively or mainly 1-septate ascospores, and persistently or predominantly 8-spored asci. The salient differences between these taxa are

summarized in Table 1. The most similar species is *C. epipolytropha* s.l., which differs mainly by host selection (epilithic *Lecanora* vs. *Siphula*) and, according to our observations and published data, by its simple to sparsely branched, relatively narrower pseudoparaphyses, (1–1.5(–2)  $\mu\text{m}$  versus 1.5–2  $\mu\text{m}$  in *C. santessonii*), and asci that can be less than 8-spored. Furthermore, the ascospores in *C. epipolytropha* are 1(–2)-septate, whereas in *C. santessonii* they are (0–)1-septate. There are also slight size differences between the two species: in *C. santessonii*, the ascomata, asci and conidia are larger, although these distinctions are subtle and require further examination. Branching of the pseudoparaphyses is not generally well described in *Cercidospora* species (see Table 1 and the references cited in the legend). Navarro-Rosinés *et al.* (2004, 2009) state that a characteristic of *Cercidospora* is that they are simple or with some anastomoses. However, in at least one other species, *C. alpina* Ihlen & Wedin, the pseudoparaphyses are also branched and anastomosed (Ihlen & Wedin 2007).

**Ecology and distribution.** This species is known from the thalli of *Siphula decumbens* and *S. fastigiata* in alpine habitats, where these host lichens are common on peaty soil or on soil in crevices in large rock outcrops. No visible damage to the host thallus was observed, except for in *Malcolm & Vězda* (H) where it had turned grey under infection. The species is recorded from Tasmania and New Zealand. A further record from Venezuela on *S. pteruloides* is uncertain as no asci or ascospores were observed in that material.

In Tasmanian specimens, *Cercidospora santessonii* was associated with *Sphaerellothecium* sp. (on *S. decumbens* and *S. fastigiata*) and with *Aabaarnia siphulicola* and *Plectocarpon gayanum* (on *S. decumbens*).

**Additional specimens examined.** **Australia:** Tasmania: Mount Bobs, 43°18'S, 146°36'E, 1080 m, on *Siphula fastigiata*, 1987, *Jarman* (HO 113705); tarn above Lake Oberon, 43°09'S, 146°16'E, 880 m, on *S. decumbens*, 2002, *Felton* (HO 520187).—**New Zealand:** South Island: Arthur's Pass, on *S. fastigiata*, 1927, *G. E. & G. Du Rietz* 1508:2 (UPS L-860067c, UPS L-860064); Mount Rochfort, 750 m, on *S. decumbens*, 1997, *Malcolm*

*& Vězda* (H).—**Venezuela:** *Territorio Federal Amazonas:* Atabapo Departamento, Cerro Marahuaca, 3°35'N, 65°20'W, 2480–2580 m, on *S. pteruloides*, 1982, *Guariglia et al.* (identification uncertain; H).

**Comparative material of *Cercidospora epipolytropha* s.l. examined** (all on *Lecanora polytropha* (Ehrh. ex Hoffm.) Rabenh.). **Estonia:** *Hiiu County:* Hõralaid islet, 58°54'N, 23°04'E, 2002, *Jüriado & Suija* (TU 23731b); Salinõmme, 58°50'N, 22°57'E, *Jüriado & Suija* (TU 25641a); Kadakalaid islet, 58°59'N, 23°00'E, 2004, *Jüriado & Suija* (TU 27792b); Hiiumaa Islets Nature Reserve, Vareslaid islet 58°59'N, 23°00'E, 2001, *Jüriado* (TU 27980a). *Harju County:* Lahemaa National Park, Mohni Island, 59°40'N, 25°47'E, 2008, *Suija* (TU 45439d); *ibid.*, 59°40'N, 25°48'E, 2008, *Jüriado* (TU 45619i).—**Greenland:** Qassiarisuk (Brattahlil), 61°06'–10'N, 45°30'–35'W, 100 m, 2005, *Motiejūnaitė* (BILAS 7567).—**Lithuania:** *Panevėžys County:* Biržai District, Juodžioniai, 56°14'N, 24°53'E, 60 m, 2006, *Stončius* (BILAS 9568). *Vilnius County:* Trakai District, Aukštadvaris, 54°36'N, 24°30'E, 150 m, 1997, *Motiejūnaitė* (BILAS 10708).—**Russia:** *Karelia Keretina:* Keret' Archipelago, Keret' Village, 66°16'N, 33°34'E, 5 m, 2000, *Himmelbrant* (LE 210292). *Putorana Plateau:* Talnakh Town, 69°28'N, 88°30'E, 1985, *Zhurbenko* (LE 206994). *Murmansk Region:* Tumannyi, 69°01'N, 35°48'E, 100 m, 1997, *Zhurbenko* (LE 261644). *Polar Ural:* Mt. Rai-Iz, 66°57'N, 65°37'E, 150 m, 1986, *Zhurbenko* (LE 261554). *Yakutiya:* Laptevykh Sea coast, E part of Kunga Range, 71°16'N, 129°22'E, 240 m, 2000, *Kunitskii* (LE 260154). *Chukotka Autonomous Okrug:* Wrangel Island, Somnitel'naya River, 70°58'N, 179°35'W, 1985, *Yurtsev* (LE 261764:a); Bezymyannoe Lake, 66°39'N, 176°40'E, 1979, *Makarova* (LE 261525); Lorino, 65°29'N, 171°43'W, 1972, *Makarova* (LE 261534); Sireniki, 64°24'N, 173°54'W, 1983, *Makarova* (LE 261784).

### **Echinothecium sp.**

**Vegetative hyphae** forming a conspicuous, dark, superficial reticulum. **Ascomata** perithecioid, superficial, 20–60  $\mu\text{m}$  diam. ( $n=10$ ), covered by protruding septate hyphae 2–5  $\mu\text{m}$  thick and up to 50  $\mu\text{m}$  long. **Asci** 35  $\times$  13–15  $\mu\text{m}$  ( $n=4$ ), 8-spored. **Ascospores** hyaline to occasionally pale brown, soleiform, with a wider upper cell, (9.5–)9.8–11.0(–11.7)  $\times$  (3.7–)3.9–4.7(–5.2)  $\mu\text{m}$ , l/w = (2.0–)2.2–2.6(–2.7) ( $n=18$ ), 1-septate, smooth-walled, non-halonate. All specimens were collected at high elevations in Venezuela.

**Notes.** This fungus closely resembles *Echinothecium reticulatum* Zopf, a species reported from various genera of the



TABLE 1. Comparison of *Cercidospora* species with 1-septate ascospores, 8-spored asci and an exciple bluish green above and hyaline below (following Navarro-Rosinés et al. 2004, 2009; Zhurbenko 2012; Calatayud et al. 2013 and present paper).

Character	<i>C. caudata</i>	<i>C. epipolytropa</i> s.l.	<i>C. epithamnolia</i>	<i>C. melanophthalmae</i>	<i>C. santessonii</i>	<i>C. solearispora</i>	<i>C. thammogalloides</i>	<i>C. verrucosaria</i>
Host	<i>Caloplaca</i> s.l.	<i>Lecanora polytropa</i> group	<i>Thamnolia</i>	<i>Rhizoplaca</i>	<i>Siphula</i>	<i>Aspicilia</i> , <i>Circinaria</i>	<i>Thamnolia</i>	<i>Megaspora</i>
Galls	no	no	no	no	no	occasionally	yes	no
Ascoma size (µm)	150–250	95–220	90–120	170–330	120–250	160–230	80–120	130–200
Exciple colour (upper part)	green-blue to brown	greenish or brownish blue	dark bluish green	blue-green, occasionally violaceous brown in the outermost part	bluish green to greenish brown or bluish green inside, olive outside	blue-green	dark bluish grey	dark bluish brown
Pseudoparaphyses: abundance	rather abundant	abundant	sparse to indistinct	abundant	abundant	abundant	sparse to indistinct	relatively abundant
width (µm)	1–1.5(–2)	1–1.5(–2)	–1.5	1.5–2	1.5–2	1.5–2	1.5–2	1.5–2
branching	no data	scarcely branched	scarcely branched	no data	richly branched and anastomosed	no data	scarcely branched	no data
Ascus size (µm)	55–75 (–80) × 8–11	50–70 × 9–13	(40–)44–60 (–63) × 10–13 (–14)	(55–)70–90 (–100) × 10–15	54–(61.5)–72 × 10– (11.7)–15	50–70 × 10–15	(41–)46–60 (–72) × (10–) 12–16(–18)	65–95 (–105) × (8–) 9–11 (4–)8
Number of spores per ascus	(4–)8	(2–)8	8	(4–)8	8	(6–)8	8	(4–)8
Ascospore dimensions (µm)	(14–)16–24 (–30) × (3–) 4–6(–7)	(14–)15–19 (–22) × (4.5–) 5–6(–7)	(12–)13–16 (–19) × (3–) 3.5–4.5(–5)	(16–)18–22 (–24) × (4–)5–6.5 (–7)	(14.7–)15.3–18.8 (–20) × (4.6–)4.9–6.7 (–7.5)	(15–)17–21 (–22) × (4.5) 5–6(–7)	(12–)14–17 (–19) × (3.5–) 4–5(–5.5)	(14.5–)15.5– 19.5 (–23) × (4.5–) 5–6(–7)
Ascospore shape	strongly heteropolar, lower cells caudate	slightly heteropolar, lower cells not caudate	strongly heteropolar, lower cells not caudate	slightly heteropolar, lower cells not caudate	heteropolar, lower cells not caudate	strongly heteropolar, lower cells not caudate	distinctly heteropolar, lower cells not caudate	slightly heteropolar, lower cells not caudate
Conidium size (µm)	3 × 0.5	3–5 × 0.5–1	no data	no data	3–6 × 1	no data	no data	no data

*Parmeliaceae* as well as from *Physcia* (Halici & Aksoy 2009; Zhurbenko *et al.* 2012; Brackel 2014). However, in a strict sense, *E. reticulatum* is confined to species of *Parmelia* s.s. and is characterized by somewhat shorter ascospores, 8–9.5 × 3.5–4.5 µm (Zopf 1898) in comparison to the material examined on *Siphula*. The second accepted species of this genus, *Echinothecium aerophilum* Alstrup & M. S. Cole, grows on species of *Alectoria* and is very distinct in its loosely interwoven vegetative hyphae with few connections to the host thallus, 4-spored asci and much larger ascospores, 27–37 × 7–9 µm (Alstrup & Cole 1998). As the material available is rather limited and the taxonomic status of *Echinothecium reticulatum* s.l. requires further revision, this fungus is identified only to genus.

*Specimens examined.* **Venezuela:** Bolívar State: Roscio Municipality, top of Tramen-tepui, NW of Macizo del Ilu-(Uru-) tepui, 5°27'N, 61°01'W, 2650 m, on *Siphula pteruloides*, 1985, Huber (H). Tachira State: around Quebrada de Pata de Judío, near to La Linea, upper part of Páramo de Tamá, the Oirá basin, 3000 m, on *Siphula* sp., 1983, Lopez-Figueiras 30286 (H). Territorio Federal Amazonas: Atabapo Departamento, Marahuaca hill, 3° 35'N, 65°20'W, 2480–2580 m, on *S. pteruloides*, 1982, Guariglia *et al.* (H).

**Endococcus hafellnerianus Motiej.,  
Suija & Kantvilas sp. nov.**

MycoBank No.: MB 827418

Lichenicolous fungus characterized by ascomata 100–130 µm diam., predominantly 4-spored asci and soleiform ascospores, 15–24 × 5–10 µm.

Type: Australia, Tasmania, Mount Norold, 43°15'S, 146°15'E, 950 m, alpine heathland-sedgeland, on thallus of *Parasiphula georginae* growing on soil, 24 February 1994, G. Kantvilas 31/94 (HO 319643—holotype).

(Fig. 3)

*Vegetative hyphae* not observed. *Ascomata* pseudothecia, abundant, subglobose in section, black, 100–130 µm diam. ( $n = 5$ ), immersed in the host thallus, breaking through the thallus cracks with only the ostiolar region clearly visible. *Ascomatal wall* pseudoparenchymatous, composed of 3–4 layers of cells (*textura intricata*) 5–10 µm

wide, cell walls thickened, dark brown, K–. *Hamathecium* of short, simple periphyses lining the ostiole; *paraphysoids* absent; *interascal gel* I+ orange. *Asci* (42.0–)42.0–49.6 (–52.0) × (14.5–)14.7–20.9(–22.0) µm ( $n = 11$ ), I–, predominantly 4-spored, occasionally 3- or 6-spored, 8-spored when immature, saccate to clavate, shortly stalked or non-stipitate, with a small, rather wide, flat, apical extension. *Ascospores* 1-septate, (15.0–)17.2–21.8 (–24.0) × (5.0–)6.6–8.9(–10.0) µm, l/w = 1.9–3.6 ( $n = 28$ ), soleiform, the upper cell usually larger than the lower one, not or only slightly constricted at the septum, dark brown and smooth-walled when mature, hyaline to greyish and minutely verruculose when young, with a halo < 1 µm thick. *Asexual morph* not observed.

*Etymology.* This species is named after the prominent Austrian lichenologist, Josef Hafellner, in acknowledgement of his enormous contribution to the study of lichenicolous fungi.

*Notes.* Of *c.* 40 species of *Endococcus* Nyl. (Lawrey & Diederich 2018), only five, including “*Microthelia*” *calcaricola* Mudd (Mudd 1861), which Hawksworth (1979) with some doubts synonymized with *Endococcus rugulosus* Nyl., have ascospores exceeding 20 µm in length (Table 2). The most similar documented species to *Endococcus hafellnerianus* is an undescribed *Endococcus* sp. (Kocourková 2000), which has larger ascomata, persistently 8-spored asci and a different, taxonomically unrelated host (*Lecidella carpathica* Körb.).

*Ecology and distribution.* This species is known only from Tasmania where it occurs on the thalli of *Parasiphula complanata*, *P. fragilis* and *P. georginae*, causing local discoloration of the host. These taxa all occur on boggy peaty soil in alpine, treeless vegetation. On *Parasiphula complanata*, the new species was associated with *Amylogalla fava*.

*Additional specimens examined.* **Australia:** Tasmania: Mount Campbell, NE of Lake Dove, 41°39'S, 145°59'E, on *Parasiphula complanata*, 1972, Bratt 72/1223 (HO 45777); Mount La Perouse, 43°30'S, 146°44'E, 1150 m, on *P. fragilis*, 1986, Kantvilas 184/86 (HO 585551).

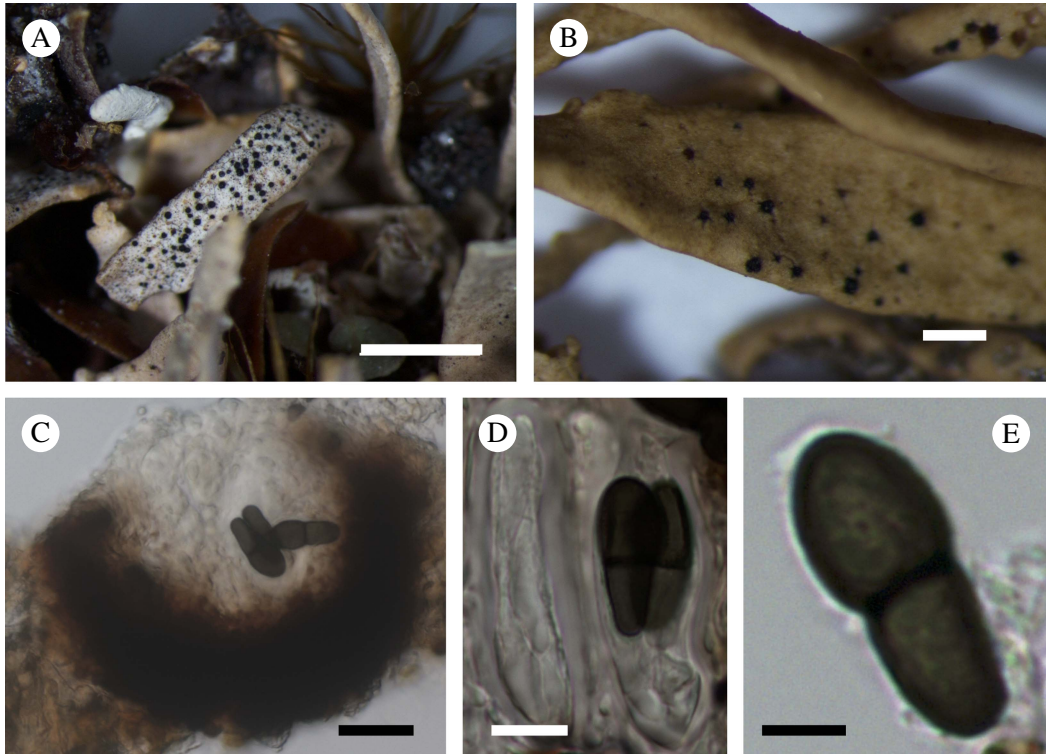


FIG. 3. *Endococcus hafellnerianus*. A & B, ascomata on the host thallus (A, holotype; B, Bratt, HO 45777); C, section through an ascoma; D, asci with ascospores; E, ascospore (in water, Kantvilas HO 122448). Scales: A = 5 mm; B = 1 mm; C = 20  $\mu$ m; D = 10  $\mu$ m; E = 5  $\mu$ m. In colour online.

### *Epigloea soleiformis* Döbbeler

*Beihefte zur Nova Hedwigia* 79: 229 (1984); type: Österreich, Salzburg, Schladminger Tauern, zwischen Hundsfeldsee und Hundskopf, 1800–2000 m, auf veralgten Moosen, 1981, Döbbeler (M Dö 4720—holotype).

**Notes.** This non-lichenized fungus is typically associated with algal films over humus, rotten wood, rock and occasionally lichens, mostly species of *Cladonia*, *Peltigera*, *Placynthiella*, *Stereocaulon* or *Trapeliopsis* (Döbbeler 1984; Zhurbenko 2010; Kukwa *et al.* 2012; Czarnota & Hernik 2013). The species is characterized by dull blackish green or grey perithecioid ascomata, 0.07–0.15 mm diam., 8-spored asci and 1-septate ascospores, 8.5–14  $\times$  3.5–5  $\mu$ m, without apical appendages (Döbbeler 1984). Our specimen concurs with the protologue. This is its first record from *Siphula*, as well as the first from South America.

**Specimen examined.** Chile: Magallanes Province: Puerto Bueno, 51°00'S, 74°12'W, over *Siphula dissoluta*, 1969, Imshaug 44580 & Ohlsson (H).

### *Neolamya* sp.

(Fig. 4)

**Vegetative hyphae** not observed. **Ascomata** perithecioid, aggregated, immersed to slightly protruding, exposed parts opaque, black and matt when dry, translucent, olive and somewhat glossy when wet, subglobose to broadly ellipsoid in section, 100–140  $\mu$ m diam. ( $n=6$ ), lacking a clypeus, with an irregular pore 20–30  $\mu$ m long. **Exciple** patchily pale to dark olive-brown, darker above. **Hymenial gel** K/I–. **Periphyses** not observed. **Paraphyses** well developed, unbranched, distantly septate, c. 2.5  $\mu$ m thick at the base, gradually tapering to 1–1.5  $\mu$ m towards the



TABLE 2. Comparison of *Endococcus* species with ascospores exceeding 20 µm in length (following Mudd 1861; Keissler 1930; David & Etayo 1995; Kocourková 2000; Kainz & Triebel 2004; Zhurbenko & Brackel 2013; Zhurbenko et al. 2016 and present paper).

Character	<i>E. caudisporus</i>	<i>E. hafellnerianus</i>	<i>E. macrosporus</i>	<i>E. sendtneri</i>	<i>Endococcus</i> sp. (Kocourková 2000)	“ <i>Microthelia</i> ” <i>calcaricola</i> Mudd
Host	<i>Lathagrium auriforme</i>	<i>Parasiphula</i>	<i>Rhizocarpon</i>	<i>Polyblastia sendtneri</i>	<i>Lecidella carpatica</i>	<i>Circinaria</i>
Ascoma size (µm)	140–165 × 125–150	100–130 diam.	130–220 diam.	100 – 250 diam.	150–185 diam.	no data
Number of ascospores per ascus	8	3–6 (8 when immature)	8	8	8	8
Ascospore wall ornamentation	smooth	minutely verruculose when young, later smooth	smooth	finely verruculose, later smooth	verruculose	no data
Ascospore colour	greenish brown, hyaline when young	dark brown, hyaline to greyish when young	medium brown, pale to olive-grey when young	pale to medium brown	no data	pale olive-green to olive-brown
Ascospore size (µm)	13–21 × (3.5–)4–5.5	(15–)17.2–21.8 (–24) × (5–)6.6–8.9 (–10)	(9.8–)15.3–18.9 (–23.2) × (5.8–)6.7–7.9 (–9.5)	(10.5 –)13.1–17.7 (–22.0) × (5.0 –)6.4 (–9.2(–12.5)	(15–)18–23 (–25) × (6–)6.5 – 8(–9)	13–22 × 6–8
Ascospore shape	caudate, tadpole-shaped	soleiform	ellipsoid to obovoid, often curved	narrowly obovate, oblong or occasionally ellipsoid	no data	ellipsoid to oblong

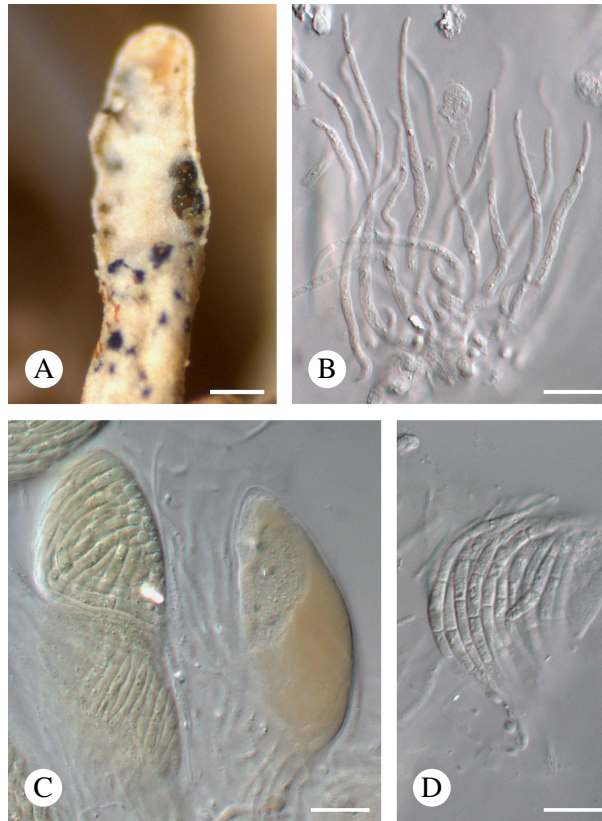


FIG. 4. *Neolamya* sp. (Ohmura 5255). A, ascomata on partly eroded wet host lobe tip; B, paraphyses (in K); C, asci (in K/I); D, ascospores (in water). Scales: A = 200  $\mu$ m; B–D = 10  $\mu$ m. In colour online.

apex, apically not enlarged. *Asci* unitunicate, K/I–,  $47\text{--}67 \times 17\text{--}21 \mu\text{m}$  ( $n = 7$ ),  $\pm$  ellipsoid, without a distinct ocular chamber, containing at least 20 spores. *Ascospores* hyaline, falcate to sigmoid (possibly due to packing inside the ascus), gradually attenuating towards the apices,  $40\text{--}50 \times 2\text{--}3 \mu\text{m}$  ( $n = 10$ ), smooth-walled, non-halonate, 3-septate, not constricted at the septa, arranged within the ascus in a bundle. *Asexual morph* not found. The fungus does not visibly damage the host thallus or induce gall formation in the host.

*Notes.* The material examined represents an undescribed species but is too scant to be formally described. It is referred to *Neolamya* Theiss. & Syd. but with some uncertainty as this genus is characterized by a dark brown exciple and distinct periphyses (Ertz 2004). It

differs clearly from the other three known species of *Neolamya* by the septation and size of the ascospores and by its host selection. *Neolamya ahtii* Zhurb., growing on species of *Cladonia* P. Browne, is characterized by mainly 1-septate and much shorter ascospores,  $6.5\text{--}34 \times 2.5\text{--}6 \mu\text{m}$ ; *N. peltigerae* (Mont.) Theiss. & H. Syd., growing on species of *Peltigera* Willd., has 3–6-septate ascospores that are much longer,  $56\text{--}90 \times 2\text{--}3.5 \mu\text{m}$ ; *N. xanthoparmeliae* Kocourk., growing on species of *Xanthoparmelia* (Vain.) Hale, has 3–10-septate and likewise much longer ascospores,  $55\text{--}111.5 \times 3\text{--}5 \mu\text{m}$  (Ertz 2004; Kocourková 2009; Zhurbenko & Pino-Bodas 2017). This fungus also strongly resembles *Spirographa fusisporella* (Nyl.) Zahlbr., the type of the genus *Spirographa* Zahlbr. However, the species of this genus

are characterized by cleistohymenial ascospores (Diederich 2004).

*Specimen examined.* **USA:** *Hawaii:* Maui Island, trail between Puu Kukui and Kaulalewelewe, 20°53'N, 156°35'W, 1500–1600 m, on *Siphula pickeringii*, 1998, *Ohmura* 5255 (TNS).

### **Plectocarpon gayanum Etayo**

*Biblioth. Lichenol.* **98:** 171 (2008); type: Chile, Navarino, campamento del lago Róbaló, 54°58'23.3"S, 67°40'59.9"W, 290 m, on cf. *Siphula* indet., 2005, *Etayo* 2462, *Sancho*, *Gómez-Bolea* & *Søchting* (MAF—holotype; hb. Etayo, UMAG—isotype).

*Notes.* This fungus is characterized by black, stromatic ascospores, 350–700 µm diam., a hymenium that is I+ red, K/I+ blue, later turning red, clavate, 8-spored asci and ellipsoid, 1–2-septate ascospores (Etayo & Sancho 2008). The specimens studied essentially concur with the protologue, although we recorded slightly larger ascospores ((14.8–)16.9–19.1(–20.5) × (4.8–)5.6–6.4(–7.0) µm, l/w = (2.2–)2.7–3.3(–3.7), n = 80) with larger locules (100–240 µm diam.) compared to Etayo & Sancho (2008) (ascospores: 12.5–18 × 4.5–6 µm; locules: 110–150 µm diam.). Whereas the sterile, stromatic tissue is typically black-brown and K–, in one specimen (*Imshaug* 40154 & *Harris*) it was olivaceous brown to black-brown, K± greenish, or reddish brown and becoming less reddish in K. The brown pigment dissolves in K and is analogous to pigment 2 of Ertz *et al.* (2005). We also noted that the fungus occasionally causes local discoloration of the host thallus.

*Ecology and distribution.* This species was initially described from Chile, growing on an unidentified species of *Siphula* (Etayo & Sancho 2008). Here it is also recorded from Tasmania, New Zealand and the Falkland Islands, where it grows on *Siphula decumbens*, *S. dissoluta* and *S. fastigiata*. These three host taxa have wide ecological amplitudes, ranging from relatively lowland heathland or forest habitats to treeless alpine elevations. The distribution of infected thalli reflects this broad range. On *S. fastigiata*, *Plectocarpon gayanum* was found together with unidentified species of *Sphaerellothecium*,

whereas on *Siphula decumbens*, it was accompanied by *Cercidospora santessonii* and *Aabaarnia siphulicola*.

*Specimens examined.* **Australia:** *Tasmania:* Mount Cameron, 40°58'33"S, 147°55'59"E, 300 m, on *Siphula fastigiata*, 1997, *Kantvilas* (HO 320821); track to Mount Cameron, 40°59'S, 147°56'E, 300 m, on *S. fastigiata*, 1995, *Kantvilas* 39/95 (HO 312570); Mount Field, 760 m, on *S. decumbens*, 1963, *James* AU 2081 (H, UPS); c. 1.5 km S of Frodshams Pass, 42°49'S, 146°23'E, 370 m, on *S. decumbens*, 2004, *Kantvilas* 193/04 (HO 526342); Mount Mawson, 1000 m, on *S. decumbens*, 2007, *Motiejūnaitė* 10915 (BILAS); peak 1 km E of Mount Mueller, 42°47'S, 146°28'E, on *S. dissoluta*, 1998, *Kantvilas* 234/98 (HO 329289); lower Olga River, 42°44'S, 145°47'E, on *S. decumbens*, 1975, *Gilbert* (75/419) (HO 45829); Lake Osborne, 850 m, on *S. decumbens*, 1981, *James* & *Kantvilas* 507/81 (UPS); tarn above Lake Oberon, 43°09'S, 146°16'E, 880 m, on *S. decumbens*, 2002, *Felton* (HO 520187); Lake Osborne Track, 43°13'S, 146°45'E, 850 m, on *S. decumbens*, 1981, *Kantvilas* & *James* 507/81 (HO 118134); Mount Read, 41°51'S, 145°33'E, 1110 m, on *S. decumbens*, 1964, *Bratt* & *Lakin* 1156 (HO 46048); Ragged Range, 42°46'S, 146°19'E, 720 m, on *S. decumbens*, 1995, *Kantvilas* 8/95 (HO-310587); Lake Seal, 42°40'S, 146°34'E, 920 m, on *S. decumbens*, 1981, *Tibell* 11247 (UPS); Shadow Lake, 42°06'S, 146°08'E, on *S. decumbens*, 1987, *Moscal* 14344 (HO 62586); South Sister, 41°32'S, 148°10'E, 800 m, on *S. fastigiata*, 2004, *Kantvilas* 407/04 (HO 529054); track from Waterfall Valley to Windermere Hut, 41°46'S, 145°58'E, on *S. decumbens*, 1977, *Matthews* 77/151 (HO 33791); Gordon Road, c. 2 km S of Needles picnic area, 42°46'S, 146°24'E, 450 m, on *S. gracilis*, 2007, *Kantvilas* & *de Villiers* 287/07 (HO 544941); Savage River National Park, E side of Baretop Ridge, 41°18'37"S, 145°26'51"E, 580 m, on *S. decumbens*, 2015, *Kantvilas* 65/15 (HO 576874); Mount Read, 41°51'S, 145°33'E, 1110 m, on *S. decumbens*, 1964, *Bratt* & *Lakin* 1156 (HO 46048).—**New Zealand:** *South Island:* Arthur's Pass National Park, Avalanche Peak Track, on *S. dissoluta*, 1971, *Harris* 647 (HO 309743); Arthur's Pass, 975–1036 m, on *S. dissoluta*, 1962, *James* 1907b (UPS); *ibid.*, on *S. decumbens*, 1927, *G. E. & G. Du Rietz* 1508:2 (UPS L-860148); *ibid.*, on *S. fastigiata*, 1927, *G. E. & G. Du Rietz* 1508:2 (UPS L-860067a); track from Flora Saddle to Mount Arthur Hut, 41°11'S, 172°44'E, 1100 m, on *S. decumbens*, 1995, *Wedin* 4968 (UPS); 1.5 km ENE of Mount Arthur Hut, 41°12'S, 172°44'E, 1050 m, on *S. decumbens*, 1993, *Tibell* 19616a (UPS); Mount Brewster, Haast Pass, 1433–1524 m, on *S. dissoluta*, 1962, *James* 480/1 (UPS); Hokitika, on *S. decumbens*, 1927, *G. E. & G. Du Rietz* 1570b:1 (UPS). *North Island:* Pouakai Range, Dover Track, 39°17'S, 174°05'E, 950 m, on *S. decumbens*, 1990, *Wedin* 2146 (UPS). *Auckland Island:* Port Ross, above Erebus Cove, on *S. decumbens*, 1927, *G. E. Du Rietz* 2283:1 (UPS L-860156b); *ibid.*, on *S. dissoluta*, 1927, *G. E. Du Rietz* 2283:1 (UPS L-860150b); Ranui Cove, 60 m, on *S. decumbens*, 1962, *James* 709 (H, UPS).—**Falkland Islands:** *East Falkland:* between Mount Osborne 2 and



Ceritos Rocks, 470 m, on *S. dissoluta* (H, TNS), 1968, *Imshaug* 40154 & *Harris* (H, TNS).

### **Polycoccum** sp.

*Vegetative hyphae* not observed. *Ascomata* perithecioid, black, 70–100 µm diam. ( $n = 10$ ), slightly protruding or occasionally semi-immersed; wall brown, K–, in surface view composed of strongly elongate cells 1.5–3.5 µm wide. *Hymenial gel* K/I–, I–, sometimes I+ blue. *Interascal filaments* abundant, septate, branched, 1–3 µm diam., sometimes indistinct. *Asci* 43–70 × 19–28 µm ( $n = 6$ ), (2–)4(–8)-spored, I–, K/I–, clavate, ellipsoid, oblong or narrowly ovoid, with a short or indistinct stalk. *Ascospores* (16.5–)18.7–23.9(–27.6) × (6.6–)7.6–9.2(–10.4) µm, l/w = (1.9–)2.2–2.8(–3.1) ( $n = 85$ ), medium to dark greyish olive to olive at maturity, irregularly uni- to biseriolate in the ascus, 1-septate, usually slightly constricted at the septum, narrowly obovoid, with a wider and slightly longer upper cell (ratio 6:5); wall distinctly granular, sometimes with a halo 0.5–1.5(–3) µm thick. The fungus does not visibly damage the host thallus or induce gall formation, although the ascomata may sometimes lift surrounding host tissues and induce gall-like swellings.

*Notes.* The material examined is very similar to *Endococcus hafellnerianus* as described above, which differs by lacking interascal filaments. It is possible that both taxa belong to the same species in which some specimens have poorly developed interascal filaments but additional collections are required to verify this hypothesis.

*Specimens examined* (all on *Parasiphula complanata*). **Chile:** Magallanes Province: Puerto Bueno, 51°00'S, 74°13'W, 1868, *Cunningham* (UPS).—**Argentina:** Isla de los Estados: Capitan Canepa Bay, 54°49'S, 64°27'W, 120 m, 1971, *Imshaug* 53147b & *Ohlsson* (H).—**New Zealand:** *Stewart Island:* track from Rakeahua Hut to Mount Rakeahua Peak, 46°56'S, 167°53'E, 640 m, 1995, *Wedin* 4885b (UPS).

### **Pyrenidium actinellum** Nyl. s.l.

*Flora (Regensburg)* 48: 210 (1865); type: England, Co. of Kent (Maidstone), Boxley Hill, on *Leptogium teretiusculum*, *Jones* (H-NYL 41028—lectotype).

*Notes.* This fungus is characterized by the following features: pseudothecia subglobose, ovoid or obpyriform, 150–200 µm diam., with a brown wall; hamathecium of abundantly branched and anastomosing paraphysoids, 1.5–2.0 µm diam., and periphyses which are green-pigmented at the top of the ostiolar region; asci clavate to subcylindrical, 4–8-spored, 60–90 × 12–18 µm; and ascospores (2–)3(–4)-septate, brown, with paler apices, 19–32 × 7–12 µm (*Hafellner & Mayrhofer* 2007; *Navarro-Rosinés & Roux* 2007). Our material concurs well with these descriptions, including the characteristic blue-green pigmentation of the hamathecium near the ostiole, and the ascospore size: (18.9–)22.6–27.0(–31.9) × (7.6–)9.2–11.6(–13.0) µm, l/w = (1.8–)2.1–2.7(–3.5) ( $n = 100$ ). In its broad sense, this is a common cosmopolitan species (or group of species) which has been reported on all continents from many, distantly related lichen genera (*Brackel* 2014). It is newly documented here as occurring on *Siphula*.

*Specimens examined.* **South Africa:** *Western Cape Province:* Caledon District, 610 m, on *Siphula* aff. *decumbens*, 1944, *Leighton* 709 (UPS); *Outeniqua Mountains,* Duiwelskop Pass, c. 1000 m, on *S. decumbens*, 1970, *Degelius* SA 207 (UPS); *Stellenbosch Flats,* on *S. torulosa*, 1930, *Duthie* 5038 (UPS).

### **Pyrenidium cf. coccineum** Aptroot

*Bryologist* 117: 286 (2014); type: Solomon Islands, Guadalcanal Island, central part, Mount Popomansiu, summit area, c. 2200 m, on *Siphula decumbens*, 1965, *Hill* 10854 (BM—holotype; ABL—isotype).

*Notes.* This taxon is characterized by 3-septate ascospores, black ascomata covered by a red, K+ purple pruina and by the way it changes the colour of the infected host to pink (*Aptroot* 2014). Our specimen agrees with the protologue with respect to the host species and ascospore length (*Aptroot* 2014) but it has slightly narrower ascospores (19–22 × 6–7 µm vs. 17–21 × 7.5–8.5 µm), does not have red pruina on the ascomata, and does not induce a change of colour in the infected host thallus. More material is needed to confirm our hypothesis regarding their conspecificity.

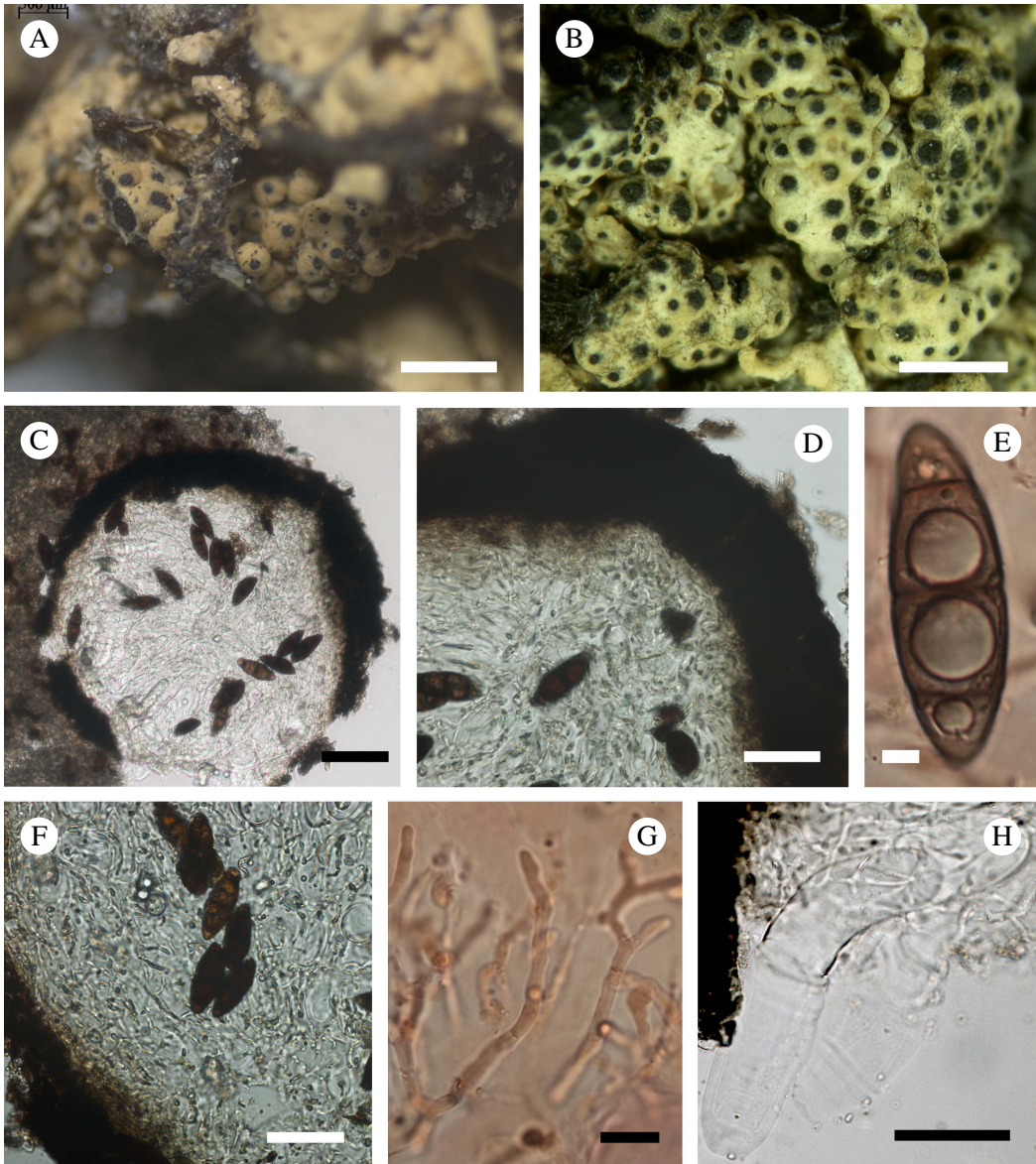


FIG. 5. *Pyrenidium macrosporum*. A & B, galls with ascomata (A, holotype; B, *Roivainen*, H); C, vertical section through an ascoma (in water); D, ostiolar region showing green pigmentation (in water); E, ascospore (in K); F, lower part of an ascoma, showing structure of the ascomatal wall and ascospores; G, paraphyses (in Congo red); H, fissitunicate ascus (in water); C–H: *Kanvilas*, HO 113190. Scales: A & B = 1 mm; C = 100  $\mu$ m; D, F & H = 50  $\mu$ m; E & G = 5  $\mu$ m. In colour online.

*Ecology and distribution.* *Pyrenidium coccineum* was hitherto known only from the type locality. The Tasmanian specimen is from a thallus of

*Siphula decumbens* growing on peaty soil in crevices in outcrops of Ordovician conglomerate in scrubby heathland.

*Specimen examined. Australia: Tasmania: Ragged Range, 42°46'S, 146°19'E, 720 m, on Siphula decumbens, 1995, Kantvilas 8/95 (HO-310587).*

**Pyrenidium macrosporum Motiej., Zhurb., Suija & Kantvilas sp. nov.**

Mycobank No.: MB 827420

Lichenicolous fungus similar to *Pyrenidium actinellum* s.l. but distinguished by the larger ascospores,  $32\text{--}55.5 \times 12.5\text{--}18 \mu\text{m}$  compared to  $19\text{--}32 \times 7.5\text{--}13 \mu\text{m}$ .

Type: Australia, Tasmania, The Hermit, 42°49'S, 146°08'E, 450 m, buttongrass moorland, on thallus of *Parasiphula jamesii*, 19 January 1984, G. Kantvilas 56/84 (HO 113212—holotype).

(Fig. 5)

*Vegetative hyphae* brown, 4–5  $\mu\text{m}$  wide, torulose. *Ascomata* single or aggregated in groups of 50–100 or more, 90–415  $\mu\text{m}$  diam. ( $n = 10$ ), perithecioid, ostiolate, black, subglobose in section, immersed to 1/3 protruding. *Exciple* brown, K+ green-black throughout, 40–65  $\mu\text{m}$  thick in the ostiolar region, 25–35  $\mu\text{m}$  thick below, pseudoparenchymatous, composed of several layers of elongate cells 6–10  $\times$  5–6  $\mu\text{m}$ . *Periphyses* 20–30  $\times$  3.0–3.5  $\mu\text{m}$ , unbranched or sometimes bifurcate. *Paraphysoids* hyaline, abundant, branched and anastomosing, 1.0–4.0  $\mu\text{m}$  thick; both periphyses and paraphysoids associated with dispersed pale to medium green to mostly blue-green granules, most abundant in the ostiolar area. *Hymenial gel* I–, K/I–. *Asci* clavate, (50–)80–120 (–160)  $\times$  (11–)20–35 (–40)  $\mu\text{m}$  ( $n = 13$ ), 4–8-spored, I–, with an apical dome and short, blunt ocular chamber. *Ascospores* (32.0–)42.5–51.1 (–55.3)  $\times$  (12.5–)14.5–17.1 (–18.0)  $\mu\text{m}$ , l/w = (1.8–)2.7–3.3 (–3.6) ( $n = 96$ ), hyaline or very pale brown when immature within the asci, later dark brown, sometimes with paler apical cells, fusiform to ellipsoid, straight or slightly curved, smooth-walled, with a halo c. 1  $\mu\text{m}$  thick, 3-septate, with apical cells smaller than central ones, slightly constricted at the septa (more markedly so at the central septum), with a pore in the central part of each septum and a single guttule in every cell. *Asexual morph* not observed.

*Etymology.* The specific epithet refers to the large size of the ascospores.

*Notes.* Ten species are currently accepted in the genus *Pyrenidium* Nyl. (Lawrey & Diederich 2018), among which *P. macrosporum* stands out clearly by its much larger asci and ascospores. Furthermore, *Pyrenidium macrosporum* is known only from *Parasiphula*, whereas two other species of the genus occur on *Siphula* s.s.: *P. actinellum* s.l., found on *S. decumbens* and *S. torulosa*, and *P. coccineum*, recorded on *S. decumbens*. Hafellner & Mayrhofer (2007) and Navarro-Rosinés & Roux (2007) considered the green to blue-green pigmentation of the ostiolar area to be a character peculiar to *Pyrenidium actinellum*. However, *P. aggregatum* Knudsen & Kocourk., described subsequently by Knudsen & Kocourková (2010), as well as *P. macrosporum*, both share this feature. The new species does not cause distinct discoloration of the host thallus but it does induce gall-like swellings around the ascomata.

*Ecology and distribution.* The new species has been found in Tasmania, Argentina and Chile, growing on thalli of *Parasiphula complanata*, *P. fragilis*, *P. georginae* and *P. jamesii*. The Tasmanian specimens are from host thalli growing on boggy, peaty soil in treeless alpine heathland and buttongrass (*Gymnoschoenus*)-dominated moorland.

*Additional specimens examined. Australia: Tasmania: Green Head, c. 3 km SSE of Greystone Bluff, 43°06'S, 146°04'E, 880 m, on Parasiphula georginae, 1991, Kantvilas 67/91 (HO 129674); head of Spring River, Port Davey Track, 180 m, on P. jamesii, 1984, Kantvilas 514/84 (HO 113190); Turrana Bluff, 41°46'S, 146°21'E, 1330 m, on P. fragilis, 2012, Kantvilas (HO 564518).—Chile: Fuegia occidentalis: Bahia Cordoba, 350 m, on P. complanata, 1929, Roivainen (H). Magallanes Province: E side of Juan Island, 50°39'S, 74°36'W, on P. complanata, 1969, Imshaug 44233a & Ohlsson (H).—Argentina: Isla de los Estados: Bahia Capitan Canepa, 54°49'S, 64°27'W, 120 m, on P. complanata, 1971, Imshaug 53147a & Ohlsson (H); *ibid.*, 54°50'S, 64°30'W, 150 m, on P. complanata, 1971, Imshaug 52995a & Ohlsson (H).*

**Saania mobergii Zhurb. gen. et sp. nov.**

Mycobank No.: MB 827282 (genus) and MB 827283 (species)



Lichenicolous fungus. Ascomata stromatic, multilocular, superficial, blackish, convex, up to 1200  $\mu\text{m}$  wide and 350  $\mu\text{m}$  thick, in section brown, K+ olive, N+ red, composed of  $\pm$  isodiametric or tangentially elongate cells. Hymenial gel I-, K/I-. Exciple indistinct. Hamathecium of persistent periphysoids. Asci bitunicate, elongate-clavate, 51–105  $\times$  17–31  $\mu\text{m}$ , 4(–8)-spored; wall I-, K/I-. Ascospores narrowly obovate to ellipsoid, (17.5–)21.5–26.0(–29.0)  $\times$  (7.0–)9.5–12.0(–15.0)  $\mu\text{m}$ , 1(–3)-septate, irregularly biseriolate to diagonally uniseriate in the ascus, initially hyaline and smooth-walled, later sometimes brown and verruculose.

Type: South Africa, Cape Province, Cape District, Table Mountain, near Upper Cableway station, on thallus of *Siphula torulosa* growing on ground, 9 August 1953, O. Almborn 1935 (UPS—holotype).

(Fig. 6)

*Vegetative hyphae* not observed. *Ascomata* stromatic, multilocular, superficial, single or sometimes contiguous to confluent, dark brown to almost black, glossy, convex, often irregular in shape, (120–)230–710(–1200)  $\mu\text{m}$  wide ( $n=68$ ), (80–)150–290(–350)  $\mu\text{m}$  thick ( $n=19$ ), with a clearly delimited margin; surface tuberculate due to elevations above the locules, sometimes inconspicuously radially striate. *Ascostromata* in section brown, darker brown towards the outer edge, K+ olive, N+ red, composed of  $\pm$  isodiametric (5–10  $\times$  5–8  $\mu\text{m}$ ) or tangentially elongate (around locules) cells, with intercellular spaces 2–4  $\mu\text{m}$  wide; pores in cell walls not observed. *Locules* up to 40 within the stroma, arranged in one or occasionally several layers, sometimes merging with each other, roundish, broadly ellipsoid, ovoid or ampulliform in section, (40–)60–110(–180)  $\mu\text{m}$  wide ( $n=60$ ), without a distinct ostiolar canal, but extending to the surface of the stroma and exhibiting gaping holes at later stages; *hymenial gel* I-, K/I-. *Exciple* similar in structure and colour to the stromatal tissue. *Hamathecium* of persistent periphysoids, consisting of (1–)2–3(–4)-celled filaments 20–40  $\mu\text{m}$  long and 1.5–2.5(–5.5)  $\mu\text{m}$  thick, constricted at the septa, sometimes dichotomously branched but not anastomosing, attached at the apex and walls of the locules and not reaching their base when mature; since the ostiolar canal is indistinct, periphyses are not clearly differentiated. *Subhymenium* hyaline,

pseudoparenchymatous, c. 20  $\mu\text{m}$  thick. *Asci* bitunicate, elongate-clavate, shortly stalked, (51–)70–97(–105)  $\times$  (17–)21–29(–31)  $\mu\text{m}$  ( $n=30$ ), 4(–8)-spored, I-, K/I-, except for the ascoplasm which stains I+ orange, K/I+ orange, with apex thickened to 4–8(–13)  $\mu\text{m}$  and lacking a distinct internal apical beak. *Ascospores* (17.6–)21.5–26.1(–28.8)  $\times$  (7.1–)9.3–12.1(–15.1)  $\mu\text{m}$ , l/w = (1.7–)2.0–2.6(–3.4) ( $n=169$ ), 1(–3)-septate, occasionally slightly constricted at the septa, central pore in the septa not observed, narrowly obovate (with slightly wide upper half) to ellipsoid, irregularly biseriolate to diagonally uniseriate in the ascus, initially hyaline, smooth-walled and occasionally with a halo < 1  $\mu\text{m}$  thick, later sometimes evenly pale brown to brown, verruculose and non-halonate.

*Asexual morph* rare, similar in structure and colour to the locules containing asci; *conidiophores* absent; *conidiogenous cells* hyaline, short-ampulliform; *conidia* hyaline, bacilliform, 6.5–7.2  $\times$  1.6–1.9  $\mu\text{m}$  ( $n=8$ ).

*Etymology.* The generic name refers to the “San” or “Saan”, the first nation people of southern Africa, whereas the specific epithet honours the eminent Swedish lichenologist, Roland Moberg, who collected one of the paratypes of the new species.

*Notes.* This new species does not correspond with other genera of lichenicolous fungi with stromatic multilocular ascomata and consequently a new genus is proposed. *Clypeococcum* D. Hawksw., *Homostegia* Fuckel, *Macrographa* Etayo, *Perigrapha* Hafellner and *Plectocarpon* Fée all differ from the new genus by having interascal filaments (Hafellner 1996; Ertz 2004; Hawksworth *et al.* 2004; Ertz *et al.* 2005; Etayo & Sancho 2008). Furthermore, the stromata of *Clypeococcum* form a clypeus; *Homostegia* differs in having 8-spored asci and usually pigmented, 3-septate ascospores; *Macrographa* differs in having N- stroma and hyaline, 1-septate ascospores; *Perigrapha* and *Plectocarpon* differ in their K/I+ blue hymenial gel and their asci with a K/I+ blue apical ring. A further genus, *Lasiosphaeriopsis* D. Hawksw. & Sivan, differs from *Saania* in having unitunicate asci without any distinct

apical apparatus and in the occurrence of pores in the stromatic cell walls (Hawksworth 1980).

*Stigmidium eucline* (Nyl.) Vězda, growing on species of *Varicellaria* Nyl., forms a stroma-like plexus of vegetative hyphae around tightly aggregated ascomata (Zhurbenko 2017) and thus may resemble the new species. However, it differs from the latter by having interascal filaments (Sérusiaux *et al.* 2003; Kocourková & Knudsen 2010), and the stroma-like structures of this species are unusual for the genus *Stigmidium* Trevis. in general, as typified by *S. schaeferi* (A. Massal.) Trevis. (Roux & Triebel 1994; Triebel & Cáceres 2004). *Lichenostigma* Hafellner s.l. also has stromatic ascomata but does not form locules and lacks hamathecial filaments (Ertz *et al.* 2014).

When compared to other siphulicolous fungi, in habit *Saania mobergii* most closely resembles *Plectocarpon gayanum*. However, the latter clearly differs in having anastomosing interascal filaments attached at the base of the locules, I+ red, K/I+ blue hymenial gel and consistently hyaline, smaller ascospores.

**Ecology and distribution.** The new species is known only from South Africa where it grows on thalli of *Siphula decumbens*, *S. torulosa*, *S. verrucigera* and an undescribed species of *Siphula* related to *S. fastigiata*. It does not visibly damage or induce gall formation in the host thallus.

**Additional specimens examined. South Africa:** *Western Cape Province:* Bainskloof Pass, on *Siphula decumbens*, 1953, *Almborn* 5083 (UPS); 4 miles N of Bainskloof Pass, on *S. verrucigera*, 1953, *Almborn* (H); N Cedarberg, 1600 m, on *Siphula* sp., 1945, *Esterhuysen* 12279 (UPS L-860155, UPS L-860078); Deception Peak, 1524 m, on *Siphula* sp., 1942, *Stoke* (UPS); Groot Drakenstein Mountains, on *S. decumbens*, 1943, *Esterhuysen* 9559 (UPS); top of Mount Paarl, on *S. torulosa*, 1963, *Kofler* (UPS); Piketberg, N of Noupooort Farm, 32°47'S, 18°39'E, 800 m, on *S. torulosa*, 1996, *Moberg* 11757 (H); Table Mountain, 914 m, on *S. decumbens*, 1953, *Almborn* 1747 (UPS).

### **Skyttea sp.**

*Vegetative hyphae* not observed. *Ascomata* apothecioid, urceolate, erumpent, superficial

when mature, greyish black, 100–150 µm diam. ( $n=4$ ); pore *c.* 20% of the ascomatal diameter; margin whitish, with several fissures. *Exciple* greenish, comprised of rectangular cells (*textura angularis*), K+ olivaceous then brown, N+ olivaceous green, with marginal, hyaline to slightly greenish excipular hairs with roundish tips, 6–9 × 2.5–3 µm. *Epithymenium* hyaline to slightly greenish, K–, N–. *Hymenium* hyaline, I–, 30–40 µm thick. *Paraphyses* filiform, simple, distantly septate, *c.* 1 µm thick, not easily separating in K; apices not thickened. *Asci* 37–39 × 5–12 µm ( $n=3$ ), 8-spored, I–, unitunicate, subcylindrical, with apex thickened and without a distinct apical apparatus. *Ascospores* hyaline, fusiform or slightly falcate, (9.0–)9.5–11.5(–12) × (2.5–)2.6–3.0(–3.0) µm, l/w = 3–4.4 ( $n=15$ ), aseptate, smooth, halonate. *Asexual morph* not observed.

**Notes.** The inclusion of this presumably undescribed species in the genus *Skyttea* Sherwood *et al.* is provisional due to the limited material available and additional specimens are needed to ascertain its taxonomic relationships. Almost all known *Skyttea* species grow on crustose lichens, with the few exceptions of *S. aff. fusispora* growing on *Physciaceae* (Diederich & Etayo 2000) and *S. anziae* Etayo & Diederich on *Anzia* sp. (Etayo 2002). In its general characteristics, our specimen is most similar to *S. lecanorae* Diederich & Etayo, a species growing on *Lecanora* with ascospores of similar length but wider (7–13 × 2–4.5 µm; Diederich & Etayo 2000). Furthermore, the excipular hairs are longer in *S. lecanorae* (8–13 µm) and both fungi inhabit different, taxonomically unrelated hosts.

**Specimen examined. Australia:** *Tasmania:* Mount Eliza, on *Parasiphula georginae*, 1985, *Kantvilas* (HO 316101).

### **Sphaerellothecium siphulae Zhurb.**

*Nova Hedwigia* 101: 420 (2015); type: Russia, Murmansk Region, Barents Sea coast, mouth of Olenka River, 69°02'N, 36°24'E, 50 m, tundra with puddles, on *Siphula ceratites*, 1997, Zhurbenko 97398 (LE 264400—holotype!; GZU—isotype!).

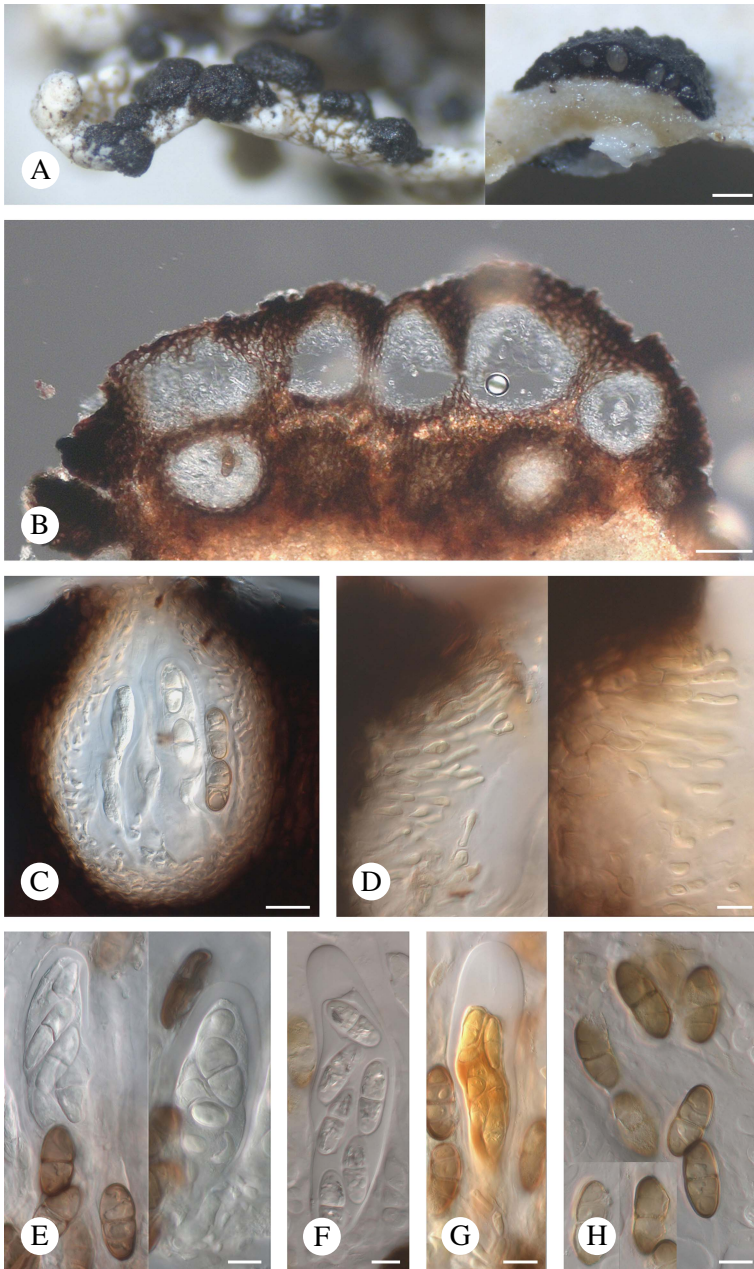


FIG. 6. *Saania mobergii*. A, stromatic ascomata, note section through ascoma on the right (holotype on the left, *Esterhuysen* 12279 on the right); B, stromatic ascomata in section in water (1942, *Stoke*); C, locule in section in water (*Esterhuysen* 12279); D, hamathelial filaments in K/I (*Almborn* 5083 on the left, *Moberg* 11757a on the right); E, asci and ascospores in water (*Almborn* 5083 on the left, holotype on the right); F, ascus and ascospores in K (*Almborn* 5083); G, ascus and ascospores in K/I (*Almborn* 5083); H, ascospores in K (*Almborn* 5083). Scales: A = 200  $\mu$ m; B = 50  $\mu$ m; C–H = 10  $\mu$ m. In colour online.



**Notes.** The species is characterized by densely aggregated ascomata, only sometimes associated with a macroscopically visible net of dark hyphae, the absence of interascal filaments, 1-septate ascospores, (8.5–)10.0–11.5(–14.0) × (3.5–)4.0–5.0(–6.0) μm, with the wall BC<sup>–</sup>, the host genus and a strong pathogenicity (Zhurbenko 2015). Ascomata are rarely associated with conidiomata, which contain hyaline, fusiform, 1(–3)-septate, smooth-walled conidia, (8.3–)10.3–13.3(–13.6) × (1.1–)1.3–1.7(–1.8) μm, l/w = (5.5–)6.6–8.8(–10.2) (*n* = 26). Hitherto, no asexual morph had been reported for this species.

Thirty additional specimens of *Sphaerellothecium* species from South America, South Africa and Australasia, growing on various species of *Parasiphula* and *Siphula*, were also examined. The morphological variations and host selection of these specimens suggest that more than one species is involved. For the moment, however, these specimens remain unnamed pending a comprehensive revision of *Sphaerellothecium* using molecular methods. Although some of these specimens are similar to *S. siphulae*, this name is retained only for specimens growing on *Siphula ceratites* from the Northern Hemisphere, from where this species was described.

**Ecology and distribution.** *Sphaerellothecium siphulae* was known previously from the Russian Arctic (Zhurbenko 2015) and the British Isles (Paul 2016) but it has a wide, circumpolar distribution similar to its host *Siphula ceratites*, a characteristic species of moist habitats in northern coastal regions. It is recorded here for the first time from North America (Canada and the USA), Finland and Norway.

**Specimens examined** (all on *Siphula ceratites*). **Norway:** *Finnmark:* East Finnmark, Båtsfjord, between Gammelvelve and Hursi, 1974, *Kvist* (H); Elvenes, 1864, *Fries* (H); Porsanger, Stabbursdalens nasjonalpark, Coarvosavzze, 1970, *Ryvarden* 6432 (O-L28875). *Nordland:* Tysfjord, Bognes (E6) south of Lodingen, 40 m, 1985, *Ross* (O-L28793); Brønnøy, near Horn at 10.5 km marker N of Brønnøysund, 50 m, 1989, *Ross* (O-L28787); Salten, Salfjell ved Balvann, 1966, *Ryvarden* (O-L28850). *Nord-Trøndelag:* Flatanger Municipality, Nordstraumen, 64-50522°N, 10-79483°E, 2015, *Suija* (TU-75652). *Sør-Trøndelag:* Oppdal, Falkfangarhoa h.

1399 SW, 1350 m, 1983, *Sæbo & Sivertsen* (O-L28827); Oppdal, Skrinko sør., 1060 m, 2003, *Bjørn & Ognedal* Bpl-L10355 (O-L123492); Rissa, Traugheia, 350 m, 1960, *Rui* (O-L28837). *Troms:* Kvænangen/Nordreisa, Kvænangsfjellet, 135 km S of Alta, 300 m, 1987, *Ross* (O-L28785).—**Russia:** *Chukotka:* Cape Schmidt, 68° 55'N, 179°27'E, 1981, *Laanetu* (TU-56799); *Murmansk Region:* Borisoglebski (Koltaköngäs), 69°39'N, 30°08' E 1927, *Lippmaa* (TU-63682, TU-63684).—**USA:** *Alaska:* Seward Peninsula, Cape Prince of Wales, 65°48'N, 168° W, 1978, *Flock* FL-737 (H).—**Canada:** *British Columbia:* Kaien Island, Prince Rupert, Mount Hays, 1963, *Schofield & Boas* 21542 (H); without exact locality, 1931, *Kujala* (H); Kunghit Island, 52°00'N, 131°03'W, 1971, *Schofield & Brodo* 17674 (H, TNS).

### ***Stigmatidium kashiwadani* Zhurb. sp. nov.**

MycoBank No.: MB 827284

Lichenicolous fungus similar to *Sphaerellothecium siphulae* but distinguished by the 1(–)3-septate or, rarely, submuriform vs. 1-septate, larger ascospores, (12–)14.5–17.5(–20) × (5–)6–8(–9) μm vs. (8.5–)10–11.5(–14) × (3.5–)4–5(–6) μm.

Type: Australia, Western Australia, Snake Rocks, 28 miles SE of Perth, 32°22'S, 116°03'E, 270 m, on thallus of *Siphula coriacea* growing on exposed rocks, 13 December 1965, *S. Kurokawa* 6631 (TNS—holotype).

(Fig. 7)

**Vegetative hyphae**—mostly immersed, pale to medium brown, 2.5–4.5 μm diam., not forming a dark, superficial reticulum. **Ascomata** perithecioid, black, dull or slightly glossy, subglobose in section, sometimes slightly papillate, ostiolate, without appendages, 60–110 μm diam. (*n* = 10), protruding in the upper part to rarely half-exposed, separate to occasionally contiguous, aggregated in clusters of up to 200. **Exciple** 6–10 μm thick, composed of 2–4 layers of tangentially compressed cells, in surface view composed of polygonal cells 3–15 μm long, dark brown above, medium to pale brown below, K+ olive-grey, pigmentation evenly amorphous. **Ostiolar filaments** well developed, brown, more or less isodiametric, rounded at the apex, not branched, 0(–)2-septate, 9–19 × 3–4.5 μm. **Short pseudoparaphyses** of type 'a' *sensu* Roux & Triebel (1994), rather inconspicuous, 4–9 × 1.5–3 μm. **Long interascal filaments** absent. **Interascal gel** I–, K/I–. **Asci** (41–)44.5–51.5(–56) × (14.5–)16.5–21.5(–23) μm (*n* = 16), 8-spored, bitunicate, narrowly pyriform-

ovoid (wider below the middle), shortly stiptate; endoascus markedly thickened above; wall BCr-, I-, K/I-. *Ascospores* subclavate to narrowly ovoid, (12.2-)14.7-17.7 (-20.1) × (5.0-)6.0-7.8(-8.8) µm, l/w = (1.8-)2.1-2.7(-3.7) (*n* = 129), initially hyaline, smooth-walled and 1-septate (septum median or rarely disposed towards the upper part), later sometimes brown, verruculose and (2-)3-septate or, rarely, submuriform, with an additional longitudinal or oblique septum, constricted at the median septum (at later stages often markedly so) but not disintegrating into semi-spores, in K rarely with a thin gelatinous sheath around immature ascospores, never pseudotetrablastic, irregularly arranged in the ascus; wall BCr-; plasma BCr+ blue. *Asexual morph* not seen.

*Etymology.* This species is named after the eminent Japanese lichenologist, Hiroyuki Kashiwadani, who collected several of the specimens on which the description is based.

*Notes.* On the basis of its morphological and anatomical characters alone, the new species could be placed in either *Sphaerellothecium* Zopf or *Stigmidium*. The current delimitation of these genera is based mainly on the presence or absence of a distinct net of dark, thick-walled vegetative hyphae. This feature is characteristic of *Sphaerellothecium araneosum* (Arnold) Zopf, the type of *Sphaerellothecium* (Cáceres & Triebel 2004; Triebel & Cáceres 2004), but its interpretation can be quite subjective and there are a number of species that could be placed in either genus. One such species is *Sphaerellothecium siphulae*, which also grows on *Siphula*. It resembles *Stigmidium kashiwadani* in its aggregated ascomata, distinct pathogenicity and most ascomatal characters but differs from that species in having 1-septate, smooth-walled, only exceptionally brown and much smaller ascospores, (8.5-)10-11.5(-14) × (3.5-)4-5 (-6) µm (Zhurbenko 2015). The new species is distinguished from most species of *Sphaerellothecium* and *Stigmidium* by the occurrence of 4-septate, submuriform ascospores. Ascospores with more than three

septa were formerly reported in these genera only for *Sphaerellothecium soechtingii* Zhurb. & Alstrup growing on *Arthrorhaphis alpina* (Schaer.) R. Sant. (Zhurbenko 2007), and *Stigmidium psorae* (Anzi) Hafellner growing on *Psora* spp. (Calatayud & Triebel 1999). Those of *S. soechtingii* are (1-)3(-5)-septate to occasionally submuriform but much smaller, (10-)11.5-14.5(-15) × (3.5-)4-5 µm; those of *S. psorae* are 1-3(-5)-septate but longer, (16-)17.5-22(-23.5) × (5-)5.5-7.5(-8) µm.

*Ecology and distribution.* The species is known from four collections from Western Australia, all on thalli of *Siphula coriacea*, a common terricolous species in heathland and dry sclerophyll forest. Host lobes turn grey when heavily infected.

*Additional specimens examined* (all on thalli of *Siphula coriacea*). **Australia:** *Western Australia:* Boyup Brook, 1967, *Kashiwadani* 4639 (TNS); Mount Chudalup at 31 miles S of Pemberton, 230 m, 1965, *Kurokawa* 6689 (TNS); Karagullen, 1967, *Kashiwadani* 4573 (TNS); Schannon, Mill Road, 1967, *Kashiwadani* 4681 (TNS).

### Additional Fungi Recorded

In addition to the taxa treated above, our survey also encountered other taxa, the generic positions of which remain unclear. We list these here as a record of what was found and as a basis for future investigations:

- (i) a discomycete with sessile black, shiny, apothecia lacking hairs, an olivaceous exciple and epihymenium, clavate to subcylindrical, 8-spored asci, and ellipsoid, hyaline, 1-septate ascospores, 9.0-13.0 × 4.0-5.0 µm (*n* = 10). (**Australia:** *Tasmania:* Quamby Bluff, 41°39'S, 146°42'E, on *Parasiphula complanata*, 1985, *Kantvilas*, HO 315823);
- (ii) a *Niesslia*-like pyrenomycete with superficial ascomata, 70-85 µm diam., with aseptate setae to 30 µm long, indistinct branched interascal filaments, 8-spored asci and hyaline, soleiform, 1-septate, smooth-walled ascospores, 10.0-14.0 × 4.0-5.0 µm (*n* = 10) (**New Zealand:** *South Island:* 1.5 km ENE of Mount Arthur Hut, 41°12'S, 172°44'E, 1050 m, on *Siphula decumbens*, 1993, *Tibell* 19616b, UPS);
- (iii) a *Polycoccum*-like pyrenomycete with ascomata 50-95 µm diam., surrounded by a brown mycelial net immersed in the host thallus, 4-6-spored asci and brown, 1-septate ascospores, 16.0-20.0 × 5.0-7.5 µm (*n* = 9) (**Australia:** *Tasmania:* Twelvetreets

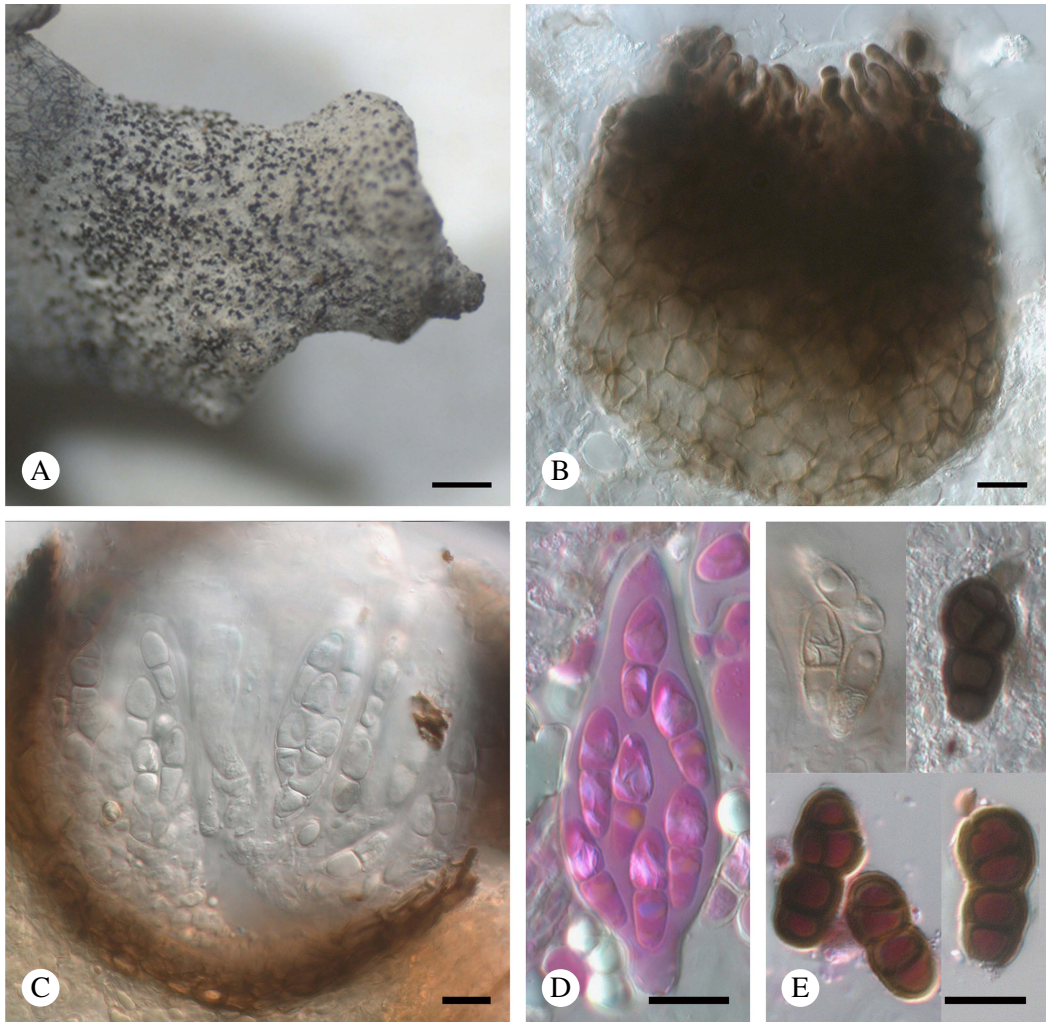


FIG. 7. *Stigmidium kashiwadani* (holotype). A, ascomata aggregated on host lobe tip; B, squashed ascoma in K, showing abundant external ostiolar filaments; C, ascoma in section with hyaline ascospores; D, ascus in phloxine after K; E, aged ascospores in K (above) and phloxine after K (below). Scales: A = 500  $\mu\text{m}$ ; B–E = 10  $\mu\text{m}$ . In colour online.

Range, 690 m, on *Parasiphula jamesii*, 1984, Kantvilas 539/84, HO 113217);

- (iv) a *Pseudostigmidium*-like pyrenomycete with black, glossy, protruding ascomata 40–80  $\mu\text{m}$  diam., triangular in section, 8-spored asci and hyaline, soleiform, 1-septate, smooth-walled ascospores, 7.8–10.0  $\times$  3.2–4.0  $\mu\text{m}$  ( $n=4$ ) (**Chile:** *Tierra del Fuego*: Isla Clarence, southern peninsula, 40 m, on *Siphula ramalinoides*, 1987, *Stenroos* 2584, H);
- (v) a pyrenomycete with black, glossy, sessile, aggregated ascomata 80–120  $\mu\text{m}$  diam., and brown, soleiform, (0–)1-septate, smooth-walled or

occasionally verruculose ascospores, (8.8–)9.8–11.4(–12.2)  $\times$  (3.9–)4.2–5.0(–5.5)  $\mu\text{m}$ , l/w = (1.9–)2.0–2.6(–2.9) ( $n=28$ ) (**USA:** *Hawaii*: Maui Island, along the trail between Puu Kukui and Kaulalewelewe, 20°53'N, 156°35'W, 1500–1600 m, on *Siphula pickeringii*, 1998, *Kashiwadani* 41074, TNS);

- (vi) a *Lichenostigma*-like coelomycete with dispersed conidiomata, 40–80  $\mu\text{m}$  diam., and brown, verruculose conidia, 8.3–14.6  $\mu\text{m}$  diam., composed of 3–10 cells, each 3.0–6.7  $\mu\text{m}$  diam. (**Colombia:** *Departamento de Santander*: Páramo de



Almorzadero, 3885 m, on *Siphula pteruloides*, 1978, Aguirre 1063 & Cleef, H);

- (vii) two hyphomycetes of uncertain affinity (New Zealand: South Island: Arthur's Pass, subalpine bog, on *Siphula fastigiata*, 1927, G. E. & G. Du Rietz 1508:2, UPS L-860067b; Otago, Old Man Range, S von Alexandra, beim Obelisk, 1800 m, on *S. foliacea*, 1985, Henssen 30381a & Lumbsch, H).

### Discussion

Our survey revealed 16 species in 14 genera of lichenicolous fungi, including the primarily algicolous *Epigloea soleiformis* which occurs occasionally on lichens. With the exception of that species and the ubiquitous *Pyrenidium actinellum* s.l., all are restricted to *Siphula*-like lichens; that is, the genera *Siphula* s.s. (*Icmadophilaceae*) and *Parasiphula* (*Coccotremataceae*). Seven species and two monotypic genera are described as new to science.

With respect to the key hypothesis underpinning this study, namely “do lichenicolous fungi support the generic delimitation of *Siphula*-like lichens (Grube & Kantvilas 2006)”, the answer is unequivocally in the affirmative. Five species (*Amylogalla fava*, *Endococcus hafellnerianus*, *Polycocum* sp., *Pyrenidium macrosporum* and *Skyttea* sp.) are found exclusively on species of *Parasiphula* whereas the rest are restricted to species of *Siphula* s.s. This pattern also holds for the most part at generic level, with only the broadly ranging genus *Pyrenidium* spanning both host genera. This in itself is a significant finding given that *Siphula*-like lichens frequently occur as intimately intermixed swards comprising several species of both genera, and yet the lichenicolous fungi in such situations distribute themselves in a highly host-specific way.

At the species level, *Siphula* s.l. can present a bewildering range of morphological variation that complicates the delimitation of taxa. At the same time, it displays a range of discrete chemical spectra. The current taxonomy of the species (Kantvilas 1996, 1998, 2002, 2004; Kantvilas & Elix 2002) is essentially based on chemical characters and their correlation with morphological and biogeographical data. Using secondary

chemistry as the critical species-level character, however, has not been without complications, and there is considerable scope in further exploring the taxonomy of *Siphula*. In this respect, the lichenicolous fungi studied offer little insight into species-level classification. Most of the more frequent taxa have been recorded from several, albeit related, host species and it is not unusual to find the same fungus on each and any of the related species, *S. decumbens* (thamnolic acid), *S. fastigiata* (baeomycesic and squamatic acids) and *S. dissoluta* (hypothamnolic acid). A possible exception is *Stigmidium kashivadamii*, which is known only from *Siphula coriacea* (barbatic acid), but this is also the only lichenicolous fungi-supporting host recorded for continental Australia. Likewise, the restriction of *Spharellothecium siphulae* to *Siphula ceratites* only (Zhurbenko 2015) is also underlain by a geographical pattern, as this host is the sole Northern Hemisphere example.

In the *Coccotremataceae*, apart from *Parasiphula*, lichenicolous fungi are known only from *Coccotrema* itself (Etayo & Sancho 2008). In the *Icmadophilaceae*, *Thamnotia* (with 23 species (Zhurbenko 2012)) shows a richness in lichenicolous fungi comparable to *Siphula*. Previous molecular investigations of *Siphula*-like lichens (Stenroos & DePriest 1998; Platt & Spatafora 2000; Stenroos *et al.* 2002; Grube & Kantvilas 2006; Ludwig *et al.* 2016) have consistently suggested that within *Siphula* itself, the so-called *S. decumbens* group is distinct from *S. ceratites*, the generic type, and is possibly deserving of separate generic status. *Siphula ceratites* is distinguished, *inter alia*, by the presence of chromones whereas the *S. decumbens* group contains depsides (Kantvilas 2002). The problem with these analyses has been that none has included a good representation of neotropical collections where, within *S. pteruloides* and *S. carassana*, there are chromone-only, chromone plus depsides and depside-only races (Kantvilas & Elix 2002). Lichenicolous fungi might well offer some insights into this taxonomic question. Unfortunately, however, although numerous collections of these taxa were examined in the



present study, they supported very few lichenicolous fungi and so this question remains unresolved.

With respect to geographical patterns, the austral region is clearly a centre of diversity for fungi inhabiting *Siphula*-like lichens, in the same way that this region is the centre of speciation for the hosts. Thus 12 of the species documented are known only from the Southern Hemisphere, including eight species known only from Tasmania. The apparent restriction of certain species to certain regions is probably an artefact of our sampling, and it is to be hoped that infected *Siphula*-like thalli attract more attention from collectors in the future. Of more interest is the fact that

particular species of lichenicolous fungi are shared between Tasmania and New Zealand, Tasmania and South America or Tasmania, New Zealand and southern South America, patterns displayed by numerous lichen, bryophyte and vascular plant taxa. In contrast, the lichenicolous fungi recorded from hosts from southern Africa, Hawaii, the Northern Hemisphere, mainland Australia and the Neotropics were, in each case, restricted to their immediate geographic region. The two strictly siphulicolous species known from the Northern Hemisphere are *Neolamyia* sp. (Hawaii) and *Sphaerellothecium siphulae* s.s., a fungus widely distributed across the entire arctic and boreal range of its host.

### Key to the lichenicolous fungi occurring on species of *Parasiphula* and *Siphula*

Note. Unidentified species of *Sphaerellothecium*, as well as species of uncertain generic position briefly characterized in the “Additional fungi recorded” section above, are not included. Species confined to *Parasiphula* or *Siphula* are denoted by <sup>P</sup> and <sup>S</sup> respectively.

- |      |   |  |
|------|---|--|
| 1    | Hymenium partly exposed at maturity . . . . .   | 2  |
|      | Hymenium not exposed at maturity . . . . .  | 4  |
| 2(1) | Ascomata greyish black, superficial, not inducing galls; ascospores (9–)9.5–11.5 (–12) × (2.5–)2.5–3 μm . . . . .   | <b>Skyttea</b> sp. <sup>P</sup>          |
|      | Ascomata pale brown, orange or red, immersed in the host thallus, inducing galls; ascospores larger . . . . .   | 3  |
| 3(2) | Vegetative hyphae, exciple and paraphyses I+ blue, K/I+ violet; ascomatal wall and hymenium yellowish to orange above; ascospores simple, (11–)11.5–14.5 (–15) × (5–)5.5–7.5 μm . . . . . | <b>Amylogalla fava</b> <sup>P</sup>      |
|      | Vegetative hyphae, exciple and paraphyses I–; ascomatal wall and hymenium hyaline; ascospores 3-septate, (23–)24.5–28(–29) × (7–)7.5–8.5 μm . . . . .                                     | <b>Abaarnia siphulicola</b> <sup>S</sup> |
| 4(1) | Asci at least 20-spored . . . . .   | <b>Neolamyia</b> sp. <sup>S</sup>        |
|      | Asci up to 8-spored . . . . .   | 5  |
| 5(4) | Ascomata with a colourless gelatinous coat 4–15 μm thick, associated with algal films overlying lichen thalli . . . . .   | <b>Epigloea soleiformis</b> <sup>S</sup> |
|      | Ascomata without a colourless gelatinous coat, not associated with algal films and developing within lichen thalli . . . . .  | 6  |

- 6(5) Ascomata stromatic ..... 7  
 Ascomata not stromatic ..... 8
- 7(6) Interascal filaments present; hymenial gel I+ red, K/I+ blue;  
 ascospores consistently hyaline, (15-)17-19(-20.5) × (5-)5.5-6.5  
 (-7) μm ..... **Plectocarpon gayanum**<sup>S</sup>  
 Interascal filaments absent; hymenial gel I-, K/I-; ascospores initially  
 hyaline, later sometimes brown, (17.5-)21.5-26(-29) × (7-)9.5-12  
 (-15) μm ..... **Saania mobergii**<sup>S</sup>
- 8(6) Ascomata covered by protruding septate hyphae 2-5 μm diam. and up to  
 50 μm long ..... **Echinothecium** sp.<sup>S</sup>  
 Ascomata not covered by protruding hyphae ..... 9
- 9(8) Ascomatal wall blue-green, greenish brown or olive-grey above,  
 hyaline below; pseudoparaphyses anastomosing; ascospores consistently  
 hyaline ..... **Cercidospora santessonii**<sup>S</sup>  
 Ascomatal wall entirely brown; interascal filaments, if present, never anastomosing;  
 at least some ascospores brown ..... 10
- 10(9) Ascospores 1-septate ..... 11  
 At least some ascospores with more than 1 septum ..... 13
- 11(10) Dark vegetative hyphae often macroscopically conspicuous; ascospores (8.5-)10-  
 11.5(-14) × (3.5-)4-5(-6) μm ..... **Sphaerellothecium siphulae**<sup>S</sup>  
 Dark vegetative hyphae macroscopically inconspicuous; ascospores much larger 12
- 12(11) Interascal filaments absent; ascospores (15-)17-22(-24) × (5-)6.5-9  
 (-10) μm ..... **Endococcus hafellnerianus**<sup>P</sup>  
 Interascal filaments present; ascospores (16.5-)18.5-24(-27.5) × (6.5-)7.5-9(-  
 10.5) μm ..... **Polycoccum** sp.<sup>P</sup>
- 13(10) Interascal filaments absent; ascospores (12-)14.5-17.5(-20) × (5-)  
 6-8(-9) μm ..... **Stigmatidium kashiwadani**<sup>S</sup>  
 Interascal filaments present ..... 14
- 14(13) Ascospores (32-)42.5-51(-55.5) × (12.5-)14.5-17(-18) μm .....  
 ..... **Pyrenidium macrosporum**<sup>P</sup>  
 Ascospores smaller ..... 15
- 15(14) Ascomata superficial, typically covered by blood red pruina,  
 without blue-green pigmentation visible in section; ascospores 17-21 × 7.5-  
 8.5 μm ..... **Pyrenidium coccineum**<sup>S</sup>  
 Ascomata mainly immersed, epruinose, with blue-green pigmentation visible in  
 section; ascospores 19-32 × 7.5-13 μm ..... **Pyrenidium actinellum** s.l.<sup>S</sup>

MZ thanks Paul Diederich, Javier Etayo and Andre Aptroot for most valuable discussions on the taxonomic status of *Saania mobergii*. The curators of H, O, TNS and UPS herbaria, and Leena Myllys, Yoshihito Ohmura and Stefan Ekman, assisted in locating and processing relevant *Siphula* specimens for study and loan. Financial support for AS was provided by IUT 20–30 and by the European Regional Development Fund (Centre of Excellence EcolChange). Financial support for JM was granted by the Lithuanian Research Council (grant no. MIP-17-5) and the Bilateral Exchange Programme between the Academies of Sciences of Lithuania and Estonia. The contribution by MZ was carried out within the framework of the research project of the Komarov Botanical Institute of the Russian Academy of Sciences “Biodiversity and spatial structure of fungi and myxomycetes communities in natural and anthropogenic ecosystems” (AAAA-A18-118031290108-6) using equipment from its Core Facility Center “Cell and Molecular Technologies in Plant Science”; his visits to the TNS and UPS herbaria were supported by JSPS Invitation Fellowship for Research in Japan (no. S16173) and by the Rolf Santesson foundation, respectively. Some of the material studied was collected by GK during field surveys co-funded by the Australian Biological Resources Study (ABRS) and BHP Billiton under the Bush Blitz Programme, with laboratory work supported by an ABRS Tactical Taxonomy Grant.

## REFERENCES

- Alstrup, V. & Cole, M. S. (1998) Lichenicolous fungi of British Columbia. *Bryologist* **101**: 221–229.
- Aptroot, A. (2014) Two new genera of *Arthoniales* from New Caledonia and the Solomon Islands, with the description of eight further species. *Bryologist* **117**: 282–289.
- Baral, H.-O. (1987) Lugol’s solution/IKI versus Melzer’s reagent: hemiamyloidity, a universal feature of the ascus wall. *Mycotaxon* **29**: 399–450.
- Baral, H.-O. (2008) Dichotomous key to *Lachnellula* (worldwide) (*Trichoscyphelloideae*, *Lachnaceae*, *Helotiales*, *Ascomycetes*), with a synoptic table of characters. Available at: [www.ascofrance.com/uploads/forum\\_file/7637.doc](http://www.ascofrance.com/uploads/forum_file/7637.doc) [28/5/2018].
- Brackel, W. von (2014) Kommentierter Katalog der flechtenbewohnenden Pilze Bayerns. *Bibliotheca Lichenologica* **109**: 1–476.
- Cáceres, M. E. S. & Triebel, D. (2004) *Sphaerellothecium*. In *Lichen Flora of the Greater Sonoran Desert Region*, Vol. 2 (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 696–699. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Calatayud, V. & Rambold, G. (1998) Two new species of the lichen genus *Immersaria* (*Porpidiaceae*). *Lichenologist* **30**: 231–244.
- Calatayud, V. & Triebel, D. (1999) *Stigmidium neofuscelliae* (*Dothideales* s. l.), a new lichenicolous fungus from Spain. *Nova Hedwigia* **69**: 439–448.
- Calatayud, V., Navarro-Rosinés, P. & Hafellner, J. (2013) Contribution to a revision of the genus *Cercidospora* (*Dothideales*) 2. Species on *Lecanora* s. l., *Rhizoplaca* and *Squamarina*. *Mycosphere* **4**: 539–557.
- Czarnota, P. & Hernik, E. (2013) Notes on two lichenicolous *Epigloea* species from Central Europe. *Acta Societatis Botanicorum Poloniae* **82**: 321–324.
- David, J. C. & Etayo, J. (1995) A new lichenicolous fungus from *Collema*: *Endococcus caudisporus* sp. nov. (*Dothideales*, *incertae sedis*). *Lichenologist* **27**: 314–316.
- Diederich, P. (2004) *Spirographa*. In *Lichen Flora of the Greater Sonoran Desert Region*, Vol. 2 (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 702–703. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Diederich, P. (2014) *Aabaarnia* and *Normanogalla*, two new lichenicolous genera of *Ostropales*, *Ascomycota*. *Bulletin de la Société des Naturalistes Luxembourgeois* **115**: 141–149.
- Diederich, P. & Etayo, J. (2000) A synopsis of the genera *Skyttea*, *Llimoniella* and *Rhymbocarpus* (lichenicolous *Ascomycota*, *Leotiales*). *Lichenologist* **32**: 423–485.
- Döbbeler, P. (1984) Symbiosen zwischen Gallertalgen und Gallertpilzen der Gattung *Epigloea* (*ascomycetes*). *Beihefte zur Nova Hedwigia* **79**: 203–239.
- Ertz, D. (2004) *Neolamyia*. In *Lichen Flora of the Greater Sonoran Desert Region*, Vol. 2 (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 677–678. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Ertz, D., Christnach, C., Wedin, M. & Diederich, P. (2005) A world monograph of the genus *Plectocarpon* (*Roccellaceae*, *Arthoniales*). *Bibliotheca Lichenologica* **91**: 1–155.
- Ertz, D., Lawrey, J. D., Common, R. S. & Diederich, P. (2014) Molecular data resolve a new order of *Arthoniomycetes* sister to the primarily lichenized *Arthoniales* and composed of black yeasts, lichenicolous and rock-inhabiting species. *Fungal Diversity* **66**: 113–137.
- Etayo, J. (2002) Aportación al conocimiento de los hongos liquenícolas de Colombia. *Bibliotheca Lichenologica* **84**: 1–154.
- Etayo, J. & Sancho, L. G. (2008) Hongos liquenícolas del Sur de Sudamérica, especialmente de Isla Navarino (Chile). *Bibliotheca Lichenologica* **98**: 1–302.
- Fleischhacker, A., Grube, M., Kopun, T., Hafellner, J. & Muggia, L. (2015) Community analyses uncover high diversity of lichenicolous fungi in alpine habitats. *Microbial Ecology* **70**: 348–360.
- Galloway, D. J. (2004) New lichen taxa and names in the New Zealand mycobiota. *New Zealand Journal of Botany* **42**: 105–120.

- Grube, M. & Kantvilas, G. (2006) *Siphula* represents a remarkable case of morphological convergence in sterile lichens. *Lichenologist* **38**: 241–249.
- Hafellner, J. (1988) Principles of classification and the main taxonomic groups. In *Handbook of Lichenology, Vol. 3* (M. Galun, ed.): 41–52. Boca Raton: CRC Press.
- Hafellner, J. (1996) Studien an lichenicolen Pilzen und Flechten VIII. *Perigrapha*, eine neue Ascomyceten-gattung für “*Melanotheca*” *superveniens* Nyl. (*Arthromiales*). *Nova Hedwigia* **63**: 173–181.
- Hafellner, J. & Mayrhofer, H. (2007) A contribution to the knowledge of lichenicolous fungi and lichens occurring in New Zealand. *Bibliotheca Lichenologica* **95**: 225–266.
- Halici, M. G. & Aksoy, A. (2009) Lichenised and lichenicolous fungi of Aladağlar National Park (Niğde, Kayseri and Adana Provinces) in Turkey. *Turkish Journal of Botany* **33**: 169–189.
- Hawksworth, D. L. (1979) Studies in the genus *Endococcus* (Ascomycotina, Dothideales). *Botaniska Notiser* **132**: 283–290.
- Hawksworth, D. L. (1980) Notes on some fungi occurring on *Peltigera*, with a key to accepted species. *Transactions of the British Mycological Society* **74**: 363–386.
- Hawksworth, D. L. (1985) A redistribution of the species referred to the ascomycete genus *Microthelia*. *Bulletin of the British Museum (Natural History), Botany Series* **14**: 43–181.
- Hawksworth, D. L., Atienza, V. & Cole, M. S. (2004) Lichenicolous species of *Homostegia* (Dothideomycetes), with the description of *H. herthelii* sp. nov., a new fungus on *Flavoparmelia* species. *Bibliotheca Lichenologica* **88**: 187–194.
- Hoffmann, N. & Hafellner, J. (2000) Eine Revision der lichenicolen Arten der Sammelgattungen *Guignardia* und *Physalospora*. *Bibliotheca Lichenologica* **77**: 1–181.
- Hue, A. (1914) Lichenes novos vel melius cognitos exposuit. *Annales Mycologici* **12**: 509–534.
- Ihlen, P. G. (1998) The lichenicolous fungi on species of the genera *Baeomyces*, *Dibaeis*, and *Icmadophila* in Norway. *Lichenologist* **30**: 27–57.
- Ihlen, P. G. & Wedin, M. (2007) *Cercidospora alpina* sp. nov. and a key to the known species in Fennoscandia. *Lichenologist* **39**: 1–6.
- Kainz, C. & Triebel, D. (2004) *Endococcus*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2* (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 648–651. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Kantvilas, G. (1996) Studies on the lichen genus *Siphula* in Tasmania I. *S. complanata* and its allies. *Herzogia* **12**: 7–22.
- Kantvilas, G. (1998) Studies on the lichen genus *Siphula* in Tasmania II. The *S. decumbens* group. *Herzogia* **13**: 119–138.
- Kantvilas, G. (2002) Studies on the lichen genus *Siphula* Fr. *Bibliotheca Lichenologica* **82**: 37–53.
- Kantvilas, G. (2004) New Australian species in the lichen genus *Siphula* Fr. *Austrobaileya* **6**: 949–955.
- Kantvilas, G. & Elix, J. A. (2002) The taxonomy, chemistry and morphology of some South American species of *Siphula*. *Herzogia* **15**: 1–12.
- Keissler, K. von. (1930) *Die Flechtenparasiten. Rabenhorsts Kryptogamenflora* 8. Leipzig: Akademische Verlagsgesellschaft.
- Knudsen, K. & Kocourková, J. (2010) *Pyrenidium aggregatum*, a new species from North America. *Opuscula Philolichenum* **8**: 71–74.
- Knudsen, K. & Kocourková, J. (2014) A new species of *Lecidea* (*Lecideaceae*, Lichenized Ascomycetes) from the mountains of California. *Opuscula Philolichenum* **13**: 80–83.
- Kocourková, J. (2000) Lichenicolous fungi of the Czech Republic (the first commented checklist). *Acta Musei Nationalis Pragae, Serie B, Historia Naturalis* **55**(3–4): 59–169.
- Kocourková, J. (2009) Observations on the genus *Neolamya*, with the description of the new species *N. xanthoparmeliae* (Ascomycota, genera incertae sedis). *Opuscula Philolichenum* **6**: 137–148.
- Kocourková, J. & Knudsen, K. (2010) *Stigmatidium eucline* is not a synonym of *Stigmatidium aggregatum*. *Opuscula Philolichenum* **8**: 101–105.
- Kukwa, M., Kowalewska, A., Śliwa, L., Czarnota, P., Czyżewska, K., Flakus, A., Kubiak, D., Wilk, K., Dimos-Zych, M., Kolanko, K. et al. (2012) Porosty i grzyby naporostowe Wdzydzkiego Parku Krajobrazowego (Pomorze Gdańskie, N Polska). *Acta Botanica Cassubica* **11**: 75–103.
- Kutorga, E. & Hawksworth, D. L. (1997) A reassessment of the genera referred to the family *Patellariaceae* (Ascomycota). *Systema Ascomycetum* **15**(1–2): 1–110.
- Lawrey, J. D. & Diederich, P. (2018) *Lichenicolous fungi – worldwide checklist, including isolated cultures and sequences available*. URL: <http://www.lichenicolous.net> (Accessed 1/5/2018).
- Ludwig, L., Knight, A. & Kantvilas, G. (2016) Discovery of ascomata in the *Siphula decumbens* group, and its placement in a separate genus. In *Abstracts of the 8th IAL Symposium, Lichens in Deep Time, 1–5 August, 2016, Helsinki, Finland*, p. 168.
- Mudd, W. (1861) *A Manual of British Lichens*. Darlington: Harrison Penney.
- Muggia, L. & Grube, M. (2018) Fungal diversity in lichens: from extremotolerance to interactions with algae. *Life* **8** (2): 15.
- Navarro-Rosinés, P. & Roux, C. (2007) *Pyrenidium*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 3* (T. H. Nash III, C. Gries & F. Bungartz, eds): 404–405. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Navarro-Rosinés, P., Calatayud, V. & Hafellner, J. (2004) *Cercidospora*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2* (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 635–639. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Navarro-Rosinés, P., Calatayud, V. & Hafellner, J. (2009) Contribution to a revision of the genus *Cercidospora* (*Dothideales*) 1. Species on *Megasporaceae*. *Mycotaxon* **110**: 5–25.



- Nylander, W. (1888) *Lichenes Novae Zelandiae*. Paris: Paul Schmidt.
- Orange, A. (2009) *Merismatium* Zopf (1889). In *The Lichens of Great Britain and Ireland* (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley, eds): 581–582. London: British Lichen Society.
- Paul, H. (2016) Lost and found lichens: visit to Sutherland 18–25 June 2016. *British Lichen Society Bulletin* **119**: 116–126.
- Platt, J. L. & Spatafora, J. W. (2000) Evolutionary relationships of nonsexual lichenized fungi: molecular phylogenetic hypotheses for the genera *Siphula* and *Thamnomia* from SSU and LSU rDNA. *Mycologia* **92**: 475–487.
- Poelt, J. (1973) Classification. In *The Lichens* (V. Ahmadjian & M. E. Hale, eds): 599–632. New York & London: Academic Press.
- Purvis, O. W. & Gilbert, O. L. (2009) *Bellemerea* Hafellner & Cl. Roux (1984). In *The Lichens of Great Britain and Ireland* (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley, eds): 210–211. London: British Lichen Society.
- Roux, C. & Triebel, D. (1994) Révision des espèces de *Stigmidium* et de *Sphaerellothecium* (champignons lichénicoles non lichénisés, Ascomycetes) correspondant à *Pharcidia epicymatia sensu* Keissler ou à *Stigmidium schaeferi* auct. *Bulletin de la Société Linnéenne de Provence* **45**: 451–542.
- Ruiz-Herrera, J. & Ortiz-Castellanos, L. (2010) Analysis of the phylogenetic relationships and evolution of the cell walls from yeasts and fungi. *FEMS Yeast Research* **10**: 225–243.
- Ruprecht, U., Lumbsch, H. T., Brunauer, G., Green, T. G. A. & Türk, R. (2010) Diversity of *Lecidea* (*Lecideaceae*, Ascomycota) species revealed by molecular data and morphological characters. *Antarctic Science* **22**: 727–741.
- Sérusiaux, E., Diederich, P., Ertz, D. & van den Boom, P. (2003) New or interesting lichens and lichenicolous fungi from Belgium, Luxembourg and northern France. IX. *Lejeunia* **173**: 1–48.
- Staiger, B. (2002) Die Flechtenfamilie *Graphidaceae*. Studien in Richtung einer natürlichen Gliederung. *Bibliotheca Lichenologica* **85**: 1–526.
- Stenroos, S. K. & DePriest, P. T. (1998) SSU rDNA phylogeny of cladoniiform lichens. *American Journal of Botany* **85**: 1548–1559.
- Stenroos, S., Myllys, L., Thell, A. & Hyvönen, J. (2002) Phylogenetic hypotheses: *Cladoniaceae*, *Stereocaulaceae*, and *Icmadophilaceae* revisited. *Mycological Progress* **1**: 267–282.
- Triebel, D. & Cáceres, M. E. S. (2004) *Stigmidium*. In *Lichen Flora of the Greater Sonoran Desert Region, Vol. 2* (T. H. Nash III, B. D. Ryan, P. Diederich, C. Gries & F. Bungartz, eds): 703–707. Tempe, Arizona: Lichens Unlimited, Arizona State University.
- Zhurbenko, M. P. (2007) New lichenicolous fungi from Eurasia. *Graphis Scripta* **19**: 1–9.
- Zhurbenko, M. P. (2010) New and interesting lichenicolous fungi from Eurasia. II. *Mycosphere* **1**: 213–222.
- Zhurbenko, M. P. (2012) Lichenicolous fungi growing on *Thamnomia*, mainly from the Holarctic, with a worldwide key to the known species. *Lichenologist* **44**: 147–177.
- Zhurbenko, M. P. (2015) *Sphaerellothecium siphulae* (Dothideomycetes *incertae sedis*), a new lichenicolous fungus on *Siphula ceratites* from the Arctic. *Nova Hedwigia* **101**: 419–425.
- Zhurbenko, M. P. (2017) Lichenicolous fungi of the Caucasus: new species, new records and a second synopsis. *Opuscula Philolichenum* **16**: 267–311.
- Zhurbenko, M. P. & Brackel, W. von (2013) Checklist of lichenicolous fungi and lichenicolous lichens of Svalbard, including new species, new records and revisions. *Herzogia* **26**: 323–359.
- Zhurbenko, M. P. & Pino-Bodas, R. (2017) A revision of lichenicolous fungi growing on *Cladonia*, mainly from the Northern Hemisphere, with a worldwide key to the known species. *Opuscula Philolichenum* **16**: 188–266.
- Zhurbenko, M. P., Hermansson, J. & Pystina, T. N. (2012) Lichenicolous fungi from the Komi Republic of Russia. II. *Folia Cryptogamica Estonica* **49**: 89–91.
- Zhurbenko, M. P., Chesnokov, S. V. & Konoreva, L. A. (2016) Lichenicolous fungi from Kodar Range, Trans-Baikal Territory of Russia. *Folia Cryptogamica Estonica* **53**: 9–22.
- Zopf, W. (1898) Untersuchungen über die durch parasitische Pilze hervorgerufenen Krankheiten der Flechten. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum* **70**: 243–288.