The Lichenologist (2020), **52**, 437–453
doi:10.1017/S002428292000047X

CAMBRIDGE UNIVERSITY PRESS

Standard Paper

Contributions to the knowledge of lichenicolous fungi growing on baeomycetoid lichens and *Icmadophila*, with a key to the species

Mikhail P. Zhurbenko[1] and Yoshihito Ohmura[2]

[1]Laboratory of the Systematics and Geography of Fungi, Komarov Botanical Institute, Russian Academy of Sciences, Professor Popov Street 2, St. Petersburg, 197376, Russia and [2]Department of Botany, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki, 305-0005, Japan

Abstract

Five species of lichenicolous fungi are described as new to science: *Buelliella ohmurae* Zhurb. & Diederich (on *Icmadophila*), with a non-granulose epihymenium, not or only slightly enlarged, pale brown apical cells of paraphysoids and 1-septate, smooth ascospores; *Catillaria japonica* Zhurb. & Hafellner (on *Dibaeis* and *Pseudobaeomyces*), with a medium to dark reddish brown epihymenium, exciple and hypothecium, rather frequently branched and anastomosed paraphyses with only slightly enlarged apical cells without a dark cap, and *Catillaria*-type asci; *Cryptodiscus ihlenii* Zhurb. (on *Dibaeis*), with persistently immersed ascomata, non-amyloid asci and hymenium, not or only slightly enlarged apical cells of paraphyses and narrowly obovate, 1-septate ascospores; *Llimoniella chilensis* Zhurb. (on *Dibaeis* and a sterile microsquamulose lichen), with a K+ green exciple and epihymenium and aseptate, broadly ellipsoid ascospores; and *Stigmidium phyllobaeidis* Zhurb., Etayo & Flakus (on apothecial discs of *Phyllobaeis*), with a hemiamyloid interascal gel, not previously reported in that genus, well-developed, 1–2(–4)-celled periphysoids, elongate asci and hyaline, 1-septate ascospores. An undescribed species of *Arthonia* (on *Pseudobaeomyces*) is briefly characterized. *Sphaerellothecium coniodes* is newly reported for Asia. A key to the 32 species of lichenicolous fungi and lichens known to occur on baeomycetoid lichens and *Icmadophila* is provided.

Key words: *Buelliella*, *Catillaria*, *Cryptodiscus*, *Llimoniella*, new species, *Stigmidium*

(Accepted 14 October 2020)

Introduction

According to Diederich *et al.* (2018*b*), most species of lichenicolous fungi seem to be confined to specific host genera. Close examination of lichenicolous fungi growing on particular lichen taxa proved to be an effective approach to reveal the taxonomic diversity of these fungi. For example, during such case studies, two species of lichen-dwelling fungi were described as new from *Arthrorhaphis* (Hafellner & Obermayer 1995), three from *Baeomyces*, *Dibaeis* and *Icmadophila* (Ihlen 1998), three from *Cladia* (Zhurbenko & Pino-Bodas 2015), seven from *Cladonia* (Zhurbenko & Pino-Bodas 2017), ten from *Graphidales* (Diederich *et al.* 2019), 13 from *Lobariella* (Flakus *et al.* 2019), four from *Peltigera* (Hawksworth 1980), one from *Phlyctis* (Muscavitch *et al.* 2017), one from *Pilophorus* (Zhurbenko & Triebel 2005), three from *Placopsis* (Brackel & Berger 2010), three from *Stereocaulon* (Zhurbenko 2010*a*) and six from *Thamnolia* (Zhurbenko 2012).

The families *Baeomycetaceae* and *Icmadophilaceae sensu* Lücking *et al.* (2016) have several morphologically similar genera in common and have sometimes been revised together (Burgaz 2015). Lichenicolous fungi growing on species of *Baeomyces* (*Baeomycetaceae*), *Dibaeis* and *Icmadophila* (both belonging to *Icmadophilaceae*) in Norway have been studied by Ihlen (1998). We revisited these and also *Phyllobaeis* (*Baeomycetaceae*) and *Pseudobaeomyces* (*Icmadophilaceae*), which are morphologically similar to *Baeomyces* (baeomycetoid), from other regions of the world preserved in the herbarium of the National Museum of Nature and Science (TNS), Tsukuba, Japan. During this process we found 11 species of lichenicolous fungi, some of which were previously unknown to science.

The aims of this paper are to present the results of the revision, including the description of five new species, and to give an identification key to the species of lichenicolous fungi and lichens growing on baeomycetoid lichens and *Icmadophila*.

Materials and Methods

This study is based on 48 specimens of lichenicolous fungi mainly deposited in TNS (42 specimens) but also in several other herbaria: KRAM (1), LE (1), LPB (2) and the private collections of J. Etayo (1) and K. Kalb (2). A Stemi 2000-CS stereomicroscope and a Zeiss Axio Imager A1 compound microscope equipped with Nomarski differential interference contrast optics, fitted with an AxioCam MRc5 digital camera were used. Microscopic characters were studied using sections hand-cut with a razor blade and mounted in water, 10% potassium hydroxide (K), Lugol's iodine directly (I) or after a K pretreatment (K/I), brilliant cresyl blue (BCr), or concentrated nitric acid (N). Measurements were taken from water mounts. Where n >10, the length, width and length/width ratio (l/w) of the ascospores are given as

Author for correspondence: Mikhail P. Zhurbenko. E-mail: zhurb58@gmail.com
Cite this article: Zhurbenko MP and Ohmura Y (2020) Contributions to the knowledge of lichenicolous fungi growing on baeomycetoid lichens and *Icmadophila*, with a key to the species. *Lichenologist* **52**, 437–453. https://doi.org/10.1017/S002428292000047X

(min−) ($\bar{x}$ − SD) − ($\bar{x}$ + SD) (−max), where 'min' and 'max' are the extreme values observed, $\bar{x}$ the arithmetic mean and SD the corresponding standard deviation. Dimensions of ascospores were rounded to the nearest 0.5 µm. Colours were named according to Kornerup & Wanscher (1978).

The Species

Arthonia sp.

Ascomata apothecia, superficial, blackish, matt, epruinose, convex, immarginate, irregularly rounded in surface view, 60–210 µm diam. (n = 10), aggregated to confluent. Epihymenium brown, *c.* 5 µm thick. Hymenium pale brown, not inspersed, 30–35 µm tall, I+ red, K/I+ blue. Hypothecium brown, 40–50 µm tall. Asci broadly clavate, *c.* 30 × 15 µm, 8-spored. Ascospores hyaline to brownish, clavate (club-shaped), irregularly arranged in the ascus, 12–13.5 × 4.5–5.5 µm (n = 6), 1-septate, halo not observed. Asexual morph not observed.

According to Diederich *et al.* (2018*b*), no *Arthonia* species have been reported on members of *Baeomycetaceae* and *Icmadophilaceae*. Keissler (1930: 97) mentioned as '*Celidium ericetorum* Rehm apud Rabh.' an *Arthonia*-like fungus growing on *Baeomyces* and *Dibaeis*, which has not been validly described. It differs markedly from the species that is mentioned above by its greenish epihymenium, I+ blue hymenium, colourless hypothecium, longer asci (60–65 × 9–10 µm) and hyaline, 1–3-septate, narrower ascospores (10–15 × 3 µm).

Rhymbocarpus ericetorum (Körb.) Etayo *et al.* growing on *Dibaeis* is somewhat reminiscent of an arthonioid fungus, but is quite distinct from the *Arthonia* species examined by having immersed apothecia, an olivaceous epihymenium and lateral exciple, a colourless to pale brown hypothecium, cylindrical to clavate asci with an only slightly thickened apical wall, and colourless, cylindrical-oblong, aseptate ascospores (Rambold & Triebel 1990; Baral & Marson 2001).

Specimen examined. **Papua New Guinea:** *Morobe District*: vicinity of Kasanombe, *c.* 30 km N of Lae, 06°22'S, 146°59'E, 1600–1700 m, on *Pseudobaeomyces* sp. (thallus, occasionally also on apothecia), 1975, *S. Kurokawa* 9560 (TNS, filed under the host).

Buelliella ohmurae Zhurb. & Diederich sp. nov.

MycoBank No.: MB 836571

Lichenicolous ascomycete. Distinguished from *Buelliella minimula* mainly by the somewhat narrower ascospores, 12.5–17.5 × 5–6.5 µm versus 14–18 × 6–8 µm, and a different host selection, *Icmadophila* versus *Pertusaria*.

Type: Japan, Honshu, Prov. Kai (Pref. Yamanashi), Mt Daibosatsu, 35°44'N, 138°50'E, on the thallus of *Icmadophila ericetorum*, 30 October 1955, *Y. Kuwata* (TNS-L-129845—holotype).

(Fig. 1)

Ascomata initially almost closed, subspherical to flattened, partly immersed, eventually becoming urceolate, 80–160 µm diam. (n = 14), erumpent, 1/2 to 3/4 exposed, blackish, matt, sometimes white pruinose, rough, with an irregularly rounded opening 10–40 µm wide surrounded by radial splits, exposing part of the hymenium, aggregated to occasionally contiguous. *Exciple* brown, K− (light brown), 15–30 µm thick, in surface view resembling textura epidermoidea and textura globulosa, in cross-section composed of circular or elongate cells up to 7 µm with walls 1–2 µm thick. *Periphyses* not observed. *Paraphysoids* rather delicate and inconspicuous in water, clearly seen in K, 1–1.5 µm diam., septate, flexuose, varying in thickness, sometimes slightly enlarged and pale brown at the apex, branched, occasionally anastomosed. *Epihymenium* pale brown, pigmentation not granulose, sometimes rather indistinct. *Hymenium* hyaline, 50–60 µm tall, I−, K/I−. *Asci* bitunicate, elongate-clavate to narrowly clavate, with a distinct foot, with an ocular chamber 1–2 µm long, 45–55 × 13–17 µm (n = 6), wall laterally rather thick, apically not to markedly thicker, I−, K/I−, 8-spored. *Ascospores* hyaline to occasionally medium brown, 1-septate, constricted at the septum, narrowly obovoid/soleiform with a broader upper cell, irregularly biseriate, partly overlapping diagonally in the ascus, (12.5–)13.5–15.5(–17.5) × 5–6(–6.5) µm, l/w = (2.1–)2.4–2.8(–3.0) (n = 22), sometimes disarticulating into semi-spores in squash mounts, wall *c.* 0.5 µm thick, smooth.

Asexual morph not observed.

Etymology. This species is dedicated to the Japanese lichenologist Yoshihito Ohmura, curator of the TNS lichen herbarium, in which material of the new species was discovered.

Distribution and host. The new species is known from four collections in Japan, growing on thalli and occasionally also on apothecia of *Icmadophila ericetorum*. Host tissues are bleached under severe infections.

Notes. The new species fits well with the concept of *Buelliella* Fink as presented in Hafellner (1979, 2004), including diagnostic characters such as cleistohymenial ascomata, a hyaline, I−, K/I− hymenium, delicate, branched and anastomosed paraphysoids, bitunicate, I−, K/I− asci, and 1-septate ascospores, remaining hyaline for a long time. We did not see the short periphyses that occur in some *Buelliella* species (Ertz & Diederich 2015) but neither were these observed in the generic type *B. minimula* (Tuck.) Fink.

The new species may be confused with other *Buelliella* species with ascospores similar in size. Among these, *Buelliella eximia* Kalb & Hafellner (on *Pyxine*) differs in the 1–3-septate, shorter and wider ascospores, 12.5–14 × 6–8 µm (Kalb 1990); *B. inops* (Triebel & Rambold) Hafellner (on *Caloplaca* s. lat.) is distinct in the markedly enlarged, brown apical cells of paraphysoids and the 1(–3)-septate, wider ascospores, 13–18 × 6–8.5 µm (Hafellner *et al.* 2002); *B. minimula* (on *Pertusaria*) is distinguished by a distinct brown, granulose epihymenium and wider ascospores, 14–18 × 6–8 µm (Hafellner 1979; specimens of *B. minimula* examined for comparison); *B. physciicola* Poelt & Hafellner (on *Phaeophyscia* and *Physcia*) has wider ascospores, 12–17 × 6–8.5 µm (Hafellner 1979); *B. protoparmeliopseos* Etayo & Pérez-Ortega (on *Protoparmeliopsis*) differs in having lirelliform young ascomata, markedly enlarged, brown apical cells of paraphysoids and larger ascospores, 14–21 × 4–10 µm (Pérez-Ortega & Etayo 2010); and *B. pusilla* Hafellner (on *Brigantiaea*) differs in the I+ light blue then red-brown hymenium and smaller, verruculose ascospores, 11–14 × 5–6 µm (Hafellner 1985).

Additional specimens examined (all on thalli and occasionally apothecia of Icmadophila ericetorum*).* **Japan:** *Honshu*: Prov. Etchu (Pref. Toyama), Mt Yakushi, 36°28'N, 137°32'E, 1600 m,

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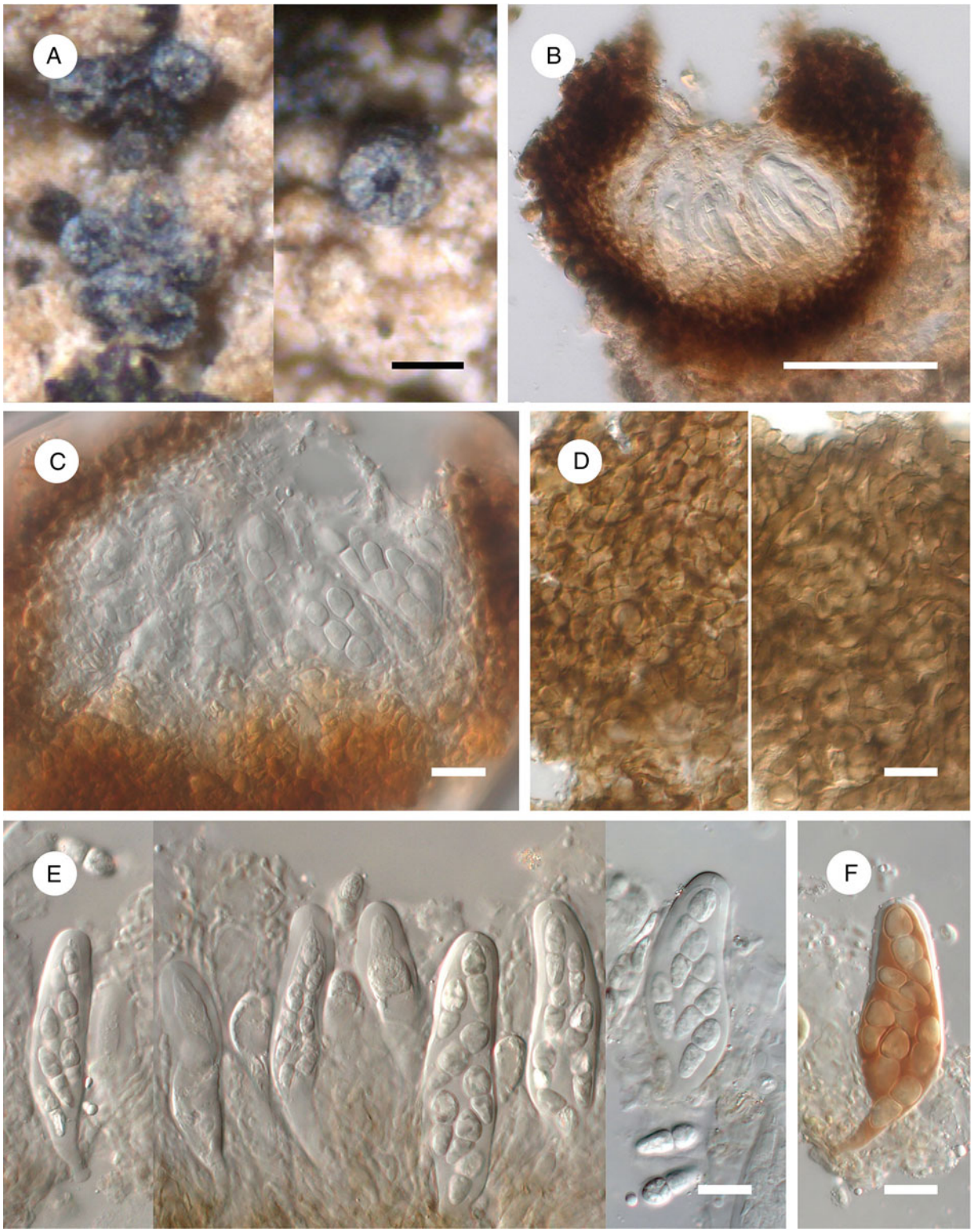

Fig. 1. *Buelliella ohmurae* (A, D–F, holotype; B, *Shibuichi* 4253; C, 1926, *Okada* (a)). A, habitus of ascomata on the thallus of *Icmadophila ericetorum*. B & C, ascoma in cross-section in water. D, different layers of the exciple in surface view in K. E, asci, ascospores and paraphysoids in K. F, ascus with spores in K/I. Scales: A = 100 μm; B = 50 μm; C–F = 10 μm. In colour online.

1976, *H. Kashiwadani* 13480 (TNS); Prov. Shinano (Pref. Nagano), Yatsugatake Mts, 35°59'N, 138°21'E, 1926, *Y. Okada* (a) (TNS); Mt Kinpu, Minamisaku-gun, 35°52'N, 138°37'E, 2550 m, 1970, *H. Shibuichi* 4253 (TNS).

Specimens of Buelliella minimula *used for comparison (both on* Pertusaria *spp.).* **Brazil:** *São Paulo Municipality*: zwischen São Lourenço und Juquií, etwa 65 km W von São Sebastião, am Rio Guaratuba, mangrove, 1980, *K. Kalb* (hb. Kalb).—**Ecuador:**

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Napo Province: zwischen Quito und Baeza, etwa 50 km NW von Baeza, in Paramovegetation, 4000 m, 1987, *K. & A. Kalb* 18669 (hb. Kalb).

Catillaria japonica Zhurb. & Hafellner sp. nov.

MycoBank No.: MB 836572

Lichenicolous ascomycete, not lichenized. Distinguished from *Catillaria stereocaulorum* by the rather frequently branched, anastomosed paraphyses, apically not or only slightly swollen, without a dark cap, medium reddish brown versus hyaline to pale yellowish brown hypothecium, and a different host selection, *Dibaeis* and *Pseudobaeomyces* versus *Stereocaulon*.

Type: Japan, Kyushu, Prov. Hyuga (Pref. Miyazaki), Ohkawauchi, Shiiba Research Forest, Kyushu University, Shiiba-son, Higashi-usuki-gun, 32°23′43"N, 131°11'10"E, 1140 m, on the thallus of *Dibaeis sorediata*, 13 November 2014, *Y. Ohmura* 11059 (TNS-L-129846—holotype).

(Fig. 2)

Ascomata apothecia, blackish, matt, epruinose, superficial, discoid, with slightly concave to slightly convex disc surrounded by an initially strongly elevated, later occasionally disappearing concolorous margin, constricted at the base, 150–450(–600) µm diam. ($n = 20$), arising singly or in small groups, occasionally contiguous. *Exciple* patchy medium to dark reddish brown, K+ slightly fading, 30–50 µm laterally, 50–250 µm basally where it sometimes forms a stipe immersed in the host thallus, in cross-section composed of circular or tangentially elongated cells up to 9 µm with walls 1.5–2.5 µm thick. *Hypothecium* medium reddish brown, K+ slightly fading, 30–70 µm tall, in cross-section of textura angularis. *Epihymenium* patchy medium to dark reddish brown, K+ slightly fading, pigmentation amorphous/non-granular, *c.* 10 µm tall. Reddish brown apothecial pigments N+ reddish orange to red. *Hymenium* hyaline to dull red, 55–70 µm tall, entirely penetrated by a hymenial gel, without oil droplets, I+ blue, K/I+ blue with greyish red patches. *Paraphyses* 1–2 µm diam., straight to sinuous (particularly above), extending beyond the asci, branched (sparingly below, rather frequently above), anastomosed, septate, with cells *c.* 3—10 µm long; tips not or slightly enlarged, without dark cap, embedded in reddish brown gelatinous gel. *Asci* of the *Catillaria*-type, subclavate, 50–65 × 10–12 µm ($n = 10$), tholus thickened, without any distinct apical apparatus, in K/I with a blue and partly reddish outer gelatinous coat and uniformly darker blue tholus, 8-spored. *Ascospores* hyaline to occasionally pale brownish orange or dull red, ellipsoid, narrowly ellipsoid, sometimes narrowly obovoid, with slightly wider upper cell, with rounded ends, (9.5–)10.5–13(–15.5) × (4–)4.5–6(–6.5) µm, l/w = (1.6–)2.0–2.6(–3.0) ($n = 78$), (0–)1(rarely 2–3)-septate, not or only slightly constricted at the median septum, with smooth wall *c.* 0.5 µm thick throughout, non-halonate, usually without distinct guttules, (1–)2(–3)-seriate in the ascus.

In one specimen (*Kashiwadani* 20272) we observed semi-immersed, applanate, 30–50 µm diam. pycnidia of unclear origin, occasionally growing on apothecial discs of *Catillaria*. They have a greenish grey wall and contain hyaline, short-bacilliform conidia, 3.5–5 × 1–1.5 µm.

Etymology. Named after Japan, where the type was collected.

Distribution and host. The new species is known from eight collections in Japan, growing on thalli of *Dibaeis* (mostly) and *Pseudobaeomyces* species, not visibly damaging the host.

Notes. To the best of our knowledge, the new species is most consistent with the broad concept of the large heterogeneous genus *Catillaria* A. Massal. (Hertel *et al.* 2007). However, reddish brown apothecial pigments and a lichenicolous lifestyle are rare in that genus, and its paraphyses are typically simple or sparingly branched, abruptly swollen and have a dark brown cap at the apex. Its type species, *C. chalybeia* (Borrer) A. Massal., additionally differs in its carbonaceous black exciple and the presence of a green apothecial pigment (Hertel *et al.* 2007). Compared to other lichenicolous species occurring in *Catillaria* (Diederich *et al.* 2018*b*), *C. japonica* seems to be most similar to *C. stereocaulorum* (Th. Fr.) H. Olivier which also has reddish brown apothecial pigments but differs in its mostly simple paraphyses, apically abruptly swollen and with a dark reddish brown cap, and hyaline to pale yellowish brown hypothecium (Zhurbenko 2010*a*).

Further genera comparable to the new species are *Catinaria* Vain. and *Scutula* Tul. The former differs in its ascospores having a compact gelatinous halo and the absence of a lichenicolous lifestyle (Gilbert 2009), and the latter in its asci with an amyloid tholus and diffuse non-amyloid axial body, and an epihymenium with a granular, greenish brown to greenish black pigment (Triebel & Kainz 2004).

With its apothecial habitus, structure and pigmentation of the exciple and epihymenium, and shape and septation of the ascospores, *Catillaria japonica* resembles species of *Sclerococcum* Fr., particularly *S. athallinum* (Müll. Arg.) Ertz & Diederich growing on *Baeomyces* (Hafellner 1979; present paper). However, species of that genus are easily distinguished by their asci with a K/I– tholus and brown ascospores (Hafellner 2004).

Additional specimens examined. **Japan:** *Hokkaido*: Prov. Kitami, Bihoro Pass, Bihoro-cho, Abashiri-gun, 43°39′N, 144°15′E, 500 m, on *Dibaeis arcuata* (thallus), 1997, *Y. Ohmura* 3604 (TNS); Prov. Tokachi, along the trail from Me-akan Hot Spring to the top of Mt Me-akan, Ashoro-cho, Ashoro-gun, 43°23'N, 144°00′E, 920–1050 m, on *D. arcuata* (thallus), 1995, *Y. Ohmura* 1699 & *H. Kashiwadani* (TNS). *Honshu*: Prov. Rikuchu (Pref. Akita), around Sukawa Hot Spring, Mt Kurikoma, 38°57′N, 140°47'E, 1200 m, on *D. arcuata* (thallus), 1983, *H. Kashiwadani* 20272 (TNS); Prov. Shimotsukue (Pref. Tochigi), Nikko-city, 13 km NW of Nikko and 5 km ESE of the village Yumoto, at the river 150 m SE of the dirt road, 36°47'49.9"N, 139°28'50.0"E, 1570 m, on *Dibaeis* sp. (thallus) growing on *Tsuga diversifolia* log, 2015, *G. Thor* 32554 (TNS). *Kyushu*: Prov. Bungo (Pref. Ohita), Mt Taisen-zan, Kujyu-cho, Naoiri-gun, 33°05'N, 131°17′E, 1400 m, on *D. arcuata* (thallus), 1987, *Y. Umezu* 144 (TNS); Mt Yufu-dake, 33°16′N, 131°23′E, on *Pseudobaeomyces pachycarpus* (thallus), 1962, *S. Kurokawa* 62261 (TNS); Prov. Ohsumi (Pref. Kagoshima), Hananoego, Mt Kuromi-dake, Yakushima Island, 30°18'45"N, 130°30'38"E, 1550 m, on *P. pachycarpus* (thallus), 2005, *K. Yoshida* 13780 (TNS).

Cryptodiscus ihlenii Zhurb. sp. nov.

MycoBank No.: MB 836573

Lichenicolous ascomycete. Distinguished from *Cryptodiscus galaninae* mainly by the I– versus I+ blue then orange to red

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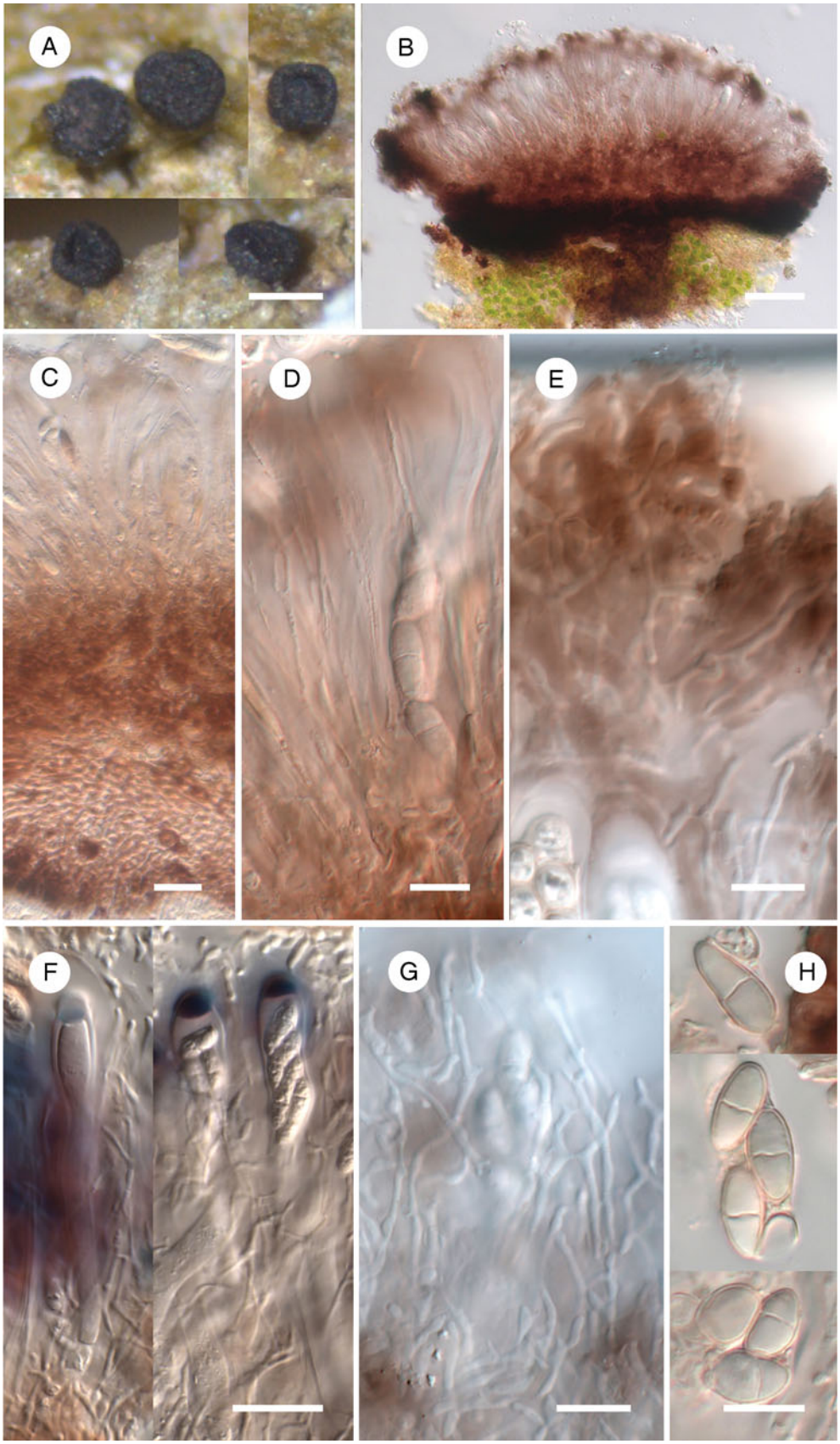

Fig. 2. *Catillaria japonica* (A & B, holotype; C & D, *Kurokawa* 62261; E–G, *Kashiwadani* 20272; H, *Umezu* 144). A, habitus of ascomata on the thallus of *Dibaeis sorediata*. B, ascoma in cross-section in water. C, exciple, hypothecium and hymenium in cross-section in water. D, hymenium and epihymenium in water. E, epihymenium in K. F, asci and paraphyses in K/I. G, paraphyses in K. H, ascospores in water. Scales: A = 200 μm; B = 50 μm; C & F = 20 μm; D, E, G & H = 10 μm. In colour online.

https://doi.org/10.1017/S002428292000047X Published online by Cambridge University Press

hymenium, narrowly obovate, 1-septate versus slightly fusiform, clavate or bacilliform, 0–2-septate and larger ascospores (14–20.5 × 5–7.5 µm versus 7–14.5 × 1.5–2 µm), and a different host selection, *Dibaeis* versus *Cladonia*.

Type: Japan, Hokkaido, Prov. Tokachi, Mt Higashi-Nupukaushi, Kami-Shihoro-cho, Kato-gun, 43°14'N, 143°06'E, *c.* 1000 m, on the thallus of *Dibaeis arcuata*, 17 September 1979, *H. Kashiwadani* 15493 (TNS-L-129847—holotype).

(Fig. 3)

Ascomata cleistohymenial apothecia, aggregated, 80–250 µm diam. ($n = 7$), persistently immersed in the host thallus, initially closed, subglobose, later opening by a small pore, finally urceolate or cupulate, with a widely exposed, concave, pale orange to orange-white, translucent, roundish to irregularly elongate (due to mutual compression) disc, inducing the formation of subglobose warts up to 0.4 mm diam. on the host thallus, containing one or several immersed apothecia. *Exciple* hyaline, without crystals, not differentiated into layers, 10–20 µm thick throughout, in cross-section composed of tangentially somewhat elongated cells 2–5 µm long, with walls 0.5–1 µm thick, K–. *Periphysoids* absent. *Epihymenium* indistinct. *Hymenium* hyaline, 70–100 µm tall, I–, K/I–. *Subhymenium* hyaline, *c.* 10 µm thick. *Paraphyses* hyaline, filiform, 1–2 µm diam., septate, branched, apically not distinctly enlarged. *Asci* narrowly ellipsoid to elongate-clavate, wall 1–3 µm thick, apically not or slightly thicker, apical structures not observed, 55–80 × 13–17 µm ($n = 3$), 8-spored, I–, K/I–. *Ascospores* hyaline, narrowly obovate, irregularly biseriate in the ascus, (14–)15.5–19(–20.5) × (5–)5.5–7(–7.5) µm, l/w = (2.0–)2.4–3.2(–3.7) ($n = 29$), 1-septate, not or slightly constricted at the septum, with smooth wall *c.* 0.5 µm thick, non-halonate, with many guttules.

Asexual morph not observed.

Etymology. The species is named after the Norwegian lichenologist Per Gerhard Ihlen who made a great contribution to the knowledge of lichenicolous fungi growing on baeomycetoid lichens.

Distribution and host. The new species is known from the type collection in Japan, growing on the thallus of *Dibaeis arcuata*, inducing gall-like warts on the host thallus; otherwise pathogenicity was not observed.

Notes. The new species fits the concept of *Cryptodiscus* Corda presented in Baloch *et al.* (2009) and Pino-Bodas *et al.* (2017). Most species of this genus are characterized by the K/I+ blue hymenium, K/I+ faintly blue ascus wall, simple, sometimes slightly forked above and apically often enlarged paraphyses, cylindrical phragmosporous ascospores and saprobic lifestyle on wood. However, three previously known species of *Cryptodiscus* are obligately lichenicolous (Diederich *et al.* 2018*b*), the hymenium and ascus wall of *C. epicladonia* Zhurb. & Pino-Bodas do not change colour with K/I, the paraphyses of *C. cladoniicola* (D. Hawksw. & R. Sant.) Pino-Bodas *et al.* are regularly branched (Pino-Bodas *et al.* 2017), and both *C. pini* (Romell) Baloch *et al.* and *C. foveolaris* (Rehm) Rehm have 1-septate ascospores (Baloch *et al.* 2009).

The other lichenicolous species of *Cryptodiscus*, viz. *C. cladoniicola*, *C. epicladonia* and *C. galaninae* Zhurb. & Pino-Bodas, all growing on *Cladonia*, are readily distinguished from *C. ihlenii* by their eventually superficial ascomata and much narrower ascospores, up to 3 µm wide (Pino-Bodas *et al.* 2017). Additionally, *C. cladoniicola* is distinct, for example, in the I+ fleetingly blue hymenium and cylindrical to slightly fusiform, 2–4-septate ascospores; *C. epicladonia* differs in its apothecia with a crystalline rim and filiform to cylindrical, 5–11-septate ascospores; and *C. galaninae* differs in the I+ blue then orange to red hymenium and slightly fusiform, clavate or bacilliform, 0–2-septate ascospores.

Cryptodiscus ihlenii is morphologically and anatomically comparable to species of *Aabaarnia* Diederich, *Absconditella* Vězda, *Dimerella* Trevis., *Gyalecta* Ach., *Lettauia* D. Hawksw. & R. Sant. s. lat., *Nanostictis* M. S. Christ. and *Stictis* Pers. *Aabaarnia* can be distinguished by its K/I+ blue hymenium, subcylindrical, 4–6-spored asci and 3-septate ascospores with a perispore (Diederich 2014). *Absconditella*, which is phylogenetically very close to *Cryptodiscus* (Baloch *et al.* 2009), mainly differs in its lichenized not lichenicolous lifestyle and asci with a distinct apical dome (Coppins 2009). *Dimerella* differs in its lichenized not lichenicolous lifestyle, sessile apothecia, I+ blue hymenium, paraphyses with a pair of swollen apical cells and asci with a K/I+ blue wall (Benfield *et al.* 2009). *Gyalecta* differs in its lichenized not lichenicolous lifestyle and trans-septate to muriform ascospores (Gilbert *et al.* 2009). The type of *Lettauia* belongs to *Cryptodiscus* (Pino-Bodas *et al.* 2017); the phylogenetic positions of the other species of this genus, viz. *L. hypotrachynae* Etayo, *L. santessonii* Ihlen & Tønsberg and *L. usneae* Etayo are still unclear but they differ in having eventually superficial apothecia with a plane disc and a K/I+ blue hymenium (Ihlen & Tønsberg 1996; Etayo 2002, 2017). *Nanostictis* mainly differs in its filiform, cylindrical or acicular, exceptionally ellipsoid, ascospores with few or many trans-septa (Christiansen 1954; Etayo & Diederich 1996; Etayo 2002, 2017; Etayo & Sancho 2008; Zhurbenko 2017). Typically, *Stictis* includes saprobic or lichenized species with the ascomatal margin lined by periphysoids and filiform ascospores (Sherwood 1977; Wedin *et al.* 2006). The generic position of the only lichenicolous species placed in this genus, *S. cladoniae* (Rehm) Sacc., is unclear; it lacks periphysoids but is well distinguished by the brown-black apothecia with blackish disc and an I+ red, K/I+ blue hymenium (Pino-Bodas *et al.* 2017).

Llimoniella chilensis Zhurb. sp. nov.

MycoBank No.: MB 836574

Lichenicolous ascomycete. Distinguished from the formerly known *Llimoniella* species by the combination of the K+ green reaction of the exciple and epihymenium, aseptate, broadly ellipsoid ascospores, and the host selection (growing on *Dibaeis*).

Type: Chile, Region X, Prov. Valdivia, Fundo San Martín (Universidad Austral de Chile), *c.* 30 km S of San José de la Mariquina, 40°38'S, 73°05'W, 10 m, mixed forest with *Nothofagus obliqua*, on the thallus of terricolous *Dibaeis* sp., 18 November 1987, *H. Kashiwadani* 35425a (TNS-L-129848—holotype).

(Fig. 4)

Ascomata apothecia, loosely aggregated, rarely confluent, erumpent, eventually 1/4 to 1/2 immersed, urceolate to cupulate, constricted at the base, roundish in surface view, 70–250 µm diam. ($n = 20$); margin prominent, often partially covering the disc, blackish, matt, rough, occasionally with radial fissures, without hairs;

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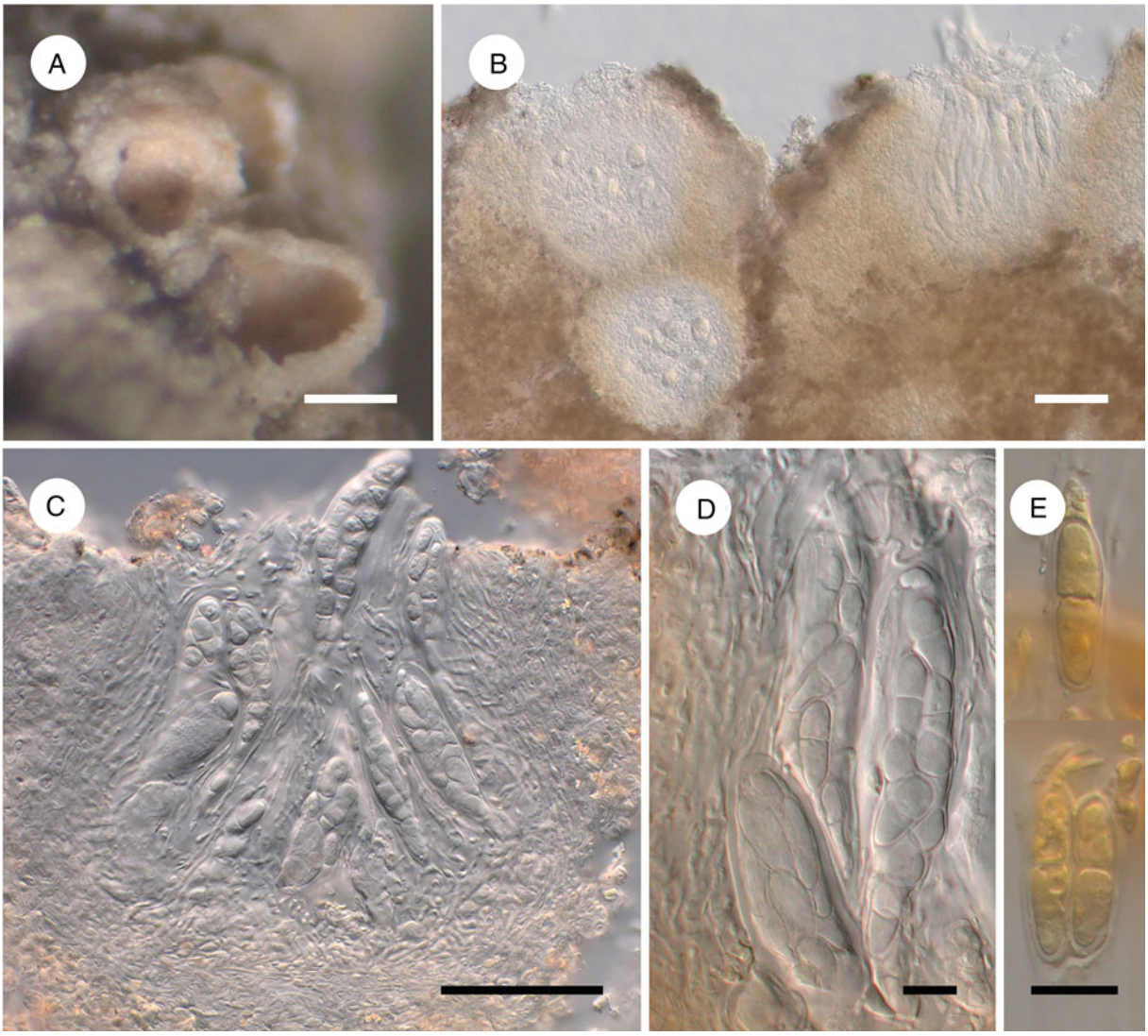

Fig. 3. *Cryptodiscus ihlenii* (holotype). A, habitus of ascomata on the thallus of *Dibaeis arcuata*. B & C, ascomata in cross-section in water. D, asci with spores in water. E, ascospores in I. Scales: A = 100 µm; B & C = 50 µm; D & E = 10 µm. In colour online.

disc initially almost enclosed, later widely exposed, blackish, not translucent, slightly concave to plane. *Exciple* in cross-section composed of circular to elongate cells up to 10 µm, with walls 1–2.5 µm thick, innermost cells usually tangentially elongated, thinner, with paler and thinner walls; laterally 20–50 µm thick, dark violet-brown, K+ greyish green to deep green, N+ reddish brown; basally 20–70 µm thick, occasionally prolonged into a short immersed stipe, pale to medium greyish or brownish orange, K–, N+ brownish orange. *Epihymenium* reddish brown and partly violet-brown (pigmentation ill-defined), K+ greyish green to deep green, K/I+ greyish red, N+ brownish orange, 10–15 µm tall. *Hymenium* pale reddish to violet-brown above, colourless below, not inspersed, 60–70 µm tall, I–, K/I–, partly K+ greenish. *Subhymenium* colourless to orangish. *Paraphyses* 2–3.5 µm thick, apically sometimes slightly swollen (to 4 µm), scarcely septate, occasionally branched, not pigmented. *Asci* subcylindrical, apically rounded to somewhat applanate, with a long foot, croziers not observed, wall 0.5–1 µm thick, not thickened at the apex, without ocular chamber, 55–75 × 7.5–10 µm ($n = 13$), 8-spored, I–, K/I–. *Ascospores* hyaline, mostly broadly ellipsoid, occasionally ellipsoid or subglobose, uniseriate in the ascus, (5–)6.5–8.5(–10.5) × (4–)4.5–5.5(–7) µm, l/w = (1.0–)1.3–1.7(–2.3) ($n = 100$), aseptate, wall *c.* 0.5 µm thick, smooth, without perispore, indistinctly guttulate.

Asexual morph not observed.

Etymology. Named after Chile, where the type was collected.

Distribution and host. The new species is known from two collections in Chile. It grows on the thalli of terricolous *Dibaeis* sp. and a sterile microsquamulose lichen, partly associated with discolorations.

Notes. The new species fits well with the generic concept of *Llimoniella* Hafellner & Nav.-Ros. in its broad sense (Hafellner & Navarro-Rosinés 1993; Diederich & Etayo 2000; Diederich *et al.* 2010) and is distinct from all its species keyed out in Diederich *et al.* (2010) and described in subsequent publications (Pérez Ortega *et al.* 2011; Vondrák *et al.* 2013; Zhurbenko 2013; Etayo 2017) by the combination of the K+ green reaction of the

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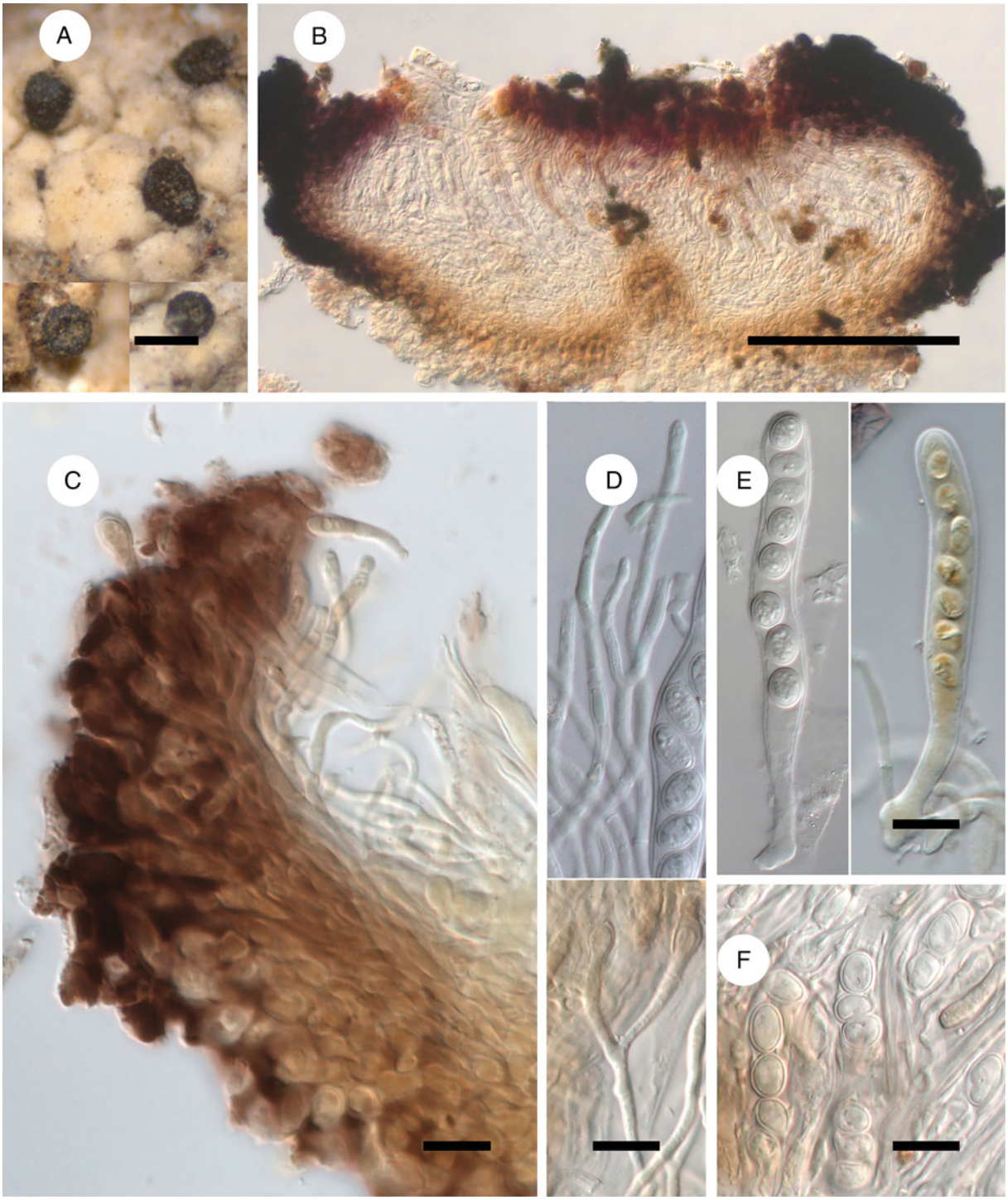

Fig. 4. *Llimoniella chilensis* (A, C, D (below) & E (on the right), holotype; B, D (above), E (on the left) & F, *Imshaug* 36984). A, habitus of ascomata on the thallus of *Dibaeis* sp. B, ascoma in cross-section in water. C, exciple in cross-section in K/I. D, paraphyses in K (above) and in K/I (below). E, asci with spores in K (on the left) and K/I (on the right). F, ascospores in water. Scales: A = 200 μm; B = 100 μm; C–F = 10 μm. In colour online.

exciple and epihymenium and aseptate, broadly ellipsoid ascospores. *Llimoniella pertusariae* Diederich & Etayo (on *Lepra ophthalmiza* and *Pertusaria glaucomela*) and *L. pyrenulae* Diederich & Etayo (on *Pyrenula*) are also characterized by the K+ green reaction and aseptate ascospores, but the latter are narrowly ellipsoid to fusiform (Diederich & Etayo 2000; Diederich *et al.* 2010, 2018*b*). In its broadly ellipsoid, aseptate ascospores the new species is similar to *Llimoniella fuscatae* Hafellner & Obermayer (on *Acarospora fuscata*), *L. gregorellae* Kocourk. & Vondrák (on *Gregorella humida*) and *L. terricola* (Arnold) M. Schultz *et al.* (on *Leptogium byssinum*) (Ertz & Diederich 2006; Hafellner & Obermayer 2007; Vondrák *et al.* 2013). However, *Llimoniella fuscatae* is distinct in its red-brown, K+ purple-violet later dark brown exciple and larger ascospores,

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9–12 × 5.5–7.5 µm; *L. gregorellae* differs in its orange-brown, K+ brown-purple exciple; and *L. terricola* differs in its orange-brown, K+ slightly darker reddish brown exciple.

In its urceolate to cupulate apothecia and hyaline, broadly ellipsoid, aseptate, uniseriate ascospores of similar size, the new species resembles *Geltingia associata* (Th. Fr.) Alstrup & D. Hawksw. However, that species, usually growing on *Ochrolechia*, differs in its more or less immersed apothecia, orange-brown, K−, N− exciple, and asci with an apically thickened wall and distinct ocular chamber (Diederich *et al.* 2010).

Additional specimen examined. **Chile:** *Valparaíso Region*: Juan Fernandez Islands, Más Afuera Island, Campo Correspondencia, 1000 m, on terricolous sterile microsquamulose lichen (thallus), 1965, *H. A. Imshaug* 36984 (TNS).

Micarea inquinans (Tul.) Coppins

This species is known from scattered reports throughout Europe (Brackel 2014) and single finds in North America (Alaska, USA; Fryday 2017) and Asia (Kai Province, Japan; Zhurbenko *et al.* 2015). *Dibaeis arcuata* is a new host species.

Specimens examined. **Japan:** *Honshu*: Prov. Shinano (Pref. Nagano), Mt Neko-dake, Ueda-city, 36°32'54.7"N, 138°23'34.5"E, 2150 m, mountain heath, on *Dibaeis baeomyces* (thallus), 2012, *A. Frisch* 12/Jp398 (TNS, filed under the host). *Hokkaido*: Prov. Kushiro, along the trail from Taro-ko to the top of Mt O-akan, Akan-gun, 43°27′N, 144°09′E, 1180–1370 m, on *D. arcuata* (thallus), 1995, *Y. Ohmura* 1619 & *H. Kashiwadani* (TNS, filed under the host).

Pyrenidium actinellum Nyl. s. lat.

This species was described from *Scytinium teretiusculum* (Nylander 1865) and subsequently reported from a wide range of lichen genera (see e.g. Brackel 2014). In its broad sense it probably includes a number of host-specific, yet undescribed species (Huanraluek *et al.* 2019). The specimens examined for this study are characterized by blue-green flecks occurring in the ostiolar region, asci with four mature spores, and 3-septate ascospores measuring (17.5–)20.5–26.5(–31) × (7–)8–9.5 µm, l/w = (2–)2.4–3.2(–4.2) (n = 48; on *Baeomyces*) and (20–)22–26.5(–30) × (7.5–)8–9(–9.5) µm, l/w = (2.2–)2.5–3.1(–3.3) (n = 19; on *Dibaeis*).

Specimens examined. **Japan:** *Hokkaido*: Prov. Kushiro, along the trail from Taro-ko to the top of Mt O-akan, Akan-gun, 43°27′N, 144°09′E, 700–1180 m, on *Dibaeis baeomyces* (thallus), 1995, *Y. Ohmura* 1550 & *H. Kashiwadani* (TNS, filed under the host); on *Baeomyces placophyllus* (thallus), 1995, *Y. Ohmura* 1551 & *H. Kashiwadani* (TNS, filed under the host); around Hyotan-numa, Akan-cho, Akan-gun, 43°25′N, 144°11′E, 460 m, on *B. rufus* (thallus), 1995, *Y. Ohmura* 2052 & *H. Kashiwadani* (TNS, filed under the host). *Honshu*: Prov. Shimotsuke (Pref. Tochigi), Nikko-city, 13 km NW of Nikko and 5 km ESE of the village Yumoto, at the river 150 m SE of the dirt road, 36°47'49.9"N, 139°28'50.0"E, 1570 m, on *Dibaeis* sp. (thallus) growing on *Tsuga diversifolia*, 2015, *G. Thor* 32553 (TNS, filed under the host); Prov. Shinano (Pref. Nagano), Yatsugatake Mts, 35°59′N, 138°21′E, on *Baeomyces rufus* (thallus), 1959, *M. Togashi & S. Kurokawa* (TNS, filed under the host); Shibunoyu Hot Spring, Yatsugatake Mts, 36°02′10"N, 138°19′43"E, 1800 m, on *B. rufus* (thallus), 1958, *S. Kurokawa* 58262 (TNS, filed under the host); Pref. Gunma, Katashina-mura, 25 km WNW of Nikko, 5 km ENE of Marunuma-kogen ski resort, 36°49'15.1"N, 139°22'35.1"E, 1780 m, on *B. placophyllus* (thallus) on log, 2015, *G. Thor* 32439 (TNS, filed under the host).—**Chile:** *Region X*: Prov. Valdivia, Fundo San Martín (Universidad Austral de Chile), *c.* 30 km S of San José de la Mariquina, 40°38′S, 5°50′W, 10 m, mixed forest with *Nothofagus obliqua*, on *Dibaeis* sp. (thallus), 1987, *H. Kashiwadani* 35425b (TNS, filed under the host).

Sclerococcum athallinum (Müll. Arg.) Ertz & Diederich

Exciple and epihymenium reddish brown, hymenium hyaline to dull red, pigmentation slightly fading in K, the K+ purplish tinge of epihymenium reported in Hafellner (1979) not observed. Ascospores (rarely 0–)1-septate, somewhat smaller than reported in Hafellner (1979) and Ihlen (1998), (6–)7–9(–10.5) × (3.5–)4–4.5(–5) µm, l/w = (1.3–)1.7–2.1(–2.4) (n = 49) versus 9–14.5 × 4–7 µm and (7.5–)9–11 × 5–6 µm respectively. In the Southern Hemisphere, *Sclerococcum athallinum* was until now known from a single report in the state of Victoria, Australia (Staatliche Naturwissenschaftliche Sammlungen Bayerns 2020) and is newly reported here from two other Australian states, New South Wales and Tasmania.

Specimens examined (both on thalli of Baeomyces heteromorphus*).* **Australia:** *New South Wales*: Blue Mountains, Mt Wilson, 33°30′S, 150°22′E, 1000 m, 1965, *S. Kurokawa* 5025 (TNS, filed under the host). *Tasmania*: SW of Hobart, Old Huon Road, 1887(?), *R. A. Bastow* (TNS, filed under the host).

Specimen of Sclerococcum athallinum *used for comparison.* **Australia:** *Victoria*: 12 km NW of Castlemaine, Harcourt-Sutton Grange Road, 36°58'S, 144°18'E, 450 m, on *Baeomyces heteromorphus* (thallus), 1994, *H. T. Lumbsch, A. Dickhäuser & H. Streimann* (D. Triebel, *Microfungi Exsiccati*, no. 129; LE 200943).

Sclerococcum attendendum (Nyl.) Ertz & Diederich

Apothecia black, sessile, discoid, with a thick, rough, elevated margin, constricted at the base, 100–310 µm diam. (n = 41), growing on thalli of *Icmadophila* species and occasionally on adjacent rotten wood. Exciple reddish brown, 20–50 µm laterally, basally sometimes forming a stipe up to 180 µm tall immersed in the host thallus. Hypothecium brown to reddish brown. Epihymenium reddish brown, *c.* 5 µm tall. Hymenium hyaline to pale reddish brown below, 30–50 µm tall. Asci 8-spored. Ascospores brown, broadly to narrowly ellipsoid or oblong, biseriate in the ascus, (6.5–)8.5–11(–13) × (3.5–)4–5(–6) µm, l/w = (1.4–)1.9–2.5(–3.0) (n = 132), (0–)1–3-septate, often slightly constricted at septa, smooth, non-halonate.

This species was described from *Pilophorus* (*Lecanorales*) and subsequently reported from a number of distantly related genera, viz. *Amygdalaria* (*Lecideales*), *Icmadophila* (*Pertusariales*) and *Porpidia* (*Lecideales*) (Triebel 1989; Ihlen 1998). According to Triebel (1989), ascospores of this species are somewhat longer than in our material ((10–)11–15(–17) × (4–)4.5–5.5(–6.5) µm), which might suggest that the specimens growing on *Icmadophila* are not conspecific with those on the other diverse host genera. However, the ascospore sizes of the additionally

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examined specimen growing on the type host *Pilophorus cereolus* (LE 207747), (6.5–)8.5–11(–13) × (3.5–)4.5–5(–6) µm, l/w = (1.4–)1.8–2.4(–2.8) (n = 102), perfectly match our material on *Icmadophila*. The species was previously known in Japan from a single collection in Honshu Province growing on *Pilophorus clavatus* (Triebel 1989); it is newly reported here for the Sakhalin Region of Russia.

Specimens examined. **Japan:** *Hokkaido*: Prov. Hidaka, foot of Mt Petegari, 42°59′N, 142°52′E, 750 m, on *Icmadophila japonica* (thallus), 1970, *S. Kurokawa* 70226 (TNS, filed under the host); Prov. Kushiro, Furebetsu Bokke, N slope of Mt Furebetsu, Akan-cho, Akan-gun, 43°24′N, 144°05′E, 780 m, on *I. japonica* (thallus), 1995, *Y. Ohmura* 1944 & *H. Kashiwadani* (TNS, filed under the host); Prov. Tokachi, Mt Higashi-Nupukaushi, Shikaoi-mura, Kato-gun, 43°14′N, 143°06′E, 1000 m, on *I. japonica* (thallus), 1979, *H. Kashiwadani* 15363 (TNS, filed under the host); foot of Mt Hakuun, Lake Shikaribetsu, Kato-gun, 43°15′N, 143°06′E, 900 m, on *I. japonica* (thallus), 1970, *M. Togashi* [Y. Ohmura, *Lichenes Minus Cogniti Exsiccati*, no. 381] (TNS, filed under the host). *Honshu*: Prov. Echigo (Pref. Niigata), on trail from the summit to Akayu Hot Spring, Mt Naeba, 36°49′N, 138°43′E, on *I. ericetorum* (thallus), 1957, *S. Kurokawa* 57199 (TNS, filed under the host); Prov. Kai (Pref. Yamanashi), Mt Kimpu, 35°52′N, 138°37′E, on *I. ericetorum* (thallus), 1953, *S. Kurokawa* 521163 (TNS, filed under the host); Prov. Kozuke (Pref. Gunma), Mt Shibutsu, Oze, 36°54′N, 139°10′E, on *I. japonica* (thallus), 1950, *Y. Asahina* 5044 (TNS, filed under the host); Prov. Shinano (Pref. Nagano), Yatsugatake Mts, 35°59′N, 138°21′E, on *I. ericetorum* (thallus), 1926, *Y. Okada* (b) (TNS, filed under the host); Mt Sannosawa-dake, Kiso-Komagatake Mts, 35°46′N, 137°47′E, 2700 m, on *I. ericetorum* (thallus), 1969, *S. Kurokawa* 69068 (TNS, filed under the host); Prov. Iwashiro (Pref. Fukushima), Oze, 36°56′N, 139°14′E, on *I. japonica* (thallus) and occasionally on neighbouring rotten wood, 1933, *S. Asahina* (TNS, filed under the host).— **Russia:** *Sakhalin Region*: Sakhalin Island, Mt Tosso, 48°03′N, 142°32′E, on *I. ericetorum* (thallus) and occasionally on neighbouring rotten wood, 1932, *M. Sato* (TNS, filed under the host).

Specimen of Sclerococcum attendendum *used for comparison.* **Russia:** *Komi Republic*: headwaters of the Pechora River, valley between Yanypupuner Range and Mt Medvezh'ya, 62°04′N, 59°08′E, 500 m, on *Pilophorus cereolus* (thallus), 1997, *M. P. Zhurbenko* 97166 (LE 207747).

Sphaerellothecium coniodes (Nyl.) Cl. Roux & Diederich

The range of ascospore sizes in the material we studied was (11–)12–14.5(–16.5) × (3.5–)4.5–5.5(–6) µm, l/w = (2.2–)2.4–3.0(–3.8) (n = 26) which is slightly greater than those presented in Ihlen (1998) and Roux & Triebel (1994), viz 11–14 × 4–5 µm and 11–13 × 3.5–5 µm respectively. To date, the species was known from Europe and North America (Hodkinson *et al.* 2009; Brackel 2014) and is newly reported here for Asia and Japan.

Specimens examined (both on thalli of Baeomyces rufus*).* **Japan:** *Hokkaido*: Prov. Tokachi, along the trail from Me-akan Hot Spring to the top of Mt Me-akan, Ashoro-cho, Ashoro-gun, 43°24′N, 143°59′E, 710–920 m, 1995, *Y. Ohmura* 1682 & *H. Kashiwadani* (TNS, filed under the host). *Kyushu*: Prov. Ohsumi (Pref. Kagoshima), Hananoego, Yakushima Island, 30°18'45"N, 130°30'38"E, 1933, *F. Fujikawa* (TNS, filed under the host).

Stigmidium phyllobaeidis Zhurb., Etayo & Flakus sp. nov.

MycoBank No.: MB 836575

Lichenicolous ascomycete growing on *Phyllobaeis*. Vegetative hyphae reduced; ascomata perithecioid, ostiolate, brownish black, glabrous, immersed to semi-immersed; exciple dark brown, K–; interascal hyphae lacking; interascal gel I+ red, K/I+ blue; periphysoids 1-2(-4)-celled; asci bitunicate, 8-spored, I–, K/I–; ascospores hyaline, 1-septate, with slightly wider upper cell, (6.5–)8–10.5(–13) × (2.5–)3–4(–5) µm.

Type: Peru, Dept. Cuzco, Prov. Paucartambo, Abra Acjanaco, near Paucartambo, 3400–3500 m, upper part of 'Ceja de Selva' zone, on apothecial discs of *Phyllobaeis erythrella* growing on soil, 17 September 1984, *H. Kashiwadani* 21946 (TNS-L-129849—holotype).

(Fig. 5)

Vegetative hyphae brown, immersed, reduced. *Ascomata* perithecioid, mostly completely immersed to semi-immersed, occasionally 1/3 protruding, brownish black, somewhat glossy, glabrous, epruinose, subglobose, 60–130 µm diam. (n = 20), with an ostiole 10–15 µm diam., aggregated. *Exciple* 10–20 µm thick, exposed upper part medium to dark brown, K–, in surface view resembling textura angularis or textura globulosa, composed of cells up to 7 µm with walls 1–1.5 µm thick; immersed lower part pale brown, in surface view resembling textura angularis or textura porrecta, mainly composed of cells up to 12 µm with walls *c.* 0.5 µm thick; in cross-section composed of *c.* 5 layers of tangentially strongly elongated cells, the innermost cells thinner, with paler and thinner walls. *Periphysoids* resemble internal periphyses (above) and pseudoparaphyses (below) *sensu* Roux & Triebel (1994: fig. 2), well-developed throughout the upper half of the inner exciple, hyaline, 1–2(–4)-celled, up to 12 µm long; external, brown periphyses absent. *Interascal hyphae* absent. *Interascal gel* I+ red, K/I+ blue and partly red (staining does not fade). *Asci* bitunicate, subcylindrical to narrowly ellipsoid, slightly wider in the central or lower part, rounded at the apex, with a distinct foot, 35–50 × 7–11 µm (n = 12), wall apically thickened, sometimes with a small ocular chamber, I–, K/I–, plasma BCr+ blue to violet, 8-spored. *Ascospores* hyaline, narrowly obovate, with slightly wider upper cell, (6.5–)8–10.5(–13) × (2.5–)3–4(–5) µm, l/w = (1.7–)2.2–3.0(–3.4) (n = 55), diagonally uniseriate to irregularly biseriate in the ascus, 1-septate, not constricted at the septum, with a smooth wall *c.* 0.3 µm thick, non-halonate, usually without distinct guttules.

Etymology. Referring to its growth on *Phyllobaeis*.

Distribution and host. The new species is known from three collections in Bolivia and Peru, growing on apothecial discs of *Phyllobaeis erythrella* and *P. imbricata*. Host tissues are bleached under severe infections.

Notes. The new species does not perfectly match any of the genera known to us and is tentatively placed in the large, almost exclusively lichenicolous genus *Stigmidium* Trevis.

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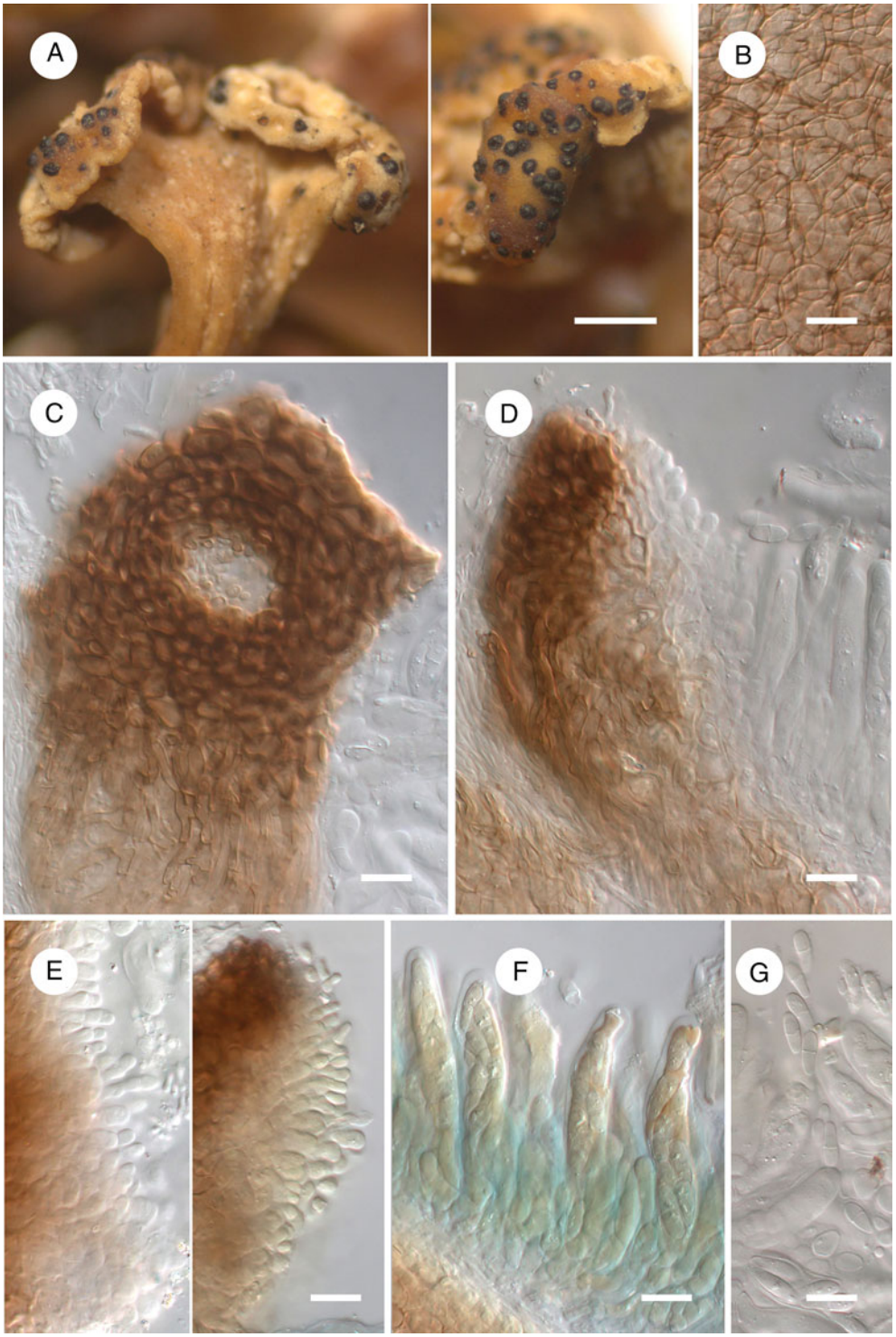

Fig. 5. *Stigmidium phyllobaeidis* (holotype). A, habitus of ascomata on apothecial discs of *Phyllobaeis erythrella*. B, basal exciple in surface view in K. C, exciple around ostiole in surface view in K. D, exciple in cross-section in K. E, periphysoids in K (on the left) and in K/I (on the right). F, asci and interascal gel in K/I. G, ascospores in K. Scales: A = 500 μm; B–G = 10 μm. In colour online.

Characteristics of *Stigmidium* fit the material examined except for the hemiamyloid reaction of the interascal gel never reported in the genus (Triebel & Cáceres 2004). However, some *Stigmidium* species, such as *S. cartilagineae* Calatayud & Triebel, *S. psorae* (Anzi) Hafellner, *S. squamarinicola* Calatayud & Triebel and *S. triebeliae* Etayo display an amyloid reaction of the interascal gel (Etayo 2000; Calatayud & Triebel 2003). A number of *Stigmidium* species, such as *S. buelliae* Zhurb. & Himelbrant, *S. cerinae* Cl. Roux & Triebel, *S. collematis* Cl. Roux & Triebel, *S. congestum* (Körb.) Triebel, *S. lecidellae* Triebel *et al.* and *S. disconephromeum* Etayo, are also confined to the apothecial discs of their host lichens (Roux & Triebel 1994;

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Roux *et al.* 1995; Etayo & Sancho 2008; Zhurbenko *et al.* 2012). With its well-developed periphysoids, hemiamyloid hymenial gel and elongate asci, the new species might fit the broad concept of *Pseudostigmidium* Etayo (Etayo & Sancho 2008). However, this genus is known to grow on foliose macrolichens of the suborder Peltigerineae and is characterized by almost exclusively 2–3-septate ascospores, though 1-septate ascospores also occur in *Pseudostigmidium disparatum* Etayo (Etayo & Sancho 2008). The generic type, *P. nephromiarium* (Linds.) Etayo, differs in having a distinct net of brown vegetative hyphae, hemispherical to subconical ascomata, I+, K/I+ light purple interascal gel and pycnidia with hyaline, bacilliform conidia (Etayo & Sancho 2008). In most respects the new species is also similar to species of *Austrostigmidium* Pérez-Ortega & Garrido-Benavent, *Clauzadella* Nav.-Ros. & Cl. Roux, *Endococcus* Nyl., *Epibryon* Döbbeler and *Sphaerellothecium* Zopf. However, *Austrostigmidium* is distinct in its I−, K/I− interascal gel and 3-septate ascospores (Pérez-Ortega *et al.* 2015), *Clauzadella* is distinguished by its comparatively thick, violet-tinged ascomatal wall and 3-septate ascospores (Navarro-Rosinés & Roux 1996), *Endococcus* is distinguished by its more or less pigmented ascospores (Kainz & Triebel 2004; Etayo & Sancho 2008), *Epibryon* differs in its typically setose ascomata and poorly developed periphyses (Döbbeler 1978; Hoffmann & Hafellner 2000), and *Sphaerellothecium* has an I−, K/I− interascal gel and typically produces a conspicuous net of dark vegetative hyphae as well as paraphysoids (Cáceres & Triebel 2004). The only species of the compared genera growing on members of the same host family *Icmadophilaceae* is *Sphaerellothecium icmadophilae* (R. Sant.) Zhurb. It grows on thalli of *Icmadophila ericetorum* and is clearly different from the new species, apart from the features noted above, in its 1(–3)-septate, hyaline to eventually brown, larger ascospores, 15–21 × 5–7 µm (Zhurbenko 2008).

In one specimen (*Etayo* 27749), perithecia of *Stigmidium phyllobaeidis* were intermixed with brown sporodochia 20–40 µm diam., originating from subhyaline to pale brownish hyphae deeply immersed in the host hymenium. They are characterized by prismatic to ellipsoid conidiophores and conidiogenous cells measuring 4–6 × 2.5–4.5 µm, producing acrogenous, simple, obpyriform, thin-walled, light brown conidia with a pointed end and truncate base, 11–14 × 2.5–3.5 µm. To the best of our knowledge, such an anamorph has not been recorded in any lichenicolous genus.

Additional specimens examined. **Bolivia:** *Dept. Cochabamba*: Carrasco Parque Nacional Carrasco, Wayra Mayu close to Monte Punku, 17°32′27″S, 65°16′14″W, 2553 m, lower montane Yungas cloud forest, on *Phyllobaeis imbricata* (discs of apothecia), 2014, *A. Flakus* 25830 (KRAM, LPB). *Dept. La Paz*: Prov. Nor Yungas, Parque Nacional y Área Natural de Manejo Integrado Cotapata, between Tunkini and Chairo villages, above Tunkini, 16°11′S, 67°52′W, 1300–1600 m, Yungas montane forest, on *P. erythrella* (discs of apothecia), 2011, *J. Etayo* 27749 (hb. Etayo, LPB).

A key to the species of lichenicolous fungi and lichens growing on baeomycetoid lichens and *Icmadophila*

This key is based on data from Keissler (1930), Hafellner (1979), Hawksworth (1979), Triebel (1989), Alstrup & Hawksworth (1990), Rambold & Triebel (1990), Gierl & Kalb (1993), Obermayer (1994), Roux & Triebel (1994), Aptroot *et al.* (1997), Ihlen (1998), Alstrup *et al.* (2000), Baral & Marson (2001), Hafellner *et al.* (2002), Punithalingam (2003), Zhurbenko (2008), Duke & Purvis (2009), Orange *et al.* (2009), Ertz *et al.* (2014), Heuchert *et al.* (2018), Diederich *et al.* (2019) and the present contribution.

1 Spores (conidia) produced on conidiogenous cells . . . 2
Spores produced in asci . . . 6

2(1) Conidiomata pycnidial, conidia hyaline . . . 3
Conidiomata not pycnidial, conidia brown . . . 5

3(2) Conidia Y-shaped, consisting of main body 9.5–11.5 × 2–2.5 µm (including basal appendage) and two divergent arms; on various host genera . . . **Spirographa ciliata** s. lat.
Conidia not Y-shaped . . . 4

4(3) Conidia cylindrical, 12–20 × 2.5–3.5 µm, with filiform lateral appendages, 18–36 × 1–2 µm, often in chains; on *Icmadophila* . . . **Acarosporium lichenicola**
Conidia narrowly ellipsoid to bacilliform, 5–6(–7) × 2–2.5 µm, without appendages, not in chains; on *Dibaeis* . . . **Phoma maculiformans**

5(2) Conidiomata stromatic; conidia composed of 4–22 cells, subspherical to ellipsoid, (10–)11–13.5(–15) × (7–)8.5–10.5(–12) µm, not in chains; on various host genera . . . **Lichenostigma alpinum**
Conidiomata not stromatic (hyphomycete); conidia (0–)1–2(–3)-septate, subcylindrical, doliiform, pyriform, ellipsoid or limoniform, 4–17 × 3–8 µm, mostly in chains; on various host genera . . . **Taeniolella delicata**

6(1) Ascomata yellow; asci multispored; ascospores hyaline, aseptate . . . 7
Ascomata blackish; asci up to 8-spored; ascospores various . . . 9

7(6) Ascomata with at least slightly exposed discs, shortly cylindrical, obconical or dish-shaped; asci cylindrical clavate; ascospores (4–)5–7.5 × 1.5–2.5 µm; on various host genera . . . **Thelocarpon lichenicola**
Ascomata without exposed discs, ovoid or conical; asci flask-shaped, tapering to a slender neck above . . . 8

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8(7) Ascospores 4–6 × 1.5–2 µm; on various host genera . . . . . **Thelocarpon epibolum** var. **epibolum**
Ascospores (6–)8–10(–12) × 2–3 µm; on various host genera . . . . . **Thelocarpon epibolum** var. **epithallinum**

9(6) Ascomata apothecioid 10
Ascomata perithecioid 26

10(9) Ascospores consistently hyaline 11
Ascospores at least partly pigmented 20

11(10) Ascospores aseptate 12
Ascospores septate 14

12(11) Apothecia completely immersed, disc brownish with black dots; ascospores (9.5–)10.5–14(–16.5) × (2.5–)3–3.5 µm; on *Dibaeis* . . . . . **Rhymbocarpus ericetorum**
Apothecia more or less superficial, disc blackish; ascospores shorter and wider 13

13(12) Apothecia urceolate to cupulate, with prominent margin; ascospores (5–)6.5–8.5(–10.5) × (4–)4.5–5.5(–7) µm, uniseriate in the ascus; on *Dibaeis* and a sterile microsquamulose lichen . . . . . **Llimoniella chilensis**
Apothecia convex, immarginate; ascospores 7–12 × 5–6 µm, irregularly arranged in the ascus; on *Dibaeis* . . . . . **Micarea inquinans**

14(11) Apothecia pale orange to orange-white, urceolate or cupulate; ascospores 1-septate, narrowly obovate, (14–)15.5–19(–20.5) × (5–)5.5–7(–7.5) µm; on *Dibaeis* . . . . . **Cryptodiscus ihlenii**
Apothecia black, not cupulate; at least some ascospores with more than one septum 15

15(14) Ascospores rod-shaped, 1–3-septate, 10–15 × 3 µm; on *Baeomyces* and *Dibaeis* . . . . . ‘**Celidium ericetorum** Rehm apud Rabh.’ *sensu* Keissler (1930: 97)
Ascospores cylindrical to acicular, 3–16-septate, 15–110 × 2–5 µm 16

16(15) Not lichenized; on *Dibaeis* . . . . . **Arthrorhaphis muddii**
Producing lichenized thallus 17

17(16) Lichenized thallus greyish, rather indistinct; on *Baeomyces* . . . . . **Arthrorhaphis grisea**
Lichenized thallus greenish yellow, distinct 18

18(17) Ascospores 3(–5)-septate; on *Baeomyces* . . . . . **Arthrorhaphis vacillans**
Ascospores 4–16-septate 19

19(18) Lichenized thallus of strongly convex areoles, not sorediate; ascospores mainly 25–45 µm long; on *Baeomyces* . . . . . **Arthrorhaphis alpina**
Lichenized thallus of flat to slightly convex areoles, sorediate; ascospores mainly 55–80 µm long; on *Baeomyces* . . . . . **Arthrorhaphis citrinella**

20(10) Ascospores hyaline to occasionally pigmented 21
Ascospores consistently pigmented (brown) 23

21(20) Apothecia eventually urceolate; ascospores 1-septate, (12.5–)13.5–15.5(–17.5) × 5–6(–6.5) µm; on *Icmadophila* . . . . . **Buelliella ohmurae**
Apothecia not urceolate; ascospores various 22

22(21) Apothecia convex, immarginate; hymenium I+ red; ascospores 1-septate, clavate, 12–13.5 × 4.5–5.5 µm; on *Pseudobaeomyces* . . . . . **Arthonia** sp. (characterized in the present paper)
Apothecia discoid, usually marginate; hymenium I+ blue; ascospores (0–)1(–3)-septate, mainly ellipsoid, (9.5–)10.5–13(–15.5) × (4–)4.5–6(–6.5) µm; on *Dibaeis* and *Pseudobaeomyces* . . . . . **Catillaria japonica**

23(20) Producing yellow to yellowish green lichenized thallus; apothecia convex, immarginate; ascospores 1-septate, (10–)11.5–14(–18) × (4–)5.5–7.5(–9) µm; on *Baeomyces* . . . . . **Epilichen scabrosus**
Lichenized thallus absent; apothecia discoid, marginate; ascospores 1- or more septate 24

24(23) Ascospores 1–3-septate, (6.5–)8.5–11(–13) × (3.5–)4–5(–6) µm; on various host genera . . . . . **Sclerococcum attendendum**
Ascospores 1-septate 25

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25(24) Epihymenium reddish brown; ascospores (6–)7–9(–10.5) × (3.5–)4–4.5(–5) µm; on *Baeomyces* . . . . . **Sclerococcum athallinum**
Epihymenium brown; ascospores (7–)10.5–14.5(–17) × (5–)6–9(–10) µm; on *Baeomyces* . . . . . **Epilichen glauconigellus**

26(9) Ascomata densely setose when young; ascospores hyaline to pale brown, 1-septate, 8–10 × 3.5–4 µm; on *Baeomyces* . . . . . **Capronia baeomycetis**
Ascomata without setae; ascospores various 27

27(26) Exciple greenish above, hyaline below; ascospores hyaline, 1-septate, 12–15(–16) × 4–5(–6) µm; on *Baeomyces* . . . . . **Cercidospora parva**
Exciple brown; ascospores various 28

28(27) Ostiolar region with blue-green flecks; asci 4-spored; ascospores brown, sometimes with paler end cells, 2–4-septate, (17.5–)21–26.5(–31) × (7–)8–9.5 µm; on various host genera . . . . . **Pyrenidium actinellum** s. lat.
Ostiolar region without blue-green flecks; asci 8-spored; ascospores various 29

29(28) Ascospores submuriform to muriform, brown, (14–)15–24.5(–32) × (6.5–)8–12(–15) µm; on various host genera . . . . . **Merismatium nigritellum**
Ascospores trans-septate, mostly or consistently hyaline 30

30(29) Ascospores (6.5–)8–10.5(–13) × (2.5–)3–4(–5) µm, hyaline, 1-septate; on *Phyllobaeis* . . . . . **Stigmidium phyllobaeidis**
Ascospores larger, hyaline to brown when overmature 31

31(30) Ascospores (11–)12–14.5(–16.5) × (3.5–)4.5–5.5(–6) µm, 1-septate; on *Baeomyces* . . . . . **Sphaerellothecium coniodes**
Ascospores (15–)16.5–19(–21) × 5–6.5(–7) µm, 1(–3)-septate; on *Icmadophila* . . . . . **Sphaerellothecium icmadophilae**

Discussion

The present study of lichenicolous fungi on baeomycetoid lichens and *Icmadophila*, coupled with recent revisions of these fungi growing on *Thamnolia* (*Icmadophilaceae*; Zhurbenko 2012) and *Siphula* (*Icmadophilaceae*; Motiejūnaitė *et al.* 2019), gives a fairly complete picture of the diversity of lichenicolous fungi growing on members of the *Baeomycetaceae* (12 species) and *Icmadophilaceae* (53 species) (Table 1). These fungi are known to grow on species of three of the five genera of *Baeomycetaceae* and on five of the eight genera of *Icmadophilaceae*. The ratio of the number of parasite species to the number of host species is 0.6 for *Baeomycetaceae* and 1.0 for *Icmadophilaceae*; at the generic

Table 1. Number of species of lichenicolous fungi and lichens growing on genera of the *Baeomycetaceae* and *Icmadophilaceae* (*sensu* Lücking *et al.* 2016). Numbers in parentheses indicate the number of species known to occur only on this genus. Based on data from Etayo (2010), Zhurbenko (2010*b*, 2012), Diederich *et al.* (2018*a*), Motiejūnaitė *et al.* (2019), Zhurbenko *et al.* (2019) and the present paper. Total counts for the 'family as a whole' may not reflect numbers in the columns as different species of lichenicolous fungi may occur on more than one host genus.

Host family	Host genus	No. of species	No. of lichenicolous fungi	No. of lichenicolous lichens
Baeomycetaceae	*Ainoa*	3	0	0
	Anamylopsora	1	1(1)	0
	Baeomyces	9	10(4)	6(6)
	Parainoa	1	0	0
	Phyllobaeis	5	1(1)	0
	family as a whole	19	12(6)	6(6)
Icmadophilaceae	*Chirleja*	1	0	0
	Dibaeis	13	10(6)	0
	Endocena	1	0	0
	Icmadophila	8	7(3)	0
	Pseudobaeomyces	1	2(1)	0
	Siphula	26	11(10)	0
	Siphulella	1	0	0
	Thamnolia	4	25(20)	0
	family as a whole	55	53(41)	0

https://doi.org/10.1017/S002428292000047X Published online by Cambridge University Press

level it ranges from 6.3 for *Thamnolia* to 0.2 for *Phyllobaeis*. In total, 62 species of lichenicolous fungi from 40 genera were recorded on lichens of these families, of which three species ('*Celidium ericetorum* Rehm apud Rabh.', *Pyrenidium actinellum* s. lat. and *Thelocarpon lichenicola*) and eight genera (*Capronia* Sacc., *Cercidospora* Körb., *Polycoccum* Körb., *Pyrenidium* Nyl., *Sclerococcum*, *Sphaerellothecium*, *Stigmidium* and *Thelocarpon* Nyl.) colonize hosts from both families. The proportion of parasite species specific to one host genus varies from 0.4 (for *Icmadophila*) to 1.0 (for *Anamylopsora* and *Phyllobaeis*). The largest numbers of associated lichenicolous fungi species are known for *Thamnolia* (25), *Siphula* (11) and *Baeomyces* (10). These numbers are relatively small, compared to those for the most 'hospitable' lichen genera, such as *Cladonia*, supporting no less than 130–140 species (Zhurbenko & Pino-Bodas 2017). Lichenicolous lichens occur within these families only on species of *Baeomyces*.

Acknowledgements. The research of MPZ was carried out within the framework of the research project of the V. L. Komarov Botanical Institute of the Russian Academy of Sciences 'Biodiversity, ecology and structural and functional features of fungi and fungus-like protists' (AAAA-A19-119020890079-6) using the equipment of its Core Facility Center 'Cell and Molecular Technologies in Plant Science'; his visit to TNS in 2017 was supported by a JSPS Invitation Fellowship for Research in Japan (no. S16173). We are indebted to A. Flakus and J. Etayo for the provision of specimens and to all staff of the Herbario Nacional de Bolivia, Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, for their generous cooperation, and to SERNAP (http://sernap.gob.bo), and all protected areas staff, for providing permits for scientific studies, as well as for their assistance during fieldwork, which resulted in the description of *Stigmidium phyllobaeidis*. Paul Diederich provided valuable remarks on the manuscript. Rod Seppelt kindly revised the English.

Author ORCIDs. Milhail P. Zhurbenko, 0000-0002-9839-4698; Yoshihito Ohmura, 0000-0003-2557-2761.

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