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Orbilia beltraniae, a new succulenticolous species from the Canary Islands

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Abstract

Orbilia beltraniae is a new succulenticolous species from the Canary Islands associated with *Euphorbia* scrubs. Phylogenetic analyses based on rDNA sequences of ITS and partial LSU were conducted to determine the relationships of the new species to others in the genus. Macro- and micromorphological, and ecology data are provided, as well as discussion in respect to closely related species. *Orbilia beltraniae* belongs to a strongly supported clade that includes non-nematophagous species of section *Arthrobotrys*, and its closest relatives are the European species *O. rectispora* and *O. cotoneastri*.

Key words

Ascomycota, ITS, LSU, morphology, *Orbiliaceae*, phylogeny, taxonomy

Introduction

Orbilia is by far the most specious genus of the *Orbiliomycetes* (Baral 2015, Baral in Jaklitsch et al. 2016). In the past its diversity was overlooked, mainly for the lack of exploration in drylands, as well as due to the morpho-taxonomical methods used (Baral 1992, 2015). Species occur in most ecosystems (from humid to arid, from subarctic to tropical) and most types of substrate (wood and bark, leaves, dung) and exposure (xeric, hygric, aquatic). In a monograph of *Orbiliomycetes*, more than 400 species are recognized in the genus (Baral 2015, Baral et al. in prep.).

Investigations on desiccation-tolerant fungi in their natural habitats are rare, although drylands occur on every continent and cover approximately 40% of the world's land area (UN 2011). Usually, such dry ecosystems have a low number of species, but a high amount of endemism (Lacoste and Salanon 1981, UN 2011, Davies et al. 2012). The studies done by E. Beltrán-Tejera and collaborators in drylands of Macaronesia have increased the knowledge of several groups, for example: (1) Basidiomycota with two new species and 23 new records, (2) Ascomycota with four new species and 10 new reports, and (3) Myxomycota with four new species and three new records (Beltrán-Tejera and Rodríguez-Armas 1999, Lado et al. 1999, Mosquera et al. 2000a, 2000b, 2003, Lado et al. 2007, Telleria et al. 2008, Beltrán-Tejera et al. 2010, Telleria et al. 2012, Quijada et al. 2012, Beltrán-Tejera et al. 2013, Quijada et al. 2014, 2015a, 2015b, 2015c).

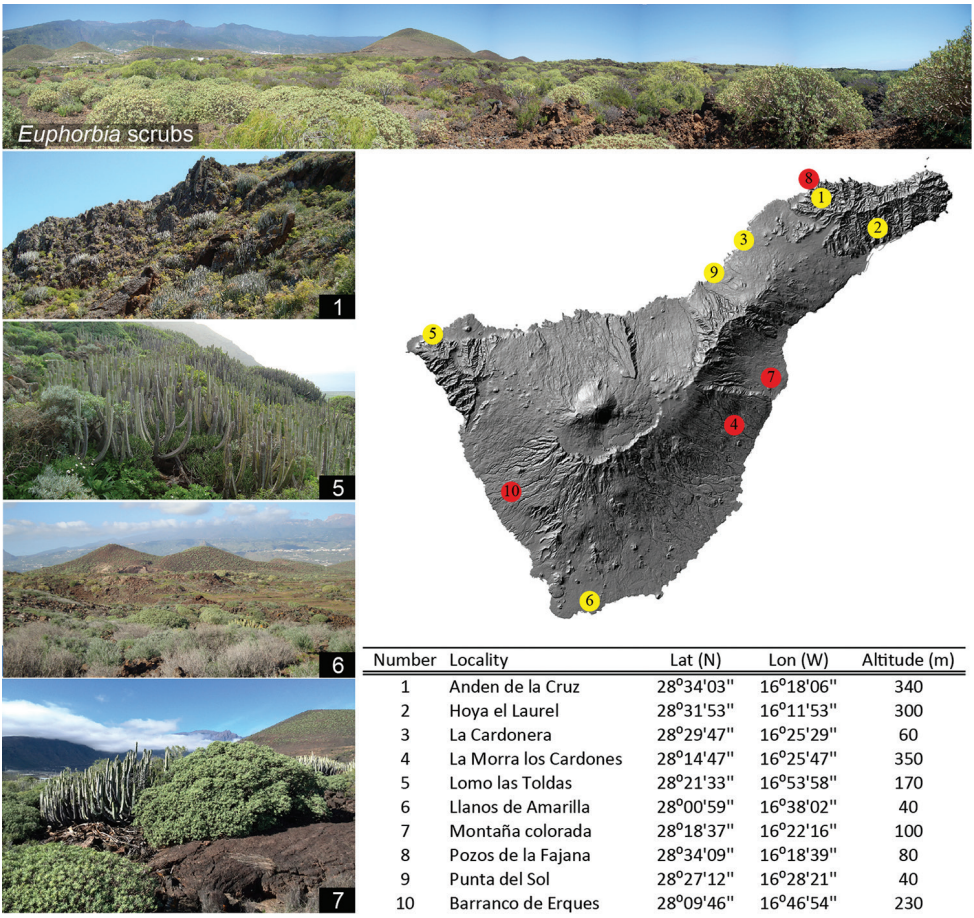
Euphorbia scrubs represents the native vegetation of drylands at lower elevations in the Canary Islands. These scrub lands are mainly composed of succulent plants (*Aeonium* Webb & Berthel, *Ceropegia* L., *Euphorbia* L., and *Kleinia* Mill) accompanied by other woody plants (*Artemisia* L., *Periploca* L., *Rubia* L.), with a high number of endemic species (>50%) (Del Arco et al. 2010). Since 2012, three new succulenticolous species of *Orbilia* have been published from this ecosystem and this type of substrate: *Orbilia asomatica* Baral, Quijada & Beltrán-Tej., *O. pisciformis* Baral, Quijada & Beltrán-Tej. and *O. succulenticola* Quijada, Baral & Beltrán- Tej. (Quijada et al. 2012, 2014). The aim of this investigation is to describe a new species of *Orbilia* that develops on the succulent remains of *Euphorbia canariensis*.

Methods

Specimens were collected in Tenerife (Canary Islands, Spain) during 2008–2014. Ten localities of *Euphorbia* scrubs were monitored in both the rainy season (September to May) and dry season (June to August), along an altitudinal transect (40–350 m) including both northern and southern slopes (Fig. 1). The sampling was restricted to the largest branches lying on the ground. Species of the following native succulent genera were sampled: *Aeonium*, *Ceropegia*, *Euphorbia*, and *Kleinia*.

Macro- and microscopic studies

Observations were made with a Motic stereomicroscope SMZ140, and with a Motic B1 light microscope. Microphotographs were taken with an USB Moticam 2500 camera and processed with the software Motic images Plus 2.0. Specimens were studied in both the living and dead state. Collection data and measurements followed methods of Quijada et al. (2012, 2014). Cell walls were sometimes contrasted with Congo Red



Number	Locality	Lat (N)	Lon (W)	Altitude (m)
1	Anden de la Cruz	28°34'03"	16°18'06"	340
2	Hoya el Laurel	28°31'53"	16°11'53"	300
3	La Cardonera	28°29'47"	16°25'29"	60
4	La Morra los Cardones	28°14'47"	16°25'47"	350
5	Lomo las Toldas	28°21'33"	16°53'58"	170
6	Llanos de Amarilla	28°00'59"	16°38'02"	40
7	Montaña colorada	28°18'37"	16°22'16"	100
8	Pozos de la Fajana	28°34'09"	16°18'39"	80
9	Punta del Sol	28°27'12"	16°28'21"	40
10	Barranco de Erques	28°09'46"	16°46'54"	230

Figure 1. Monitored localities in *Euphorbia* scrubs: number of locality, place name for locality according to IDECanarias visor 3.0 (http://visor.grafcan.es/visorweb/), latitude, longitude, and altitude. In yellow the localities where *Orbilia beltraniae* was found.

(CR). Potassium hydroxide 5% (KOH) as mountant was used to measure dead cells for comparison with old herbarium specimens of related species. The following abbreviations were adopted (Baral 1992): * = living state; † = dead state; *† = living and dead state (no difference noted); SCBs = KOH-soluble cytoplasmic bodies; SBs = spore bodies; VBs = refractive vacuolar bodies; LBs = lipid bodies. Colour coding refers to Anonymous (1976).

DNA extraction, PCR amplification, and DNA sequencing

For complete details about DNA extraction, PCR amplification, PCR purification, and cycle sequencing see Baral et al. (2017b). Sequences were obtained of the complete

Table 1. Specimens used in this study with voucher information and GenBank accession numbers. *Orbilia beltraniae* sequences are indicated in bold. Species with asterisk have at present unpublished names (Baral et al. 2017a).

Species	Collection	Section	GenBank number
Orbilia dryadum	H.B. 6876a	*Orbilia*	KT215281
Orbilia leucostigma	H.B. 6810c	*Orbilia*	KT215282
Orbilia polyspora	H.B. 7243b	*Ovoideae*	KT215276
*Orbilia sphaerospora**	H.B. 9129	*Ovoideae*	KT222429
*Orbilia ovoidea**	H.B. 6489a	*Ovoideae*	KT215275
*Orbilia canadensis**	H.B. 6826	*Ovoideae*	KT215277
Orbilia asomatica	TFC Mic. 21258	*Arthrobotrys*	KT222399
Orbilia auricolor	H.B. 6664	*Arthrobotrys*	KT215294
Orbilia beltraniae	**TFC Mic. 24363**	***Arthrobotrys***	**KT222405**
Orbilia beltraniae	**TFC Mic. 23890**	***Arthrobotrys***	**KT222406**
Orbilia cardui	H.B. 9891	*Arthrobotrys*	KT222402
Orbilia cotoneastri	CBS 116281	*Arthrobotrys*	KT215288
Orbilia quercus	HMAS 88783	*Arthrobotrys*	AY804213/DQ656669
Orbilia rectispora	H.B. 7142	*Arthrobotrys*	KT215289
*Orbilia xinjiangensis**	H.B. 9646	*Arthrobotrys*	KT222435
*Orbilia mammillata**	H.B. 7165c	*Arthrobotrys*	KT215290
Gamsylella gephyropaga	ATCC 96677	*Arthrobotrys*	EF445990
Arthrobotrys oligospora	ATCC 96709	*Arthrobotrys*	EF445989
Drechslerella brochopaga	ATCC 96710	*Arthrobotrys*	EF445987
Drechslerella doedycoides	ATCC 96778	*Arthrobotrys*	EF445992
Orbilia aristata	H.B. 6713	*Hemiorbilia*	KT596782
*Orbilia clavuliformis**	H.B. 6714	*Hemiorbilia*	KT215271
*Orbilia subaristata**	H.B. 6685a	*Hemiorbilia*	KT215270
Orbilia flavida	H.B. 6716	*Lentiformes*	KT215228
*Orbilia subocellata**	H.B. 6474	*Lentiformes*	KT215227
*Orbilia cucumispora**	H.B. 6762a	*Lentiformes*	KT215231
Orbilia gambelii	H.B. 6466	*Habrostictis*	KT215249
*Orbilia subvitalbae**	H.B. 6504a	*Habrostictis*	KT215250
*Orbilia microserpens**	H.B. 6519a	*Habrostictis*	KT215251
*Orbilia cisti**	H.B. 6500	*Habrostictis*	KT215251
Orbilia aurantiorubra	H.B. 6815a	*Aurantiorubrae*	KF741595
Orbilia comma	H.B. 6639b	*Aurantiorubrae*	KT215258
Orbilia phragmotricha	H.B. 7535a	*Aurantiorubrae*	KT215259
*Orbilia denticulata**	H.B. 6725	*Aurantiorubrae*	KT215256
*Orbilia brachychitonis**	H.B. 7578a	*Aurantiorubrae*	KT215257
Orbilia sinensis-1	YMF1.01843	*Helicoon*	DQ480727/DQ480728
Orbilia sinensis-2	HMAS 96782	*Helicoon*	DQ656642/DQ656676
Orbilia sarraziniana	H.B. 7235	*Helicoon*	KM199780
*Orbilia rosea**	H.B. 6756a	*Helicoon*	KM199779
*Orbilia fusiformis**	YMF1.01848	*Helicoon*	EF026114/EF026115
Hyalorbilia polypori	H.B. 7557a	outgroup	KT215223

internal transcribed spacer region (ITS, ~500 bp), comprising ITS1, the 5.8S ribosomal subunit, and ITS2, and the partial nuclear large subunit (LSU, D1-D2 region, ~630 bp). All sequences are deposited in GenBank (Table 1).

Phylogenetic analyses

The data matrix for alignment was constructed to explore the phylogenetic relationships. 42 sequences were included, representing eight sections (*Orbilia*, *Arthrobotrys*, *Ovoideae*, *Habrostictis*, *Hemiorbilia*, *Lentiformes*, *Aurantiorubrae*, *Helicoon*) according to Baral (2015; Baral et al. 2017a). The sequences were aligned using the L-INS-i algorithm for ITS region and the G-INS-i algorithm for LSU region with MAFFT v7.017 (Katoh et al. 2002). The program GBLOCKS v. 0.91b was used to identify and eliminate ambiguously aligned regions (Castresana 2000), using the same relaxed setting as in Quijada et al. (2014). The final alignment contained 943 bp (83% of the first alignment length). The analyses were performed using the optimal model of nucleotide substitution identified with JMODELTEST (Posada 2008; http://darwin.uvigo.es), based on the Akaike information criterion (Akaike 1974). Maximum Likelihood (ML) and Bayesian Inference (BI) analysis were performed using Geneious (v. 6.1.7). Branch support in ML analyses was inferred from 1000 rounds of bootstrap. For more details about phylogenetic methods see Quijada et al. (2014). Phylogenetic trees were drawn with FigTree 1.4 (available at http://tree.bio.ed.ac.uk/sofware/figtree/), and artwork was prepared in Adobe Illustrator CS5.

Results

Phylogenetic results

The alignment consisted of 943 bp characters, of which 322 were parsimony-informative, 415 were variable, and 528 were constant. Only the Bayesian consensus tree is shown (Fig. 2) because overall topologies of the ML and BI analyses were identical.

Each section constituted a supported clade except for section *Orbilia*, with only two species in this analysis (*O. leucostigma* and *O. dryadum*, 71.8% MLBS, 0.94 BIPP). The two sequences of *O. beltraniae* are completely identical in their overlapping part that includes also LSU (D1-D4) and a short part of SSU. This section is divided in several supported clades. *Orbilia beltraniae* clusters with five selected species (*Orbilia xinjiangensis*, *O. cotoneastri*, *O. rectispora*, *O. asomatica*, *O. cardui*) in one supported clade (clade I, 89.3% MLBS, 0.99 BIPP). The other four clades (II–V) are represented by groups of one to three selected species. Clade II includes two species of *Drechslerella* (99.9% MLBS, 1 BIPP), clade III two species of *Arthrobotrys* (100% MLBS, 1 BIPP), clade IV two species of *Dactylellina* with low support (47.6 MLBS, 0.74 BIPP), and clade V with one species of *Gamsylella*.

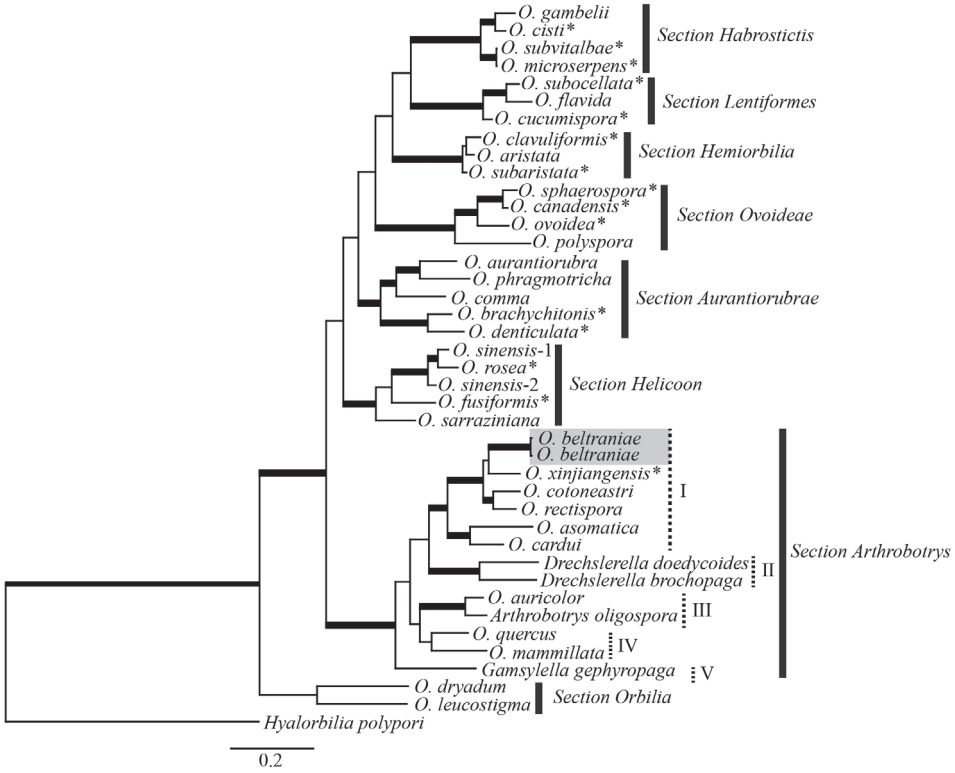


Figure 2. Bayesian 50% majority rule consensus tree based on a concatenated alignment of ITS and LSU sequences of 42 strains of *Orbiliaceae* (see Table 1). Bold branches were supported by ML bootstrap values ≥75% and BI PP≥0.95. Subgroups within section *Arthrobotrys* have been recognised by other authors in five different genera according to their asexual states and trapping devices: **I** *Dactylella* **II** *Drechslerella* **III** *Arthrobotrys* **IV** *Dactylellina* **V** *Gamsylella*. * = name at present not validly published (Baral et al. 2017a).

Taxonomy

Orbilia beltraniae **Quijada, Baral & G. Marson, sp. nov.**
Mycobank: MB813971
Fig. 3

Type. SPAIN. Canary Islands: Tenerife, Tacoronte, La Cardonera, 28°29'47"N, 16°25'29"W, 60 m alt., on detached branch of *Euphorbia canariensis* lying on the ground, 30 Oct 2013, L. Quijada (holotype: TFC Mic. 24363, isotype TFC Mic. 24359).

Diagnosis. *Similis Orbiliae cotoneastri sed ascosporae longiores, paraphyses ad apicem leniter vel modice lanceolato-lageniformes. Habitat ad ramos* Euphorbiae canariensis *in zona subtropica (semi-)arida Macaronesiae.*

Etymology. The specific epithet refers to Esperanza Beltrán-Tejera in recognition of her many contributions to the development of Canarian mycology, of her work in education and of our friendship.

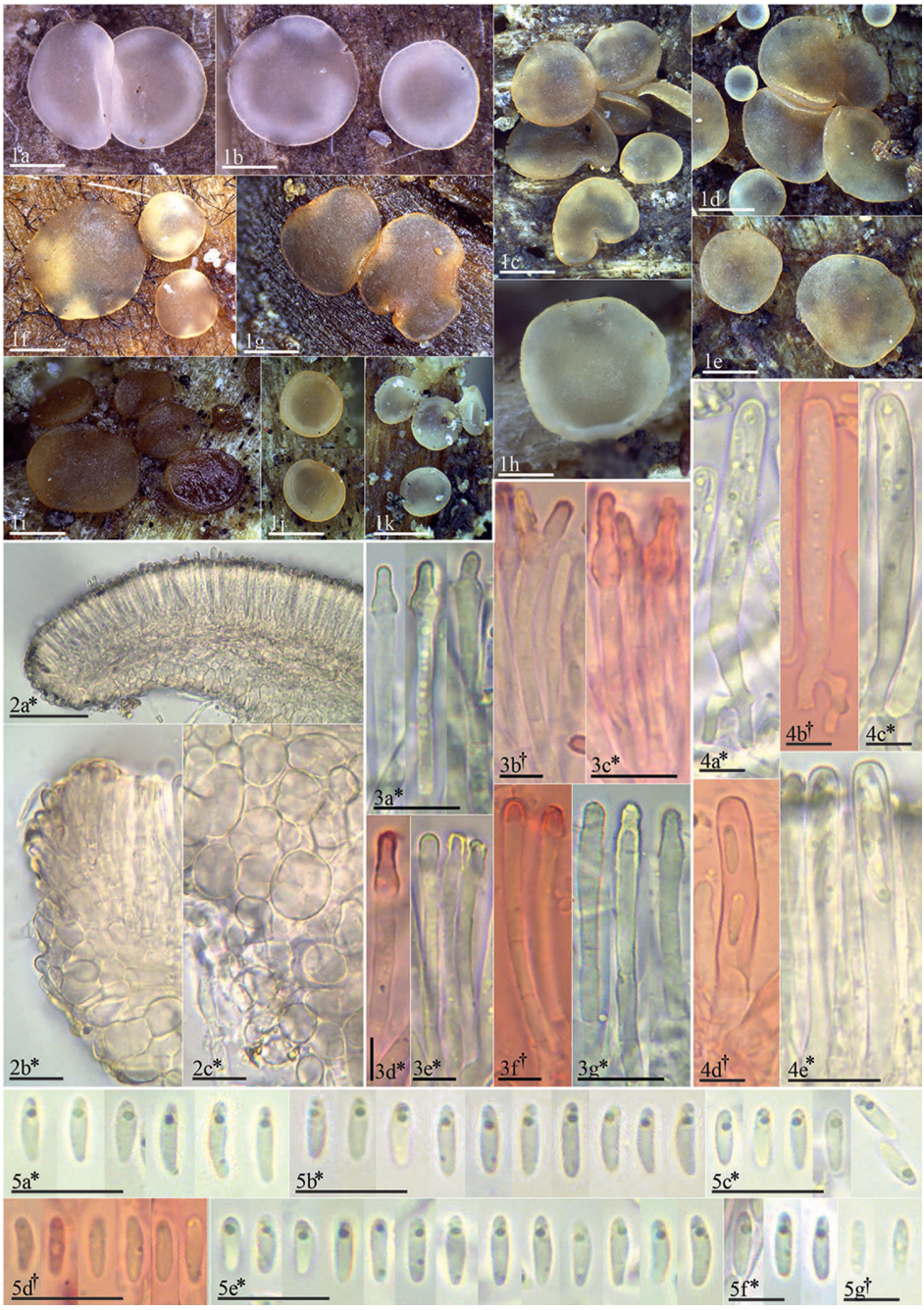


Figure 3. Morphological features of *Orbilia beltraniae*. **1** Apothecia rehydrated after 1–2 weeks **2** Excipular tissues in median section **3** Paraphyses **4** Asci **5** Ascospores. Scale bars: 500 µm= **1a–k**; 50 µm= **2a**; 10 µm= **2b–c, 3a, c, g, 4e, 5a–e**; 5 µm= **3b, d–f, 4a–d, 5f**; Mounted in: CR= **3b–d, 4b, d, 5d**; H_2O= **2a–c, 3a, e–g, 4a, c, e, 5a–c, e–g**. Photos: TFC Mic. 23771 = **1i–k, 3b–c, 4b, 5a**; TFC Mic. 23836 = **1h, 2c, 3d–e, 5b**; TFC Mic. 23890 = **1d–e, 4a, 5f**; TFC Mic. 23902 = **1f–g, 3a, 4c**; TFC Mic. 24231 = **2a, 3g, 5c, g**; TFC Mic. 24363 =**1c, 2b, 3f, 4d–e, 5d–e**; TFC Mic. 24449 = **1a–b**.

Description. *Apothecia* moist 0.4–1.2(1.5) mm diam, 0.1–0.2 mm thick (receptacle 0.06–0.07 mm), pale white (231. p White) to medium orange yellow (71. OY), rarely medium yellow brown (77. m y Br), medium translucent, round to somewhat undulating, gregarious in small groups; disc flat, margin thin, ± smooth, not protruding, sessile on a broad base, superficial. *Asci* *(32)38–40(46) × (3)3.5–4.5 µm, †(27.5)33–35(43) × (2.5)3–3.5 µm, 8-spored, 4–6 lower spores inverted, pars sporifera *14–20 µm; apex strongly truncate (not indented, not inflated), thin-walled; base with short to medium long stalk, h- or H-shaped. *Ascospores* *(4.5)5.5–6(7) × (1.2)1.4–1.6(2) µm, †(4)4.5–5 × 1–1.5 µm, cylindrical to slightly fusoid-clavate, with rounded to obtuse ends, straight or slightly curved, only slightly (rarely medium) tapered below; *SBs* *(1)1.5–2 × 0.5–1 µm, globose, often ± eccentrical, sometimes with distinct filum. *Paraphyses* uninflated to often slightly to medium lanceolate-lageniform with rounded tip, terminal cell *(13.5)17.5–19.5(25) × 2–3 µm, 3–5 µm protruding beyond living asci, lower cells *(4.5)7–9.5(10.5) × 1.5–2.5 µm, unbranched at upper septum, rarely with a bifurcate apex. *Medullary excipulum* 20–45 µm thick, of dense *textura intricata* with inflated cells, sharply delimited. *Ectal excipulum* of thin-walled *t. globulosa-angularis*, at base 40–105 µm thick, cells *(7.5)11–13(18) × (4.5)8–9.5(13) µm, at margin 10–28 µm thick, oriented at a 40–80° angle to the surface, marginal cortical cells *(5.5)7.5–8.5(12.5) × (2.5)3.5–4.5(7) µm, not forming distinct cell rows; glassy processes absent. *Anchoring hyphae* rather sparse, *1.5–3.5 µm diam, wall 0.2 µm thick. *SCBs* only present in paraphyses, globose, numerous in each terminal cell, *VBs* absent. *Exudate* forming a thin and firmly attached layer over paraphyses, up 1 µm thick on marginal cortical cells. Asexual state unknown.

Distribution and ecology. *Orbilia beltraniae* is so far only known from Tenerife island (Canarian archipelago, Macaronesia).

The species has been found between 40–340 m alt., from the coast to lowland elevations, on the northern and southern slopes where *Euphorbia* scrubs develop. All specimens have to date been collected on *Euphorbia canariensis*, so it seems that the species is host specific, growing during the rainy period between autumn and spring on succulent wood of detached, dead branches lying on the ground. Its desiccation tolerance was not thoroughly explored, but it can be said that its mature asci can survive at least one or two weeks in the herbarium. Although no apothecia of *O. beltraniae* were found in summer, several specimens were found to be fully alive during dry periods without rain in winter and spring, which permits us to conclude that the apothecia tolerate desiccation and probably survive over the summer to continue growth in autumn.

Other specimens examined. *Orbilia beltraniae* (all on detached branches of *Euphorbia canariensis* lying on the ground). SPAIN. Canary Island: Tenerife, Buena Vista del Norte, Lomo las Toldas, 28°21'33"N, 16°53'58"W, 170 m alt., 27 Dec 2012, L. Quijada (TFC Mic. 23836); La Laguna, Andén de la Cruz, 28°34'03"N, 16°18'06"W, 340 m alt., 20 May 2013, L. Quijada (TFC Mic. 24231); 29 Dec 2013, L. Quijada (TFC Mic. 24449); La Matanza de Acentejo, Punta del Sol, 28°27'12"N, 16°28'21"W, 40 m alt., 2 Mar 2013, L. Quijada (TFC Mic. 23890); S/Cruz de Tenerife, Hoya el Laurel, 28°31'53"N, 16°11'53"W, 300 m alt., 5 Mar 2013, L. Quijada (TFC Mic.

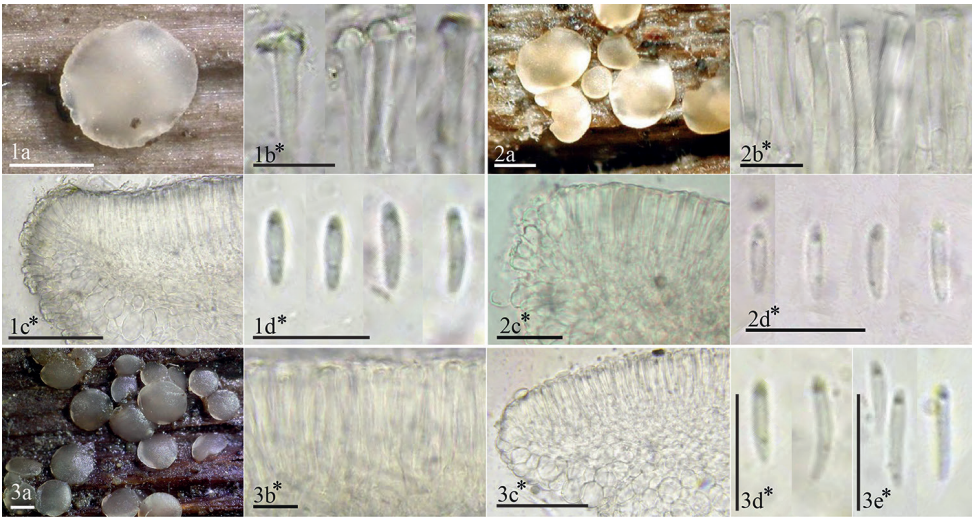


Figure 4. Morphological features of species related to *Orbilia beltraniae*. **1** *Orbilia cardui* **2** *Orbilia cotoneastri* **3** *Orbilia rectispora*. **a** Fresh apothecia **b** Paraphyses **c** Excipular tissues in median section **d–e**. Ascospores. Scale bars: 500 µm= **1a, 2a, 3a**; 50 µm= **1c, 3b**; 10 µm= **1b, d, 2b–d, 3c–e**. All mounted in H_2O. Photos: H.B. 7241a = **2a**; H.B. 9549 = **3b, d**; H.B. 9645b = **2b, d**; H.B. 9891 = **1a, c–d**; H.B. 9901 = **1b**; H.B. 9962 = **3a, c, e**; J.P.P. 28122 = **2c**.

23902); San Miguel de Abona, Llanos de Amarilla, 28°00'59"N, 16°38'02"W, 40 m alt., 16 Dec 2012, L. Quijada (TFC Mic. 23771).

Orbilia cardui. EUROPE. Germany: Sachsen, 6 km NNE of Chemnitz, 1 km E of Glösa, Indianerteich, 50°53'10"N; 12°57'23"E, 330 m alt., on stem of *Angelica sylvestris*, 15 May 2014, B. Mühler (H.B. 9891); Luxembourg: Esch-sur-Alzette, 2 km NNE of Dudelange, 1.5 km S of Bettembourg, Triage, 49°30'15"N; 06°05'50"E, 280 m alt., on herbaceous stems of undetermined dicotyledoneous, 25 Jul 2014, G. Marson (H.B. 9901).

Orbilia cotoneastri. EUROPE. France: Bretagne, Morbihan, 12 km S of Auray, 1.6 km SW of Locmariaquer, Breneguy, 47°33'35"N; 02°57'42"W, 5 m alt., on wood of branch of *Ulex europaeus*, 3 Nov 2002, J.P. Priou (H.B. 7241a); 5.3 km S of La Gacilly, 2 km N of St.- Vincent-sur-Oust, La Provostaie, 47°43'04"N; 02°08'50"W, 5 m alt., on stems of *Fallopia sachalinensis*, 3 Jun 2008, J.P. Priou (J.P.P. 28122); Galicia: La Coruña, 18 km SE of Coruña, SE of Betanzos, N of Calle de Concepción Arenal, 43°16'34"N; 08°12'21"W, 40 m alt., on bark of branch of *Quercus robur*, 31 Dec 2011, B.A. Rodríguez (H.B. 9645b).

Orbilia rectispora. EUROPE. Germany: Mecklenburg-Vorpommern, 0.5 km SE of Rehna, Radegasttal, 53°46'30"N; 11°03'30"E, 20 m alt., on culms of *Sparganium erectum*, 11 Jul 2015, T. Richter (H.B. 9962); Great Britain: Yorkshire, South Yorkshire, 3.5 km S of Barnsley, 1.5 km SW of Worsbrough, Worsbrough Country Park, 53°31'15"N; 01°28'55"W, 70 m alt., on leaves of *Typha latifolia*, 20 May 2011, H.O. Baral (H.B. 9549).

Discussion

Section *Arthrobotrys* will be proposed in the monograph of *Orbiliomycetes* (Baral et al. in prep.) as a subgroup of *Orbilia* to accomodate species with narrowly sickle-shaped, rod-shaped, or ellipsoid ascospores, desiccation-tolerant or -sensitive apothecia, and asexual states that either form various types of organs for trapping nematodes or other invertebrates or do not form trapping devices in culture when nematodes are added. *Orbilia beltraniae* is phylogenetically close to *O. cotoneastri* and *O. rectispora*, which belong to the group of section *Arthrobotrys* in which trapping organs are not formed, and that are currently referred to the asexual state genus *Dactylella* Grove. *Orbilia cotoneastri* has ascospores and spore bodies very similar to those of *O. beltraniae*, but differ in paraphysis morphology, showing uninflated or rarely capitate-clavate apices; in *O. beltraniae* they are uninflated to medium lanceolate-lageniform with rounded tips. *Orbilia rectispora* has longer ascospores than *O. beltraniae* [up to 9.5(11) µm vs. up to 6.5(7) µm]. In addition, the three species have a very different ecology: *O. beltraniae* occurs on succulent substrates in semiarid places of the Canary Islands, *O. cotoneastri* occurs on wood, bark, and herbaceous stems in moist places of Europe, and *O. rectispora* occurs on leaves of monocots in wet places of Europe (Baral et al. in prep).

Orbilia cardui is phylogenetically more distantly related to the above species, but more similar to it in size of asci, ascospores, and spore bodies. Also here, the paraphyses shape distinguishes *O. beltraniae* from *O. cardui* which has slighty capitate paraphyses. *Orbilia cardui* has a wide ecological spectrum in Europe, growing in shady forests and open ruderal places or wetlands on wood, bark, herbaceous stems, and even on other fungi (Baral et al. in prep), whereas *O. beltraniae* is apparently restricted to wood of the Canarian endemic succulent *Euphorbia canariensis*.

Orbilia beltraniae is the fourth species so far found exclusively in the *Euphorbia* scrubs of the Canary Islands. Although it seems to be host specific on *Euphorbia canariensis*, the three previously described species (*Orbilia asomatica*, *O. pisciformis*, *O. succulenticola*) share this substrate but they also develop on other succulent species like *E. balsamifera*, *E. lamarckii*, and *E. atropurpurea* (Quijada et al. 2012, 2014, 2015c).

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Resolving the species of the lichen genus *Graphina* Müll. Arg. in China, with some new combinations

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Abstract

In the framework of continuing studies on the *Graphidaceae* in China, the status of all taxa traditionally assigned to the genus *Graphina* reported from China are resolved in the present paper. Five new combinations are made, namely *Diorygma isabellinum* (Zahlbr.) Z.F. Jia & Lücking, **comb. nov**., *Fissurina adscribens* (Nyl.) Z.F. Jia & Lücking, **comb. nov.**, *Graphis lecanactiformis* (Zahlbr.) Z.F. Jia & Lücking, **comb. nov.**, *Phaeographis haloniata* (Zahlbr.) Z.F. Jia & Lücking, **comb. nov.** and *Platygramme taiwanensis* (J.C. Wei) Z.F. Jia & Lucking, **comb. nov.** Five new synonymies were found: *Graphina olivascens* Zahlbr. (= *Fissurina adscribens*), *Graphina plumbicolor* Zahlbr. (= *Phaeographis haloniata*), *Graphina roridula* Zahlbr. and its variety *platypoda* Zahlbr. [= *Diorygma pachygraphum* (Nyl.) Kalb, Staiger & Elix], and *Graphina taiwanensis* f. *obscurata* J.C. Wei (= *Platygramme taiwanensis*).

Key words

Lichens, taxonomy, Graphidaceae, Ostropales, Lecanoromycetes, Ascomycota

Introduction

The lichen genus *Graphina* Müll. Arg. entailed an artificial concept of ascospore-based genera in *Graphidaceae* Dumort., including all graphidoid species with muriform, hyaline ascospores (Müller 1880). Based on phenotypic and molecular studies, a new classification of genera within the family was recently established (Staiger 2002; Rivas Plata et al. 2012). As a result, the genus *Graphina* was placed in synonymy with *Thalloloma* Trevis., based on the systematic affinities of its presumed type species, *Graphina*

anguina Müll. Arg. [= *Thalloloma anguinum* (Mont.) Trevis.] (Staiger 2002). However, *G. anguina* had not actually been included in the protologue of *Graphina*, and therefore a new lectotype had to be selected, namely *G. puiggarii* Müll. Arg., which makes *Graphina* a synonym of *Graphis* Ach. (Lücking et al. 2007). Following the current generic concept of *Graphidaceae* (*sensu* Staiger 2002), many species of *Graphina* belong in *Graphis* s. str., whereas others have been moved into other genera based on phylogeny, apothecial morphology and/or anatomy.

During our study of Chinese *Graphidaceae*, we attempted to resolve the status of all species reported with the genus name *Graphina* from China (Wei 1991; Aptroot and Seaward 1999; Aptroot and Sipman 2001, Aptroot and Sparrius 2003). We found that 33 species were reported, which are here presented in the form of an updated 'checklist' and transferred to the corresponding genera, namely *Carbacanthographis* Staiger & Kalb, *Diorygma* Eschw., *Fissurina* Fée, *Graphis* Adans., *Phaeographis* Müll. Arg., *Platygramme* Fée, *Platythecium* Staiger and *Thalloloma* Trevis.

Materials and methods

Type material cited here was either obtained on loan from the herbaria in H, PC, and W or studied in the cited herbaria. Because many of the names discussed here have already been treated by Kalb et al. (2004), Staiger (2002), Nakanishi et al. (2003) and Lücking et al. (2009), we do not provide full synonymies and type specimen citations unless the name has not previously been treated or the type specimen is particularly relevant to the discussion. A dissecting microscope (Olympus SZX12) and a light microscope (Olympus BX51 and Nikon Eclipse-55i) were used for the morphological and anatomical studies. Measurements and illustrations were taken from the manual cross sections of fruit bodies in water. The amyloidy of the ascospores was tested using Lugol's solution. The lichen substances were detected and identified by thin-layer chromatography (Culberson and Kristinsson 1970; Culberson 1972; White and James 1985). Newly proposed taxonomic names and combinations were deposited in MycoBank.

Taxonomy

List of the Chinese species previously reported under the name *Graphina* Müll.Arg.

Below, a list of all species reported under *Graphina* from China is provided. Following modern concepts of the *Graphidaceae* (Staiger 2002; Rivas Plata et al. 2012), the current name is indicated, accompanied by brief notes.

1. *Graphina acharii* (Fée) Müll. Arg.
Mém. Soc. Phys. Hist. Nat. Genève 29(8): 38, 1887.
≡ ***Graphis acharii*** Fée, Essai Crypt. Exot. (Paris): 39, 1825.

Following Lücking et al. (2009), this taxon belongs in *Graphis* as *G. acharii* Fée. It is a corticolous species reported from Hong Kong (Aptroot and Sipman 2001) and Taiwan (Aptroot and Sparrius 2003).

2. *Graphina adscribens* (Nyl.) Müll. Arg.

Hedwigia 31: 284, 1892.

≡ ***Fissurina adscribens*** (Nyl.) Z.F. Jia & Lücking, **comb. nov.** (see below).

This taxon belongs morphologically in *Fissurina* and the combination in that genus as *F. adscribens* (Nyl.) Z.F. Jia & Lücking is required (see below). It is a corticolous species reported from Hong Kong (Thrower 1988).

3. *Graphina alpestris* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 56, 1930.

≡ ***Graphis alpestris*** (Zahlbr.) Staiger, Biblthca Lichenol. 85: 205, 2002.

Following Staiger (2002), this taxon belongs in *Graphis* as *G. alpestris* (Zahlbr.) Staiger. It is a corticolous species reported from Yunnan (Zahlbruckner 1930, 1932; Wang et al. 2008; Jia and Wei 2016) and Hainan (Jia and Wei 2011, 2016).

4. *Graphina analoga* (Nyl.) Zahlbr.

Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. 83: 107, 1909.

≡ ***Graphis analoga*** Nyl., Ann. Sci. Nat., Bot., sér. 4, 11: 244, 1859.

Following Lücking et al. (2009), this taxon belongs in *Graphis* as *G. analoga* Nyl. It is a corticolous or sometimes saxicolous species reported from Hong Kong (Aptroot and Seaward 1999; Aptroot and Sipman 2001) and Taiwan (Aptroot and Sparrius 2003).

5. *Graphina cleistoblephara* (Nyl.) Zahlbr.

Cat. Lich. Univers. 2: 401, 1923.

≡ ***Graphis cleistoblephara*** Nyl., Ann. Sci. Nat., Bot., sér. 4, 20: 265, 1863.

Following Staiger (2002), this taxon belongs in *Graphis* as *G. cleistoblephara* Nyl. It is a corticolous species reported from Hainan (Jia and Wei 2011; Wei et al. 2013; Jia and Wei 2016), Yunnan (Jia and Wei 2011, 2016); Taiwan (type location, Zahlbruckner 1940; Lamb 1963; Wang and Lai 1973, 1976), Hong Kong (Thrower 1988), and mainland China (prov. not indicated: Hue 1891).

6. *Graphina colliculosa* (Mont.) Hale

Lich. Amer. Exs.: 156, 1976.

≡ ***Platythecium colliculosum*** (Mont.) Staiger, Biblthca Lichenol. 85: 380, 2002; *Sclerophyton colliculosum* Mont., Ann. Sci. Nat., Bot., sér. 3, 16: 61, 1851.

Following Staiger (2002), this taxon belongs in *Platythecium* as *P. colliculosum* (Mont.) Staiger. It is a corticolous species reported from Hong Kong (Thrower 1988; Aptroot and Sipman 2001) and Taiwan (Aptroot and Sparrius 2003). Material under this name reported by Thrower (1988: 94) from Hong Kong contains norstictic acid and has muriform ascospores, about 15 × 5 μm in size, with four transverse

and one or two longitudinal septa and belongs to *P. dimorphodes* (Nyl.) Staiger; the other material illustrated by the same author on page 95, with ascospores 25–35 µm long, could not be identified with certainty but may represent a species of another genus, e.g. *Diorygma*.

7. *Graphina erythrella* (Mont. & Bosch) Zahlbr.

Cat. Lich. Univers. 2: 405, 1923.

≡ ***Diorygma erythrellum*** (Mont. & Bosch) Kalb, Staiger & Elix, Symb. Bot. Upsal. 34(1): 150, 2004; *Ustalia erythrella* Mont. & Bosch, in Junghuhn, Pl. Jungh. 4: 478, 1855.

Following Kalb et al. (2004), this taxon belongs in *Diorygma* as *D. erythrellum* (Mont. & Bosch) Kalb, Staiger & Elix. It is a corticolous species reported from Taiwan (Aptroot and Sparrius 2003).

8. *Graphina filiformis* Zahlbr.

Feddes Repert. 31: 214, 1933.

= ***Graphis japonica*** (Müll. Arg.) A.W. Archer & Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 437 (2009).

Following Lücking et al. (2009), this name is a synonym of *Graphis japonica* (Müll. Arg.) A.W. Archer & Lücking. It is a corticolous species reported from Zhejiang (Jia and Wei 2016), Fujian (Jia and Wei 2011, 2016), Hainan (Jia and Wei 2011, 2016; Wei et al. 2013), Hong Kong (Jia and Wei 2016) and Taiwan (type location as *Graphina filiformis* Zahlbr., Zahlbruckner 1933, 1940; Wang and Lai 1973).

9. *Graphina fissofurcata* (Leight.) Müll. Arg.

Flora 65(24): 385, 1882.

= ***Graphis streblocarpa*** (Bél.) Nyl., Flora 49: 133, 1874.

Following Lücking et al. (2009), this name is a synonym of *Graphis streblocarpa* (Bél.) Nyl. It is a corticolous or rarely saxicolous species reported from Zhejiang (Wu and Qian 1989), Fujian (Jia and Wei 2011, 2016) and Hong Kong (Aptroot and Seaward 1999; Aptroot and Sipman 2001).

10. *Graphina galactoderma* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 57, 1930.

≡ ***Graphis galactoderma*** (Zahlbr.) Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 436 (2009)

Following Lücking et al. (2009), this taxon belongs in *Graphis* as *G. galactoderma* (Zahlbr.) Lücking. It is a corticolous species reported from Yunnan (type location, Zahlbruckner 1930, 1932) and Guizhou (Jia and Wei 2016).

11. *Graphina haloniata* Zahlbr.

Feddes Repert. 31: 216, 1933.

≡ ***Phaeographis haloniata*** (Zahlbr.) Z.F. Jia & Lücking, **comb. nov.** (see below).

The presence of brownish ascospores, an exposed, broad disc, and a slightly carbonized exciple shows that this taxon has to be transferred to *Phaeographis* (see below). It is a corticolous species reported from Taiwan (type location, Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973; Aptroot and Sparrius 2003).

12. *Graphina hiascens* (Fée) Müll. Arg.

Mém. Soc. Phys. Hist. nat. Genève 29(8): 42, 1887.

= ***Graphis hiascens*** (Fée) Nyl., Ann. Sci. Nat., Bot., sér. 4, 11: 226, 1859; *Opegrapha hiascens* Fée, Essai Crypt. Exot., Suppl. Révis. (Paris): 25, 1837.

Following Lücking et al. (2009), this taxon belongs in *Graphis* as *G. hiascens* (Fée) Nyl. It is a corticolous species reported from Hainan (Jia and Wei 2011, 2016), Hong Kong (Thrower 1988; Jia and Wei 2016) and Taiwan (Aptroot and Sparrius 2003).

13. *Graphina hologlauca* Zahlbr.

Cat. Lich. Univers. 2: 408, 1923.

= ***Diorygma hieroglyphicum*** (Pers.) Staiger & Kalb, in Kalb et al., Symb. Bot. Upsal. 34(1): 151, 2004.

Following Kalb et al. (2004), this taxon is a synonym of *Diorygma hieroglyphicum* (Pers.) Staiger & Kalb. It is a corticolous species reported from Fujian (Jia and Wei 2016), Hainan (Meng and Wei 2008; Wei et al. 2013; Jia and Wei 2016), Yunnan (Meng and Wei 2008; Jia and Wei 2016), Hong Kong (Thrower 1988) and Taiwan (Aptroot and Sparrius 2003). The material illustrated in Thrower (1988: 97) should be *Diorygma hololeucum* (Mont. & Bosch) Kalb, Staiger & Elix, not *D. hieroglyphicum*, because of its morphological characteristics and the presence of protocetraric acid.

14. *Graphina hunanensis* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 54, 1930.

≡ ***Graphis hunanensis*** (Zahlbr.) M. Nakan. & Kashiw., in Nakanishi, Kashiwadani & Moon, Bull. Natn. Sci. Mus., Tokyo, B 29(2): 87, 2003.

Following Nakanishi et al. (2003), this taxon belongs in *Graphis* as *G. hunanensis* (Zahlbr.) M. Nakan. & Kashiw. It is a saxicolous species reported from Hunan (type location, Zahlbruckner 1930, 1932).

15. *Graphina incrustans* (Fée) Müll. Arg.

Mém. Soc. Phys. Hist. nat. Genève 29(8): 47, 1887.

≡ ***Fissurina incrustans*** Fée, Essai Crypt. Exot. (Paris) : 60, 1825.

Following Staiger (2002), this taxon belongs in *Fissurina* as *F. incrustans* Fée. It is a corticolous species reported from Hong Kong (Thrower 1988; Aptroot and Seaward 1999; Aptroot and Sipman 2001).

16. *Graphina isabellina* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 58, 1930.

≡ ***Diorygma isabellinum*** (Zahlbr.) Z.F. Jia & Lücking, **comb. nov.** (see below).

This species has a *Diorygma*-like thallus and ascomata and large, muriform, hyaline ascospores 110–120 × 35–48 µm. It is similar to *Diorygma hieroglyphicum*, but the latter differs by its larger ascospores, 170–250 × 42–58 µm (Kalb et al. 2004). Hence, we transfer the species to *Diorygma* as *D. isabellinum* (Zahlbr.) Z.F. Jia & Lücking (see below). It is a corticolous species reported from Hunan (type location, Zahlbruckner 1930, 1932).

17. *Graphina japonica* var. *major* Zahlbr.

Feddes Repert. 31: 213, 1933.

= ***Graphis japonica*** (Müll. Arg.) A.W. Archer & Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 437, 2009.

Following Lücking et al. (2009), this taxon is a synonym of *Graphis japonica* (Müll. Arg.) A.W. Archer & Lücking. It is a corticolous species reported from Zhejiang (Jia and Wei 2016), Fujian (Jia and Wei 2011, 2016), Hainan (Jia and Wei 2011, 2016; Wei et al. 2013), Hong Kong (Jia and Wei 2016) and Taiwan (type location as *Graphina japonica* var. *major* Zahlbr., Zahlbruckner 1933, 1940; Wang and Lai 1973).

18. *Graphina lapidicola* (Fée) Müll. Arg.

Flora 68: 513, 1885.

≡ ***Graphis lapidicola*** Fée, Bull. Soc. Bot. Fr. 21: 28, 1874.

Following Lücking et al. (2009), this taxon belongs to *Graphis* as *G. lapidicola* Fée. As the epithet suggests, it is a mainly saxicolous or sometimes corticolous species reported from Hainan (Jia and Wei 2011, 2016; Wei et al. 2013) and Hong Kong (Thrower 1988).

19. *Graphina lecanactiformis* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 57, 1930.

≡ ***Graphis lecanactiformis*** (Zahlbr.) Z.F. Jia & Lücking, **comb. nov.** (see below).

This species has a laterally carbonized exciple and hyaline, muriform ascospores 37–45 × 15–18 µm (Zahlbruckner 1933). The remaining type material is badly developed, but suggests placement in *Graphis*. Hence, we transfer it to *Graphis* as *G. lecanactiformis* (Zahlbr.) Z.F. Jia & Lücking (see below). It is a corticolous species reported from Yunnan (type location, Zahlbruckner 1930, 1932).

20. *Graphina marcescens* (Fée) Müll. Arg.

Mém. Soc. Phys. Hist. nat. Genève 29(8): 42, 1887.

≡ ***Carbacanthographis marcescens*** (Fée) Staiger & Kalb, in Staiger, Biblthca Lichenol. 85: 109, 2002.

Following Staiger (2002), this taxon belongs in *Carbacanthographis* as *C. marcescens* (Fée) Staiger & Kalb. It is a corticolous species reported from Hong Kong (Aptroot and Sipman 2001) and Guangxi (Jia et al. 2017).

21. *Graphina mendax* (Nyl.) Müll. Arg.
Revue Mycol. Toulouse 10(40): 177, 1888.
= ***Diorygma junghuhnii*** (Mont. & Bosch) Kalb, Staiger & Elix, Symb. Bot. Upsal. 34(1): 157, 2004.
Following Kalb et al. (2004), this taxon is a synonym of *Diorygma junghuhnii* (Mont. & Bosch) Kalb, Staiger & Elix. It is a corticolous species first reported under the name *Graphina mendax* from Hong Kong (Thrower 1988; Aptroot and Seaward 1999) and Taiwan (Aptroot and Sparrius 2003) and later as *Diorygma junghuhnii* from Fujian (Meng and Wei 2008; Jia and Wei 2016), Guangdong (Jia and Wei 2016), Guanxi (Jia and Wei 2016), Hainan (Meng and Wei 2008; Wei et al. 2013; Jia and Wei 2016), Guizhou (Jia and Wei 2016), Yunnan (Jia and Wei 2016) and Hong Kong (Jia and Wei 2016).

22. *Graphina olivascens* Zahlbr.
in Handel-Mazzetti, Symb. Sin. 3: 57, 1930. (non Zahlbruckner 1933: 215; see below *G. taiwanensis*)
= ***Fissurina adscribens*** (Nyl.) Z.F. Jia & Lücking (see below).
Based on characteristics of thallus and lirellae, this species has to be included in *Fissurina*. It agrees morphologically with *Fissurina adscribens* and its ascospore size falls in the range of the latter. Hence, we consider it a synonym to *F. adscribens* (see below). It is reported from Hunan (as *Graphina olivascens*, Zahlbruckner 1930, 1932).

23. *Graphina oxyspora* Zahlbr.
Feddes Repert. 31: 214, 1933.
≡ ***Graphis oxyspora*** (Zahlbr.) Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 439, 2009.
Following Lücking et al. (2009), this taxon belongs in *Graphis* as *G. oxyspora* (Zahlbr.) Lücking. It is a corticolous species reported from Taiwan (type location, Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973).

24. *Graphina petrophila* Zahlbr.
Feddes Repert. 31: 213, 1933.
= ***Graphis japonica*** (Müll. Arg.) A.W. Archer & Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 437, 2009.
Following Lücking et al. (2009), this taxon is a synonym of *G. japonica* (Müll. Arg.) A.W. Archer & Lücking. It is a saxicolous species reported from Taiwan (type location as *Graphina petrophila* Zahlbr., Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973).

25. *Graphina plumbea* Zahlbr.
in Handel-Mazzetti, Symb. Sin. 3: 55, 1930.
≡ ***Graphis plumbea*** (Zahlbr.) Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 440, 2009.

Following Lücking et al. (2009), this taxon belongs in *Graphis as G. plumbea* (Zahlbr.) Lücking. It is a corticolous species reported from Fujian (type location, Zahlbruckner 1930, 1932; Jia and Wei 2011, 2016), Zhejiang (Jia and Wei 2016), Hainan (Jia and Wei 2011, 2016; Wei et al. 2013) and Hong Kong (Jia and Wei 2016).

26. *Graphina plumbicolor* Zahlbr.

Feddes Repert. 31: 217, 1933.

= ***Phaeographis haloniata*** (Zahlbr.) Z.F. Jia & Lücking (see below).

From the characteristics of thallus and lirellae, this species is also a *Phaeographis*. It agrees with *Graphina haloniata* Zahlbr. and hence is placed in synonymy with the newly combined *Phaeographis haloniata* (Zahlbr.) Z.F. Jia & Lücking (see below). It is a corticolous species reported from Taiwan (type location, Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973).

27. *Graphina roridula* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 59, 1930.

incl. var. ***platypoda*** Zahlbr., in Handel-Mazzetti, Symb. Sin. 3: 60, 1930.

= ***Diorygma pachygraphum*** (Nyl.) Kalb, Staiger & Elix, Symb. Bot. Upsal. 34(1): 163, 2004.

From the characteristics of thallus and lirellae, this species belongs in *Diorygma*. It is very similar to *Diorygma pachygraphum* (Nyl.) Kalb, Staiger & Elix and here added as a further synonym to that species, including its variety *platypoda* Zahlbr. *Diorygma pachygraphum* is a corticolous species reported from Hunan and Yunnan (type locations of *Graphina roridula* Zahlbr. and *G. roridula* var. *platypoda* Zahlbr., Zahlbruckner 1930, 1932), and also reported from Fujian (Meng and Wei 2008; Jia and Wei 2016), Guangxi (Jia and Wei 2016), Hainan (Wei et al. 2013; Jia and Wei 2016), Guizhou (Jia and Wei 2016) and Yunnan (Jia and Wei 2016).

28. *Graphina soozana* Zahlbr.

Feddes Repert. 31: 215, 1933.

≡ ***Diorygma soozana*** (Zahlbr.) M. Nakan. & Kashiw., in Nakanishi, Kashiwadani & Moon, Bull. Natn. Sci. Mus., Tokyo, B 29(2): 86, 2003.

Following Nakanishi et al. (2003), this taxon belongs in *Diorygma* as *D. soozana* (Zahlbr.) M. Nakan. & Kashiw. It is a corticolous species reported from Taiwan (type location, Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973), Zhejiang (Wu and Qian 1989), and then reported from Fujian, Sichuan, Guizhou and Yunnan (Meng and Wei 2008; Jia and Wei 2016).

29. *Graphina subpulicaris* Zahlbr.

Feddes Repert. 31: 212, 1933.

= ***Graphis cleistoblephara*** Nyl., Ann. Sci. Nat., Bot., sér. 4 20: 265, 1863.

This name is a synonym of *Graphina cleistoblephara* (Nyl.) Zahlbr. (Wei 1991). Following Staiger (2002) the latter belongs to *Graphis* as *G. cleistoblephara* Nyl. It is

a corticolous species reported from Taiwan under the name *Graphina subpulicaris* Zahlbr. (type location, Zahlbruckner 1933).

30. *Graphina symplocorum* Zahlbr.

in Handel-Mazzetti, Ann. K. K. Naturh. Hofmus. Wien 40: 142, 1926.

= ***Graphis renschiana*** (Müll. Arg.) Stizenb., Ber. Tät. St Gall. Naturw. Ges.: 184, 1891.

Following Lücking et al. (2009), this taxon is a synonym of *Graphis renschiana* (Müll. Arg.) Stizenb. It is a corticolous species reported under the name *Graphina symplocorum* Zahlbr. from Hunan (type location, Zahlbruckner 1930), and as *Graphis renschiana* (Müll. Arg.) Stizenb. from Hainan, Guizhou and Yunnan (Wei et al. 2013; Jia and Wei 2011, 2016).

31. *Graphina taiwanensis* J.C. Wei

An Enumeration of Lichens in China (Beijing): 99, 1991; nom. nov. pro *Graphina olivascens* Zahlbr., in Feddes Repert. Spec. Nov. Regni Veg. 31: 215, 1933; nom. illeg. ICBN Art. 53 [non Zahlbr. 1930].

≡ ***Platygramme taiwanensis*** (J.C. Wei) Z.F. Jia & Lücking, **comb. nov.** (see below).

Graphina taiwanensis J.C. Wei was introduced as replacement name for *Graphina olivascens* Zahlbr. 1933 (based on the type from Taiwan, Asahina no. 346), [non *Graphis olivascens* Zahlbr. 1930: type from Hunan, Handel-Mazzetti no. 11220] (Wei 1991). It is unclear why Zahlbruckner described a new species under the same name as another species he had described three years prior.

From the characteristics of the thallus and lirellae and the large, muriform ascospores (80–105 × 15–18 µm), it is evident that this species belongs to *Platygramme*. It is similar to *P. platyloma* (Müll. Arg.) M. Nakan. & Kashiw. (Nakanishi et al. 2003), but the latter differs in having larger ascospores (more than 120 µm long) and absence of lichen substances; therefore the name is here recombined as *P. taiwanensis* (J.C. Wei) Z.F. Jia & Lücking (see below).

Graphina taiwanensis* f. *obscurata (Zahlbr.) J.C. Wei, An Enumeration of Lichens in China (Beijing): 99, 1991; *Graphina olivascens* f. *obscurata* Zahlbr., in Feddes Repert. Spec. Nov. Regni Veg. 31: 215, 1933 (legitimate acc. to ICN Art. 55.2).

= ***Platygramme taiwanensis*** (J.C. Wei) Z.F. Jia & Lücking, **comb. nov.** (see below).

Graphina olivascens f. *obscurata* was described by Zahlbr. (1933) as a variety of *G. olivascens* Zahlbr. (1933), which is a later homonym of *G. olivascens* Zahlbr. (1930). Wei (1991) introduced a replacement name for the species and then correctly recombined the infraspecific name with Zahlbruckner as basionym author. The type of the latter is clearly conspecific with the type of *G. olivascens* Zahlbr. (1933) (≡ *G. taiwanensis* J.C. Wei) and hence the two names are added as synonyms to *Platygramme taiwanensis* (J.C. Wei) Z.F. Jia & Lücking.

Graphina taiwanensis is a corticolous species reported from Taiwan (type location, Zahlbruckner 1933; Lamb 1963; Wang and Lai 1973; Wei 1991).

32. *Graphina verruculina* Zahlbr.

in Handel-Mazzetti, Symb. Sin. 3: 58, 1930.

= ***Graphis japonica*** (Müll. Arg.) A.W. Archer & Lücking, in Lücking, Archer & Aptroot, Lichenologist 41(4): 437, 2009.

Following Lücking et al. (2009), this taxon is a synonym of *G. japonica* (Müll. Arg.) A.W. Archer & Lücking. It is a corticolous species reported under the name *Graphina verruculina* Zahlbr. from Fujian (type location, Zahlbruckner 1930; 1932).

33. *Graphina virginea* (Eschw.) Müll. Arg.

Bull. Herb. Boissier 3(2): 47, 1895.

= *Diorygma poitaei* (Fée) Kalb, Staiger & Elix, Symb. Bot. Upsal. 34(1): 164, 2004.

Following Kalb et al. (2004), this taxon is a synonym of *D. poitaei* (Fée) Kalb, Staiger & Elix. *Graphina virginea* (Eschw.) Müll. Arg. was reported from Hong Kong (Thrower 1988, p. 101), but according to her photograph and description, the material has norstictic acid, non-pruinose discs, 1-spored asci and hyaline muriform ascospores 50–60 × 15–25 µm in size and may represent a species of *Thalloloma*, such as *T. anguinaeforme* (Vain.) Staiger.

Nomenclatural novelties

1. *Fissurina adscribens* (Nyl.) Z.F. Jia & Lücking, comb. nov.

MycoBank No. 821429

Figure 1A–B

Bas.: ***Graphis adscribens*** **Nyl.,** in Bull. Soc. Linn. Normandie, ser. 2., 2: 117, 1868; *Graphina adscribens* (Nyl.) Müll. Arg. in Hedwigia 31: 284, 1892.

= *Graphina olivascens* Zahlbr., in Feddes Repert. Spec. Nov. Regni Veg. 31: 215, 1930 (non Zahlbr. 1933); Type: China (Hunan), *Handel-Mazzetti 11220* (holotype W!)

Description. Thallus corticolous, crustose, surface grey to olive, waxy and smooth; apothecia lirelliform, elongate, *Fissurina*-morph, single and rarely branched, 2–4.5 mm long and 0.2–0.35 mm wide; discs closed, slit-shaped; proper margin unconspicuous, concolorous with thallus; proper exciple not carbonized; hymenium clear, at most 150 µm high, I–; 8 ascospores per ascus, hyaline, ellipsoid, muriform, 8/3–4 locular, I–, 22–30 × 8–9 µm.

Chemistry. No substances present.

Notes. Because of the characteristics of thallus and lirellae, this species belongs to *Fissurina*. It is similar to *Fissurina subnitida* (Nyl.) Nyl. but differs by having smaller ascospores (*F. subnitida*: 27–35 × 13–16 µm; Staiger 2002). Therefore, we accept the name in *Fissurina* as *F. adscribens* (Nyl.) Z.F. Jia & Lücking. The type material of *Graphina olivascens* has *Fissurina*-like lirellae, hyaline, muriform ascospores (8/3–4

Figuer 1. A, B Type *Graphina olivascens* (*Handel-Mazzetti 11220*) **C, D** Type *Graphina isabellina* (*Handel-Mazzetti 11437*) **E, F** Type *Graphina lecanactiformis* (*Handel-Mazzetti 7147*).

locular, I–, 20–25 × 8–9 µm; Zahlbruckner 1930) and lacks lichen substances, and its characteristics fall within the range of *F. adscribens*, and it is here placed as synonym of the latter. *Fissurina adscribens* is a corticolous species reported from Hunan (as *Graphina olivascens*, Zahlbruckner 1930, 1932). Unfortunately, the material reported from Hong Kong as *Graphina adscribens* (Thrower 1988: 92) could not be studied but based on its reported chemistry (stictic and constictic acids) and larger ascospores (30–35 × 5–10 µm) represents another species of *Fissurina*.

2. *Diorygma isabellinum* (Zahlbr.) Z.F. Jia & Lücking, comb. nov.
MycoBank No. 821431
Figure 1C–D

Bas.: *Graphina isabellina* Zahlbr., in Handel-Mazzetti, Symb. Sin. 3: 58, 1930; Type: China (Hunan), *Handel-Mazzetti 11437* (holotype W!).

Description. Thallus corticolous, crustose, surface milk-white, somewhat yellowish, warty and rough; apothecia lirelliform, elongate, single and rarely branched, 2–4.5 mm long and 0.2–0.35 mm wide; labia obvious; discs closed to slightly opened; proper margin conspicuous, concolorous with the thallus; proper exciple not carbonized; hymenium clear, 160–180 µm high. I–; 1 ascospore per ascus, hyaline, ellipsoid, muriform, I+ violet, 110–120 × 35–48 µm.

Chemistry. Norstictic acid (major), connorstictic acid (minor or trace).

Notes. Because of the characteristics of thallus, lirellae and ascospores, this species belongs to *Diorygma* and is here recombined as *D. isabellinum* (Zahlbr.) Z.F. Jia & Lücking. It is similar to *D. pachygraphum*, but differs by smaller ascospores, the latter having ascospores 170–250 × 42–58 µm; it also similar to *D. junghuhnii* (Mont. & Bosch) Kalb, Staiger & Elix, but the latter differs in a I+ blue-violet hymenium and and smaller ascospores (60–)80–125 × 21–42 mm (Kalb et al. 2004). In the recent world key to *Diorygma* (Feuerstein et al. 2014), this species would key out at couplet 41.

3. *Graphis lecanactiformis* (Zahlbr.) Z.F. Jia & Lücking, comb. nov.
MycoBank No. 821432
Figure 1E–F

Bas.: *Graphina lecanactiformis* Zahlbr., in Handel-Mazzetti, Symb. Sin. 3: 57, 1930; Type: China (Yunnan), *Handel-Mazzetti 7147* (holotype W!).

Description. Thallus corticolous, crustose, surface grey-yellowish, slightly rough; apothecia lirelliform, sessile, oval to elongate, single, not branched, 1–1.2 mm long and 0.6–0.9 mm wide; discs open in the type material and appearing yellow-brown pruinose, but this could be due to damage; labia entire; proper margin conspicuous, black; proper exciple laterally carbonized; hymenium clear, 240–290 µm high. I–; 8 ascospores per ascus, hyaline, ellipsoid, muriform, 7–8/1–3 locular, I+ violet, 37–45 × 15–18 µm.

Chemistry. No substances present.

Notes. Because of the characteristics of thallus and lirellae, this species belongs to *Graphis* and is here recombined as *G. lecanactiformis.* It is similar to *Graphis tenuirima* (Shirley) A.W. Archer in anatomy, but differs in ascoma morphology (*dussii* morph according to Lücking et al. 2009) and the larger ascospores. In the world key to *Graphis* (Lücking et al. 2009), this species would key out at couplet 23 in Group 5.

4. *Phaeographis haloniata* (Zahlbr.) Z.F. Jia & Lücking, comb. nov.
MycoBank No. 821433
Figure 2A–D

Bas.: *Graphina haloniata* Zahlbr., Feddes Repert. 31: 216, 1933; Type: China (Taiwan), *Asahina 356* (holotype W!)
= *Graphina plumbicolor* Zahlbr., Feddes Repert. 31: 217, 1933; Type: China (Taiwan), *Asahina 340* (holotype W!)

Description. Thallus corticolous, crustose, thick, surface grey to olive-green, waxy and slightly warty; apothecia lirelliform, elongate, single and rarely branched, at most 9.0 mm long and 0.5 mm wide; discs open, brownish, slightly pruinose, flat to somewhat concave; proper margin obvious, concolorous with thallus; proper exciple slightly carbonized basally; hymenium inspersed, 100–125 µm high, I–; 8 ascospores per ascus, brownish, ellipsoid, muriform, 8/1–3 locular, I+ violet-brown, 30–35 × 10–14 µm.

Chemistry. Stictic acid.

Notes. Because the material of *Graphina haloniata* in W has the typical characteristics of *Phaeographis*, such as open discs and brownish ascospores, it is here transferred to *Phaeographis*. The reported differences between *Graphina haloniata* and *G. plumbicolor* were in ascospore size: 30–34 × 12–14 µm in *G. haloniata* and 29–30 × 10–11 µm in *G. plumbicolor* (Zahlbruckner 1933), but in the studied material these measurements largely overlap. The two names were only reported from their type locations in Taiwan (Zahlbruckner 1933, 1940; Lamb 1963; Wang and Lai 1973; Wei 1991).

Figuer 2. A, B Type *Graphina haloniata* (*Asahina 356*) **C, D** Type *Graphina plumbicolor* (*Faurie 83*).

5. *Platygramme taiwanensis* (J.C. Wei) Z.F. Jia & Lücking, comb. nov.
MycoBank No. 821436
Figure 3A–D

Bas.: *Graphina taiwanensis* J.C. Wei, An Enumeration of Lichens in China (Beijing): 99, 1991; nom. nov. pro *Graphina olivascens* Zahlbr., in Feddes Repert. Spec. Nov. Regni Veg. 31: 215, 1933; nom. illeg. ICBN Art. 53 [non Zahlbr. 1930]; Type: China (Taiwan), *Asahina 346* (holotype W!)

= *Graphina taiwanensis* f. *obscurata* (Zahlbr.) J.C. Wei, An Enumeration of Lichens in China (Beijing): 99, 1991; *Graphina olivascens* f. *obscurata* Zahlbr., in Feddes Repert. Spec. Nov. Regni Veg. 31: 215, 1933 (legitimate acc. to ICN Art. 55.2). Type: China (Taiwan), *Asahina 375* (holotype W!)

Description. Thallus corticolous, crustose, thin, surface cervine to slightly olive, smooth; apothecia lirelliform, elongate, strong, adpressed, single and short branched, 1.5–3 mm long and 0.2–0.3 mm wide; labia entire, distinctly; discs closed or very narrow, epruinose; proper margin obvious, concolorous with the thallus; proper exciple laterally carbonized; hymenium clear, 130–150 µm high. I–; asci long clavate, 1-spored; ascospores, hyaline to grayish, subcylindrical to oblong, ends obtuse, muriform with dense locules, I+ red-brown, 80–105 × 15–18 µm.

Chemistry. Stictic acid.

Figuer 3. A, B Type *Graphina taiwanensis* (*Asahina 346*) **C, D** *Graphina taiwanensis* f. *obscurata* (*Asahina 346*).

Notes. The material of *Graphina taiwanensis* and f. *obscurata* in W shows the characteristics of *Platygramme* such as the distinctly labiate lirellae, closed discs, a laterally carbonized exciple and hyaline to grayish ascospores. *Platygramme taiwanensis* is most similar to *P. platyloma*, but the latter differs in having an inspersed hymenum, larger ascospores (more than 120 µm long) and lack of lichen substances. *Platygramme pudica* (Mont. & Bosch) M. Nakan. & Kashiw. differs in having an inspersed hymenum, larger ascospores (150–180 × 18–25 µm) and echinocarpic acid (Jia and Kalb 2013). The form *obscurata* only differs from the nominal taxonby the darker thallus, which is largely caused by the bark, and hence we include it in *P. taiwanensis*. The species was only reported from the type location in Taiwan (Zahlbruckner 1933; Lamb 1963; Wang and Lai 1973, Wei 1991).

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RESEARCH ARTICLE

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Morphologic and molecular data help adopting the insect-pathogenic nephridiophagids (Nephridiophagidae) among the early diverging fungal lineages, close to the Chytridiomycota

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Abstract

Nephridiophagids are poorly known unicellular eukaryotes, previously of uncertain systematic position, that parasitize the Malpighian tubules of insects. Their life cycle includes merogony with multinucleate plasmodia and sporogony leading to small, uninucleate spores. We examined the phylogenetic affiliations of three species of *Nephridiophaga*, including one new species, *Nephridiophaga maderae,* from the Madeira cockroach (*Leucophaea maderae*). In addition to the specific host, the new species differs from those already known by the size of the spores and by the number of spores within the sporogenic plasmodium. The inferred phylogenetic analyses strongly support a placement of the nephridiophagids in the fungal kingdom near its root and with a close, but unresolved, relationship to the chytids (Chytridiomycota). We found evidence for the nephridiophagidean speciation as being strongly coupled to host speciation.

Key words
Cryptomycota, entomoparasitic, entomopathogenic, Fungi, Haplosporidia, Microsporidia, Molecular phylogeny, protozoa, Rozellomycota, small subunit ribosomal DNA (SSU, 18S), spore morphology

Introduction

Arthropods may be infected by a range of unicellular pathogens of disparate taxonomic affiliations (Lange and Lord 2012). The majority of entomopathogenic spore-forming protists belong to the supertaxa Opisthokonta (e.g. Microsporidia) and SAR (Alveolata with the Apicomplexa; Rhizaria with the Haplosporidia and Paramyxea; Adl et al. 2012). Nephridiophagids (Nephridiophagidae) are unicellular, spore-forming parasites previously of uncertain systematic position. They infect the Malpighian tubules of insects and are mainly found in the lumen of these tubules (e.g., Woolever 1966, Radek and Herth 1999). The life cycle of nephridiophagids includes a merogony phase with vegetative multinucleate plasmodia that divide into oligonucleate and uninucleate cells. Sporogonial plasmodia form internal, 5–10 µm long, oval, flattened spores, generally with one nucleus. Residual nuclei of the mother cell remain in the cytoplasm between the developing spores.

The systematic position of the nephridiophagids has been discussed intensively. Morphologically, this lineage could not be assigned unambiguously to any of the known major taxa of spore-forming protists. Some authors place them with the haplosporidians (Ivanić 1937, Woolever 1966, Purrini and Weiser 1990) while others disagreed with this grouping (Toguebaye et al. 1986, Purrini and Rhode 1988, Lange 1993). With the aid of a light microscope, the nephridiophagid stages resemble microsporidians (Microsporidia), and by tradition some nephridiophagids have been given names in microsporidian genera (e.g., *Nosema periplanetae* and *Pleistophora periplanetae*; Lutz and Splendore 1903, Perrin 1906). A preliminary molecular analysis placed them within the Fungi, close to 'zygomycota' (Wylezich et al. 2004, White et al. 2006). Since then, the Microsporidia have been placed near the root of the fungal kingdom (Capella-Gutiérrez et al. 2012, Xiang et al. 2014) as have the Cryptomycota (Lazarus and James 2015). The genus *Nephridiophaga* was introduced by Ivanić (1937) for *N. apis*, which infects honey bees. Insects, which represent the metazoan group with the highest species richness, appear to be remunerative to screen for novel fungal taxa which were hidden in habitats insulated from the free environment (Hawksworth 2001).

The Fungi comprise upwards of 6 million extant species, of which some 135,400 have been described formally (Blackwell et al. 2011, Hibbett et al. 2011, Taylor et al. 2014; www.speciesfungorum.org as of May 2017). Although all true fungi are heterotrophs, they occupy a very wide range of niches and nutritional modes. About 1% of the described species – 750-1,000 species from about 100 genera – are pathogens of insects. These entomopathogens are distributed over most fungal phyla, and their hosts are spread among 20 orders of insects (Araújo and Hughes 2016). All insect developmental stages from egg to adult may be subject to infection. Molecular data have

increased our understanding of insect-fungal relationships considerably. A wide range of associations and infection types has been discovered, ranging from parasitic through commensal and even beneficial (Suh et al. 2005, Vega et al. 2012, Douglas 2015). High-throughput sequencing is rapidly gaining in popularity as a means of studying fungus-insect interactions, and published studies have uncovered surprising diversity even within single insect individuals (e.g., Dhami et al. 2013). This is in line with the results from other environmental fungal sequencing efforts, where tens to hundreds of previously unknown (or at least not sequenced) species are usually found in each new study undertaken (Nilsson et al. 2016). It is thus not speculative to assume that a significant number of insect pathogenic fungi await discovery and formal description.

Many early diverging fungi are associated with insects, however, this region of the fungal tree of life suffers from poor taxon sampling and phylogenetic resolution. The last few years have seen the description of numerous new species and lineages of early diverging fungi, even at the phylum level (e.g., James et al. 2006, Corsaro et al. 2014, Karpov et al. 2014a, b, Bauer et al. 2015). The nephridiophagids belong in this part of the fungal kingdom (Wylezich et al. 2004), but they have yet to be addressed using phylogenetic methods in the context of a rich taxon sampling of closely related taxa. The present study uses a molecular phylogenetic approach to examine the phylogenetic relationships of the nephridiophagids. We included three species of *Nephridiophaga* from cockroaches, viz. *N. blattellae*, *N. blaberi,* and a new species from the Madeira cockroach (*Leucophaea maderae*). Increasing the number of analyzed species we aim to clarify the relationships among the deep lineages of the Fungi. Our molecular, morphological, and ultrastructural results show that the nephridiophagids may represent a distinct clade at the root of the Fungi.

Materials and Methods

Animal material

Specimens of the Death´s Head Cockroach *Blaberus craniifer*, the German Cockroach *Blattella germanica,* and the Madeira Cockroach *Leucophaea* (*Rhyparobia*) *maderae* were retrieved from the Federal Environment Agency (UBA; https://www.umweltbundesamt.de/en) in Berlin, Germany. Cockroaches of different ages and sex were dissected, and their Malpighian tubules were removed and processed for further examination through light and electron microscopy as well as molecular analysis.

Light microscopy

For fresh preparations, parts of the tubules were ground with fine forceps in a drop of 0.6% NaCl solution. The infected tubules were then smeared on a microscopic slide, air dried, and fixed in methanol for 5 min prior to staining with Giemsa solution (Ac-

custain, Sigma; 1:10 in tap water for 45 min). Dried smears were mounted in Entellan (Merck). Extracted bundles of Malpighian tubules were embedded in paraffin (Paraplast) for histological examination. Fixation was carried out in Bouin's fluid, modified after Dubosq-Brasil (Böck 1989). Sections of 7 µm were stained with hematoxylin-eosin (Böck 1989) and embedded in Malinol (Chroma). The chitinous spore walls of native spores were fluorescently labeled with 0.01% Calcofluor White M2R in a 50 mM phosphate buffer of pH 7.2 for 15 min. Photos were taken with a Zeiss Axiophot equipped with an Inteq digital camera and the software EasyMeasure 1.4.

Scanning electron microscopy

Cover glasses were coated with 0.01% poly-L-lysine to promote attachment of spores. Malpighian tubules were ground in a drop a fixative (1% OsO_4, 2.5% glutardialdehyde, 0.1 M cacodylate buffer, pH 7.2) on the cover glasses and fixed for 1 h. After dehydration in a graded series of ethanol, the prepared cover glasses were critical point dried in a Baltec CPD 030 and sputtered with gold in a Baltec SCD 040. Images were taken with a Quanta 200 scanning electron microscope from FEI Company.

Transmission electron microscopy

Stages of *N. blattellae* were fixed (glutaraldehyde, reduced osmium) and embedded according to Radek and Herth (1999).

DNA extraction

For molecular analysis of the nuclear small subunit (SSU, 18S) rRNA encoding rDNA sequences of microscopically identified *Nephridiophaga* species, dissected Malpighian tubules of *Blattella germanica, Blaberus craniifer,* and *Leucophaea maderae* were transferred into 1.5 ml PCR-clean reaction tubes (Eppendorf, Hamburg, Germany) with 50 µl of distilled water and stored at -20°C pending further analysis. Alternatively, the tubules were put into 50 µl of lysis buffer. (0.5% sodium dodecyl sulfate, 200 mM TRIS-HCl pH 8.0). For DNA extraction, specimens were centrifuged at 13,200 *g* for 5 min using the Eppendorf benchtop centrifuge 5415R with a F45-24-11 rotor. The supernatant was removed, and total DNA was extracted from the obtained pellets using the DNeasy Plant Mini Kit from Qiagen (Hilden, Germany). Briefly, each pellet was thoroughly resuspended in 400 µl of warm buffer AP1 and 4 µl RNase A (100 mg/ml). Samples were incubated at 65°C for 10 min and 20 min at room temperature. Next, 130 µl of AP2 buffer was added and samples were incubated for 5 min on ice. Lysate was transferred into the QIA shredder column and the column was centrifuged

for 2 min at 13,200 *g*. The flow-through was gently mixed with 1.5 volume AP3/E buffer, transferred to a DNeasy spin column, and centrifuged for 1 min at 6000 *g*. The column was placed into a new 2 ml collecting tube and washed with 500 µl AW buffer. The column was centrifuged for 1 min at 6,000 *g*, after which the flow-through was removed and the column was washed again with 500 µl AW buffer. Centrifugation was performed at 13,200 *g* for 2 min. Finally the column was placed into a 1.5 ml PCR-clean reaction tube and DNA was eluted with 50 µl AE buffer. After 5 min incubation at room temperature, the column was centrifuged at 6,000 *g* for 2 min. The extracted DNA was stored at -20°C pending further analysis.

For amplification of the SSU sequences of *N. blattellae*, *N. blaberi,* and *N. maderae*, the eukaryotic universal primers published by Medlin et al. (1988) without polylinker were used that span the complete 18S (Table 1). Additionally, we designed a bridging *Nephridiophaga*-specific primer (Nephbla3 rv) based on the public SSU sequence of *N. blattellae* (NCBI GenBank accession no. AY603958) using PrimerBLAST (http://www.ncbi.nlm.nih.gov/tools/primer-blast/). Since *Nephridiophaga* DNA was extracted from ground cockroaches, primer specificity was essential, so that the primers do not match the host. The tiny amount of fungal DNA compared to host DNA could lead to preferential amplification of cockroach DNA unless specific primers were used. The primers used targeted nucleotide position 1-21 (Euc Uni 18S fw), nucleotide position 872-891 (Nephbla3 rv and Nephbla3 fw) and nucleotide position 1787-1810 (Euc Uni 18S rv) of the complete 18S ribosomal RNA gene of *N. blattellae* (NCBI GenBank accession no. AY603958), resulting in sequences of 891 nt (Euc Uni 18S fw and Nephbla3 rv) and 939 nt (Nephbla3 fw and Euc Uni 18S rv) (Table 1). All primer sets were synthesized by Eurofins MWG Operon (http://www.eurofinsgenomics.eu/).

PCR amplification of SSU rDNA

PCR amplification of the 18S rRNA gene was performed using HotStarTaq *Plus* DNA polymerase kit (Qiagen) and 10 mM dNTP mix (Peqlab, Erlangen, Germany) according to the manufacturers' protocols. PCR reactions were performed with an initial DNA denaturation step at 95°C for 5 minutes followed by 35 cycles of 94°C for 1 min, 59°C for 1 min for each primer set (Table 1), 72°C for 1 min, and a final elongation step at 72°C for 10 min. Amplification products were separated on a 1% agarose gel, stained with ethidium bromide, and visualized under UV light.

Table 1. Primer sets used to amplify the SSU rDNA of *Nephridiophaga blattellae*, *N. blaberi,* and *N. maderae.*

Source	Primer	Sequence 5′-3′	Product size
Medlin et al. 1988	Euc Uni 18S fw	AACCTGGTTGATCCTGCCAGT	891 nt
this study	Nephbla3 rv	AATACTGACGCCCCCAACTG	
this study	Nephbla3 fw	CAGTTGGGGGCGTCAGTATT	939 nt
Medlin et al. 1988	Euc Uni 18S rv	TGATCCTTCTGCAGGTTCACCTAC	

Sequencing of amplified the SSU rDNA

The PCR amplicons were purified using the QIAquick PCR Purification Kit from Qiagen. Briefly, 20 µl of each PCR-product was resuspended in 100 µl PB-buffer and transferred to a QIAquick DNA column, centrifuged at 16,100 *g* for 30 s and the flow-through was aspirated. The column was washed with 750 µl PE-buffer and centrifuged at 16,100 *g* for 30 s. The flow-through was aspirated and the column was centrifuged at 16,100 *g* for 30 s to remove any residual ethanol. The column was placed into a 1.5 ml PCR-clean reaction tube (Eppendorf), and 50 µl of warm EB-buffer was added onto the membrane. To elute the PCR amplicons, the columns were centrifuged at 8,000 *g* for 2 min. The purified PCR products were sent to Eurofins-Genomics (http://www.eurofinsgenomics.eu/) for sequencing. The short sequences (Table 1) were edited and processed using the VectorNTI software from Invitrogen™ Life Technologies (Darmstadt, Germany). Two new SSU rDNA sequences were generated, one each for *N. blaberi* (1,697 bases) and *N. maderae* (1,784 bases). These were deposited in GenBank (Benson et al. 2017) under accession numbers KU900289-KU900290. For further phylogenetic analysis we also used the *N. blattellae* SSU rDNA sequence AY603958 (1,807 bases) from GenBank.

Phylogenetic inference

The generated sequences were aligned against the SILVA SSU reference database (v119) using SINA (Pruesse et al. 2012), which accounts for secondary structures of the ribosomal RNA. We added the zygomycete sequences from White et al. (2006) to the reference database to increase the coverage of fungal lineages at the root of the fungal kingdom. For the general placement of *Nephridiophaga* into the eukaryotic tree of life we took the multiple sequence alignment of all 62k reference database entries and removed all overly short sequences as well as sequences with anomalies (Ashelford et al. 2005), thus reducing the dataset to 40k entries with 22,404 analyzed characters. A maximum likelihood tree with the multithread version of FastTree (version 2.1, Price et al. 2010) was inferred, specifying 10k resamplings using a GTR model. *Nephridiophaga* was recovered within the Holomycota (syn.: Nucletmycea; Suppl. material 1, Fig. S1), and we thus compiled a representative dataset of 196 taxa from all Holomycota and close neighbors. The final alignment was adjusted manually in AliView 1.17 (Larsson 2014). We only allowed full length sequences ranging from SILVA SSU position 1132 to 43048 for all subsequent phylogenetic inferences, including all variable regions, resulting in a total of 2,773 analyzed characters, of which 1,057 were invariable. Phylogenetic inference was done using Bayesian inference in MrBayes v. 3.2.6 (Ronquist et al. 2012) and maximum likelihood in FastTree with 10,000 bootstrap replicates. The Bayesian inference of phylogeny was based on 20 million generations under the GTR model and INVGAMMA substitution rates as suggested by MrModelTest 2.3 (Nylander et al. 2004). Chain mixing and convergence were satisfactory (the latter approaching an average split frequency of 0.008). Sequence similarities were

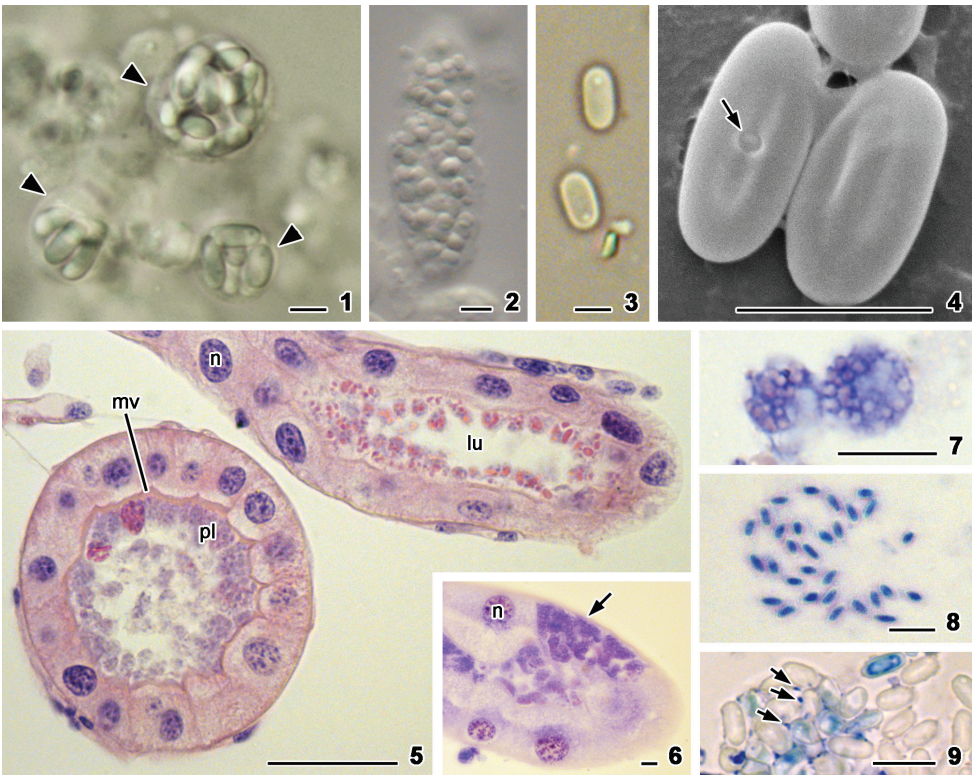
calculated based on Jukes and Cantor (1969) distances. The multiple sequence alignment and the phylogenetic trees were deposited in TreeBASE at https://treebase.org/ (study no. S19000).

Results

Characterization of the new species Nephridiophaga maderae

While species of *Nephridiophaga* from *Blattella germanica* (Blattellidae, Blattellinae) and *Blaberus craniifer* (Blaberidae, Blaberinae) were already known, there is no formal description of a nephridiophagid from *Leucophaea maderae* (Blaberidae, Oxyhaloinae). In nine out of ten dissected Madeira cockroaches, the Malpighian tubules were infected by a spore-forming nephridiophagid. The degree of infection was generally low (6–10 sec of microscopy necessary before finding first stages). Two animals were infected more heavily (1–5 sec of microscopy). None of the infected cockroaches showed obvious symptoms of illness. In fresh smears, spore-containing plasmodia (Fig. 1), vegetative multinucleate plasmodia (Fig. 2), and single spores were seen, which jointly form the typical stages of species from the genus *Nephridiophaga.* The number of spores in a sporogenic plasmodium varied between 6 and 26, with a mean number of 15 (n = 34). As long as the plasma membrane of the plasmodium is intact (Fig. 1, arrows), the spores are kept together in groups. Single spores have a flattened oval form, measuring 6.3–7.9 (7.2) x 3.1–4.7 (3.7) µm in fresh preparations (n = 50) and 4.8–7.5 (6.4) x 2.4–4.5 (3.3) µm in Giemsa-stained smears (n = 50). Scanning electron micrographs reveal a centrally localized, plugged spore opening on the upper side (Fig. 4, left spore). The lower side has no opening but may be slightly folded (Fig. 4, right spore). The rim of the spore is thickened. In hematoxylin-eosin stained paraffin sections, the localization of the parasites in the lumen of the Malpighian tubules can be seen clearly (Fig. 5). Many cells attach to the microvilli border of the epithelial cells while others are free in the lumen. Only very rarely, intracellular vegetative plasmodia are found in the epithelial cells of the Malpighian tubules (Fig. 6). Giemsa staining of smears also reveals the different stages, viz. multinucleated vegetative plasmodia (Fig. 7), young spores whose interior can be stained (Fig. 8), and mature spores into which the stain cannot penetrate. Typical for nephridiophagids are the residual vegetative nuclei of the mother cell in the cytoplasm between the spores (Fig. 9).

Characteristic ultrastructural features of the genus *Nephridiophaga* are demonstrated using the example of *N. blattellae* (Figs 10–13). Vegetative plasmodia have a variable cell form and contain one to several nuclei, numerous mitochondria, and an endoplasmic reticulum (Fig. 10). The mitochondria are of the tubular to sac-like type rather than of the cristae type. Sporogenic plasmodia internally form flattened-oval, thick-walled spores with one nucleus; residual vegetative nuclei remain in the cytoplasm of the mother cell (Fig. 11). The spores contain typical eukaryotic cell structures such as a nucleus, mitochondria, and an endoplasmic reticulum but no obvious extra elements (Fig. 12). A layer of small vesicles attaching to the lining of the developing

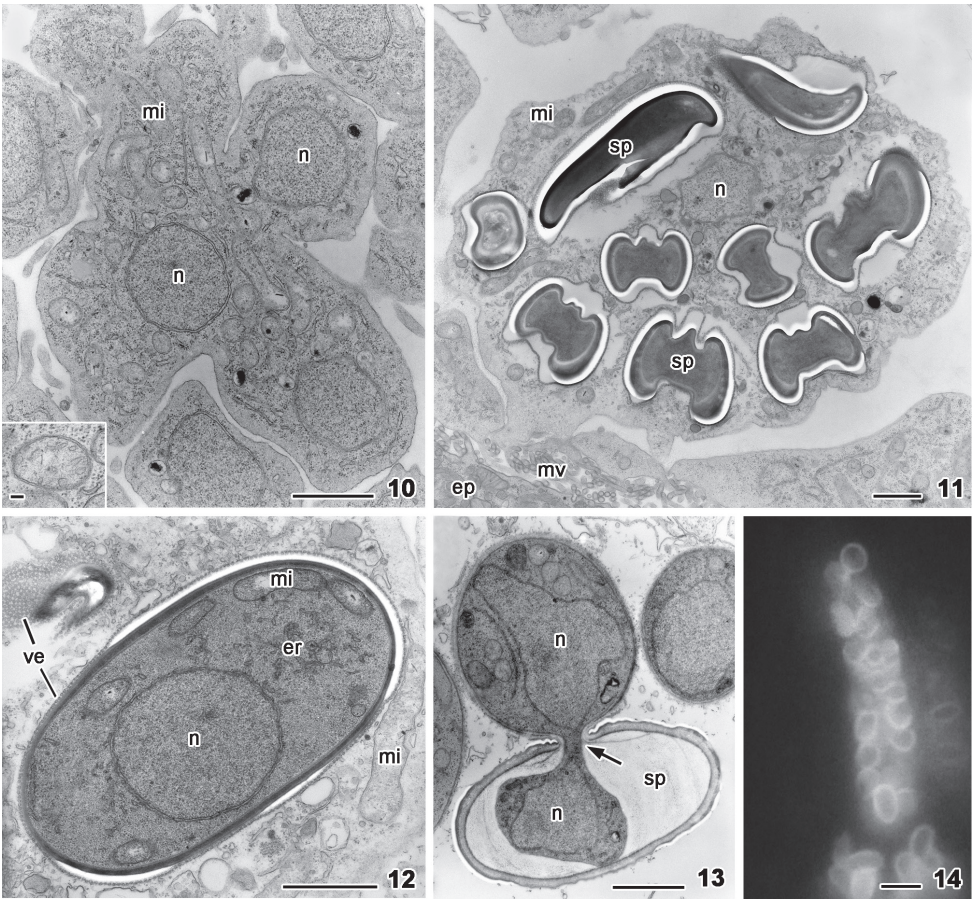


Figures 1–9. *Nephridiophaga maderae*, **1, 2, 5–9** bright field **3** phase contrast **4** scanning electron microscopy. **1** Three sporogonial plasmodia with different numbers of included spores. Arrows point to plasma membrane. **2** Merogonial plasmodium with numerous nuclei. **3** Mature spores. **4** The upper surface of the spore possesses a central spore opening (arrow, left spore) while the lower surface of the spore lacks an opening (right spore). **5, 6** Paraffin sections stained with hematoxylin-eosin. Generally, the plasmodia (pl) are found in the lumen of the Malpighian tubule but are often attached to the microvilli (mv) (**5**). Rarely, aggregates of vegetative plasmodia (arrow) occur in the epithelial cells of the Malpighian tubules (**6**). n = nuclei of epithelial cells. **7–9** Smears of macerated tubules stained with Giemsa depicting vegetative plasmodia (**7**), stained young spores (**8**), and unstained mature spores with residual nuclei (arrows) of the mother sporoplasm. Scale bars: 5 µm (**1–4**), 50 µm (**5**), 10 µm (**6–9**).

sporoblasts is probably involved in the formation of the spore wall (Fig. 12). The only structure apparently aiding in hatching of the sporoplasm is a central spore opening through which the sporoplasm can escape (Fig. 13). Calcofluor staining reveals the presence of chitin in the spore wall (Fig. 14).

Phylogenetic position of Nephridiophaga

Since we wanted to clarify the phylogenetic relationship of *Nephridiophaga* with respect to other spore-forming pathogens, we included members of the former Zygomycota as well as the Haplosporidia and Microsporidia (Suppl. material 1, Fig. S1). The genus



Figures 10–14. *Nephridiophaga blattellae*, **10–13** transmission electron microscopy, **14** Calcofluor white staining. **10** Meront with several nuclei (n) and mitochondria (mi) in the lumen of Malpighian tubule. Inset: Mitochondrium with tubular to sac-like cristae. **11** Sporogenic plasmodium containing mature spores (sp), mitochondria (mi), and vegetative nuclei (n) in the cytoplasm. The plasmodium is anchored to the microvilli (mv) of epithelial cells (ep) of the tubule. **12** Young spore within the cytoplasm of a sporogenic plasmodium, surrounded by a layer of vesicles. The spore cytoplasm contains one nucleus (n), mitochondria (mi), and endoplasmic reticulum (er). **13** An infectious sporoplasm hatches through the central spore opening, leaving behind the spore wall of the emptying spore (sp). The nucleus (n) is squeezed through the tiny spore opening. **14** Calcofluor white stains the spore wall indicating the presence of chitin (bluish color). Scale bars: 1 μm (**10–13**), inset 0.1 μm (**10**), 5 μm (**14**).

Nephridiophaga is clearly positioned within the Fungi but does not cluster together with any of the long branches of Microsporidia (Cryptomycota), Haplosporidia (SAR group), or *Dimargaris* (Dimargaritales, Kickxellomycotina, 'zygomycota'). We further selected a representative set of entries from the Holomycota phyla and its sister clades in order to find the most probable position of *Nephridiophaga* in the backbone tree. Again we recovered strong support for the *Nephridiophaga* within the Fungi (Fig. 15).

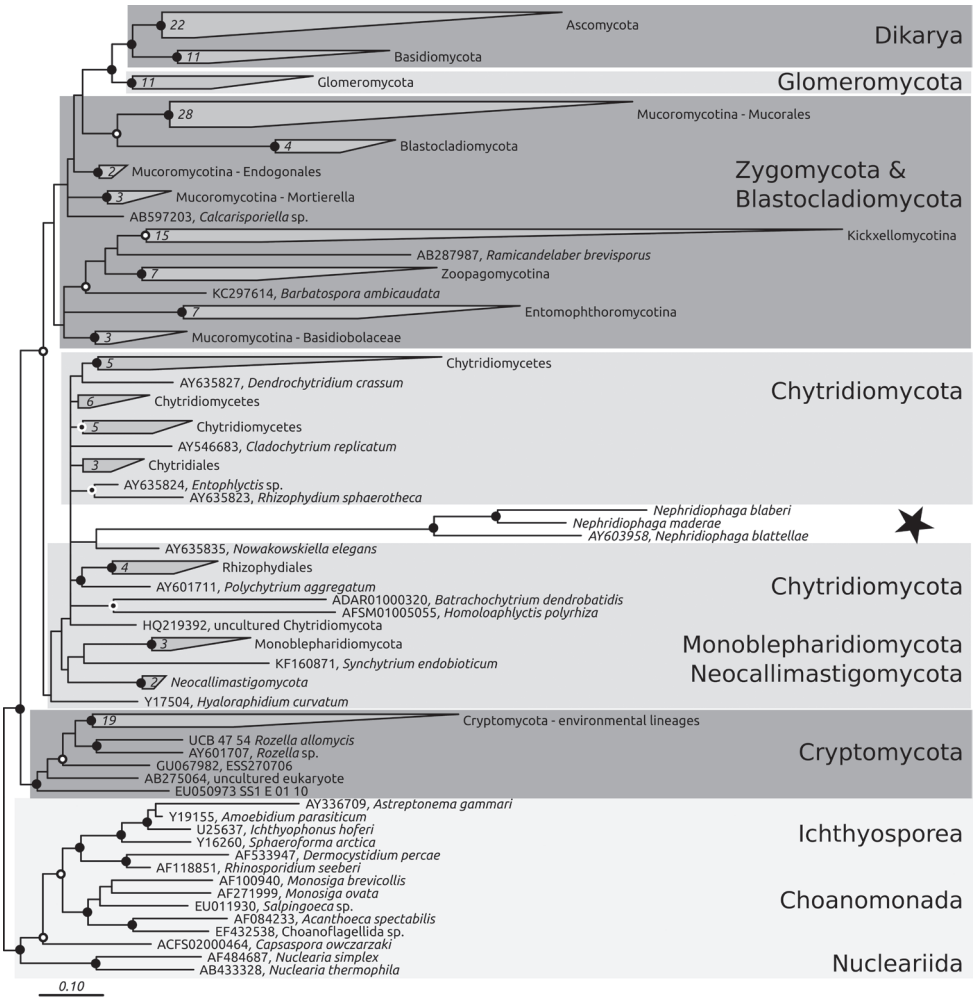


Figure 15. Bayesian phylogenetic tree including major lineages of the Holomycota (Liu et al. 2009; syn.: *Nucletmycea*, Brown et al. 2009), i.e. Fungi, Cryptomycota, and the basal Nucleariida, together with Holomycota sister clades Choanomonada, Ichthyosporea, and Filasterea (Holozoa; Lang et al. 2002). *Nephridiophaga* species (star) form a clade together with the flagellate fungi, here indicated as Chytridiomycota *s.l.* The scale indicates expected changes per site. Branch support is given as Bayesian posterior probabilities above 0.95 (black circles) and maximum likelihood resampling values above 90% (white circles). Filled black circles mark support from both methods.

The clade could not be assigned to the Cryptomycota but instead formed a clade with the Chytridiomycota *sensu lato*. The fully supported branch leading to *Nephridiophaga* points to an independent lineage near the root of the fungal kingdom. In addition, the strong branch support obtained for data from each of the three samples of *Nephridiophaga* from different cockroach species supports the notion that the isolates indeed

represent three distinct species. The new species *Nephridiophaga maderae* differed from described taxa by approximately 12-14% at the intrageneric level and by more than 20% at the inter-phylum level in its small subunit ribosomal DNA sequence (as referred to pairwise sequences similarity). The *Nephridiophaga* clade is not known from environmental sequences.

Taxonomy

***Nephridiophaga maderae* Radek, Owerfeldt, Gisder & Wurzbacher sp. nov.**
Registration identifier: 552000

Diagnosis. Flattened, oval to elongate, uninucleate spores measuring 6.3–7.9 (7.2) x 3.1–4.7 (3.7) µm in fresh preparations and 4.8–7.5 (6.4) x 2.4–4.5 (3.3) µm in Giemsa-stained smears. 6–26 (15) spores per sporogenic plasmodium. Vegetative and sporogenic life cycles stages in lumen of Malpighian tubules. Vegetative plasmodia are rarely intracellular in epithelial cells of Malpighian tubules.

Holotype. Two slides were deposited in the Upper Austrian Museum in Linz, Austria (Giemsa stained smear with slide number 2014/58 and hemalaun-eosin stained paraffin sections with slide number 2014/59).

Distribution / host locality. Culture at the Federal Environment Agency (UBA), Berlin, Germany. Naturally occurring in tropical regions world-wide.

Ecology: Infection of the host by oral ingestion of spores. Life cycle stages develop in the Malpighian tubules. Spores released via the feces.

Etymology and host. Named after its host, the Madeira cockroach, *Leucophaea maderae.*

Discussion

The phylogenetic position of *Nephridiophaga* has been a longstanding enigma in the systematics community. As a result of the re-appraisal of fungal phylogeny during the Deep Hypha project (Blackwell et al. 2006), *Nephridiophaga blattellae* was reported to cluster among the fungi and not among other eukaryotes as previously described using the SSU sequence generated by Wylezich et al. (2004). *Nephridiophaga blattellae* appeared to have some statistically supported phylogenetic relationship with the Kickxellales-Dimargaritales-Zoopagales clade among the zygomycetes (White et al. 2006). Here we report the generation of SSU sequence data from another species which was previously described, *N. blaberi*, and from the new species of *Nephridiophaga* in order to re-evaluate the phylogenetic position for the nephridiophagids. We were able to provide robust phylogenetic support (100%) for the position of the nephridiophagids near the root of the fungal kingdom.

The identification of Nephridiophaga maderae *as novel species*

All nephridiophagids found so far in cockroaches belong to the genus *Nephridiophaga*: *N. archimandrita* (Radek et al. 2011), *N. blaberi* (Fabel et al. 2000), *N. blattellae* (Crawley 1905, Woolever 1966, Radek and Herth 1999), *N. lucihormetica* (Radek et al. 2011), *N. periplanetae* (Lutz and Splendore 1903, Lange 1993), and *N. tangae* (Purrini et al. 1988). Characteristics of these species were compiled and tabulated by Radek et al. (2011) and the species studied so far seem to be host specific. Furthermore, they differ slightly in the size of spores and the number of spores within the sporogenic plasmodium. The localization of the life stages is mostly in the lumen of the Malpighian tubules, but in some species intracellular vegetative plasmodia have also been found. Due to these characters we believe that an as-yet unknown species of *Nephridiophaga* occurs in *Leucophaea maderae*. Woolever (1966) already mentioned the occurrence of a nephridiophagid in this host but did not provide any details. Our sequence data strongly support the existence of this un-named species and the general occurrence of different species of nephridiophagids in different hosts, indicating that speciation in *Nephridiophaga* is strongly linked to host speciation. The new species differs from *N. blattellae* by 12% and from *N. blaberi* by 14% in their nuclear small subunit ribosomal DNA which is a sufficient phylogenetic distance, according to Marshall and Berbee (2011), to justify a new species. *Nephridiophaga maderae* sp. nov. joins four other species of *Nephridiophaga* in having been recovered from cockroaches (Woolever 1966, Fabel et al. 2000, Radek et al. 2011), hinting at the unique and diverse life forms that can be found by investigating taxa inhabiting divergent host species.

Phylogenetic position of the genus Nephridiophaga

The results confirmed the finding of Wylezich et al. (2004) that *Nephridiophaga* belongs to the fungal kingdom rather than being related to non-fungal eukaryotes. It was, however, not possible to resolve the branching order of the non-Dikarya fungi in a robust way. We found a polytomy where the nephridiophagids were embedded within the flagellate fungi, the Chytridiomycota sensu lato (Voigt 2012). There is strong phylogenetic and ultrastructural support not to assign the nephridiophagids to any of the newly erected/redefined phyla Blastocladiomycota, Chytridiomycota *sensu stricto*, Monoblepharidomycota, and Neocallimastigomycota, all of which stem from the former phylum Chytridiomycota *s.l.* (see Voigt (2012) for an overview).

It is interesting that sequences from species of *Nephridiophaga* have never been recovered in studies based on environmental sequencing, although primer mismatches can be hypothesized to be the culprit (cf. Tedersoo et al. 2015). Alternatively, *Nephridiophaga* sequences may be rare enough to be below the detection limit in bulk environmental samples. So far, we have only recovered sequences from the cockroach clade (Blattodea), which is an early-diverging lineage. Thus, species of *Nephridiophaga* from other arthropods will be extremely helpful to retrace the evolutionary history

of this cryptic and enigmatic group of fungi. During the past, the placement of one novel fungal group (Archaeorhizomycetes) discovered using DNA-based methods shifted when more characters from additional rDNA and protein-coding regions were added to the analysis (Rosling et al. 2011). Multiple markers such as the nuclear large subunit (LSU, 28S) ribosomal DNA (rDNA) in addition to the nuclear small subunit (SSU, 18S) ribosomal DNA sequences and protein coding genes will be very helpful for future phylogenetic efforts involving the *Nephridiophaga* clade. Indeed, the LSU has been proposed as a good genetic marker for non-Dikarya fungi (e.g., Letcher et al. 2006). Obtaining additional genes for *Nephridiophaga* is, however, very laborious and resource intensive, given the endobiotic nature of these minute fungi. Herein, we decided to opt for SSU rDNA sequences with the aim to expose the uniqueness of *Nephridiophaga.* Increased research interest in this genus and related lineages will hopefully bring about the developments needed in primer design to support the generation of additional genetic marker data, and even full genomes, to fully resolve the precise phylogenetic position of *Nephridiophaga* within the kingdom Fungi. We are in the process of generating additional ribosomal (ITS and LSU) and nuclear gene sequences (Elongation factor alpha) for *Nephridiophaga.*

While about 98% of the described fungi belong to the Dikarya, comprising the two phyla Ascomycota and Basidiomycota, the relationships among the remaining lineages of fungi are less well resolved (Carr and Baldauf 2011, Bauer et al. 2015). Our molecular analyses provide strong support for *Nephridiophaga* as a distinct lineage closely related to the Chytridiomycota *s.l. Nephridiophaga* probably originates from flagellate fungi but has secondarily lost its flagella. Morphological and ultrastructural characters that support the inclusion of *Nephridiophaga* in the Fungi include a heterotrophic lifestyle, propagation by spores, an intranuclear position of the spindle during nuclear division, the presence of chitin in the spore wall, and chitosome-like vesicles on the surface of the maturing spore (Radek et al. 2002).

Significant rDNA sequence divergence above 20%, distinctive morphology, and unique life cycle traits support the delimitation of *Nephridiophaga* from other fungus-like organisms – the ARM clade (Aphelida, Cryptomycota, and Microsporidia; cf. Karpov et al. 2014a, Corsaro et al. 2016) – found near the root of the kingdom Fungi. The ARM clade is presently not included in the Fungi. Nephridiophagids are different from Microsporidia by not possessing a polar tube, polaroplast, and posterior vacuole – structures that are involved in the hatching process of Microsporidia. Endoparasitic trophonts of the Aphelida and Cryptomycota (syn.: Rozellomycota) are able to phagocytose whereas nephridiophagids do not engulf particulate food (Powell 1984, Karpov et al. 2013). The morphology and the life cycle of *Nephridiophaga* deviate from the Chytridiomycota *s.l.,* which possesses typical flagellate stages (zoospores) and centrioles. These structures are missing in nephridiophagids. The only microtubules detected in nephridiophagids so far are intranuclear spindle microtubules formed during nuclear division (Radek and Herth 1999). Thus, the morphology of the kinetosome-associated structures useful in the determination of families and genera of zoosporic fungi cannot be used for classification here (Powell and Letcher 2014). In

general, the Blastocladiomycota, Chytridiomycota *s.str.*, Neocallimastigomycota, and Monoblepharidomycota – the Chytridiomycota *s.l.* – develop posterior flagellate zoospores when free-living but lose the flagella when the life cycle is endoparasitic in all stages (James et al. 2006, Voigt 2012, Powell and Letcher 2014). The nephridiophagids appear to have lost the ability to produce flagella, much like the endoparasitic Microsporidia. This may be due to the completely endobiotic life style, which renders active motility less of a useful trait.

In contrast to many other organisms at the root of the Fungi, the habitat of nephridiophagids is quite restricted – they represent one of the comparatively few groups of fungal endoparasites of arthropods known so far. Further morphological differences are the lack of mycelia (a thallus) and microbody-lipid complexes (MLCs). The MLCs, assemblages of lipid globules, endoplasmic reticulum, mitochondria, and microbodies in Chytridiomycota *s.l.* are suggested to be involved in the conversion of energy from lipids (Powell 1976, Powell and Letcher 2014). Lipid globules to date have not been identified in nephridiophagids, and the presence of microbodies is similarly unclear. In *N. blattellae*, opaque vesicles with homogenous content have been observed (Radek and Herth 1999), but catalase activity could not been shown (unpublished, RR). Compared to agile zoospores, the various life stages of nephridiophagids probably do not need much, if any, energy for motility. Nephridiophagids possess mitochondria with tubular to sac-like inner membrane structures, which stands in strong contrast to mitochondria with cristae in the other fungi. On the whole, there are no specific morphological traits in nephridiophagids that can be used to support a close relationship with chytridiomycete lineages. Molecular analyses presently seem to be the only clue to resolve their phylogenetic relationships – and the molecular results support the nephridiophagids as a distinct lineage among the early diverging fungi.

Conclusion

The molecular, morphological, and ultrastructural evidence brought forward in this study point to the fact that the nephridiophagids form a distinct clade of fungi whose precise taxonomic affiliation cannot be settled at the present time. But we refrain from assigning a rank to this clade in the context of insufficient sampling and clade stability.

Fortunately, we have come far in the generation of molecular data from additional genes and genetic markers, such that we hope to be able to resolve the phylogenetic position of the nephridiophagids in the not too distant future. Studies closing in on the very root of the Fungi have the potential to cast light not only on those particular lineages, but also on the evolution of all extant fungal groups and their nutritional modes and biotic interactions. The increasingly ambitious sampling efforts undertaken by the mycological and molecular ecology communities leave no doubt that the next few years will witness substantial scientific progress in understanding and delimiting the root of the kingdom Fungi. Targeting the cockroach habitat will be worthwhile to consider for future environmental sequencing studies.

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Supplementary material 1

Figure S1

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Data type: molecular data

Explanation note: SSU phylogenetic tree of all eukaryotic lineages (40 k sequences) including spore-forming protist taxa and fungal groups. The *Nephridiophaga* species (purple) cluster closely to Cryptomycota and several long branches of Chytridiomycota and 'zygomycota' sequences at the base of the fungal tree. Holomycota sequences are yellow whereas Haplosporidia and Microsporidia are highlighted in red. The scale indicates expected changes per site. Branch support is given as maximum likelihood resampling values.

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RESEARCH ARTICLE

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Taxonomic novelties and new records of Fennoscandian crustose lichens

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Abstract

We present taxonomic, distributional and ecological notes on Fennoscandian crustose lichens and lichenicolous fungi, based on new collections as well as revision of herbarium material. Two new combinations are proposed: *Frutidella furfuracea* comb. nov. for *F. pullata* and *Puttea duplex* comb. nov. for *Fellhanera duplex*. *Lecidea byssoboliza*, *L. carneoglauca* and *Variolaria torta* are all reduced to synonymy with *Bacidia antricola*, *Bacidia invertens* is synonymized with *B. igniarii*, *B. atrolivida* with *Mycobilimbia tetramera*, and *Gyalidea fruticola* with *Thelenella pertusariella*. A new description is provided for *Micarea hylocomii*. 25 species of lichens and lichenicolous fungi are reported as new to Finland, Norway and/or Sweden: *Absconditella lignicola* (Norway), *Bacidia antricola* (Norway), *B. polychroa* (Norway), *B. pycnidata* (Sweden), *Bacidina adastra* (Sweden), *Biatora veteranorum* (Norway), *Briancoppinsia cytospora* (Finland), *Catillaria scotinodes* (Norway), *Cliostomum subtenerum* (Norway), *Dirina fallax* (Sweden), *Fellhaneropsis almquistiorum* (Norway), *Gyalidea subscutellaris* (Sweden), *Lecania inundata* (Norway), *L. suavis* (Norway), *Micarea capitata* (Norway), *M. deminuta* (Norway), *M. hylocomii* (Sweden), *M. lynceola* (Sweden), *M. soralifera* (Sweden), *M. subconfusa* (Sweden), *Mycoblastus sanguinarioides* (Finland, Sweden), *Paralecia pratorum* (Sweden), *Puttea duplex* (Sweden), *Sarcogyne algoviae* (Finland) and *Toninia subnitida* (Norway). Lectotypes are designated for *Bacidia antricola*, *Lecidea byssoboliza*, *Lecidea carneoglauca*, *Lecidea subconfusa* and *Lecidea submoestula*.

Key words
Ascomycota, lectotypification, lichens, Ramalinaceae, Pilocarpaceae

Introduction

The diversity of lichen-forming and lichenicolous fungi in Fennoscandia is often considered to be reasonably well-known, yet new species are discovered continuously. In 2004, the Fennoscandian checklist included 2414 lichen-forming species (Santesson et al. 2004), while the most recent one includes 2538 species (Nordin et al. 2017). Although new discoveries of macrolichens are indeed made (e.g., Arvidsson et al. 2012, Frödén and Thell 2010, Klepsland 2013, Westberg et al. 2015, 2016), the main uncharted territory is found within the world of small, crustose lichens (e.g., Arup et al. 2014, Ekman 2015, Svensson and Palice 2009, Westberg et al. 2011, 2015, 2016). Crustose lichens comprise about two thirds of all lichens in Fennoscandia, but the taxonomic status, distribution and ecology of several hundred of these species are virtually unknown. The aim of this paper is to contribute to the understanding of Fennoscandian crustose lichen species by reporting a number of species as new to one or more Fennoscandian countries and by providing taxonomic and nomenclatural novelties, including new combinations, synonymizations and lectotypifications, on a series of crustose lichens and lichenicolous fungi.

Material and methods

Light microscopy measurements were made on material mounted in water using an oil-immersion lens, with a precision of 1 µm. Only well-developed ascospores lying outside the asci were measured. Measurements of asci and paraphyses of *Micarea hylocomii* were made on material cut to sections 12–18 µm thick using a freezing microtome and stained with lactophenol cotton blue. HPTLC was performed using the method described by Arup et al. (1993). Coordinates are in the WGS84 map datum unless otherwise stated.

Taxonomy

Absconditella lignicola Vězda & Pišút

Nova Hedwigia 40: 344 (1985, "1984"). – Type: Slovakia, Carpates, in valle torrentis Hincov potok supra lacum Strbské pleso, ad truncum decorticatum *Piceae exselsae* in Piceeto montano, alt. 1300 m, 22 Aug 1983, I. Pišút & A. Vězda (PRA-V, holotype, not seen; BRA, GZU, M, isotypes, not seen).

New to Norway. Reported from much of the Northern hemisphere as well as Tasmania (Coppins 2009a, Urbanavichus 2010).

In Norway, this species has usually been collected from the upper side of large, relatively recently decorticated logs of *Picea abies*, but once also on a stump (not cut). It has, however, also been collected on logs of *Populus tremula* and *Pinus sylvestris*. The species is mostly found in association with slimy biofilms, in Norway often accompanied by *Micarea peliocarpa* (Anzi) Coppins & R.Sant. All Norwegian finds have been made in lowland *Picea* forests in the Oslofjord area. Most of the localities are characterized by high productivity with moderate to large amounts of dead wood.

Specimens examined: NORWAY: Buskerud, Øvre Eiker, Knivfjellet-Snaukollen, på middels nedbrutt, barkløs granlåg, gammel blåbær-granskog med mye død ved, MGRS NM 5403 3438 [=59.8436°N 9.9642°E], alt. 590 m, 15 May 2016, J. T. Klepsland JK16-229a (O-L-206462). Buskerud, Lier, Storkollen S, på stor barkløs granstubbe i tett granbestand ved skiløype, svak lågurtskog, MGRS NM 6458 3228 [=59.8232°N 10.1518°E], alt. 375 m, 31 May 2016, J. T. Klepsland JK16-247 (O-L-206548). Oslo, Oslo, Solbergvannet S, barkløs granlåg, lite nedbrutt, eldre blåbær-granskog i terrengforsenkning/liten bekkedal, MGRS PM 0452 4146 [=59.8974°N 10.8683°E], alt. 235 m, 23 April 2014, J. T. Klepsland JK14-L033 (O-L-200173). Oslo, Oslo, Solbergvannet S, barkløs, lite nedbrutt granlåg, eldre blåbær-granskog i terrengforsenkning/liten bekkedal, MGRS PM 0450 4139 [=59.8968°N 10.8680°E], alt. 235 m, 27 April 2014, J. T. Klepsland JK14-L039 (O-L-200180). Oslo, Oslo, Solbergvannet S, barkløs, middels nedbrutt furulåg, eldre blåbær-barblandingsskog, MGRS PM 0447 4143 [=59.8971°N 10.8675°E], alt. 235 m, 27 April 2014, J. T. Klepsland JK14-L038c (O-L-200179). Oslo, Oslo, Solbergvannet SØ, på barkløs ospelåg, middels nedbrutt, eldre blåbær-granskog i terrengforsenkning, MGRS PM 0466 4133 [=59.8962°N 10.8708°E], alt. 240 m, 27 April 2014, J. T. Klepsland JK14-L042 (O-L-200183). Oslo, Oslo, Sarabråten N, barkløs, lite nedbrutt granlåg, rik sørboreal blandingsskog (grandominert), MGRS PM 0522 4098 [=59.8929°N 10.8806°E], alt. 220 m, 27 April 2014, J. T. Klepsland JK14-L049 (O-L-200188).

Bacidia antricola Hulting

Lichenol. exkurs. vestra Bleking 17 (1872). – Type: Sweden, Blekinge, Hällaryd par., "Valhall", 1871, J. Hulting (UPS L-753472, lectotype, designated here by SE; GB 0151489, LD, S L4637, S L69089, isolectotypes, seen by SE).

Variolaria torta Taylor in Mackay, Fl. Hibern. 2: 114 (1836), *nom. rejic. prop.* (ICN Art. 56.1). – Type: Ireland, Co. Kerry, "shaded rocks, Askew Wood", T. Taylor (BM 000974464, holotype or syntype, seen by SE).

Lecidea carneoglauca Nyl., Flora 56: 295 (1873). *Bacidia carneoglauca* (Nyl.) A.L.Sm., Monogr. Brit. Lich. 2: 155 (1911). – Type: Jersey, "shady rocks near Rozel", 1873, C. Du Bois Larbalestier (BM 000974466, lectotype, designated here by SE; H-NYL 17406, isolectotype marked "Jersey", seen by SE).

Lecidea byssoboliza Nyl., Flora, Regensburg 62: 206 (1879). *Bilimbia byssoboliza* (Nyl.) A.L.Sm., Monogr. Brit. Lich. 2: 141 (1911). *Bacidia byssoboliza* (Nyl.) H.Olivier, Bull. Géogr. Bot. 21: 170 (1911). – Type: Ireland, Co. Galway, "in antro, Killery Bay prope Kylemore", 1878, C. Du Bois Larbalestier (H-NYL 21838, lectotype, designated here by SE; no obvious isolectotypes in BM).

New synonyms. New to Norway. Previously known from the United Kingdom, Ireland, Sweden, the Netherlands, Luxembourg, Belgium, Germany, Austria, and the Czech Republic (Hulting 1872, Bouly de Lesdain 1910, van den Boom et al. 1999, Palice 1999, Aptroot et al. 2004, Coppins and Aptroot 2009, Berger and Türk 1993, Wirth et al. 2013, Diederich et al. 2014). Previously reported from Norway by Santesson et al. (2004), but the material on which this report was based has later been shown to be misidentified.

The types of *Variolaria torta*, *Bacidia antricola*, *Lecidea carneoglauca*, and *L. byssoboliza* are clearly conspecific. *Variolaria torta*, by far the oldest name, has after its introduction only been briefly mentioned by Adams (1909) and Zahlbruckner (1928) as a dubious name. Therefore, in the interest of nomenclatural stability, a proposal to reject *Variolaria torta* has been submitted (Ekman 2017). The type material of this name in BM consists of a small but well preserved and readily identifiable specimen with abundant pycnidia but no apothecia, sent to W. J. Hooker by Taylor. Among the remaining names, the combination *Bacidia carneoglauca*, introduced by Smith (1911) is currently the most widely used. However, *Bacidia antricola* was validly published in the dissertation of Johan Hulting no later than 27 May 1872 (Hulting 1872) and is consequently older than *Lecidea carneoglauca*. *Bacidia antricola* has been included in every subsequent lichen flora or checklist of Swedish lichens (e.g., Fries 1874, Forssell and Blomberg 1880, Magnusson 1936, Santesson 1984, Foucard 1990, Foucard 2002). Furthermore, there are reports under this name from Belgium (Bouly de Lesdain 1910), as well as a further Swedish record (Hulting 1925). Therefore, this name is adopted here. The lectotype of *Bacidia antricola* selected here is the largest and most well developed of the five available syntypes, with numerous pycnidia and several apothecia in various states of development.

Although geographically widely separated, both of the newly discovered Norwegian sites for *B. antricola* are situated close to the west-coast, with an oceanic climate. At both sites, the species grew on somewhat metal-enriched rocks in shady and humid situations, below overhanging cliffs and sheltered from rain. At the southernmost locality, the species was largely confined to steep or almost vertical rock walls at the entrance of an old (copper?) mine. The entrance to the cave is situated in a steep ESE-facing hillside, close to but well above the fjord, and is surrounded by a lush forest dominated by *Corylus avellana*, *Fraxinus excelsior*, and *Ulmus glabra*. At the northern locality, the species was mainly found on horizontal or slightly inclined rocks along a small stream, deep underneath an overhang at the bottom of a small but topographically uneven south-facing hill. The surrounding forest is dominated by *Betula pubescens* and *Populus tremula*, with scattered *Corylus avellana*.

Additional specimens examined: NORWAY: Hordaland, Kvinnherad, Djupevika (Varaldsøy naturreservat), på skyggefullt, jernrikt berg i gruveåpning. Rik edelløvskog,

MGRS LM 3575 6867 [=60.1220°N 6.0437°E], alt. 130 m, 12 September 2015, J. T. Klepsland JK15-L139 (O-L-204535). Nord-Trøndelag, Leka municipality, Gjertrudvika N, on shaded pebbles and rocks by a small stream beneath an overhanging rock wall in a forest dominated by birch and aspen, 65.0448°N 11.5696°E, alt. 40 m, 3 July 2016, J. T. Klepsland JK16-461 (O). SWEDEN: Blekinge, Edestad par., c. 700 m WNW of Edestad, on small boulder on the ground in humid, deciduous forest, 56.21966°N 15.35112°E, alt. 25 m, 26 April 2013, S. Ekman 5640 (UPS L-782502). Södermanland, mellan Kvarsebo och Säter, på gneis (på en mycket skuggig lokal), 1909, J. Hulting (S L69092). Södermanland, Kvarsebo prope Säter, 19 August 1898, J. Hulting (S L69091); Ibid., 28 June 1910, J. Hulting (S L69090).

Bacidia igniarii (Nyl.) Oxner

Flor. Lish. Ukraini 2: 166 (1968). *Lecidea igniarii* Nyl., Flora 50: 328 (1867). – Type: Finland, "ad Polyp. igniarium in Tavastia", 1863, J. P. Norrlin (H-NYL 17232, lectotype selected by Ekman 1996, seen by SE).

Bacidia invertens Vain., Acta Soc. Fauna Flora Fenn. 53 (1): 149 (1922), non *Bacidia invertens* (Nyl.) Zahlbr., Cat. Lich. Univ. 4: 252 (1926). – Type: Finland, Etelä-Häme, "Tammela prestgård", 1868, A. Kullhem (H, holotype or possibly syntype, seen by SE).

New synonym. *Bacidia invertens* was listed as an accepted species by Stenroos et al. (2016). The type material, however, consists of a well developed and typical specimen of *Bacidia igniarii*, and the former is consequently reduced into synonymy. There is some doubt whether the specimen in H was the only one available to Vainio at the time of description. Surprisingly, there does not seem to be any material of *B. invertens* deposited in TUR (Alava 1988).

Bacidia polychroa (Th.Fr.) Körb.

Parerga Lich., fasc. 2: 131 (1860). – *Biatora polychroa* Th.Fr., Öfvers. Kongl. Vetensk.-Akad Förh. 12 (1): 17 (1855). – Type: Ukraine, "in Acere campestri", (UPS L-106162, lectotype selected by Ekman 1996, seen by SE).

New to Norway. This species is distributed across Europe and eastern temperate North America (Ekman 1996). Reports from other areas of the world probably represent other species. *Bacidia polychroa* is red-listed as threatened or regionally extinct in a number of countries where it has been assessed, *viz.* Sweden (ArtDatabanken 2015), Finland (Jääskeläinen et al. 2010), Germany (Wirth et al. 2011), and the United Kingdom (Woods and Coppins 2012).

The Norwegian find of *B. polychroa* was made at the base of an old *Acer platanoides* situated in a narrow and rather deep ravine in a region of mixed temperate woodland composed of e.g. *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior, Picea abies*, *Pinus sylvestris*, *Quercus robur*, and *Ulmus glabra*. The site is sheltered and characterized

by high humidity and minimal sun exposure. Several additional lichen species with oceanic preferences or a demand of high and stable air humidity grow in the vicinity, *viz. Bacidia biatorina* (Körb.) Vain., *B. laurocerasi* (Delise ex Duby) Zahlbr., *Bacidina phacodes* (Körb.) Vězda, *Coenogonium luteum* (Dicks.) Kalb & Lücking, *Gyalecta flotowii* Körb., *Lobaria virens* (With.) J.R.Laundon, *Pyrenula nitida* (Weigel) Ach., and *Thelotrema lepadinum* (Ach.) Ach.

Specimen examined: NORWAY: Vestfold, Larvik municipality, Fjærevardåsen E, on bark at base of old *Acer platanoides* in a deep, narrow wooded ravine, 59.1873°N 10.0515°E, alt. 150 m, 23 June 2016, J. T. Klepsland JK16-420 (UPS L-785596).

Bacidia pycnidiata Czarnota & Coppins

Fig. 1A–B

Lichenologist 38: 407 (2006). – Type: Czech Republic, Eastern Sudetes, Rychlebské hory Mts, W of Bila Voda village, vicinity of worked-out quarry of marble 'Kukačka' near the border of Poland, 50°26'18"N 16°53'14"E, alt. c. 360 m, on bryophytes over marble rock within mixed spruce-ash forest, 23 April 2004, P. Czarnota 4157 (GPN, holotype, not seen; E, UGDA, isotypes, not seen).

New to Sweden. *Bacidia pycnidiata* has been reported from Belgium, Poland, the Czech Republic, Slovakia, Lithuania, Estonia, Finland, Ukraine, and Russia (Republic of Mordovia and Republic of Adygea) in Europe, as well as the Republic of Buryatia south of Lake Baikal in Asian Russia (assuming that the watershed through Greater Caucasus is taken as the geographic border between Europe and Asia) (Czarnota and Coppins 2006, Suija et al. 2007, Ertz et al. 2008, Pykälä 2008, Motiejūnaitė et al. 2011, Dymytrova 2013, Malíček et al. 2014, Urbanavichus and Urbanavichene 2013, Urbanavichene and Urbanavichus 2014, Urbanavichene and Palice 2016). The species is mostly found on trunks of deciduous trees and shrubs, either directly on the bark or over bryophytes, in more or less shady and humid habitats. The autecological amplitude seems to be wide, however, and there are scattered finds on coniferous trees, more or less moribund cyanolichens, soil, as well as stones (or bryophytes on stones) on the ground, including metal-rich waste (Vondrák et al. 2010, Czarnota and Hernik 2014 in addition to references above). It has been suggested that the species is favoured by anthropogenic impact (Czarnota and Hernik 2014), although its ecological repertoire also includes semi-natural old-growth forests (Suija et al. 2007).

The Swedish find was made on bark of an old *Acer platanoides* in a semi-open stand of *Quercus robur* in a grazed field. The locality is situated at the outskirts of the town of Kalmar, and the surroundings consist partly of cultivated fields, partly of urbanized land (roads, housing, manufacturing, commerce, small airport etc.). Although frequently reported only in an anamorphic state, *B. pycnidiata* was found to produce abundant apothecia in the Swedish site.

Specimens examined: SWEDEN: Småland, Kalmar par., Hagbygärde, ekbacke S om Lantmännen, grov lönn i ekdominerad betad hagmark, 56.67492°N 16.30616°E,

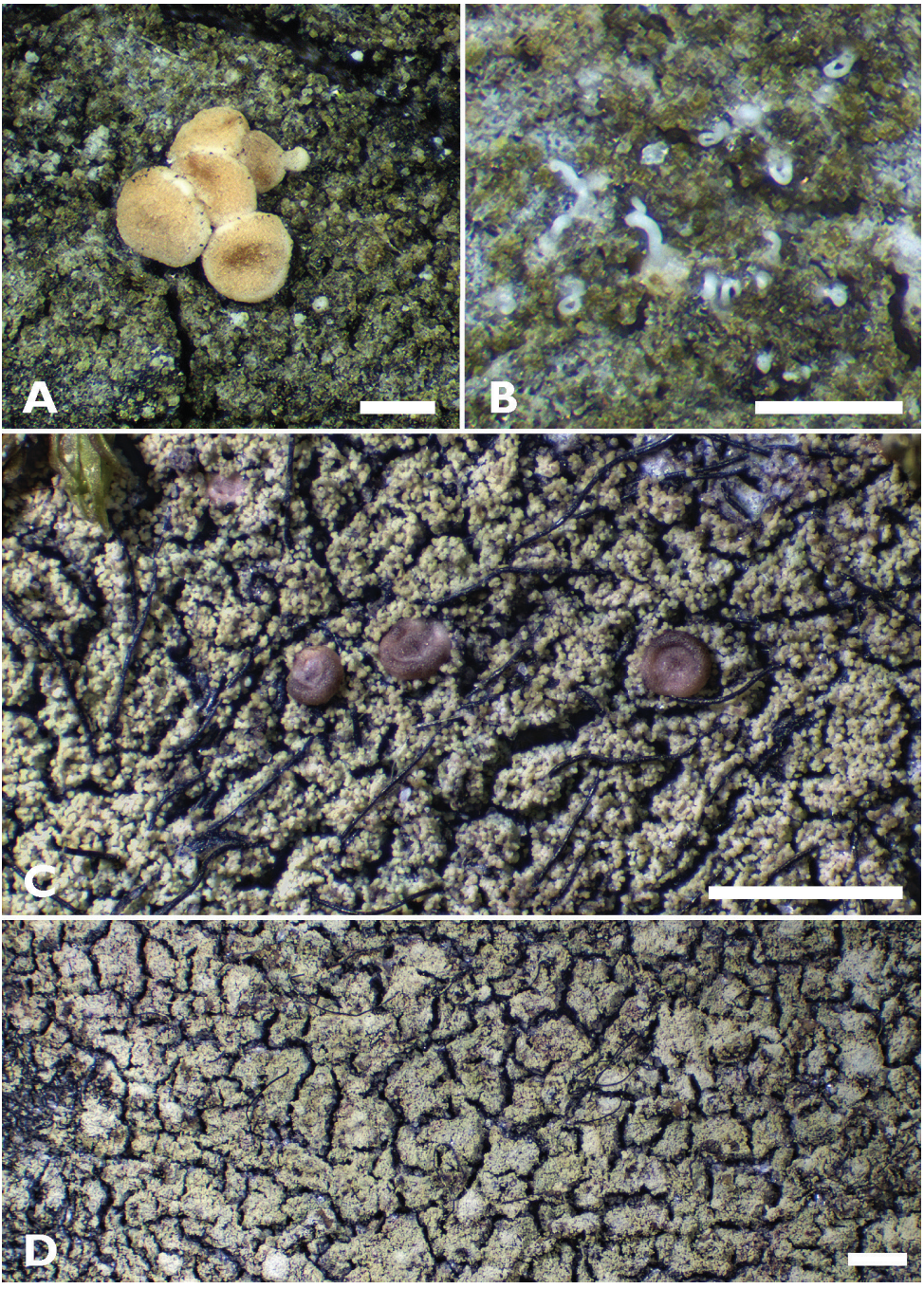

Figure 1. A–B *Bacidia pycnidiata* (UPS L-681835), **A** group of apothecia **B** pycnidia with long and curved necks. **C–D** *Bacidina adastra*, **C** close-up of thallus with apothecia, note intermingled black fibers belonging to the polypropylene fabric on which the specimen grows (UPS L-779918) **D** overview of thick, sterile thallus (UPS L-779932). Scale bars: 0.25 mm (**A–B**), 1 mm (**C–D**).

27 September 2011, T. Knutsson 2011-067 (UPS L-681835). ESTONIA: Jõgevamaa, Puurmani comm., Altnurga village, Pikknurme forestry, Altnurga ash forest, alt. 20–30 m, 58°32'40"N 26°17'00"E), on a fallen *Prunus padus*, 22 June 2005, G. Thor 18981 (UPS L-159702).

Bacidina adastra (Sparrius & Aptroot) M.Hauck & V.Wirth

Fig. 1C–D)

Herzogia 23: 16 (2010). *Bacidia adastra* Sparrius & Aptroot, Lichenologist 35: 275 (2003). – Type: The Netherlands, Zuid-Holland, Gouda, Goudse Hout, landscape garden 'Heemtuin Goudse Hout', on fallen branch of *Salix alba*, 9 February 2001, L. B. Sparrius 4566 (L, holotype, not seen; ABL, herb. Sparrius, isotypes, not seen; E-00250877, isotype, seen by SE).

New to Fennoscandia. This species has been reported from the Netherlands, Belgium, United Kingdom, Ireland, Germany, Poland, Estonia, Czech Republic, Austria, Switzerland, France, Ukraine, Armenia, and Ecuador (Sparrius and Aptroot 2003, Kubiak and Sparrius 2004, Aptroot et al. 2005, Aptroot and Honegger 2006, Vondrák 2006, Coppins and Aptroot 2009, Khodosovtseva 2009, Berger and Priemetzhofer 2010, Roux 2012, Gasparyan and Sipman 2016). In several instances, however, reports have been based on sterile material, a questionable practice given that the species does not produce any secondary substances. In an addendum to Smith et al. (2009) (available at http://www.britishlichensociety.org.uk/recording-mapping/downloads, accessed 21 November 2016), *Bacidina adastra* is considered rare and strongly over-reported, being confused with crusts of free-living green algae. Morphologically, *B. adastra* is somewhat reminiscent of *B. neosquamulosa* (Aptroot & Herk) S. Ekman, which in its current delimitation may turn out to include more than one species. *B. neosquamulosa* in the strict sense forms imbricate, finely dissected microsquamules that may later disintegrate to form goniocysts. *B. adastra*, on the other hand, starts out as minute, sometimes somewhat flattened, granules that soon bud off new granules in a more or less coralloid manner, the end result being a thick, finely granular and pale green crust. In addition, the thallus surface tends to be more shiny in *B. neosquamulosa* than in *B. adastra*.

In Fennoscandia, *Bacidina adastra* is currently known from two sites in southern Skåne. The first find was made in a churchyard surrounded by houses in an otherwise open, agricultural landscape, where the species occurred in fair quantity and sparingly fertile on a young, planted *Ulmus*. The second find was made in the northern outskirts of the town of Lund, in public plantations with a variety of shrubs where the ground had been covered by a black fabric of non-woven polypropylene to prevent weeds from establishing. This fabric is colonized by a variety of lichens, mostly crustose lichens during the first years, whereas later successional stages are dominated by *Peltigera didactyla* (With.) J.R.Laundon and species of *Cladonia*. The crustose lichen flora is richest in species and individuals in slopes with moderate shade from shrubs.

Slopes seem to be preferred because leaf litter does not easily accumulate on the fabric. The richest spots are downhill from fences cutting through the plantations, where the concentration of metal ions is probably high. Apart from large spots of abundantly fertile *Bacidina adastra*, other lichens encountered on the ground cover fabric were *Agonimia globulifera* M.Brand & Diederich, *Bacidina chloroticula* (Nyl.) Vězda & Poelt, and *Peltigera didactyla*.

Additional specimens examined: SWEDEN: Skåne, Norra Nöbbelöv par., 75 m WNW of the church, on ground cover fabric in plantation of shrubs, 55.7321°N 13.1639°E, alt. 25–30 m, 15 October 2011, S. Ekman 5635 (UPS L-779932). Skåne, Norra Nöbbelöv par., 150 m WSW of the church, on ground cover fabric in plantation of shrubs, 55.7315°N 13.1627°E, alt. 25–30 m, 15 October 2011, S. Ekman 5632 (UPS L-779918). Skåne, Norra Nöbbelöv par., 170–190 m W of the church, on ground cover fabric in plantation of shrubs, 55.7318°N 13.1621°E, alt. 25–30 m, 15 October 2011, S. Ekman 5628, 5629, 5630, 5631 (UPS L-779914, L-779915, L-779916, L-779917). Skåne, Södra Åby par., at S side of the church, just outside the bordering hedge, on young *Ulmus*, 55.3853°N 13.3104°E, 13 August 2001, S. Ekman 5637 (UPS L-781595).

Biatora veteranorum Coppins & Sérus.

in Sérusiaux et al., Bryologist 113: 337 (2010). *Catillaria alba* Coppins & Vězda in Vězda, Lichenes Rariores exsiccati 53 (1993), non *Biatora alba* (Schleich.) Hepp. – Type: Austria, Tirol, Hohe Tauern, Virgen, Hinteregg, ad truncum putridum *Laricis*, alt. ca. 1600 m, 1 Sept 1988, A. Vězda (PRA-V, holotype, not seen; UPS L-030528, isotype, seen by SE).

New to Norway. Previously known from Sweden, Denmark, Scotland, France, Germany, Poland, the Czech Republic, Slovakia, Austria, Spain, Italy, Ukraine, Russia, and Rwanda (Vězda 1993, Palice 1999, Czarnota 2003, Killmann and Fischer 2005, Coppins et al. 2005, Sérusiaux et al. 2010, Knutsson 2014, Urbanavichus and Urbanavichene 2014).

The Norwegian finds were made on old and hard wood, in one case on the underside of a decorticated, leaning trunk of *Sorbus aucuparia* in a rain-sheltered site under an over-hanging rock, and in two other cases on wood of very old but living *Taxus baccata*, both on the underside of decorticated branches and on vertical surfaces inside a hollow trunk. All known localities consist of humid oldgrowth forests dominated by spruce and aspen or by birch and aspen. No apothecia were observed in the Norwegian sites, but numerous white and stalked pycnidia were present. Conidia in the Norwegian specimens measure c. 4 × 1.5 µm, and the photobiont is chlorococcoid, 6–15 µm diam. By comparison, conidia and photobiont cells in an isotype of *Catillaria alba* (UPS L-030528) measure 3.1–4.2 × 1.5–1.9 and 7–13 µm, respectively.

Additional specimens examined: NORWAY: Aust-Agder, Evje og Hornnes, Prestøygardsvatnet Ø, på hard ved på undersiden av lutende gammel rogn, skyggefull

eldre blåbær-røyrkvein-ospedominert skog med gran og rogn, MGRS MK 3915 9650 [=58.6046°N 7.9528°E], alt. 445 m, 12 October 2013, J. T. Klepsland JK13-L740 (O-L-206558). Aust-Agder, Evje og Hornnes, Svartebergli, på hard ved inni stammeskadet gammel barlind, middelaldret edelløvblandet bjørk-ospeskog med gammel barlind, MGRS MK 2268 9427 [=58.5820°N 7.6702°E], alt. 325 m, 26 December 2016, J. T. Klepsland JK16-926 (O-L-206549). Aust-Agder, Evje og Hornnes, Svartebergli, på undersiden av gamle, hengende døde greiner på gammel barlind, eldre edelløvblandet bjørk-ospeskog med gammel barlind, MGRS MK 2255 9425 [=58.5818°N 7.6680°E], alt. 370 m, 26 December 2016, J. T. Klepsland JK16-928 (O-L-206550).

Briancoppinsia cytospora (Vouaux) Diederich et al.

In Diederich et al., Fungal Diversity 52: 8 (2012). *Phyllosticta cytospora* Vouaux, Bull. Trimestr. Soc. Mycol. Fr. 30: 193 (1914). *Phoma cytospora* (Vouaux) D. Hawksw., Trans. Br. Mycol. Soc. 67: 56 (1976). – Type: Luxembourg, N of Reckange (Mersch), Enelter Kapelle, on old trunk of *Aesculus*, on degenerate thalli of cf. *Lecanora conizaeoides*, 3 September 2009, P. Diederich 16849 (BR, neotype, selected by Diederich, Ertz, Lawrey and van den Boom in Diederich et al. 2012, not seen; GMUF, herb. Diederich, herb. van den Boom, isoneotypes, not seen).

New to Finland. *Briancoppinsia cytospora* is widespread in Europe and has also been reported from the United States. (Diederich et al. 2012). In Fennoscandia, the species has previously been reported from Norway and Sweden (Santesson 1993). A member of the Arthoniaceae (Arthoniales), this species is a lichenicolous fungus on *Lecanora conizaeoides* Nyl. ex. Cromb., *Cladonia* spp., *Pertusaria* spp., and various parmelioid lichens (Diederich et al. 2012). It is recognized by the globose pycnidia with initially punctiform ostioles that later expose the white conidial mass, the KI+ red pycnidial gel, and the slightly curved conidia measuring 5.8–6.8 × 1.6–2.0 µm (Diederich et al. 2012).

Briancoppinsia cytospora was first encountered on *Hypogymnia physodes* (L.) Nyl. growing on *Ulmus*. Subsequently, we examined all Finnish collections of *H. physodes* in herbarium UPS, which resulted in five additional finds.

Specimens examined: FINLAND: Nylandia, 3 km SE Helsinki downtown, Suomenlinna (Sveaborg) fortress, on *Ulmus glabra*, elev. 15 m, 60°08'38"N 24°59'08"E (WGS84, ±150 m), 31 July 2016, G. Thor 33920 (UPS). Regio Aboënsis, Raisio, base of Kullavuori hill, 26 May 1969, R. Alava, K. Alho & U. Laine (UPS L-189538, filed under *H. physodes*). Tavastia australis, Toijala, 15 August 1931, G. Degelius (UPS L-086913, filed under *H. physodes*). Tavastia australis, Kylmäkoski, Taipale in vicinity of the farm Matti Seppälä, 28 March 1965, L. Kärenlampi (UPS L-189542, filed under *H. physodes*). Savonia borealis, Pielavesi, W-Säviä, Alava prope Matopuro, 10 October 1960, A. J. Huuskonen (UPS F-785388). Ostrobottnia Media, Nykarleby, Döbeln-monumentet, 27 June 1957, G. Degelius (UPS L-086920, filed under *H. physodes*).

***Catillaria scotinodes* (Nyl.) Coppins**
Fig. 2A

Lichenologist 21: 223 (1989). *Lecidea scotinodes* Nyl., Flora 56: 295 (1873). *Kiliasia scotinodes* (Nyl.) Coppins in Gilbert et al., Lichenologist 20: 238 (1988). – Type: Scotland, Perth and Kinross, V. C. 88, 'Craig Tulloch, Blair Athole, ad saxa micaceo-schistosa', August 1871, J. M. Crombie (H-NYL, BM, syntypes, not seen, UPS L-196597, potential but undated syntype, seen by SE).

New to Norway. Previously reported from Sweden (Coppins 1994), United Kingdom (Coppins 1989), and Switzerland (Groner 2006). Reports from the Ukraine of *'Catillaria* aff. *scotinodes'* (Khodosovtsev et al. 2007), based on material that is similar to *C. scotinodes* except in having brown instead of green pigment in the epihymenium, possibly refers to *Catillaria aphana* (Nyl.) Coppins or *Bacidia freshfieldii* (Vain.) Zahlbr.

The Norwegian locality is situated close to the Barents Sea, just within the southern part of the arctic climate zone. The site is characterized by dwarf-shrub heath and sharp rocky ridges of layered, steeply inclined, metamorphic rocks of varying composition, both acid and base-rich. *Catillaria scotinodes* was found growing on a fairly exposed ridge of calciferous sandstone with layers of dolomite.

Additional specimens examined: NORWAY: Finnmark, Vardø municipality, Persfjord NW, on ridge of calciferous sandstone in subarctic heath, fairly exposed, 70.4253°N 30.7574°E, alt. 40 m, 1 July 2014, J. T. Klepsland JK14-L355 (UPS L-785594). SWEDEN: Dalarna, Idre par., Mount Vålåberget (just E of Idre), at the top of the very steep uppermost part of the mountain, on rocks in open situation, 61°50'N 12°49'E, alt. 600 m, 7 October 1989, R. Moberg 9040 (UPS L-13858). Jämtland: Åre par., Handöl Rapids in river Handölån, W of lake Ånnsjön, E shore of the river, S of the suspension bridge and N of the small hill with boulders c. 400 m SSW of the bridge, on flat part of schistose rock on the shore, 63°23'N 12°45'E, alt. 570 m, 31 July 1993, B. Owe-Larsson H93-47a (UPS L-696344). Lycksele lappmark, Tärna par., Ume älv, Strimasund, udde S om Strimasundet, svagt lutande kalkstrandklippa i övre geolitoral, 66°03'N 14°52'E, alt. 520 m, 1 September 1963, G. E. Du Rietz 700b (UPS L-132194).

***Cliostomum subtenerum* Coppins & Fryday**

In Fryday & Coppins, Lichenologist 44: 724 (2012). – Type: Great Britain, Wales, V. C. 52, Anglesey, NE of Amlwch, cove E of Llam Carw, 23/460.936, on vertical siliceous ('green' schist) coastal rocks above HWM, 11 June 1995, S. P. Chambers s. n. (E, holotype, not seen).

New to Norway. This species was recently described from two sites in the British Isles, one in Wales and one in Scotland (Fryday and Coppins 2012).

C. subtenerum was encountered at the Helgeland coast in central Norway, only 200 m from the coastline, where it occupied a shelf appearing on a roughly horizontal rock

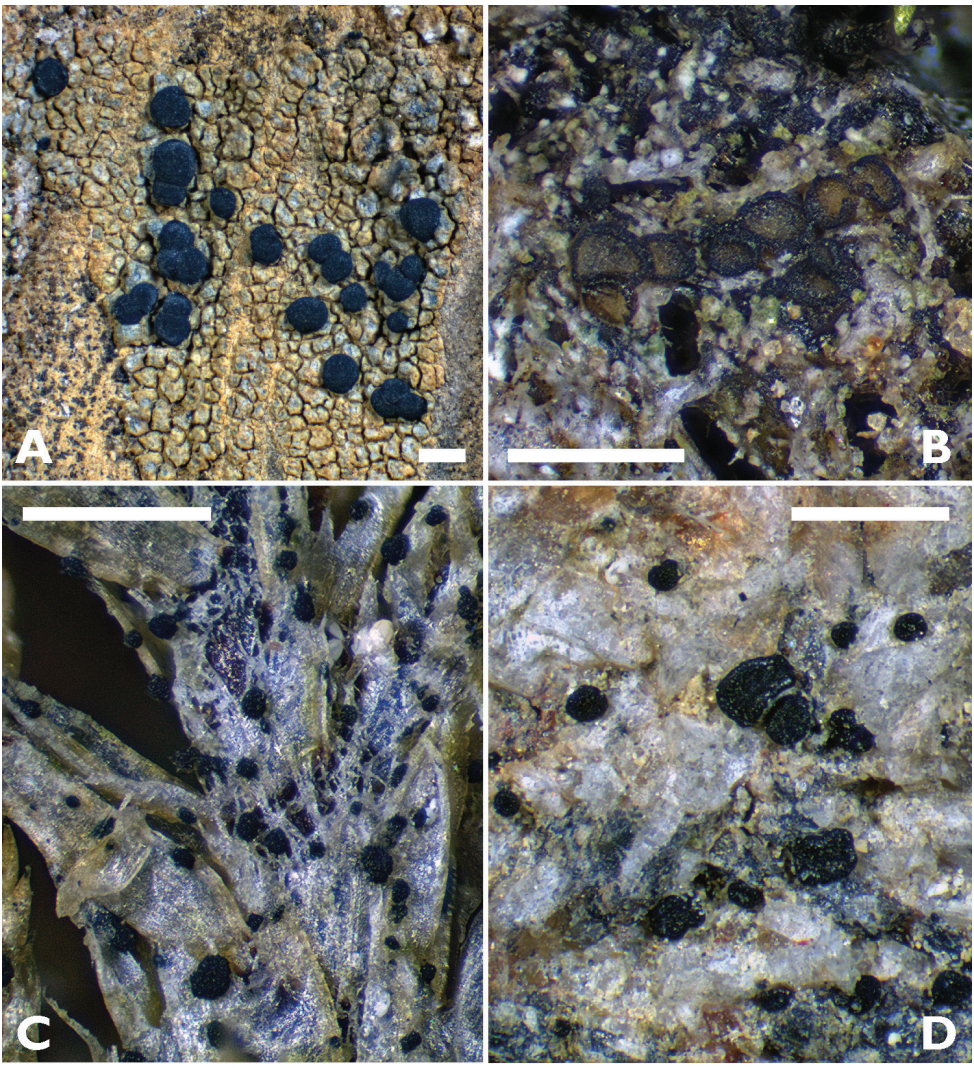

Figure 2. A *Catillaria scotinodes* (UPS L-785594) **B** *Gyalidea subscutellaris* (UPS L-679028) **C** *Micarea hylocomii* (UPS L-803526) **D** *Micarea lynceola* (UPS L-778164). Scale bars: 0.5 mm.

face under an overhang formed by a big mica-schist boulder. This site is part of an extensive boulder field at the nearly horizontal north foot of the very steep Mt. Skjeggen. The boulder field is partly covered by open birch forest, while flat patches between the boulders are mostly covered by small bogs. Other notable lichens found at the site include *Coccotrema citrinescens* P.James & Coppins, *Pannaria hookeri* (Borrer ex Sm.) Nyl., *Spilonema paradoxum* Bornet, and *Sporodictyon cruentum* (Körb.) Körb. Although extensively searched for in the surrounding area, no additional finds were made.

Specimen examined: NORWAY: Nordland, Gildeskål, Skjeggen N, på horisontalt berg under stort overheng, åpen bjørkeskog, MGRS VQ 4084 2625 [= 66.9482°N 13.6461°E], alt. 30 m, 7 June 2013, J. T. Klepsland JK13-L211 (O-L-204569).

***Dirina fallax* De Not.**

Giorn. Bot. Ital. 2: 189 (1846). – Type: Italy, Sardinia, Prov. Sassari: Nurra, Capo (Punta) Falcone, Monte della Crocetta, near sea, alt. c. 50 m, macchia on schistose (silicious) rocks, 1987, T. Ahti 47193 (S F184389, neotype, selected by Tehler et al. 2013, not seen; H, isoneotype, not seen). For synonyms, see Tehler et al. (2013).

New to Sweden. *Dirina fallax* is mainly distributed in the western part of the Mediterranean Region and along the Atlantic coast from northern Morocco to Scotland, with an outpost locality in the Canary Islands. Records from Baden-Württemberg in Germany and the South Bohemian and South Moravian Regions of the Czech Republic are geographically closest to the the Swedish locality (Tehler et al. 2013). However, Norwegian material determined as *D. massiliensis* Durieu & Mont. has not been examined by us and may partly represent *D. fallax*.

Dirina fallax was first collected in Sweden 1998 on Mt. Omberg in the province of Östergötland and was reported as *D. massiliensis* f. *sorediata* by Nordin and Hermansson (1999). They noted the siliceous substrate and the thin, dark thallus. The species was again observed at the same locality when visited by the Swedish Lichenological Society during an excursion in 2015 (Westberg and Arup 2016). The Swedish material is sorediate and lacks apothecia (see photograph in Westberg and Arup 2016, Fig. 3).

For a long time, *Dirina fallax* was treated as a synonym of *D. massiliensis*. Molecular data, however, show that they are distinct species, although closely related (Tehler et al. 2013). The shape and size of apothecia, ascospores and conidia as well as the secondary chemistry (erythrin, ± lecanoric acid and unidentified substances) are the same in both species. *D. fallax*, however, has a thinner and usually more brownish grey thallus compared to the thicker, whitish and chalk-like thallus of *D. massiliensis* (Tehler et al. 2013). The thallus and apothecial thalline margin of *D. fallax* vary considerably in colour, from dark brown over greyish to creamy white. *D. fallax* is confined to acidic rocks, *D. massiliensis* to calcareous rocks. Sorediate specimens of *Dirina fallax* are morphologically indistinguishable from sorediate specimens of *D. canariensis* Tehler & Ertz, which is considered endemic to the Canary Islands (Tehler et al. 2013).

Specimens examined: SWEDEN: Östergötland, Västra Tollstad par., Mt Omberg, Alvastra, beech forest N of the ruins, 58°17'N 14°39'E, alt. 150 m., on overhanging rock, 9 May 1998, A. Nordin 5056 (TLC: erythrin and unknown substance) (UPS L-099094); ibid., 25 April 2015, U. Arup L-15009 (LD).

***Fellhaneropsis almquistiorum* S.Ekman**

Nord. J. Bot. 33: 641 (2015). – Type: Sweden, Medelpad, Liden par., eastern escarpment of Mt Vättaberget, on shaded stones on the ground just below vertical rock face, 62.69496°N 16.77550°E, 150 m a.s.l., 13 September 2011, S. Ekman 5607 and M. Svensson (UPS L-684029, holotype, seen by SE; GZU, isotype, seen by SE).

New to Norway. Previously reported from central Sweden, central Germany (Ekman 2015), and Finland (Pykälä 2017).

The Norwegian finds are located c. 20 km apart in the area between the Oslofjord and lake Øyeren, in sheltered sites with old-growth bilberry-spruce forest. At both sites, the species was found exclusively on mineral-rich black biotite rock in deep shade, sheltered from rain and trickling water by overhanging rocks. The only associated lichen species recorded was *Brianaria lutulata* (Nyl.) S.Ekman & M.Svensson (found at both sites).

Additional specimens examined: NORWAY: Akershus, Enebakk municipality, Gaupestein, on deeply shaded rock (biotite gneiss) below huge overhang in old-growth bilberry-spruce forest, MGRS PM 1203 2028 [= 59.7054°N 10.9910°E], alt. 235 m, 17 May 2014, J. T. Klepsland JK14-L118 (O-L-206531, UPS L-785595). Oslo, Oslo kommune, Sarabråten N, på nesten vertikal bergflate (glimmergneis) i skyggefull bergsprekk, bergskrent i eldre granskog, MGRS PM 0522 4106 [=59.8937°N 10.8806°E], alt. 230 m, 27 April 2014, J. T. Klepsland JK14-L678 (O-L-206547).

Frutidella furfuracea **(Anzi) M.Westb. & M.Svensson, comb. nov.**
MycoBank: MB819390

Biatora furfuracea Anzi, Comment. Soc. Crittog. Ital. 2: 13 (1864). *Biatora amaurospoda* Anzi, Comment. Soc. Crittog. Ital. 2: 13 (1864), *nom. inval.* [ICN Art. 32.1a] or *nom. illeg.* [ICN Art. 52.1]. *Lecidea furfuracea* (Anzi) Jatta, Sylloge Lich. Ital. 326 (1900), non Pers., *nom. illeg.* [ICN Art. 53.1]. *Lecidea anziana* Zahlbr., Cat. Lich. Univ. 3: 733 (1925). – Type: Italy, Lombardy, "sui tronchi marcidi dei pini nell' alpe Suena, Bormio", M. Anzi [?] (MOD, lectotype selected by Printzen 1995 [ICN Art. 9.9], not seen; UPS L-202807, isolectotype, seen by MW and MS).

Biatora pullata Norman, Öfvers. Kongl. Vet.-Akad. Förhandl. 27: 803 (1870). *Lecidea pullata* (Norman) Th.Fr., Lichenogr. Scand. 2: 471 (1874). *Frutidella pullata* (Norman) Schmull, Mycologia 103: 990 (2011). – Type: Norway, Nordland, Maalselven, ad Kirkennaes convallis, J. M. Norman, (BG, syntype, not seen).

Lecidea perobscurans Nyl., Flora 58: 11 (1875). – Type: Finland, Korpilahti, Soima, supra cort[icem] Betulae vetust[um], 1873, E. A. Vainio, (TUR-V 22982, lectotype, selected by Printzen 1995 [ICN Art. 9.9], not seen; H, H-NYL 21097, isotypes, not seen).

Lecidea ostrogothensis Nyl. in Hulting, Bot. Not. 1892: 123 (1892). – Type: Sweden, Ostrogothia, Kvarsebo, ad cortices ligna Pini silvestris, 1891, J. Hulting (H-NYL 21210, holotype, not seen).

Remarks. The complicated nomenclature of this species was clarified by Jørgensen et al. (2002, see also Printzen 1995). In summary, the oldest name is *Biatora furfuracea*, validly and legitimately described in 1864, while *B. amaurospoda* is either an invalid or illegitimate name (depending on whether it is considered effectively published or

not). *Lecidea furfuracea* (Anzi) Jatta is, however, not available in *Lecidea* because of the existence of an earlier homonym, *L. furfuracea* Pers., described in 1826. As pointed out by Jørgensen et al. (2002), the younger synonym *L. pullata* should therefore be used as long as the species is treated in *Lecidea*. However, when transferred to *Frutidella*, as was done by Schmull et al. (2011), the oldest epithet becomes available and *F. furfuracea* is consequently the correct name.

***Gyalidea subscutellaris* (Vězda) Vězda**
Fig. 2B

Folia Geobot. Phytotax. Bohemoslov. 1: 327 (1966). *Gyalecta subscutellaris* Vězda, Biológia, Bratislava 15: 173 (1960). – Type: Slovakia, Tatra Magna, in ascensu occid. alpis Ostrva, supra muscos destructos, 1750 m.a.s.l., 22 August 1958, A. Vězda (PRA-V-03129, holotype, not seen, PRA-V-05551, isotype, not seen; UPS L-093370, L-159273, isotypes, seen by AN and MW).

New to Fennoscandia. When originally described, *Gyalidea subscutellaris* was placed in *Gyalecta* (Vězda 1960). It was found overgrowing mosses at a high-elevation locality in the Tatra Mountains of Slovakia. Later, it was reported from the Polish part of the Tatra Mountains (Flakus 2007) and in the United Kingdom (Gilbert et al. 2009). The species is characterized by small apothecia (up to 0.5 mm diam., but usually smaller) with a dark brown to black rim and a brownish concave disc, developed on an inconspicuous thallus encrusting soil and bryophytes on basic, metal-rich (Britain) or slightly acidic ground (Tatra). According to Gilbert et al. (2009), the ascospores are muriform and measure (15–)17–20(–22) × 7–10 µm. The Swedish material agrees well with the isotypes at UPS, except that ascospores in Nordin 6631 are poorly developed and do not exceed 16 × 8 µm. In addition, the disc is black and concolourous with the rim in this specimen, a phenomenon potentially caused by environmental factors. In southern Sweden (Gotland and Uppland), *G. subscutellaris* was collected on calcareous ground, whereas the northern sites in Jämtland are situated on metal-rich soil at an old copper mine as well as on acidic ground.

Additional specimens examined: SWEDEN: Gotland, Kräklingbo par., c. 1.9 km SE of Kräklingbo church, along the small road towards Torsburgen, 57.438668°N 18.740235°E, on mosses on calcareous ground, 13 September 2016, M. Westberg & M. Wedin (UPS L-785598). Gotland, Östergarn par., Herrvik, just W of the harbour, 57.42288°N 18.910357°E, on mosses over limestone outcrops, 13 September 2016, M. Westberg & M. Wedin (UPS L-785599). Jämtland, Åre par., Fröå copper mines, E of the building with the pumps, on dead mosses on sandy ground, 63.40361°N 13.21028°E, alt. 645 m, 30 August 2008, A. Nordin 6631 (UPS L-182990). Jämtland, Åre par., Handöl, Handöl rapids, E river bank at the dam above the rapids, on open gravelly ground, 63.24394°N 12.44044°E, alt. 640 m, 29 August 2014, A. Nordin 7633 (UPS L-679028). Uppland, Djurö par., Runmarö, Norestranden c. 450 m NE of Nore, 59.27935°N 18.79779°E. 25 October 2008, M. Westberg 08-429 (S F297927).

Lecania inundata (Hepp ex Körb.) M.Mayrhofer

In Nimis & Poelt, Stud. Geobot. 7 (suppl. 1): 111 (1987). *Biatorina inundata* Hepp ex Körb., Parerga Lichenol. 2: 145 (1860). – Type: Germany, Baden-Württemberg, Heidelberg, an Granitblöcken im Neckar, W. E. von Ahles (L, lectotype, selected by Mayrhofer 1988 [ICN Art. 9.9], not seen)

New to Norway. This species is widely distributed in Europe and North America (Mayrhofer 1988, van den Boom and Ryan 2004).

The Norwegian specimen is typical of the species in having a coarsely papillate thallus surface. The papillae have a cortex and are larger than the blastidia in the otherwise similar *L. erysibe* (Ach.) Mudd. The material was collected in a steep, south-facing rock wall composed of calciferous meta-sandstone subjected to trickling water. The site is located close to the large river Lågen, near the bottom of the valley Gudbrandsdalen. This part of Gudbrandsdalen is one of the driest and most summer-warm places in Norway, with a weakly continental climate. Several saxicolous lichen species are, at least in modern times, largely confined to a limited inner section of this or a few neighbouring valleys, e.g. *Lecanora margacea* Poelt, *Lobothallia praeradiosa* (Nyl.) Hafellner, *Peltula placodizans* (Zahlbr.) Wetmore, *Rhizocarpon vorax* Poelt & Hafellner, *Squamarina magnussonii* Frey & Poelt, *S. pachylepidea* (Hellb.) Poelt, *Toninia cinereovirens* (Schaer.) A.Massal., and *T. ruginosa* (Tuck.) Herre.

Specimens examined: NORWAY: Oppland, Sør-Fron municipality, Steberg S, kalkrikt skråberg, sigevannspåvirket, MGRS NP 5352 2443 [= 61.5496°N 10.0071°E], alt. 260 m, 4 August 2011, J. T. Klepsland JK11-L552 (O L-183713). GERMANY: Baden-Württemberg, "an Granitfelsen im Neckar bei Heidelberg", before 1860, W. von Zwackh-Holzhausen in Zwackh-Holzhausen: Lichenes exsiccati 258 (UPS, probable topotype, seen by SE, according to Körber 1860 collected at the same or nearby locality as the lectotype).

Lecania suavis (Müll.Arg.) Mig.

Flora von Deutschland: 331 (1926). *Callopisma suave* Müll.Arg., Flora (Regensburg) 55: 472 (1872). *Lecanora suavis* (Müll.Arg.) Stizenb., Ber. Tät. St Gall. naturw. Ges. 1880-1881: 373 (1882). – Type: France, Haute-Savoie, in saxis dolomiticus montis jurassici, Reculet, 1872, J. Müller Argoviensis (G, syntypes, not seen).

New to Norway. Apparently widespread in much of Europe, although with a concentration of finds in Central Europe and relatively few finds in eastern Europe (Mayrhofer 1988, Gavrylenko and Khodosovtsev 2009, Urbanavichus and Urbanavichene 2011).

Currently known from two sites in northern Norway, both in the county of Troms. At both sites, the species was found growing on calcareous rock under overhangs, on

limestone and marble, respectively. Despite being sheltered from rain, both sites are fairly open and sun-exposed. The Balsfjord locality lies at the rim of a lake and is surrounded by birch forest, whereas the Lavangen locality is situated in the low-alpine zone.

Specimens examined: NORWAY: Troms, Lavangen, Kolbanelva S, på berghylle (marmor) under overheng, lavalpin sone, MGRS CB 7976 2104 [=68.6752°N 18.0363°E], alt. 650 m, 23 August 2015, J. T. Klepsland JK15-L853 (O-L-207256). Troms, Balsfjord, Sagelvvatnet NV, på soleksponert kalkberg, under overheng, ferskvannsstrandsone, MGRS DB 2433 7833 [=69.2024°N 19.0902°E], alt. 96 m, 22 August 2015, J. T. Klepsland JK15-L827 (O-L-206522).

Micarea capitata M.Svensson & G.Thor

Lichenologist 43: 401 (2011). – Type: Sweden, Härjedalen, "Tännäs parish, the E slope of Mt. Ramundberget, above the holiday village of Kvarnbäcken, subalpine deciduous forest, on *Hylocomium splendens* on boulder", 62°41'654"N 12°23'662"E, alt. 730 m, 2 June 2007, M. Svensson 1004 (UPS L-532764, holotype, seen by MS).

New to Norway. Previously known only from two Swedish collections (Svensson and Thor 2011).

A small patch of this species was found growing on the upper side of a leaning (almost horizontal), moss-covered trunk of a living *Sorbus aucuparia* in an old-growth forest dominated by *Betula pubescens* and *Populus tremula*. The site lies close to the coast at the island Meløya in Nordland county, northern Norway. The site is further characterized by big boulders and a few vertical rock walls, which contribute to a sheltered and humid microclimate. *M. capitata* inhabited both *Hylocomium splendens* (Hedw.) Schimp and *Hypnum cupressiforme* Hedw. Another rare muscicolous lichen, *Gyalideopsis muscicola* P.James & Vězda, was found on the same trunk.

Micarea capitata is perhaps most likely to be confused with *M. hylocomii* Poelt & Döbbeler (see note under that species below). Another species similar to *M. capitata* is *M. olivacea* Coppins, which was not discussed by Svensson and Thor (2011). Our observations indicate that *M. olivacea* differs from *M. capitata* by having apothecia without a clearly constricted base, a dark olivaceous K+ green pigment in the hymenium and hypothecium, and abundant pycnidia (unknown in *M. capitata*). *M. olivacea* has been found growing on lignum and on rock, not over bryophytes (Coppins 1983, 2009b).

Additional specimen examined: NORWAY: Nordland, Meløy, Meløytinden N, på mosekledd, nesten liggende stamme av rogn, eldre bærlyng-osp-bjørkeskog omgitt av bergvegger og store steinblokker, MGRS VQ 3154 1489 [=66.8444°N 13.4397°E], alt. 25 m, 14 July 2016, J. T. Klepsland JK16-609 (O-L-206446).

Specimen examined of *Micarea olivacea*: Scotland, Caledonia, "Mid Ebudes: Mull, Aros, Druimfin, on V. C. 1o3, on a stump by a conifer plantation", 15 May 1968, P. W. James (BM 000975572, holotype, seen by MS).

Micarea deminuta Coppins

Bibl. Lich. 58: 58 (1995). – Type: Scotland, Stirlingshire (VC 86): Inversnaid, Pollochro Woods, grid 27/334108, on decaying log, 30 April 1987, A. Orange 4928 (NMW, holotype, not seen; E, isotype, not seen).

New to Fennoscandia. Initially described on material from Belgium and Great Britain (Coppins 1995), the distribution of *M. deminuta* has proven to be wide. Apart from additional European records (e.g., the Czech Republic, Palice 1999; Poland, Czarnota 2007), the species is now also known from Japan, North America, and Tasmania (Coppins 2009b, Czarnota 2004).

The species was found colonizing an extensive area of soft wood on the upper side of a large, moderately to well decomposed log of *Populus tremula*. The site is an old-growth forest dominated by *Picea abies* and *Populus tremula*, between a lakelet in the east and a steep hill to the west, and consequently sheltered from direct sun. We also found an additional Norwegian specimen in UPS, where the species grew over plant debris, but any other ecological information is lacking.

Specimen examined: NORWAY: Aust-Agder, Åmli, Lyngvatn V, på myk yteved av morken ospelåg, eldre blåbær-smyle-granskog med osp, MGRS ML 6334 1262 [=58.7521°N 8.3665°E], alt. 455 m, 10 August 2016, J. T. Klepsland JK16-723 (O-L-206476). Hordaland, Ulvik, Finse, L. Finsenut, 21 July 1916, G. Einar Du Rietz (UPS L-598807).

Micarea hylocomii Poelt & Döbbeler

Fig. 2C

Bot. Jahrb. Syst. 96: 341 (1975). – Type: Austria, "Rhätische Alpen, Samnaun-Gruppe, Tirol: Bergwald am Weg von Serfaus nach Madatschen, gegen 1500 m nahe am Madatschen", 15 September 1972, J. Poelt (GZU, holotype, seen by MS).

Thallus forming small patches on leaves of *Hylocomium splendens*, thin, faint grey-greenish grey, episubstratal. *Photobiont* cells regularly globose, 4–7 µm diam. (–10 µm according to Poelt and Döbbeler 1975), occurring in clusters inside the thallus. *Apothecia* numerous, scattered, immarginate, convex-hemispherical, ± adnate or sometimes with slightly constricted base, black or rarely grey (when young or when lacking green pigment), when wet often with a faint blue-green tinge, 0.06–0.12 mm diam. *Epihymenium* indistinct, light–dark blue-green, sometimes with dark brown tinges, c. 5 µm high, K–, C–, N+ red. *Hymenium* hyaline to light-dark blue-green in streaks, 19–35 µm tall, C– (blue-green pigment rapidly fading), N± red, I+ blue, K–, KI+ blue. *Hypothecium* hyaline to light brown without any red or purple tinge, K–, C–, N– (N± red if the blue-green pigment reaches the hypothecium). *Paraphyses* few and difficult to discern, simple or sparingly branched, colourless, 1–1.5(–2) µm wide, apices not or slightly thickened (–3 µm wide), hyaline. *Exciple* not seen, even in sections of young

apothecia. *Asci* clavate, apically thickened, 8-spored, with wall KI+ blue throughout the length of the ascus, 18–32 × 8–13 µm. *Ascospores* narrowly ellipsoid, straight or slightly curved, 0–1-septate, (7–)8–10(–15) × (1.5–)2(–3) µm. *Pycnidia* not seen.

Chemistry. Thallus K–, C–, Pd–, UV–. No lichen substances detected by HPTLC.

New to Sweden. Initially described from Austria (Poelt and Döbbeler 1975), *M. hylocomii* has subsequently been reported from Norway and Switzerland (Poelt and Buschardt 1978, Poelt, Plantae Graecenses, Lichenes, no. 94).

After noting some discrepancies between the Scandinavian material and the original description, we examined all available material of *M. hylocomii*, including the holotype. The main difference between our new description and the original one concerns the paraphyses, which Poelt and Döbbeler (1975) described as having spherical apices with dark brown or black pigment hoods. Generally, the extremely small size of the apothecia and the scarcity of paraphyses make these characters difficult to observe, but although the apices are slightly thickened in the Scandinavian material, no dark brown or black pigment hoods were seen. Subsequent examinations revealed that there are no such apical pigment hoods in the holotype either. However, the dark blue-green and brown pigments present in *M. hylocomii* are often concentrated to the upper part of the apothecium and seemingly adhere to the outer surface of the paraphyses, thus sometimes giving the impression of faint pigment hoods. Another discrepancy concerns the ascospores, which Poelt and Döbbeler (1975) described as 1-septate, but there are non-septate ascospores present in the holotype. There is generally some variation in the proportion of simple and 1-septate ascospores between the specimens, ranging from the exclusively simple ascospores in Svensson 725 to the mostly 1-septate ascospores in Svensson 1050.

The anatomy of the paraphyses as well as the uniformly KI+ blue ascus wall led Poelt and Döbbeler (1975) to suggest that *M. hylocomii* belongs in an undescribed genus, an opinion that was shared by Coppins (1983). As described here, however, the anatomy of the paraphyses is not clearly inconsistent with a placement in *Micarea*, which is true of most other characters as well (e.g. ascospores, size of the photobiont). Unfortunately we were, in spite of many attempts, unable to observe a well-developed apical apparatus. As noted by the original authors, however, the asci do seem somewhat unusual in displaying a strong, uniformly KI+ blue reaction throughout their length. Whether this is an indication of a different generic affiliation than *Micarea* should be further investigated using molecular methods.

In Norway and Sweden, *Micarea hylocomii* has always been collected on *Hylocomium splendens*, usually where the bryophyte is hanging down the vertical side of a boulder, though not in rain-protected situations. The species has been found on one- to three-year-old shoots of its host, indicating that its substrate is short-lived and that *M. hylocomii* is adapted to frequent dispersal. The ubiquitousness of its host suggests that *M. hylocomii* is likewise common. Jørgensen (1996) suggested that *M. hylocomii* could be a suboceanic species. Although the number of collections is too low to enable an evaluation of this suggestion, *M. hylocomii* may at least turn out to have quite

specific requirements in terms of humidity, since most of the localities are quite humid, either because they are situated in swampy forests or close to a stream.

M. hylocomii is most likely to be confused with *M. capitata*, which also inhabits *Hylocomium splendens*. *M. capitata*, however, differs from *M. hylocomii* by having larger apothecia (0.10–0.35 mm diam.) with a more clearly constricted base, broader ascospores (–4 µm), and by possessing a blue-green pigment that does not fade rapidly in C (Svensson and Thor 2011). Furthermore, *M. capitata* has numerous, branched and anastamosing paraphyses, while paraphyses are scarce and difficult to discern in *M. hylocomii*. Other *Micarea* species with a thin or immersed thallus and minute (–0.2 mm diam.), black apothecia, such as *M. contexta* Hedl., *M. deminuta* Coppins, *M. eximia* Hedl., and *M. olivacea*, may also be confused with *M. hylocomii*, although none of them is known to grow on *H. splendens* (Coppins 1983, Czarnota 2007). *M. deminuta* is readily distinguished by its dark brown pigment in the hypothecium and broader (3–6 µm wide) ascospores (Coppins 1995). More care is needed to separate the other three species, since they too have a green, N+ red pigment in their apothecia. *M. contexta* differs in having constantly 1-septate ascospores with one cell larger than the other. Also, it has a dark green and/or a dark purple pigment in the hypothecium, reacting K+ green (Coppins 1983). *M. eximia* has a light reddish brown, K+ green hypothecium (Coppins 1983). *M. olivacea* has numerous paraphyses, mostly 1-septate ascospores, and a dark olivaceous or olive brown hypothecium that reacts K+ green (Coppins 1983).

Additional specimens examined: NORWAY: Hordaland, Lindås-Halvöya, kleiner Mischwald in geschützter Lage bei Syslak, wenige Meter über dem Lurefjord, 8 September 1976, A. Buschardt, P. M. Jørgensen & J. Poelt (two collections with the same label data, GZU). SWEDEN: Härjedalen, Tännäs par., the W slope of Mt. Trappåsen, 150 m E of the road to Ramundberget, by the small stream Röllekbäcken, subalpine deciduous forest, on *Hylocomium splendens* on boulder by the stream, alt. 725 m, 62º40'N 12º25'E, 4 June 2007, M. Svensson 1038 & 1045 (UPS L-803528, L-803529). Tännäs par., 1.6 km NNE of Bodrösten, old-growth mixed coniferous forest, on *Hylocomium splendens* on an old stump of *Pinus sylvestris*, alt. 730 m, 62º35'N 12º29'E, 4 June 2007, M. Svensson 1050 (UPS L-803556). Jämtland, Kall par., 3.5 km E the small village Öster-Kjoland, S side of the small river Öster-Kjolån, old-growth *Picea abies* forest, on *Hylocomium splendens* on a boulder, alt. 420 m, 63º35'N 12º54'E, 26 May 2006, M. Svensson 725 (UPS L-803526). Västerbotten, Degerfors par., 6 km NE the village Vindeln, 500 m SW the house Nymyrkälen, on c. 1.5 m high boulder in clear-cut with scattered old *Pinus sylvestris*, alt. 200 m, 64º13'55"N 19º49'05"E, 30 May 2012, G. Thor 27772 (UPS L-803527). Åsele Lappmark, Dorotea par., Måntorp, alt. 400 m, 64º23'N 16º26'E, 9 June 2011, M. Lif 240 (UPS L-803525). SWITZERLAND: Graubünden, Oberengadin, Gemeinde Silvaplana, God Surlej, SO Champfer, WNW-seitige, locker von Arven und Lärchen bewaldete Hänge, alt. 1800-1900 m, 11 September 1970, J. Poelt (Pl. Graec. Lich. no 94, GZU, absent from duplicate UPS L-047264).

***Micarea lynceola* (Th.Fr.) Palice**
Fig. 2D

Preslia 71: 313 (1999). *Lecidea lynceola* Th.Fr., Lichenogr. Scand. 2: 561 (1874). *Leimonis lynceola* (Th.Fr.) Aptroot, Index Fungorum 331 (2017). – Type: Norway, Akershus, Oslo, Tveten, 20 May 1868, N. G. Moe 257 (UPS L-094388, lectotype, selected by Hertel 1975 [ICN Art. 9.9], seen by MS).

Micarea excipulata Coppins, Notes RBG Edin. 45: 161 (1988). – Type: Austria, Kärnten, Karawanken: Am Eingang zu Trögener Klam (ca. 7 km WSW Eisenkappel), 46°28'N 14°31'E, 700m, Pioniervegetation auf lose am Grunde liegenden, weich verwitterenden Silikatsteinchen, 5 August 1973, J. Poelt in Hertel, Lecid. Exs. no 54 (M, holotype, not seen; UPS, isotype, seen by MS).

New to Sweden. *M. lynceola* was described from Norway in 1874, but has so far not been correctly reported from Sweden. The species has also been recorded from Ireland, United Kingdom, the Netherlands, Belgium, Germany, Austria, the Czech Republic, Poland, Finland, and the Murmansk Region of Russia (Palice 1999, Aptroot and van Herk 1999, Ertz et al. 2008, Urbanavichus et al. 2008, Coppins 2009b, Czarnota 2011).

M. lynceola is a pioneer species of siliceous rocks and the Swedish collection was made on a loose rock on a road-bank. It is easily confused with *M. polycarpella* (Erichsen) Coppins & Palice, which has similar ecology and to which earlier Swedish records of *M. lynceola* belong (Palice 1999). *M. lynceola*, however, has a well-developed, 30–40 µm wide exciple which is readily distinguished as a non-amyloid zone after treatment with KI, while *M. polycarpella* has 7–10 µm wide excipular rim of pigmented hyphae that does not contrast with the hymenium in KI (Palice 1999).

Additional specimens examined: NORWAY: Akershus, Oslo, Tveten, 20 September 1868, N. G. Moe 257 (UPS L-094386, topotype). SWEDEN: Östergötland, Risinge par., 2.5 km NNW of Lotorp, 250 m N of the tarn Skirgölen, E side of the road, 58.754343°N 15.803343°E, alt. 70 m, 31 May 2011, M. Svensson 2129 (UPS L-778164).

***Micarea soralifera* Guz.-Krzemiń. et al.**

Lichenologist 48: 165 (2016). – Type: Poland, Równina Bielska, Białowieża Primeval Forest, Białowieża National Park, forest section no. 256, Circeo-Alnetum, on log, October 2014, M. Kukwa 13001 & A. Łubek (UGDA, holotype, not seen).

New to Fennoscandia. This recently described species was originally reported from Poland and the Czech Republic (Guzow-Krzemińska et al. 2016). It belongs to the *Micarea prasina* group and is characterized by having distinct soralia and containing micareic acid. In Sweden it has been found in the nature reserve Fiby urskog near Uppsala, where it occurs on decaying logs in an old-growth forest dominated

by conifers, and in one locality in the outskirts of Uppsala, where it grew on wood of *Salix*.

Specimens examined. SWEDEN: Uppland, Husby-Ärlinghundra par., Östra Steninge, along jogging trail c. 500 m NW of the Syrian Orthodox Church, on dead mossy boughs of *Salix* on the ground, 59.62033°N 17.81340°E, 4 October 2016, A. Nordin 8056 (UPS L-797384, HPTLC: micareic acid). Uppland, Vänge par., Fiby urskog Nature Reserve, S part of the reserve, c. 350 m west of Kvarnberg, on decaying log by the trail in old-growth forest dominated by conifers, 59.8827°N 17.3514°E, 8 April 2016, M. Westberg, S. Ekman & G. von Hirschheydt (UPS L-790650, HPTLC: micareic acid). Ibid., E part of the reserve, 50 m E of the river Fibyån and 600 m S of the lake Fibysjön, on dry spruce twig in spruce-dominated forest (old overgrown hayfield from the 1930s), 59.8873°N 17.3457°E 11 May 2016, G. von Hirschheydt, M. Westberg & S. Ekman (UPS L-790652, HPTLC: micareic acid).

Micarea subconfusa **(Nyl.) Alstrup**
Fig. 3A

in Alstrup et al., Fróðskaparrit 40: 96 (1994). *Lecidea subconfusa* Nyl., Flora 52: 84 (1869). – Type: Faeroe, Strömsö, "Torshavn", August 1867, E. Rostrup (C-L-76663, lectotype, selected by Alstrup in Alstrup et al. 1994 [ICN Art. 9.9], specified here by MS [ICN Art. 9.17]).

Lecidea submoestula Nyl., Flora, Jena 59: 235 (1876). *Micarea submoestula* (Nyl). Coppins in Coppins et al., Lichenologist 24: 367. – Type: Ireland, Co. Galway, "route de Westport", 1876, C. Du Bois Larbalestier, (H-NYL 19033, lectotype, designated here by MS).

New to Fennoscandia. *Micarea subconfusa* is a rarely recorded species, currently known from Ireland, Scotland, and the Faeroe Islands (Alstrup et al. 1994, Coppins 2009b, Coppins and James 1992).

M. subconfusa belongs to the *M. assimilata* group and inhabits acid rocks in the lowlands. It is similar to the alpine *M. paratropa* (Nyl.) Alstrup, but lacks K+ violet pigmentation in the hymenium and has a K – hypothecium. The Swedish specimen grew on wood of an old pilework close to the seashore, which likely represents a case of a primarily saxicolous species occasionally growing on dust-enriched wood. Due to superficial similarities with other, not closely related saxicolous lecideoid lichens, *M. subconfusa* is possibly an overlooked species.

Alstrup in Alstrup et al. (1994) referred to the collections C-L-76662 and C-L-76663 as the "holotype" of *Lecidea subconfusa*, thus effectively designating both as lectotype. We here further specify this by designating the specimen C-L-76663 as lectotype. This specimen has the words "specimen primarium" written with red ink on the sheet to which it is glued, as well as an indication that the specimen has been sent to Nylander ("a Rostrup Nylandro missum"). According to Alstrup et al. (1994), the handwriting is that of Rostrup.

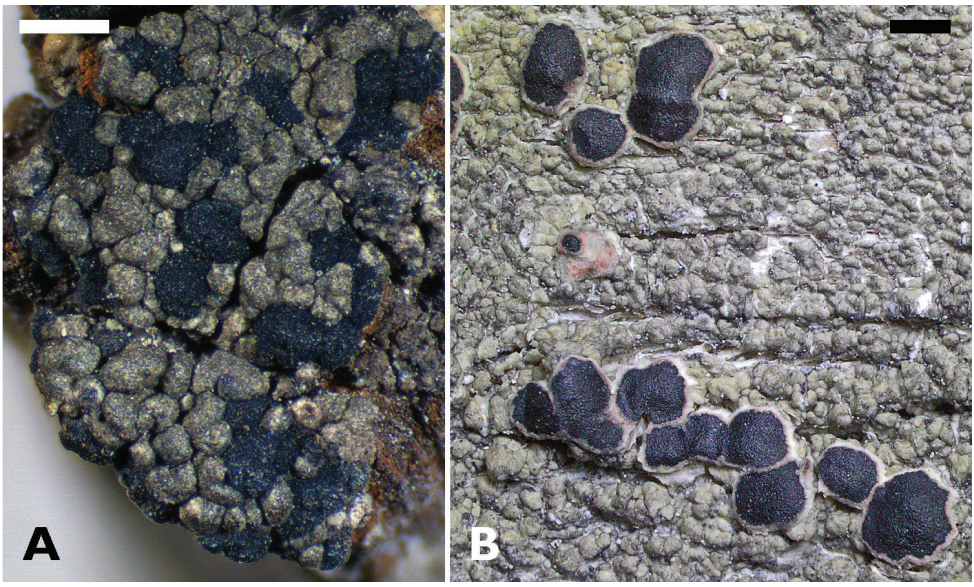

Figure 3. A *Micarea subconfusa* (UPS L-578286) **B** *Mycoblastus sanguinarioides* (UPS L-550384). Scale bars: 0.5 mm (**A**), 1 mm (**B**).

Syntypes of *Lecidea submoestula* are available in BM and H-NYL. The specimen H-NYL 19033 only gives the locality as "route de Westport" and the year as 1876. Two collections in BM are possible duplicates of the Nylander specimen, but give the date as February 1876 and March 1876 respectively, which means that it cannot be ascertained which constitutes a duplicate of the specimen in H-NYL. Consequently, the specimen H-NYL 19033 is chosen here as lectotype of *L. submoestula*.

Additional specimens examined: FAEROE ISLANDS: Strömsö, Kirkuböfjelet, July 1867, E. Rostrup (H-NYL 16944). Strömsö, Thorshavn, July 1867, E. Rostrup (C-L-76662). Strömsö, August 1867, E. Rostrup (C-L-76661). IRELAND: Co. Galway, road to Westport 5 miles from Kylemore, February 1876, C. Du Bois Larbalestier (BM 001062221). Road to Westport, March 1876, C. Du Bois Larbalestier (BM 001062222). Road to Westport, 5 miles from Kylemore Castle, Connemara, 1877, C. Du Bois Larbalestier (BM 001062223). SWEDEN: Gästrikland, Gävle par., Barsagrundet, at Inre Fjärden, 60.68333°N 17.18333°E, 2 January 1988, A. Nordin 2265 (UPS L-578286).

Mycobilimbia tetramera (De Not.) Vitik. et al. ex Hafellner & Türk

Stapfia 76: 154 (2001). *Bilimbia tetramera* De Not., Giorn. Bot. Ital. 2 (1): 191 (1846). *Biatora tetramera* (De Not.) Coppins in Coppins et al., Lichenologist 24: 367 (1992). – Type: Norway, S. C. Sommerfelt (RO, lectotype, selected by Printzen 1995 [ICN Art. 9.9], not seen).

Lecidea atrolivida Vain., Medd. Soc. Fauna Flora Fenn. 10: 10 (1883). *Bilimbia atrolivida* (Vain.) H. Olivier, Bull. Géogr. Bot. 21: 186 (1911). *Bacidia atrolivida* (Vain.) Zahlbr., Cat. Lich. Univ. 4: 101 (1926). – Type: Finland, Kainuu, "Kianta, Saarenmylly, kallion juurella (länttä kohd.)", 1877, E. Vainio (TUR-V 21424, holotype, seen by SE).

New synonym. *Bacidia atrolivida* was listed as an accepted species by Stenroos et al. (2016). The type material, however, consists of typical *Mycobilimbia tetramera*, and the former is consequently reduced into synonymy. According to Vainio (1922), *Bacidia atrolivida* is supposed to differ from '*Bilimbia obscurata*' (i.e., *Mycobilimbia tetramera*) in having a sparsely sorediate thallus, an observation we were unable to confirm. The type material in TUR-V is cited here as the holotype, because it appears to have been the only specimen available to Vainio at the time of description (Alava 1988).

Mycoblastus sanguinarioides Kantvilas

Fig. 3B

Lichenologist 41: 172 (2009). – Type: Australia, Tasmania, Pelion Plains, 1 km W of Pelion Hut, 41°50'S 146°02'E, 890 m altitude, on eucalypt stump in *Eucalyptus delegatensis* open forest, 11 March 1992, G. Kantvilas 267/92 (HO, holotype, not seen; BM, isotype, not seen).

Lecidea sanguinaria var. *lecanoroidea* Nyl., Lichenes Japoniae: 77 (1890). – Type: Japan, Itchigômé, 1879, E. Almquist (H-NYL 10912, syntype, seen by TS).

New to Finland and Sweden. This species was described from Tasmania, Australia (Kantvilas 2009), but has later been shown to be widespread in the Northern Hemisphere (Canada, Japan, Russia, USA; Spribille et al. 2011). There is one collection each from Finland and Sweden in herbarium UPS. Both localities are apparently very humid (near a waterfall and a rapid, respectively). The Swedish locality harbours several rare lichens, such as *Pannaria conoplea* (Ach.) Bory, *Pilophorus robustus* Th.Fr., *Placopsis gelida* (L.) Lindsay, and *Ramalina thrausta* (Ach.) Nyl. (herbarium material in UPS). The Fennoscandian localities are in keeping with the occurrence of the species in humid regions in eastern Eurasia and coastal western and eastern North America.

Mycoblastus sanguinarioides is similar to *M. sanguinarius* (L.) Norman but can be distinguished by often having flat apothecia surrounded by a thin ring of whitish thalline tissue. In contrast, small apothecia of *M. sanguinarius* are usually distinctly convex with a constricted base. Furthermore, the hymenium of *M. sanguinarioides* contains birefringent hymenial crystals, visible in polarized light (see Spribille et al. 2011, Fig. 2). The chemistry of the two Fennoscandian specimens (bourgeanic acid and atranorin) agrees with the chemistry of *M. sanguinarioides* elsewhere in the Northern Hemisphere. Both compounds occur in *M. sanguinarius* as well, but always together with one or several additional compounds. *M. sanguinarius* has four chemotypes (Spribille, unpublished data), three of which are found in northern Europe: (1) rangiformic acid and atranorin (common, northern), (2) bourgeanic acid, caperatic acid and atranorin (mainly in the south), (3) bourgeanic acid, rangiformic acid and atranorin (northern)

and (4) lichesterinic and protolichesterinic acid (currently known from a single saxicolous specimen from the Yukon). Some of these chemotypes might warrant recognition as distinct species (Spribille et al. 2011).

Specimens examined. FINLAND: Karelia borealis [=Pohjois-Karjala], Koli [=Koli National Park], Tarhapuro [water fall], on *Betula* at the water fall, 16 June 1954, G. Degelius (UPS L-202809). SWEDEN: Lule lappmark, Jokkmokk socken, Muddus nationalpark, V-sidan av Mudduskanjon, blockravin några km S om fallet, torr gran, 28 August 1944, B. H. Svenonius MS423 (UPS L-550384).

Paralecia pratorum Brackel et al.

In Liu et al. Fungal Diversity 72: 167 (2015). – Type: Italy, Toscana, Prov. di Massa-Carrara, Prati di Logarghena above the city of Pontremoli, 44°22.848N, 9°56.573E, elev. 845 msl., growing on *Protoparmeliopsis muralis* (Schreb.) M. Choisy, on schistose rock outcrops in a meadow, 7 Oct. 2013, W. von Brackel (M-0045925, holotype, not seen).

New to Fennoscandia. The recently proposed monotypic genus *Paralecia* has been suggested to belong in the Squamarinaceae (Liu et al. 2015). The single species *P. pratorum*, a lichenicolous fungus on *Protoparmeliopsis muralis*, has brown, lecideine apothecia growing on the lobes and apothecial margins of the host. It is further characterized by asci with an I+ dark blue tube-like apical structure, and hyaline and simple ascospores. *Paralecia pratorum* was found growing on its host on the island Runmarö in the Stockholm archipelago. The locality is rich in lichens and with a variety of calcareous and non-calcareous rocks facing the Baltic Sea. The species is so far known only from Italy and Sweden.

Specimen examined. SWEDEN: Uppland, Djurö par., Runmarö, Norestranden, NE of Nore, 59.27868°N 18.79664°E, alt. 20 m, 30 June 2009, M. Westberg & T. Berglund 09-399 (UPS F-787462).

Puttea duplex (Coppins & Aptroot) M.Svensson, comb. nov.

MycoBank #MB819389

Fellhanera duplex Coppins & Aptroot, Lichenologist 40: 368 (2008). – Type: Wales, V.C. 46, Cardigan, Cwm Rheidol, Coed Simdde-lwyd NNR 22/(SN)/718.785, alt. 200 m, open valley-side *Quercus petraea* woodland, on *Hypnum* 'drip tassel' on trunk of fairly well-lit, S-facing *Q. petraea*, 15 April 2001, S. P. Chambers (E-00169970, holotype, seen by MS; GZU, isotype, not seen).

Remarks. New to Sweden. Originally described from Scotland and Wales (Coppins and Aptroot 2008), and was recently reported from Norway (Tønsberg 2016).

When describing this species, Coppins and Aptroot (2008) assigned it to *Fellhanera* on account of its similarity to *F. margaritella* (Hulting) Hafellner. Subsequently, *F. margaritella* was transferred to *Puttea* by Stenroos et al. (2009). *Puttea* was initially

monotypic, but Stenroos et al. listed several other candidates for inclusion, of which two were later combined into the genus: *P. exsequens* (Nyl.) Printzen & Davydov (Davydov and Printzen 2012) and *P. caesia* (Fr.) M.Svensson & T.Sprib. (Dillman et al. 2012). *P. duplex* is distinct from the other three species by having 16–24 ascospores per ascus, but otherwise fits well in *Puttea* on account of having minute, pale apothecia, asci with a KI+ blue tholus penetrated by a canal that slightly widens towards the apex, and crystals that dissolve in K in the epihymenium and hymenium.

According to Coppins and Aptroot (2008), the exciple of *P. duplex* is paraplectenchymatous, which would be consistent with a placement in *Fellhanera* (Lücking 2008), while *Puttea margaritella* (the type species of that genus) has a strongly gelatinized exciple composed of branched, parallel hyphae (Stenroos et al. 2009). Although the exciple of *P. duplex* is often poorly developed and difficult to observe, we found that it is in fact quite similar to that of *P. margaritella*, being strongly gelatinized and consisting of dichotomously branched hyphae with narrowly cylindrical cell lumina.

The Swedish specimen was found on bark of *Betula* in a mature coniferous production forest. The specimen differs from the original description in having longer ascospores (–9 µm versus –5 µm) and by growing directly on bark and not over bryophytes. However, as the original description of *F. duplex* was based on only three specimens, the range of variation in ascospore size is possibly larger than indicated there and the ecology of the species may likewise be broader. Since the Swedish specimen agrees well with the holotype in other respects, we prefer to include it in *P. duplex* pending further studies.

Additional specimen examined: SWEDEN: Hälsingland, Bollnäs par., 8,5 km SW of Hanebo church, 1 km S of Hällbo, SE of Skidtjärnen, on stem of living *Betula pubescens* (23 cm diam.) in mature coniferous forest, alt. 120 m, 61°12'N 16°25'E, 22 August 2012, F. Jonsson FU9206 (UPS L-786606).

Sarcogyne algoviae H.Magn.

In Rabenh. Krypt.-Fl., Edn 2 (Leipzig) 9(5.1): 78. 1935. – Type: Germany, Bayern, "Obere Seealpe in den Allgäuer Alpen bei Oberstdorf, c. 5000'", 1860, H. Rehm (S L2741, holotype, seen by MW).

New to Finland. Previously known from the Alps, *Sarcogyne algoviae* was recently reported from Sweden and Norway (Westberg et al. 2015).

The newly discovered specimen was collected on calcareous rock in northernmost Finland. The species is characterized by apothecia with a strongly carbonized margin, a colourless hypothecium, and narrowly ellipsoid ascospores (Westberg et al. 2015).

Additional specimen examined: FINLAND: Lapponia inarensis, Utsjoki, Kevo Subarctic Research Station, c. 3 km SW cliff Kotkapahta in Kevojoki valley, 20 August 1965, T. Ahti 20905 (H).

***Thelenella pertusariella* (Nyl.) Vain.**

Acta Soc. Fauna Fl. Fenn. 49 (2): 155 (1921). *Verrucaria pertusariella* Nyl., Flora 47: 367 (1864). *Microglaena pertusariella* (Nyl.) Norman, Kongel. Norske Vidensk. Selsk. Skr. 5: 366 (1868). – Type: Russia, Lapponia ponojensis, nära Triostroff, 1863, N. I. Fellmann (H-NYL 1594, lectotype, selected by Mayrhofer 1987 [ICN Art. 9.9], not seen).

Phlyctis submuriformis H.Magn., Arkiv Bot. 33A (1): 117 (1946). – Type: Sweden, Lycksele lappmark, Tärna par., Långfjället, on *Sorbus*, 20 July 1924, A. H. Magnusson 8938a (UPS L-108344, holotype, seen by MS).

Gyalidea fruticola M.Svensson & G.Thor, Lichenologist 39: 335 (2007). – Type: Sweden, Uppland, Häggeby par., 3 km NW of Häggeby church, along the road between Skadevi and Eknäs, broadleaved deciduous forest, on decaying bark on old *Lonicera xylosteum*, alt. 20 m, 59°41'N 17°32'E, 15 January 2006, M. Svensson 616 (UPS L-167526, holotype, seen by MS and GT; S F68480, isotype, seen by MS and GT).

New synonym. *Gyalidea fruticola* was described mainly from material collected on *Lonicera xylosteum* in southern Sweden and seemingly fit into *Gyalidea* on account of having a KI– hymenium (the KI+ pale red-brown reported by Svensson and Thor 2007 is the colour of the iodine), sparingly branched paraphyses, and submuriform ascospores (Svensson and Thor 2007). However, subsequent collections have made it clear that *G. fruticola* cannot be separated from *Thelenella pertusariella*. Like *Gyalidea*, the genus *Thelenella* belongs to the Ostropomycetidae (Nelsen et al. 2017) and displays similar hymenial and ascospore characters. *Thelenella*, however, differs by having perithecia instead of apothecia. Southern morphs of *T. pertusariella* are often very small and perithecia in poor condition often get a gyalectoid appearance, hence the mistaken assignment to *Gyalidea*.

Additional specimens examined: ITALY: Trentino Alto Adige, Trento Prov., Stelvio National Park, Val de la Mare, 400 m SE of Malga Prabon, Bosco di Celvestré, mixed old growth coniferous forest, on dead twig of *Lonicera alpigena*, alt. 1780 m, 46°24'N 10°41'E, 27 July 2006, M. Svensson 853 (UPS L-167599). NORWAY: Varanger, Båtsfjord municipality, the top of the valley Skogdalen, subalpine deciduous forest, on bark of *Salix* sp., alt. 200 m, 70°53'N 29°69'E, 2 July 2014, M. Svensson 2912 (UPS L-803559). SWEDEN: Härjedalen, Ljusnedal par., 1.2 km WNW of Djupdalsvallen, along the track to Mt Gruvvålen, small stream in open subalpine deciduous forest, on dead stem of *Salix lanata* close to the water, alt. 900 m, 62.71832°N 12.43697°E, 24 August 2007, M. Svensson 1114 (UPS L-176178). Jämtland, Kall par., Skäckerfjällen Nature Reserve, 600 m N of Sågen, E side of the river from Lake Nedre Ottsjön, deciduous forest on the shore of the river, on decaying bark of *Alnus incana*, alt. 450 m, 63°44'N 12°33'E, 17 August 2008, M. Svensson 1351 (UPS L-803565). Södermanland, Aspö par., 150 m NW of Aspö church, deciduous forest, at the base of dead stem of *Lonicera xylosteum*, alt. 5 m, 59°29'N 17°23'E, 26 March 2006, M. Svensson 632 (UPS L-166883). Södermanland, Sköldinge par., N of Lake Silingen, by the ruins of the ancient fortress Tjugesta skans, broadleaved deciduous forest, on decaying bark on old *Lonicera xylosteum*, alt. 55 m, 59°01'N 16°16'E, 19

November 2006, M. Svensson 931 (UPS L-167524). Uppland, Alsike par., 300 m N of Dragontorpet, just W of road 255, broadleaved deciduous forest, on decaying bark on old *Lonicera xylosteum*, alt. 20 m, 59°45'N 17°39'E, 8 January 2006, M. Svensson 609 (UPS L-167525). Uppland, Alsike par., 300 m N of Grönvreten, just E of road 255, near ditch, edge of mixed coniferous forest, on decaying bark of *Lonicera xylosteum*, alt. 20 m, 59°46'N 17°39'E, 7 July 2006, M. Svensson 868 (UPS L-167522). Uppland, Gryta par., 3.2 km N the village Örsundsbro, just W of gravel road, near ditch, coniferous forest, on *Lonicera xylosteum*, alt. 40 m, 59°45'N 17°18'E, 2 October 2006, G. Thor 20100 (UPS L-166884). Uppland, Knivsta parish, 1.7 km W of Valloxsäby, c. 400 m N of lake Valloxen, broadleaved deciduous forest, on decaying bark on old *Lonicera xylosteum*, alt. 25 m, 59°44'N 17°50'E, 29 January 2006, M. Svensson 623 (UPS L-167527). Uppland, Sånga par., 1.5 km SE of Sånga church, S of Svartsjö djurgård, E of the road, broadleaved deciduous forest, on decaying bark on *Lonicera xylosteum*, alt. 10 m, 59°20'N 17°43'E, 10 March 2006, M. Svensson 628 (UPS L-167251). Uppland, Söderby-Karl par., 5 km SW of Söderby-Karl church, along the road between Koludden and N. Järsö, Svartbäcksviken, broadleaved deciduous forest, on decaying bark of *Lonicera xylosteum*, alt. 15 m, 59°51'N 18°37'E, 2006, M. Svensson 624 (UPS). Västmanland, Vittinge par., 700 m SE of Månsbo, N shore of Lake Ekholmssjön, deciduous forest, on decaying bark of *Lonicera xylosteum*, alt. 70 m, 59°51'N 17°02'E, 4 February 2007, M. Svensson 947 (UPS L-167523). Östergötland, S:t Anna par., Djursö, 300 m NW of the farm, broadleaved deciduous forest, on decaying bark on old *Lonicera xylosteum*, alt. 5 m, 58.40098°N 16.79018°E, 6 May 2007, M. Svensson 994 (UPS L-171652).

Toninia subnitida (Hellb.) Hafellner & Türk

Stapfia 76: 159 (2001). *Catillaria subnitida* Hellb., Nerikes lafflora 92 (1871). – Type: Sweden, Närke, Tysslinge par., Hjulåsen, 1869, P. J. Hellbom, (O, lectotype, selected by Kilias 1981: 372, not seen; GB-0128121, isolectotype, not seen).

Patellaria tristis Müll.Arg., Mém. Soc. Phys. Hist. Nat. Genève 16: 398 (1862). *Catillaria tristis* (Müll.Arg.) Arnold, Verh. Zool.-Bot. Ges. Wien 29: 362 (1879). *Kiliasia tristis* (Müll.Arg.) Hafellner, Beih. Nova Hedwigia 79: 265 (1984). – Type: France, Ain, "au-dessus de Chésery dans le Jura français", 28 August 1852, J. Müller (G, holotype, not seen).

Probably new to Norway. Kilias (1981) reported this species from one locality in Nordland in northern Norway based on a specimen collected by G. Degelius. We have, however, been unable to trace this specimen. The same specimen was reported as *Catillaria hypochlorella* (Vain.) Zahlbr. (syn. *Lecidea hypochlorella* Vain., Vainio 1883) by Degelius (1955), who discussed the distinction from *Catillaria subnitida* Hellb. Degelius pointed out the agreement with Vainio's descriptions (1881, 1934), and the identification of this specimen, along with another specimen from Torne lappmark in northern Sweden (Magnusson 1952) as *L. hypochlorella* was upheld by Santesson (1984, and later editions). Vainio (1934) discussed the similarity between *L. hy-*

pochlorella and *T. subnitida*, mentioning that they differ only in the hymenium being entirely green in the former, whereas the latter has a bluish epihymenium. There are, however, additional differences. In *L. hypochlorella*, the hypothecium contains a mixture of green and dull brown pigments, which contrast to the strongly darker proper exciple. In *T. subnitida*, on the other hand, the hypothecium and proper exciple are very similar in hue (dark red-brown) and do not contrast. Furthermore, ascospores in *L. hypochlorella* are 1(–2)-celled, whereas they are consistently 2-celled in *T. subnitida*. The material from Torne lappmark in Sweden (UPS L-785614) represents *L. hypochlorella*. The Norwegian specimens of *Toninia subnitida* had been misidentified as *Bacidia coprodes* (Körb.) Lettau and were discovered while revising material filed under that species (Ekman 2014).

Kilias (1981) reported *T. subnitida* (as *Catillaria tristis*) also from Sweden, Finland, Russia, Germany, Czech Republic, Switzerland, Austria, and Italy. It has later been recorded also from Spain and Montenegro (Hladun and Gómez-Bolea 1982, Knežević and Mayrhofer 2009). Reports from North America are doubtful, as the name was introduced in the checklist of Egan (1987) with reference to Kilias (1981). The latter author, however, does not mention any North American finds.

Additional specimens examined: NORWAY: Akershus, Oslo, Ormø, 5 May 1867, N. G. Moe (UPS L-138580). Akershus, Nordmarken, Tømter, 9 September 1868, N. G. Moe (UPS L-138579). Akerhus, Nordmarken, Tømter, 1868, N. G. Moe 230 (UPS L-138578). Nord-Trøndelag, Snåsa, Bergåsen nature reserve, humid spruce-birch forest in NW-facing slope WSW of lake Heimsjøen, alt. 260 m, 64°15.19'N 12°24.28'E, 12 September 2006, Z. Palice (PRA).

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