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Phylogeny, evolution and a re-classification of the *Lichinomycetes*

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Abstract: The *Lichinomycetes* is an independent lichenized lineage within the *Ascomycota* comprising *ca*. 390 species and 50 genera. Very few studies have dealt with family and genus classification using molecular data and many groups are in need of thorough revision. Thus, we constructed a multilocus phylogeny (mtSSU, *RPB2* and *mcm7* gene regions) including 190 specimens of *Lichinomycetes* belonging to 126 species. Ancestral state reconstruction analyses were carried out to trace the evolution of selected characters. The current classification scheme of the *Lichinomycetes* based on morphological and anatomical characters is in great conflict with the phylogenetic relationships resulting from the present study. The results suggest substantial non-monophyly at the family and genus levels. A revised classification is proposed here and an overview of genera accepted in the *Lichinomycetes* is given. Ancestral *Lichinomycetes* are reconstructed as crustose with pycnoascocarps and octosporous asci. We used a combination of characters to delineate groups including the ascoma development and the type of asci. The revised classification includes 11 new genera, five resurrected genera, and 54 new combinations distributed in four families (three emended and one new). Three new species are also described.

Key words: ancestral reconstruction, ascoma ontogeny, *Heppiaceae*, *Gloeoheppiaceae*, *Lichinaceae*, new taxa, *Peltulaceae*.

Taxonomic novelties: New family: *Lichinellaceae* M. Schultz & M. Prieto. **New genera:** *Allopyrenis* M. Schultz & M. Prieto, *Gonotichia* M. Schultz & M. Prieto, *Lapismalleus* M. Schultz & M. Prieto, *Lingolemma* M. Schultz & M. Prieto, *Paludolemma* M. Schultz & M. Prieto, *Paracyphus* M. Schultz & M. Prieto, *Peltolemma* M. Schultz & M. Prieto, *Pseudocarpon* M. Schultz & M. Prieto, *Pseudotichia* M. Schultz & M. Prieto, *Pycnolemma* M. Schultz & M. Prieto, *Tichocyphus* M. Schultz & M. Prieto. **New species:** *Paracyphus gotlandicus* M. Schultz & M. Prieto, *Pseudocarpon persimile* M. Schultz & M. Prieto, *Tichocyphus gotlandicus* M. Schultz & M. Prieto. **New combinations:** *Allopyrenis grumulifera* (Nyl.) M. Schultz & M. Prieto, *Allopyrenis haemaleella* (Nyl.) M. Schultz & M. Prieto, *Allopyrenis impolita* (Th. Fr.) M. Schultz & M. Prieto, *Allopyrenis phaeococca* (Tuck.) M. Schultz & M. Prieto, *Allopyrenis reducta* (Th. Fr.) M. Schultz & M. Prieto, *Allopyrenis sanguinea* (Anzi) M. Schultz & M. Prieto, *Allopyrenis tenuis* (Henssen) M. Schultz & M. Prieto, *Cladopsis densisidiata* (Aptroot *et al.*) M. Schultz & M. Prieto, *Cladopsis foederata* (Nyl.) M. Schultz & M. Prieto, *Cladopsis guyanensis* (M. Schultz *et al.*) M. Schultz & M. Prieto, *Cladopsis palmana* (J. Steiner) M. Schultz & M. Prieto, *Cladopsis polycocca* (Nyl.) M. Schultz & M. Prieto, *Forssellia canariensis* (Henssen) M. Schultz & M. Prieto, *Forssellia concordatula* (Nyl.) M. Schultz & M. Prieto, *Gonotichia octosporella* (Lettau) M. Schultz & M. Prieto, *Lapismalleus lugubris* (A. Massal.) M. Schultz & M. Prieto, *Lemmopsis lutophila* (Arnold) M. Schultz & M. Prieto, *Lempholemma segregatum* (Nyl.) M. Schultz & M. Prieto, *Lichinella baicalensis* (Makryi) M. Schultz, *Lichinella etoshica* (Brusse) M. Schultz, *Lichinella lusitanica* (Henssen) M. Schultz, *Lichinella pulvinata* (E. Dahl) M. Schultz, *Lichinella schleicheri* (Hepp) M. Schultz, *Lichinella terrestris* (Makryi) M. Schultz, *Lingolemma lingulatum* (Tuck.) M. Schultz & M. Prieto, *Paludolemma syreniarum* (C.J. Lewis & M. Schultz) M. Schultz & M. Prieto, *Peltolemma socotranum* (M. Schultz) M. Schultz & M. Prieto, *Phylliscum aotearoa* (Henssen & B. Bartlett) M. Schultz & M. Prieto, *Phylliscum cylindrophorum* (Vain.) M. Schultz, *Phylliscum laatokkaense* (Vain.) M. Schultz & M. Prieto, *Phylliscum neglectum* (Henssen) M. Schultz & M. Prieto, *Phylliscum permiscens* (Nyl.) M. Schultz & M. Prieto, *Phylliscum rhodostictum* (Taylor) M. Schultz & M. Prieto, *Porocyphus antarcticus* (Cromb.) M. Schultz & M. Prieto, *Porocyphus macrosporus* (Henssen *et al.*) M. Schultz & M. Prieto, *Porocyphus minutissimus* (Henssen) M. Schultz, *Porocyphus rosulans* (A. Henssen) M. Schultz, *Porocyphus tasmanicus* (A. Henssen) M. Schultz, *Porocyphus willeyi* (Tuck.) M. Schultz & M. Prieto, *Pseudotichia vermiculata* (Nyl.) Schultz & M. Prieto, *Pycnolemma polycarpum* (M. Schultz) M. Schultz & M. Prieto, *Synalissina botryosa* (A. Massal.) M. Schultz & M. Prieto, *Synalissina cladodes* (Tuck.) M. Schultz & M. Prieto, *Synalissina condensata* (Arnold) M. Schultz & M. Prieto, *Synalissina degeliana* (P.M. Jørg.) M. Schultz & M. Prieto, *Synalissina dispansa* (H. Magn.) M. Schultz & M. Prieto, *Synalissina intricatissima* (J. Steiner) M. Schultz & M. Prieto, *Synalissina isidiodes* (Nyl. *ex* Arnold) M. Schultz & M. Prieto, *Synalissina vesiculifera* (Henssen) M. Schultz & M. Prieto, *Thelignya arnoldii* (Frauenf.) M. Schultz & M. Prieto, *Thelignya lacustris* (P.M. Jørg. & R. Sant.) M. Schultz & M. Prieto, *Thelignya neglecta* (Erichsen) M. Schultz & M. Prieto, *Thelignya obtenebrans* (Nyl.) M. Schultz, *Thyrea osorioi* (Henssen) M. Schultz. **New status and combination:** *Gonotichia depauperata* (Servít) M. Schultz & M. Prieto. **Emended description:** *Lempholemma* Körb., *Lichina* C. Agardh, *Thelignya* A. Massal., Lichinaceae Nyl., Phylliscaceae Th. Fr., Porocyphaceae Körb. **Resurrection:** *Cladopsis* Nyl., *Collemopsis* Nyl. *ex* Crombie, *Forssellia* Zahlbr., *Pleopyrenis* Clem., *Synalissina* Nyl.

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INTRODUCTION

The *Lichinomycetes* is an independent lichenized lineage within the *Ascomycota* which includes one order, *Lichinales*, and comprises *ca*. 390 described species and 50 genera (Jaklitsch *et al.* 2016, Lücking *et al.* 2016, Wijayawardene *et al.* 2020). Its independent phylogenetic position was already observed by Spatafora *et al.* (2006) and Schoch *et al.* (2009), whose results placed the group close to *Geoglossomycetes*. Recent phylogenetic studies place the *Lichinomycetes* as sister to the *Coniocybomycetes* (Prieto *et al.* 2013, Beimforde *et al.* 2014, Voglmayr *et al.* 2019) in a divergent clade in *Ascomycota*. Recently, Diaz-Escandón *et al.* (2022) proposed a much broader concept of *Lichinomycetes,* including six different fungal classes (*Coniocybomycetes*, *Geoglossomycetes*, *Xylonomycetes*, *Candelariomycetes* and *Sareomycetes*). This was based on similarities on genome content and gene repertoires.

Following the narrow concept, the *Lichinomycetes* are mostly small and gelatinous when wet but at a closer view they develop all lichen growth forms (*i.e.* crustose, squamulose, foliose, fruticose and filamentous forms; Fig. 1). The species possess a wide variety of growth forms, anatomy, ascoma development, ascus types or number of spores per asci (Henssen 1963a, Moreno & Egea 1991). Ascomata include typical apothecia, but other types such as pycnoascocarps and thallinocarps also occur (Henssen 1963a, 1980, Henssen & Jahns 1974) (Fig. 2). The asci are mainly thin-walled, prototunicate, usually with eight spores, but unitunicate or polysporous asci are present in some species and genera. However, based on previous studies (*e.g.* Henssen 1980, Eriksson 1981, Büdel 1987, Henssen *et al.* 1987), and own microscopic observations, Moreno & Egea (1991) observed different structures

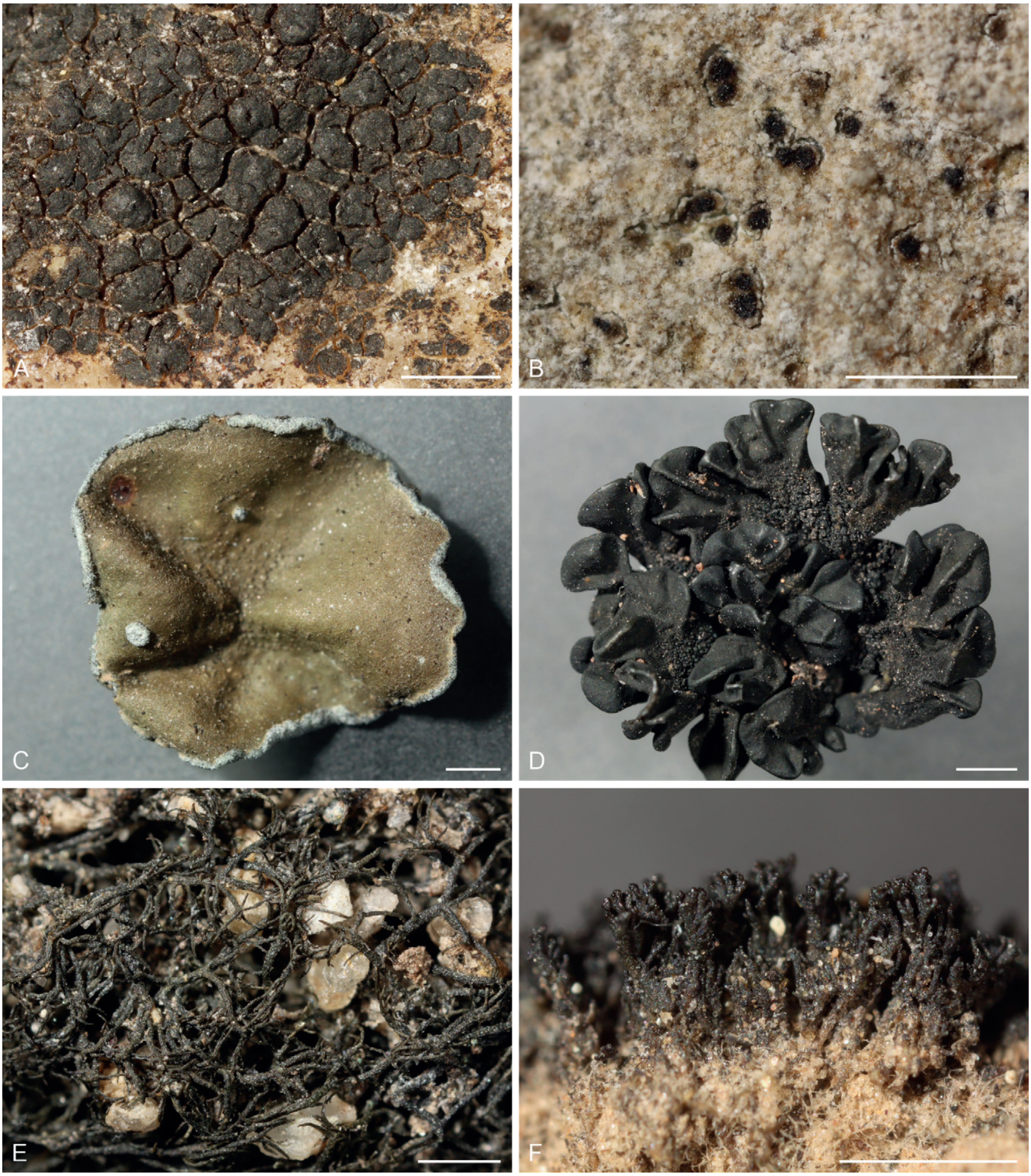

Fig. 1. Main types of thallus growth forms in the *Lichinomycetes*. **A.** *Pterygiopsis atra*, crustose, margin slightly effigurate (Beeching 6938). **B.** *Watsoniomyces obsoletus*, endolithic with immersed, blackish apothecia (Powell). **C.** *Peltula euploca*, squamulose-peltate, concave with grey sorediate margin (Marques 1246). **D.** *Digitothyrea polyglossa*, foliose, divided into furcate, plicate lobes, surface isidiate (Schultz 16124). **E.** *Ephebe lanata*, filamentous, irregularly branched, shape determined by *Stigonema* cyanobiont (Schultz 16606a). **F.** *Lichinella stipatula*, fruticulose or dwarf-fruticose with short, erect branchlets (Schultz 16610b). A, D. *Lichinaceae*. B, E. *Porocyphaceae*. C. *Phylliscaceae*. F. *Lichinellaceae*. Scale bars = 1 mm.

in the asci and proposed additional types of asci in the *Lichinaceae*: the *Lichinella*, *Lichina*, *Peccania*, *Pyrenopsis* and *Synalissa* types (Fig. 3). Büdel (1987) also described the *Peltula* type asci.

Primary photobionts are cyanobacteria including various filamentous and coccoid groups (*e.g.*, *Calothrix*, *Chroococcidiopsis*, *Gloeocapsa*, *Scytonema* or *Stigonema*) apart from *Nostoc* (Bubrick

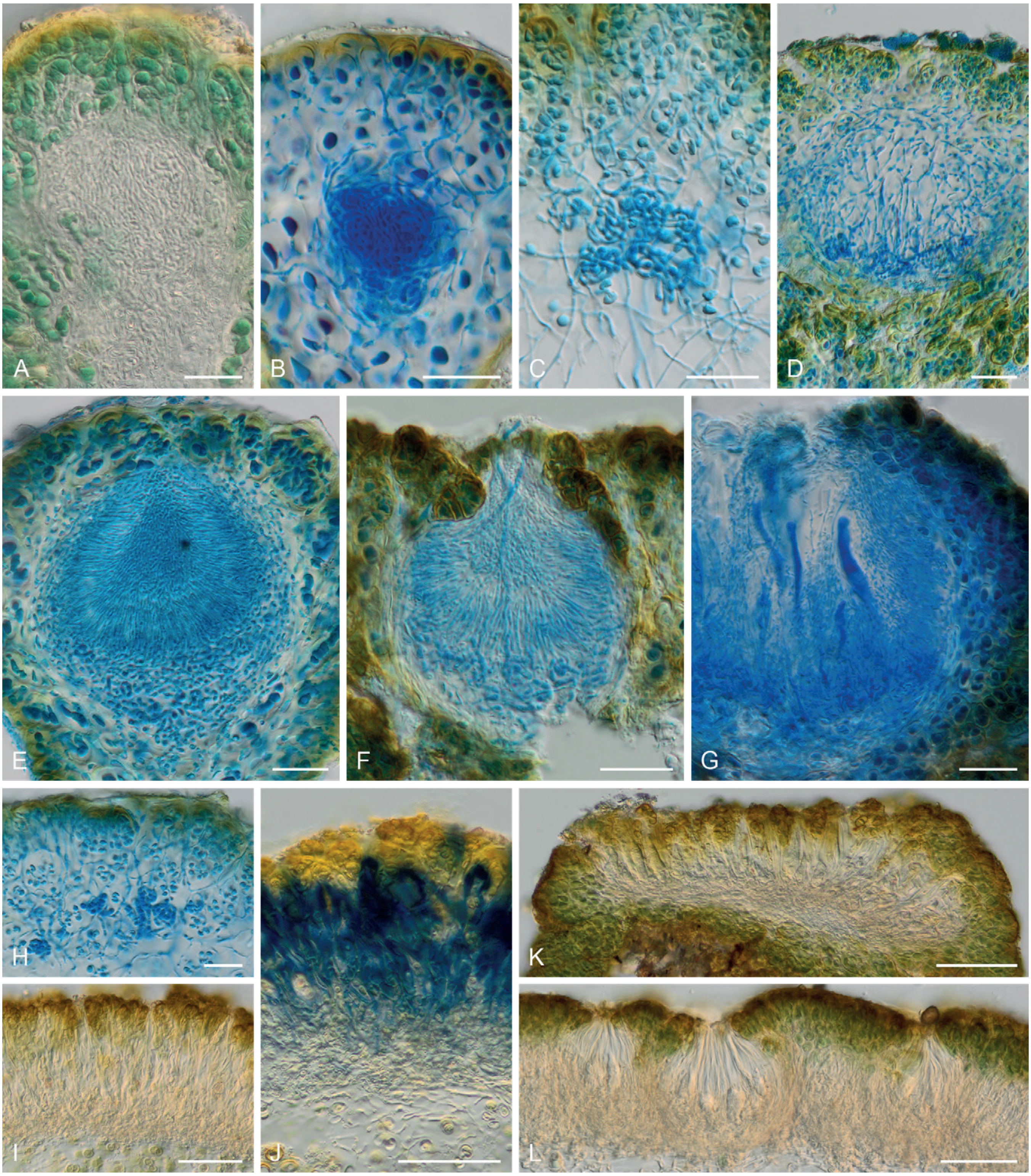

Fig. 2. Ascoma ontogeny main pathways in the *Lichinomycetes.* **A.** *Lichina confinis*, spheroid tangle of generative hyphae in tip of thallus branch developing into an apothecium (Schultz 07195). **B.** *Phloeopeccania pulvinulina*, tangle of generative hyphae with densely coiled ascogones in LPCB (Brown 50910). **C.** *Peccania fontqueriana*, group of coiled ascogones developed directly from thallus hyphae in LPCB (Schultz 14102b). **D.** *Psorotichia frustulosa*, spheroid ascoma primordium formed by reticulate hyphae and first ascogenous hyphae at the base in LPCB (Palice 12703). **E.** *Porocyphus antarcticus*, early stage of pycnoascocarp with ascogones formed beneath a still fully functional pycnidium in LPCB (Eaton, holotype). **F.** *Tichocyphus gotlandicus*, somewhat later stage with trichogynes protruding into pycnidial cavity in LPCB (Schultz 05569, paratype). **G.** *Collemopsis schaereri,* medium stage of pycnoascocarp, juvenile asci and first paraphyses formed in pycnidial cavity and conidiophores still producing small conidia in LPCB (Schultz 03440b). **H.** *Lichinella algerica* aggr., earliest stage of thallinocarp development with coiled ascogones below thallus surface in LPCB (Groner 4354). **I.** *Lichinella minnesotensis*, young thallinocarp with sparse paraphyses and juvenile asci below almost continuous thallus cover (LaGreca 4245). **J.** Thallinocarp hymenium with strong blue staining in KOH/Lugol and sterile, yellowish brown thallus cover (LaGreca 4245). **K.** *Lichinella myriospora*, mature thallinocarp, irregular hymenium with sparse asci and paraphyses covered by almost continuous layer of sterile thallus plectenchyma containing coccoid cyanobionts (Palice 15858). **L.** *Lichinella cribellifera*, mature thallinocarp, hymenium divided into partial hymenia with punctiform discs and separated by intrusions of sterile thallus (Feuerer). Scale bars: A–H = 25 µm, I–L = 50 µm.

1978, Büdel 1982, 1985, Büdel & Henssen 1983, Jung *et al.* 2021, Sanders & Masumoto 2021, Chrismas *et al.* 2023). Most species are saxicolous or terrestrial, and rarely corticolous (Henssen 1980). Worldwide distributed, members of *Lichinomycetes* are considered pioneers on environmental extreme substrates. They grow on seeping moist or irrigated rocks, maritime and littoral zones,

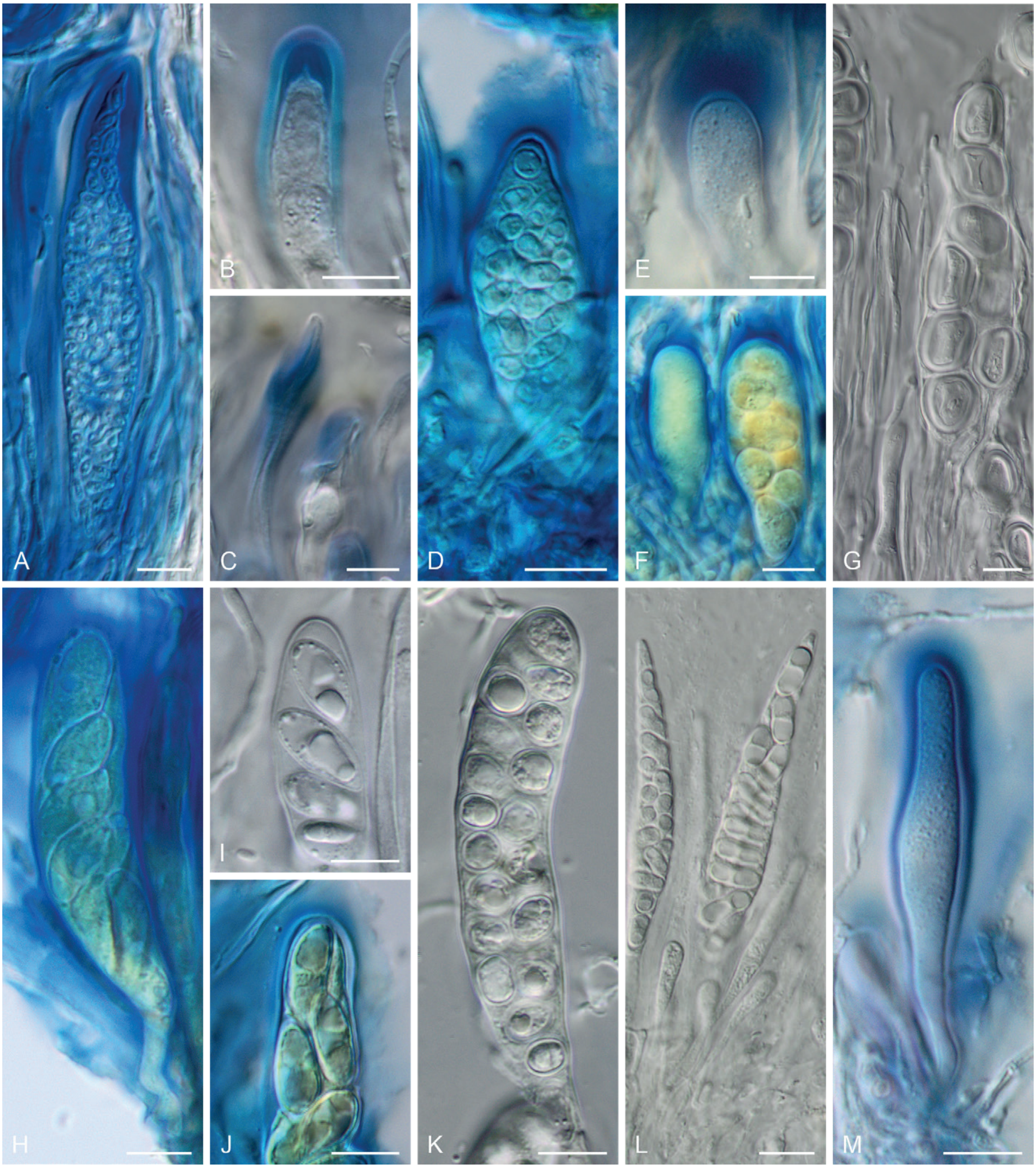

Fig. 3. Ascus types and ascospores in the *Lichinomycetes*. **A.** *Peltula euploca*, narrow clavate, polysporous, unitunicate-rostrate ascus in KOH/Lugol, tip thickened and distinctly amyloid (Marques 1247). **B.** *Pyrenopsis furfurea/haematina*, unitunicate-rostrate ascus, tip amyloid in KOH/Lugol with small ocular chamber. **C.** Emptied ascus with amyloid rostrum (Schultz 16930). **D.** *Lichinella cribellifera*, *Lichinella* type ascus, irregularly clavate, thin walled, no apical wall thickening, but outer wall coat distinctly staining in KOH/Lugol and tip with bluish outer gelatinous cap (Feuerer). **E.** *Peccania coralloides*, *Peccania* type ascus *sensu* Moreno & Egea (1991), broadly clavate, thin walled, with distinct amyloid outer cap, but no apical dome, KOH/Lugol (Schultz 08477). **F.** *Anema tumidulum*, *Peccania* type ascus *sensu* Moreno & Egea (1991) in KOH/Lugol (Henssen 17744b, isotype). **G.** *Lichina confinis*, *Lichina* subtype ascus, wall very thin, non amyloid in KOH (Schultz 05548). **H.** *Psorotichia murorum*, *Psorotichia* subtype ascus *sensu* Moreno & Egea (1991), 8-spored, wall thin with thin amyloid outer coat and only indistinct amyloid cap, KOH/Lugol (Schultz 19162). **I.** *Collemopsis schaereri*, *Psorotichia* subtype ascus *sensu* Moreno & Egea (1991), wall thin throughout, no distinct outer gelatinous cap in KOH (Schultz 05573). **J.** Wall non amyloid with indistinct, somewhat amyloid outer cap in KOH/Lugol (Schultz 05573). **K.** *Synalissa ramulosa*, *Synalissa* subtype ascus *sensu* Moreno & Egea (1991) in KOH, same as *Psorotichia* subtype but polysporous (Schultz 08946). **L.** *Phylliscum demangeonii*, *Phylliscum* type ascus, wall thin throughout, tip pointed, non amyloid, polysporous, in KOH (Schultz 16884). **M.** *Phylliscum aotearoa*, *Phyllisciella* type ascus, wall thick, with strongly amyloid outer coat and amyloid cap but no apical dome in KOH/Lugol (Kantvilas 113-16). Scale bars = 10 µm.

seepages, rivers and lakes, often submerged by water (Jørgenssen 2007), or as soil crust components growing predominantly in arid and semi arid areas (Moreno & Egea 1991, Büdel *et al.* 2009).

The circumscriptions of families and genera in *Lichinomycetes* have varied historically (see Moreno & Egea 1991 for further details). The first family classifications (*i.e.* *Lichinaceae*, *Ephebaceae*, *Pyrenopsidaceae*; Zahlbruckner 1926) were based on the photobionts, until Henssen (1963a) used the ascoma development instead. According to the variability of ascus types (*i.e.* prototunicate asci and unitunicate rostrate) within the group, families were placed within different orders (*i.e. Lecanorales* or *Lichinales*) by several authors. Thus, the order *Lichinales* was erected by Henssen & Büdel in Eriksson & Hawksworth (1986) to contain the families *Lichinaceae* and *Peltulaceae*, and later *Gloeoheppiaceae* (Henssen 1995), arguing differences with the *Lecanoromycetes* in the ascoma development. The family *Heppiaceae* was placed in the *Lecanorales* by some authors (*e.g.* Henssen 1994, Eriksson & Hawksworth 1998, Eriksson 2000), while others (*i.e.* Tehler 1996) placed the *Peltulaceae* among the *Lecanorales* and transferred the *Heppiaceae* to the *Lichinales*. Phylogenetic analyses of rDNA data supported the inclusion of *Heppiaceae* within *Lichinaceae* (Schultz *et al.* 2001), resulting in the synonymy of the family name *Heppiaceae* under the older name *Lichinaceae* (Schultz & Büdel 2003). In these later studies, the monophyly of the class was also supported based on a wider taxon sampling (Schultz *et al.* 2001, eight taxa; Schultz & Büdel 2003, 34 taxa). Currently, three families are accepted (*i.e.* *Gloeoheppiaceae*, *Lichinaceae* and *Peltulaceae*, with three, 36–44 and one genus respectively and 7–10, 335–355 and 32–40 species, Jaklitsch *et al.* 2016, Wijayawardene *et al.* 2020). However, the total diversity of this group of lichens is still insufficiently known and new species are described continuously (Lewis & Schultz 2019, Yang *et al.* 2022, Kitaura *et al.* 2023). Furthermore, only one study has dealt with family delimitation in the *Lichinomycetes* using molecular data (Schultz & Büdel 2003) and the results suggests that families as currently circumscribed should be revised.

Recent studies have excluded several genera from the class, as the case of *Epiphloea* (belonging to *Collemataceae*; Schultz *et al.* 2015), *Lichinodium* (belonging to the *Leotiomycetes*, Prieto *et al.* 2019). Based on unpublished data and preliminary results communicated by Amo *et al.*, the genera *Euopsis* and *Harpidium* which may constitute an undescribed independent lineage of lichenized fungi. Also, some species have been recently included in the *Lichinomycetes* (Diaz-Escandón *et al.* 2021; *Watsoniomyces*). Regarding generic delimitation, the circumscription of genera is one of the major challenges in the family (Henssen 1963a, 1980, Ellis 1981, Moreno & Egea 1992a), and there are very few studies including molecular data (Schultz & Büdel 2003, Kauff *et al.* 2018). Almost all groups are taxonomically confused, phylogenetically unclear, and in urgent need of collecting and taxonomic revision (Moreno & Egea 1991, Kauff *et al.* 2018). Crustose species and genera (*e.g. Psorotichia*, *Pterygiopsis*, *Pyrenopsis*) which are poorly delimited and poorly known (Moreno & Egea 1994) need particular attention. Additionally, phenotypical variation caused by environmental conditions has been reported to be a serious problem in the species identification (Moreno & Egea 1991) which may also affect the generic delimitation.

Thus, the aim of this study was to investigate the phylogenetic relationships within the *Lichinomycetes* in order to revise the current classification accordingly. A second aim was to study the characters used in genera delimitation by ancestral state reconstruction analyses and to evaluate their use as circumscribing characters.

MATERIAL AND METHODS

Taxon sampling

We used a representative sample of the *Lichinomycetes* to cover the three families currently recognized within the class and most of the genera, especially species-rich ones such as *Lempholemma*, *Lichinella*, *Psorotichia* and *Pyrenopsis*. The collections used are mostly from M. Prieto and M. Schultz and deposited in S and HBG fungaria, respectively. For the most difficult and doubtful species, we have included several specimens. In total, we have included 190 specimens representing 126 species of *Lichinomycetes* (Table 1) covering roughly one third of all known species.

Morphology

Anatomy of the samples was studied employing an Olympus BX51 compound microscope set to differential interference contrast (DIC) and equipped with an Olympus XC50 camera to obtain digital images. Freezing microtome sections 14–16 µm thick were produced, stained and fixed with lactophenol cotton blue.

The circumscriptions of families and genera in *Lichinomycetes* have been based on different characters including growth form, ascoma development, spore number and type of asci (see Moreno & Egea 1991 for further details). Thus, to test whether the currently used diagnostic characters represent synapomorphies according to molecular phylogenetic reconstructions we have traced the evolution of these four characters scored as discrete binary and multistate as follows (Supplementary Table S1).

Growth forms include 0) crustose, 1) endolithic, 2) squamulose, 3) foliose, 4) filamentose and 5) fruticulose species (Fig. 1). Ascoma ontogeny follows three major paths (Henssen 1963a): 0) typical apothecia formed from ascogons arising single or in groups prior or after formation of a usually spheroid tangle of generative hyphae, trichogynes single or in groups protruding towards the thallus surface and getting fertilized by spermatia and initiating formation of ascogeous hyphae and a juvenile hymenium (Fig. 2A–D), 1) pycnoascocarps initiated by ascogones formed beneanth pycnidia with trichogynes protruding into the pycnidial cavity or ± along the outer pycnidial wall towards the thallus surface and getting fertilized by spermatia most likely originating from the pycnidium, primary paraphyses formed by former conidiophores and juvenile asci formed within the pycnidial cavity and pycnidium subsequently replaced by growing young hymenium with secondary paraphyses (Fig. 2E–G) or 2) thallinocarps that are formed from groups of free acscogones and trichogynes, a distinct tangle of generative hyphae lacking and thus excipular structures much reduced with asci and sparse paraphyses remaining ± covered by sterile thalline plectenchyma, sometimes becoming divided by protruding sterile thalline plectenchyma into small partial hymenia (Fig. 2H–L). Asci can be 0) octosporous or 1) polysporous (Fig. 3D, F–L). For ascus type we integrated information taken from Henssen & Jahns (1974), Henssen (1980), Büdel (1987), Moreno & Egea (1991) as well as own observations obtained from sequenced and other relevant material and here we accept the following types: 0) Unitunicate-rostrate type (adopting the *Peltula* type *sensu* Büdel (1987) for all species of *Pyrenopsis s. l.* possessing asci with strongly amyloid apical dome forming a rostrum upon ascospore discharge) (Fig. 3A–C), 1) *Lichinella* type (thin walled with distinctly amyloid outer coat and gelatinous cap) (Fig. 3D), 2) *Lichina* type (wall very thin, disintegrating or opening by apical ruptures, amyloid outer coat absent or thin; and not thick walled and bitunicate as claimed by Janex-Favre (1967), see Henssen & Jahns 1974: 81–82; includes *Synalissa* and *Psorotichia* subtypes (Fig. 3G–K), 3) *Peccania* type (thin wall with a distinct gelatinose amyloid cap which may be lacerate or not; includes the "*Pyrenopsis*" type *sensu* Moreno & Egea (1991) which applies only for the non unitunicate-rostrate species, *i.e. Cladopsis*) (Fig. 3E, F), 4) *Phylliscum* type (thin walled with distinctly pointed tips; Henssen 1980, Henssen & Büdel 1984) (Fig. 3L), 5) *Phyllisciella* type (bottle shaped, thick walled, polysporous; Henssen & Büdel 1984) (Fig. 3M), and 6) prototunicate with ascospores released very early and present in mazaediate *Coniocybomycetes*.

Due to the low variability observed (*e.g.* presence of paraphyses, conidia shape or secondary metabolites) or the lack of reliable data related to an unexpected high diversity (*e.g.* vegetative thallus anatomy, type of cyanobionts), these other characters have been studied for species delimitation, but not included in the ancestral state reconstruction analyses.

Extraction, PCR and sequencing

Genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen) according to the manufacturer's instructions. For this purpose, a small piece of the thallus was cleaned under a dissecting microscope merged in liquid nitrogen and ground to a powder using a pestle and mortar. On the basis of a pilot study comparing different gene regions, according to its phylogenetic resolution and ease of amplification, we selected two protein-coding genes, *RPB2* and *mcm7*, and the mtSSU rDNA region for analysis. The mtSSU rDNA region was amplified with mtSSU1 and mtSSU3R (Zoller *et al.* 1999). We used the primers mcm7-709for and mcm7-1348rev (Schmitt *et al.* 2009) for amplification of the *mcm7* region and in some cases we carried out a nested PCR using 1 µL of the PCR product and the internal primers mcm7-CalicF and mcm7-CalicR (Prieto *et al.* 2013). The protein coding *RPB2* was amplified using the primers RPB2-5F and RPB2-7cR (Liu *et al.* 1999) and the newly designed primer RPB2-Lich-1045R (ATCATGCTNGGATGRATCTCRCARTG).

The PCR amplifications were performed using Illustra™ Hot Start Mix RTG PCR beads (GE Healthcare, UK) in a 25 µL volume, containing 3 µL of diluted genomic DNA, 10 µM of each primer and distilled water. Amplifications were performed using the following program: initial denaturation at 95 °C for 15 min, followed by 35–40 cycles of 95 °C for 45 s, 54–56 °C for 50 s, 72 °C for 1 min, followed by a final extension at 72 °C for 5 min. The RPB2 program for the combination RPB2-5f and RPB2-Lich-1045R was as follows: initial denaturation at 95 °C for 5 min, followed by 40 cycles of 95 °C for 30 s, 60 °C for 90 s, with a Ramp up 0.2 °C/s, 72 °C for 75 s, followed by a final extension at 72 °C for 8 min. The PCR products were subsequently purified using the enzymatic method Exo-sap-IT (USB Corporation, Santa Clara, California, USA). The purified PCR products were sequenced at Macrogen Europe service (www.macrogen.com), using the same amplification primers. Sequences were assembled and edited using Sequencher v. 4.10.1. (Genes Codes Corporation, Ann Arbor) and deposited in GenBank (Table 1).

Alignments and phylogenetic analyses

Sequences were aligned with MAFFT v. 6 (Katoh & Toh 2008), adjusted manually and translated to amino acids for protein coding loci using Aliview v. 1.26 (Larsson 2014). Ambiguous regions (*sensu* Lutzoni *et al.* 2000) and introns were delimited manually and excluded from the phylogenetic analyses. We also used Gblocks v. 0.91b (Castresana 2000) to identify ambiguous regions following the relaxed conditions described by Talavera & Castresana (2007). Since the Maximum Likelihood results were very similar using Gblocks and manually excluding ambiguous regions, we used the latter for the rest of analyses.

Individual gene regions were analysed using maximum likelihood-based inference (ML) in RAxML v. 8.2.12 (Stamatakis 2014) with a GTRGAMMA model for tree inference and rapid bootstrapping with a GTRCAT model. Gene-tree incongruence was checked by comparing likelihood bootstrap values (ML-BS) between the individual gene trees. Clades were considered in conflict when a supported clade (bootstrap support > 70 %) for one marker was contradicted with significant support by another. Bestfitting substitution models and partitioning scheme for the concatenated 3-locus alignment were inferred with PartitionFinder 2 (Lanfear *et al.* 2017) using the Akaike Information Criterion (AIC).

Based on previous phylogenies (Prieto *et al.* 2019), two members of the *Coniocybomycetes* were used as outgroups and to root the trees. Rapid bootstraping was run with the GTRCAT model. We also carried out a Bayesian analysis using MrBayes v. 3.2.7a (Ronquist & Huelsenbeck 2003, Altekar *et al.* 2004, Ronquist *et al.* 2012) with BEAGLE (Ayres *et al.* 2012). The analyses consisted of two parallel searches, each with four chains, run for 50 M generations, and initiated with random starting trees. The chains were sampled every 1 000 generations from the posterior distribution. To determine if the chains had converged, verify if mixing was appropriate, and choose a suitable burn-in, we plotted the log-likelihood values against the time generation with Tracer v. 1.5.0 (Rambaut & Drummond 2007). We assumed stationarity of the chains when log-likelihood values reached the same stable equilibrium value for each independent run (Huelsenbeck & Ronquist 2001) and when average standard deviation of split frequencies across runs dropped below 0.01. A burn-in sample of 25 000 trees was discarded for each run. The remaining 50 000 trees (pooled from both independent runs) were used to assemble a majority rule consensus tree and to estimate branch lengths and Posterior Probabilities (PPs).

Maximum likelihood, Bayesian analyses and the selection of models were run on the CIPRES Science Gateway v. 3.3 (Miller *et al.* 2010). The resulting trees were edited with Figtree v. 1.4.4. (https://github.com/rambaut/figtree/releases).

Ancestral state reconstruction

We inferred ancestral states and traced the evolution of growth form, ascoma development, spore number and type of asci. Maximum likelihood ancestral state reconstruction was performed with the program Mesquite v. 3.61 (Maddison & Maddison 2019) with the Mk1 model. For this purpose, the last 5 000 trees that resulted from the first run from the Bayesian analysis of the concatenated data set were employed using the "trace character over trees" option, which summarizes the ASR over a series of trees. Stochastic character mapping (SCM) was performed with 100 replicates using the dated tree (from BEAST analysis) in phytools (Revell 2012) with the R function make.simmap and the SYM model. The best-fitting model was selected by comparing the log-likelihoods among the models equal rates (ER), symmetrical (SYM) and all rates different (ARD) using a likelihood ratio test.

Table 1. Species used for the phylogenetic analysis with voucher and GenBank numbers. New combinations and new species are marked in bold.

Species	mtSSU	*RPB2*	*mcm7*	Voucher
Allopyrenis californica ined.	**PQ160697**	**PQ161131**	**PQ161267**	Schultz 16579a (HBG-015146)
Allopyrenis grumulifera (5210)	**PQ160698**	—	**PQ161268**	Schultz 08611 (HBG-015119)
Allopyrenis grumulifera (SL39)	**PQ160699**	—	—	Prieto SL39 (S-F490746)
Allopyrenis haemaleella (4977)	**PQ160700**	**PQ161132**	**PQ161269**	Schultz 08607b (HBG-015121)
Allopyrenis haemaleella (4998)	**PQ160701**	**PQ161133**	**PQ161270**	Schultz 08608 (HBG-015147)
Allopyrenis impolita (SL159)	**PQ160702**	—	**PQ161271**	Prieto SL159 (S)
Allopyrenis impolita (SL46)	**PQ160703**	—	**PQ161272**	Prieto SL46 (S-F490756)
Allopyrenis phaeococca (4596)	**PQ160704**	**PQ161134**	**PQ161273**	McCune 34101 (OSC, HBG-015249)
Allopyrenis phaeococca (5018)	**PQ160705**	**PQ161135**	**PQ161274**	Rosentreter 18855 (SRP)
Allopyrenis reducta (4811)	**PQ160706**	**PQ161136**	**PQ161275**	Schultz 16950 (HBG-015107)
Allopyrenis reducta (SL132)	**PQ160707**	**PQ161137**	**PQ161276**	Prieto SL132 (S)
Allopyrenis sanguinea (4807)	**PQ160708**	**PQ161138**	**PQ161277**	Schultz 16932a (HBG-015116)
Allopyrenis sanguinea (4810)	**PQ160709**	**PQ161139**	**PQ161278**	Schultz 16954a (HBG-015114)
Allopyrenis sanguinea (4978)	**PQ160710**	**PQ161140**	**PQ161279**	Schultz 08607a (HBG-015120)
Allopyrenis tenuis	**PQ160711**	**PQ161141**	—	Schultz 16422 (HBG-015148)
Anema decipiens	**PQ160712**	**PQ161142**	**PQ161280**	Schultz 08410 (HBG-015149)
Anema notarisii	**PQ160713**	**PQ161143**	**PQ161281**	Schultz 08479 (HBG-015150)
Anema nummularium	**PQ160714**	**PQ161144**	**PQ161282**	Marques 659 (PO, HBG-015595)
Anema prodigulum	**PQ160715**	**PQ161145**	**PQ161283**	Hollinger 16274 (hb. Hollinger)
Anema tumidulum	**PQ160716**	**PQ161146**	**PQ161284**	Prieto SL57 (S-F472943)
Chaenotheca furfuracea	JX000121	**PQ161147**	JX000158	Wedin 6366 (UPS)
Chaenotheca gracilenta	JX000119	**PQ161148**	JX000157	Wedin 7022 (S)
Cladopsis densisidiata	MT739518	—	—	Caceres_Aptroot_42415
Cladopsis foederata	JN206655	—	—	Lumbsch (F)
Cladopsis guyanensis	**PQ160717**	—	—	Schultz 20004 (HBG-015151)
Cladopsis palmana	**PQ160718**	—	**PQ161285**	Feuerer (HBG-015152)
Cladopsis polycocca (2692)	**PQ160719**	**PQ161149**	—	Beeching 3152 (HBG-015580)
Cladopsis polycocca (2693)	**PQ160720**	**PQ161150**	**PQ161286**	Beeching 3151 (HBG-015591)
Cladopsis cf. triptococca (SL78)	**PQ160721**	**PQ161151**	**PQ161287**	Schultz 16602a (HBG-015153)
Cladopsis triptococca (3577)	**PQ160722**	—	**PQ161288**	Marques 928 (PO, HBG-015100)
Collemopsis schaereri (3716)	**PQ160723**	**PQ161152**	**PQ161289**	Teuber 1527 (HBG-010202)
Collemopsis schaereri (SL125)	**PQ160724**	**PQ161153**	**PQ161290**	Prieto SL125 (S-F472957)
Collemopsis schaereri (SL126)	**PQ160725**	**PQ161154**	**PQ161291**	Prieto SL126 (S)
Digitothyrea divergens	**PQ160726**	**PQ161155**	**PQ161292**	Schultz 14245a (HBG-015055)
Digitothyrea polyglossa	**PQ160727**	**PQ161156**	**PQ161293**	Schultz 16124 (HBG-015056)
Ephebe cf. hispidula	**PQ160728**	**PQ161157**	**PQ161294**	Prieto SL34 (S-F472977)
Ephebe lanata	**PQ160729**	—	**PQ161295**	Schultz 16606a (HBG-015054)
Ephebe ocellata	**PQ160730**	**PQ161158**	**PQ161296**	Hutten 14639 (HBG-015105)
Ephebe perspinulosa	**PQ160731**	**PQ161159**	**PQ161297**	Prieto SL35 (S-F472971)
Forssellia affinis	**PQ160732**	**PQ161160**	**PQ161298**	Yoshi 100198 (KOLRI, HBG-015136)
Forsellia canariensis	**PQ160733**	**PQ161161**	**PQ161299**	Feuerer (HBG)
Forsellia concordatula (SL123)	**PQ160734**	**PQ161162**	**PQ161300**	Prieto SL123 (S-F490747)
Forssellia concordatula (SL36)	**PQ160735**	**PQ161163**	**PQ161301**	Prieto SL36 (S-F490748)
Forssellia umbilicata	**PQ160736**	**PQ161164**	**PQ161302**	Guttova, Halda & Palice 6203 (PRA)
Gloeoheppia erosa	**PQ160737**	**PQ161165**	**PQ161303**	Feuerer (HBG-015144)
Gloeoheppia turgida (GB12)	—	**PQ161166**	**PQ161304**	Brown 50805 (HBG-015254)
Gloeoheppia turgida (SL118)	—	**PQ161167**	**PQ161305**	Feuerer (HBG)
Gonotichia depauperata	**PQ160738**	**PQ161168**	**PQ161306**	Schultz 08299 (HBG-015060)

Table 1. (Continued).

Species	mtSSU	*RPB2*	*mcm7*	Voucher
Gonotichia octosporella	**PQ160739**	**PQ161169**	**PQ161307**	Prieto SL28 (S)
Heppia adglutinata	—	**PQ161170**	—	Prieto SL97 (S-F473114)
Heppia despreauxii	**PQ160740**	**PQ161171**	**PQ161308**	Feuerer (HBG)
Heppia solorinoides	**PQ160741**	—	**PQ161309**	Prieto SL153 (S)
Jenmania goebelii	—	**PQ161172**	**PQ161310**	Kato (HBG-015184)
Lapismalleus lugubris **(SL1)**	**PQ160742**	**PQ161173**	**PQ161311**	Prieto SL1 (S-F472941)
Lapismalleus lugubris **(SL101)**	**PQ160743**	**PQ161174**	**PQ161312**	Schultz 05566 (HBG-015155)
Lecidopyrenopsis corticola	**PQ160744**	—	**PQ161313**	van den Boom 47145 (BR)
Lemmopsis lutophila	**PQ160745**	**PQ161175**	**PQ161314**	Palice 1959 (PRA, HBG-015250)
Lemmopsis pelodes	**PQ160746**	**PQ161176**	**PQ161315**	Prieto SL20 (S-F473076)
Lempholemma chalazanum	**PQ160747**	**PQ161177**	**PQ161316**	Feuerer (HBG)
Lempholemma elveloideum	**PQ160748**	**PQ161178**	**PQ161317**	Egea (BCN)
Lempholemma polyanthes	**PQ160749**	**PQ161179**	—	Prieto SL71 (S-F473081)
Leprocollema americanum	**PQ160750**	**PQ161180**	**PQ161318**	van den Boom 34547 (BR)
Lichina confinis	**PQ160751**	**PQ161181**	**PQ161319**	Schultz 07195 (HBG-025080)
Lichina intermedia	**PQ160752**	**PQ161182**	**PQ161320**	Galloway (CHR528471, HBG-024418), epitype
Lichina pygmaea	**PQ160753**	**PQ161183**	**PQ161321**	Schultz 04069 (HBG-015171)
Lichinella algerica (4079)	**PQ160754**	—	—	Feuerer (HBG-015185)
Lichinella algerica (4082)	**PQ160755**	—	—	Feuerer (HBG-015186)
Lichinella cf. cribellifera (4028)	**PQ160756**	—	—	Feuerer (HBG-015063)
Lichinella cf. cribellifera (4030)	**PQ160757**	—	—	Feuerer (HBG-015063)
Lichinella cribellifera (3784)	**PQ160758**	**PQ161184**	—	Ertz 16312 (BR, HBG-015094)
Lichinella cribellifera (4035)	**PQ160759**	**PQ161185**	—	Feuerer (HBG-015095)
Lichinella iodopulchra (4746)	**PQ160760**	**PQ161186**	**PQ161322**	Schultz 16023j (HBG-015145)
Lichinella myriospora	**PQ160761**	—	**PQ161323**	Palice 15858 (PRA, HBG-015251)
Lichinella nigritella (3821)	**PQ160762**	—	**PQ161324**	Urbanavichus 0905075 (HBG-015583)
Lichinella nigritella (3971)	**PQ160763**	—	—	Schultz 08487 (HBG-015189)
Lichinella nigritella (3982)	**PQ160764**	—	—	Schultz 08472 (HBG-015190)
Lichinella schleicheri (3662)	**PQ160765**	—	**PQ161325**	Dirig & Werier L-8435 (CUP, HBG-015191)
Lichinella schleicheri (4902)	**PQ160766**	—	**PQ161326**	Schultz 17158 (HBG-015192)
Lichinella stipatula	**PQ160767**	**PQ161187**	—	Schultz 16610b (HBG-015062)
Lingolemma lingulatum **(4714)**	**PQ160768**	**PQ161188**	—	Berger (hb. Berger, HBG-015206)
Lingolemma lingulatum **(4715)**	**PQ160769**	**PQ161189**	—	Berger 24056a (hb. Berger, HBG-015042)
Lingolemma lingulatum **(GB16)**	**PQ160770**	—	**PQ161327**	Berger (Schultz 12208)
Metamelanea umbonata (3841)	**PQ160771**	**PQ161190**	**PQ161328**	Orange 15053 (NMW, HBG-015233)
Metamelanea umbonata (SL48)	**PQ160772**	**PQ161191**	**PQ161329**	Prieto SL48 (S-F473079)
Paludolemma syreniarum	**PQ160773**	—	—	Lewis 1414a (HBG-024775)
Paracyphus gotlandicus **(SL134)**	**PQ160774**	**PQ161192**	**PQ161330**	Prieto SL134 (S)
Paracyphus gotlandicus **(SL18)**	**PQ160775**	**PQ161193**	**PQ161331**	Prieto SL18 (S)
Paracyphus gotlandicus **(SL19)**	—	**PQ161194**	—	Prieto SL19 (S)
Paulia aldabrensis	**PQ160776**	**PQ161195**	**PQ161332**	Schultz 18183 (HBG-015193)
Paulia caespitosa	**PQ160777**	**PQ161196**	**PQ161333**	Elix 42467 (CBG, HBG-015194)
Paulia myriocarpa	**PQ160778**	**PQ161197**	**PQ161334**	Berger 24057 (hb. Berger, HBG-015045)
Paulia nitidula	**PQ160779**	**PQ161198**	**PQ161335**	Schultz 18155b (HBG-015195)
Paulia perforata	**PQ160780**	**PQ161199**	**PQ161336**	Brown 08022012-1 (hb. Brown, HBG-015253)
Peccania cernohorskyi	**PQ160781**	**PQ161200**	**PQ161337**	Candan 22 (ANES17287, HBG-024803)
Peccania coralloides	**PQ160782**	**PQ161201**	**PQ161338**	Schultz 08484 (HBG-015059)
Peccania fontqueriana	**PQ160783**	**PQ161202**	**PQ161339**	Seelemann L036 (HBG-015196)

Table 1. (Continued).

Species	mtSSU	*RPB2*	*mcm7*	Voucher
Peccania subnigra	**PQ160784**	**PQ161203**	**PQ161340**	Bratt 12585 (SBBG)
Peccania teretiuscula	**PQ160785**	**PQ161204**	**PQ161341**	van den Boom 34531 (BR)
Peccania terricola	**PQ160786**	**PQ161205**	**PQ161342**	Urbanavichus 0905060a (HBG-015584)
Peltolemma socotranum **(14042)**	**PQ160787**	**PQ161206**	**PQ161343**	Schultz 14042c (HBG-015199)
Peltolemma socotranum **(14045)**	**PQ160788**	**PQ161207**	**PQ161344**	Schultz 14045a (HBG-015198)
Peltolemma socotranum **(GB18)**	**PQ160789**	**PQ161208**	**PQ161345**	Schultz 14303a (HBG-015197)
Peltula aff. tenuis	**PQ160790**	—	**PQ161346**	Beeching s.n. (HBG-015586)
Peltula auriculata	**PQ160791**	—	—	Gröger 18, AFTOL 892 (Büdel 24901)
Peltula bolanderi	**PQ160792**	**PQ161209**	**PQ161347**	Hutten 14883 (SBBG000900L)
Peltula clavata	—	**PQ161210**	**PQ161348**	Sérusiaux (BR, HBG-015200)
Peltula euploca	**PQ160793**	**PQ161211**	**PQ161349**	Marques 1246 (HBG-015596)
Peltula lingulatum	**PQ160794**	**PQ161212**	**PQ161350**	Sérusiaux (BR, HBG-015201)
Peltula radicata	—	**PQ161213**	—	Schultz 19135a (HBG-019535)
Peltula rodriguezii	**PQ160795**	**PQ161214**	**PQ161351**	Prieto SL68
Peltula tortuosa	**PQ160796**	**PQ161215**	**PQ161352**	Büdel 24058 (HBG-015111)
Peltula umbilicata	DQ92295	—	—	AFTOL 891 (Büdel 14901a-1, B)
Phloeopeccania fruticosa ined.	**PQ160797**	**PQ161216**	—	Brown 50529 (hb. Brown, HBG-015202)
Phloeopeccania pulvinulina	**PQ160798**	**PQ161217**	**PQ161353**	Brown (HBG-015203)
Phylliscum aotearoa	**PQ160799**	—	—	Kantvilas 113/16 (HO583182, HBG-015585)
Phylliscum demangeonii (SL130)	**PQ160800**	GCA_026026795	—	Prieto SL130 (S-F472980)
Phylliscum granuliforme **(SL29)**	**PQ160801**	—	—	Prieto SL29 (S-F472975)
Phylliscum granuliforme **(SL82)**	**PQ160802**	—	—	Lewis 1303 (HBG-015140)
Phylliscum permiscens **(4794)**	**PQ160803**	**PQ161218**	—	Schultz 16877 (HBG-015122)
Phylliscum permiscens **(SL47)**	**PQ160804**	**PQ161219**	**PQ161354**	Prieto SL47 (S)
Pleopyrenis cf. picina **(SL158)**	—	**PQ161220**	**PQ161355**	Prieto SL158 (S-F490749)
Pleopyrenis picina **(4999)**	**PQ160805**	—	**PQ161356**	Schultz 08609 (HBG-015204)
Pleopyrenis picina **(5209)**	**PQ160806**	—	**PQ161357**	Schultz 08627 (HBG-015205)
Porocyphus coccodes (SL14)	**PQ160807**	**PQ161221**	**PQ161358**	Prieto SL14 (S)
Porocyphus coccodes (SL163)	**PQ160808**	**PQ161222**	**PQ161359**	Prieto SL163 (S)
Porocyphus coccodes (SL184)	**PQ160809**	**PQ161223**	**PQ161360**	Prieto SL184 (S-F251637)
Porocyphus macrosporus	—	**PQ161224**	—	Ertz 12986 (BR, HBG-015207)
Porocyphus rehmicus (SL135)	**PQ160810**	—	**PQ161361**	Prieto SL135 (S)
Porocyphus rehmicus (SL26)	**PQ160811**	**PQ161225**	**PQ161362**	Prieto SL26 (S)
Porocyphus willeyii	**PQ160812**	**PQ161226**	**PQ161363**	Beeching 10219 (NYS, HBG-015587)
Pseudocarpon persimile **(SL21)**	**PQ160813**	**PQ161227**	**PQ161364**	Prieto SL21 (S)
Pseudocarpon persimile **(SL75)**	—	**PQ161228**	**PQ161365**	Schultz 05557 (HBG-015208)
Pseudocarpon persimile **(SL76)**	**PQ160814**	**PQ161229**	**PQ161366**	Prieto SL76 (S)
Pseudotichia vermiculata **(SL12)**	**PQ160815**	—	**PQ161367**	Prieto SL12 (S)
Pseudotichia vermiculata **(SL64)**	**PQ160816**	**PQ161230**	**PQ161368**	Prieto SL64 (S)
Psorotichia columnaris	**PQ160817**	**PQ161231**	**PQ161369**	Feuerer (HBG-015209)
Psorotichia diffracta (SL144)	**PQ160818**	**PQ161232**	**PQ161370**	MUB 8682 (BCN)
Psorotichia diffracta (SL178)	—	**PQ161233**	**PQ161371**	MUB 8737 (BCN)
Psorotichia frustulosa (3332)	**PQ160819**	—	**PQ161372**	Palice 12703 (PRA, HBG-015252)
Psorotichia frustulosa (SL96)	**PQ160820**	**PQ161234**	**PQ161373**	Prieto SL96 (S)
Psorotichia murorum (SL141)	**PQ160821**	—	**PQ161374**	MUB 8039 (BCN)
Psorotichia murorum (SL146)	**PQ160822**	—	**PQ161375**	Prieto SL146 (S-F490757)
Psorotichia polyspora	—	**PQ161266**	**PQ161376**	Canêz, Spielmann, Lorenz-Lemke & Fava 3357 (CGMS 31710, HBG-015593)

Table 1. (Continued).

Species	mtSSU	*RPB2*	*mcm7*	Voucher
Pterygiopsis atra (3172B)	—	—	**PQ161377**	Beeching 6938 (NYS, HBG-015578)
Pterygiopsis atra (3414)	—	**PQ161235**	—	Beeching 9855 (NYS, HBG-015577)
Pterygiopsis atra (3560)	—	**PQ161236**	**PQ161378**	Beeching 9855 (NYS, HBG-015577)
***Pycnolemma polycarpum* (4327)**	**PQ160823**	**PQ161237**	**PQ161379**	Schultz 18125 (HBG-015210)
***Pycnolemma polycarpum* (SL88)**	**PQ160824**	**PQ161238**	**PQ161380**	Schultz 18291 (HBG-015212)
***Pycnolemma polycarpum* (SL89)**	**PQ160825**	**PQ161239**	**PQ161381**	Schultz 18280 (HBG-015211)
Pyrenocarpon thelostoma (2954)	**PQ160826**	**PQ161240**	**PQ161382**	Hyerczyk 2400 (HBG-015213)
Pyrenocarpon thelostoma (SL151)	**PQ160827**	**PQ161241**	**PQ161383**	Hyerczyk 2400 (HBG-015213)
Pyrenopsis conferta (5078)	**PQ160828**	—	**PQ161384**	van den Boom 26043 (BR, HBG-015549)
Pyrenopsis conferta (SL157)	—	**PQ161242**	**PQ161385**	Prieto SL157 (S)
Pyrenopsis conferta (SL42)	—	—	**PQ161386**	Prieto SL42 (S-F490750)
Pyrenopsis furfurea (SL38)	**PQ160829**	**PQ161243**	**PQ161387**	Prieto SL38 (S-F490751)
Pyrenopsis furfurea/haematina (4805)	**PQ160830**	—	—	Schultz 16925 (HBG-015106)
Pyrenopsis furfurea/haematina (SL131)	**PQ160831**	—	**PQ161388**	Prieto SL131 (S-F490758)
Pyrenopsis furfurea/haematina (SL33)	—	**PQ161244**	**PQ161389**	Prieto SL33 (S)
Pyrenopsis furfurea/haematina (SL40)	**PQ160832**	—	—	Prieto SL40 (S)
Pyrenopsis furfurea/haematina (SL41)	**PQ160833**	—	**PQ161390**	Prieto SL41 (S)
Pyrenopsis furfurea/haematina (SL95)	**PQ160834**	—	**PQ161391**	Prieto SL95 (S-F473115)
Pyrenopsis furfurea/haematina (2952)	**PQ160835**	**PQ161245**	**PQ161392**	Schultz 16389 (HBG-015214)
Pyrenopsis subareolata (5378)	**PQ160836**	—	—	Westberg 4.8 (S)
Pyrenopsis subareolata (SL128)	**PQ160837**	**PQ161246**	**PQ161393**	Arup (S-L13190)
Pyrenopsis subareolata (SL160)	**PQ160838**	**PQ161247**	**PQ161394**	Prieto SL160 (S)
Synalissa ramulosa (3987)	**PQ160839**	**PQ161248**	**PQ161395**	Schultz 08483 (HBG-015215)
Synalissa ramulosa (SL16)	**PQ160840**	**PQ161249**	**PQ161396**	Prieto SL16 (S-F472974)
Synalissina botryosa	**PQ160841**	—	**PQ161397**	Prieto SL136 (S-F490752)
Synalissina cladodes	**PQ160842**	**PQ161250**	**PQ161398**	Prieto SL137 (S-F490753)
Synalissina condensata	**PQ160843**	—	**PQ161399**	Groner 4014 (hb. Groner, HBG-015047)
Synalissina degeliana	**PQ160844**	—	**PQ161400**	Prieto SL5 (S-F490754)
Synalissina intricata	**PQ160845**	**PQ161251**	**PQ161401**	Schultz 08404 (HBG-015216)
Synalissina isidiodes	**PQ160846**	**PQ161252**	**PQ161402**	Prieto SL61 (S-F490755)
Synalissina vesiculifera	**PQ160847**	—	**PQ161403**	Rosentreter 18798 (SRP, HBG-015048)
Thelignya lacustris	**PQ160848**	**PQ161253**	**PQ161404**	Prieto SL50 (S-F473080)
Thelignya lignyota	**PQ160849**	**PQ161254**	**PQ161405**	Prieto SL31 (S-F472976)
***Thelignya neglecta* (SL43)**	**PQ160850**	**PQ161255**	**PQ161406**	Prieto SL43 (S)
***Thelignya neglecta* (SL77)**	**PQ160851**	**PQ161256**	**PQ161407**	Schultz 07226 (HBG-025110)
Thermutis velutina (SL53)	**PQ160852**	**PQ161257**	**PQ161408**	Prieto SL53 (S)
Thermutis velutina (SL79)	**PQ160853**	**PQ161258**	**PQ161409**	Westberg (S, F138195)
Thyrea confusa (3774)	**PQ160854**	**PQ161259**	**PQ161410**	Vust (G00057823)
Thyrea confusa (3775)	**PQ160855**	**PQ161260**	**PQ161411**	Vust (G00057823)
Thyrea girardii	**PQ160856**	**PQ161261**	**PQ161412**	Urbanavichus 0905071a (hb. Urbanavichus, HBG-015582)
Thyrea plectopsora	**PQ160857**	—	—	Schultz 18162a (HBG-015052)
Thyrea sp.	**PQ160858**	—	—	Schultz 18175 (HBG-015051)
Tichocyphus gotlandicus	**PQ160859**	**PQ161262**	**PQ161413**	Schultz 05538b (HBG-015244)
Tichocyphus gotlandicus	**PQ160860**	**PQ161263**	**PQ161414**	Schultz 05569 (HBG-015246)
Watsoniomyces obsoletus	MW370265	GCA_026025055	—	Powell 2930
Zahlbrucknerella calcarea	**PQ160861**	**PQ161264**	**PQ161415**	Schultz 08211 (HBG-015243)
Zahlbrucknerella patagonica	**PQ160862**	**PQ161265**	**PQ161416**	Feuerer (HBG-015221)

Divergence time estimates

We implemented a Bayesian Markov chain Monte Carlo algorithm for estimating divergence times using the BEAST v. 1.10.4 software package (Drummond *et al.* 2012). The tree topology and divergence times were estimated simultaneously. Five different unlinked partitions (as in the ML analysis), with the GTR+I+G substitution model for each partition were used, with uncorrelated lognormal relaxed clock model, and a Yule tree prior. We used a secondary calibration constraining the ingroup (*Lichinomycetes*) with a uniform distribution with a lower value of 114 Mya and an upper value of 238 Mya (based on Scenario 2 from Prieto & Wedin 2013) and following Prieto & Wedin (2017). A first relaxed log-normal clock with default priors to estimate prior distributions was run to be used in a final analysis. The BEAST analysis was run for 10 M generations, logging parameters and trees every 1 000 generations. Convergence, mixing, and effective sample sizes (ESS) of parameters were checked using Tracer v. 1.7.2 (Rambaut & Drummond 2007). A burn-in of 1 000 trees was removed from each analysis. The remaining trees were used to generate a maximum clade credibility tree with TreeAnnotator v. 1.10.4 (Drummond *et al.* 2012).

Tests of monophyly

For those clades without enough statistical support or those with lower values, a comparison of marginal likelihood estimates between two models was carried. For this purpose, one topologically constrained tree and one topologically unconstrained, were used to evaluate monophyly. This have been done for clade 3 including *Heppia* (77 % BS support and 95 % pp) and for *Forsellia* (not supported in the combined analysis) with IQ-TREE (Nguyen *et al.* 2015) and based on the approximately unbiased AU test (Shimodaira 2002).

RESULTS

The combined alignment included 683 characters for mtSSU, 917 for *RPB2* and 552 for *mcm7*, with a total of 2 152 characters. The total number of invariant (constant or ambiguous constant) sites was 822 (38.21 % of all sites) corresponding to 292, 321 and 209 from the mtSSU, *RPB2* and *mcm7* respectively. The number of parsimony informative sites was 1 221 in total, with 354, 562 and 305 sites from the mtSSU, *RPB2* and *mcm7*. Bestfitting partitioning scheme was as follows: mtSSU, 1st and 2nd position of *RPB2*, 3rd position of *RPB2*, 1st and 2nd position of *mcm7*, 3rd position of *mcm7* which was applied with a GTRGAMMA model in RAxML and GTR+I+G model in the Bayesian analyses.

Individual gene trees did not have supported nodes in conflict, and data were concatenated. However, differences in main clades were observed. In both the mtSSU and *mcm7* trees, clades 1, 4 and 5 were highly supported, meanwhile in *RPB2* trees only clades 1 and 5 were supported. Clade 3, including *Heppia*, was only supported by *RPB2* (93 % BS). The relationship between clade 4 and 5 was only supported by the *mcm7* tree (88 % BS). Most shallow relationships were similarly supported by the three genes, except in the case of *Forsellia* which was only supported by mtSSU and *RPB2* (83 % and 94 % BS respectively).

The results from Maximum Likelihood and Bayesian analyses were congruent and combined in Fig. 4. Topologies of both analyses were similar, and both trees showed four major lineages (clades 1–4) with significant support. Few clades that were not supported in BS-ML were supported in the Bayesian analysis, including *Pyrenopsis s. str.* and its relationship with the rest of members of clade 3. In both analyses both *Phylliscum* and *Synalissina* showed long branches. The relationship between clades 4 and 5 were not supported by any of the analyses.

The monophyly test did not reject any of the possibilities for clade 3, although the unconstrained tree (as showed in Fig. 4) had a lower log likelihood (-69171.22 *vs* -69176.96). The results were similar for *Forsellia,* where the test did not reject any hypothesis but the constrained tree in which *Forsellia* was monophyletic had a slightly lower log likelihood (-72110.12 *vs* -72111.08).

A high number of genera is not monophyletic: *Cryptothele*, *Lemmopsis*, *Lempholemma*, *Lichina*, *Metamelanea*, *Psorotichia*, *Pterygiopsis* and *Pyrenopsis*. Thus, we here describe new genera in order to achieve a revised classification based on supported clades. Most of these genera (recircumscribed or described as new) are supported and resolved except *Gonotichia*, *Forssellia*, *Phylliscum-Phyllisciella* and *Thyrea-Watsoniomyces*. We describe three new species in three new monotypic genera (*Paracyphus*, *Pseudocarpon* and *Tichocyphus*).

The delimitation of families has been done based on the combined results of the ML-Bayesian analyses considering the morphology, anatomy, and the evolutionary context with the ASR of selected traits and dating results (see below). Thus, Clades 2–5 recovered are considered as different families, which have been emended and redefined here except in the case of clade 5 which does not have a family-level name and that is provided later.

The ancestor for the *Lichinomycetes* and for Clades 2–5 (Fig. 4) is reconstructed as crustose with octosporous asci (Fig. 5). All growth forms have evolved multiple times (except endolithic in the present taxon sampling) and although it is conserved in certain genera, there is a mix of growth forms in other genera being crustose forms overrepresented. Polysporous asci have evolved at least ten times. Regarding ascoma development, *Lichinomycetes* ancestor and clades 2–4 are reconstructed as having pycnoascocarps except for clade 5 which has thallinocarps. Type of asci is not reconstructed with confidence in these nodes except for clade 2 reconstructed as *Lichina* type (Fig. 5 and Supplementary Table S2).

As stated, within the *Lichinales*, five main clades are supported. Clade 1 contains most genera previously included in *Lichinaceae*, together with *Gloeoheppia* (*Gloeoheppiaceae*), *Heppia* (*Heppiaceae*) and three clades previously included in *Pyrenopsis*: *Pyrenopsis s. str.*, *Cladopsis* (*Pyrenopsis p.p.*) and *Pleopyrenis* (*Pyrenopsis p.p.*). Within this big clade, two clades (Clades 2 and 3) are well supported and here recognized as families *Lichinaceae* and *Porocyphaceae* respectively. Clade 2 (*Lichinaceae*) includes *Anema*, *Collemopsis*, *Digitothyrea*, *Forssellia*, *Gloeoheppia*, *Jenmania*, *Lemmopsis*, *Leprocollema*, *Lichina*, *Lingolemma*, *Metamelanea*, *Paludolemma*, *Paulia*, *Peltolemma*, *Phloeopeccania*, *Pseudotichia*, *Psorotichia*, *Pterygiopsis s. str.*, *Pycnolemma*, *Pyrenocarpon*, *Synalissa*, *Thelignya* and *Zahlbrucknerella*. It is mostly characterized by predominantly typical apothecia, also including pycnoascocarps, (but no thallinocarps) and asci of *Peccania* and *Lichina* types. All except endolithic growth forms are present in this clade and polysporous asci have evolved at least three times. Clade 3 (*Porocyphaceae*) is formed by *Cladopsis*, *Ephebe*, *Heppia*, *Lapismalleus*, *Lecidopyrenopsis*, *Paracyphus*, *Pleopyrenis*, *Porocyphus*, *Pseudocarpon*, *Pyrenopsis s. str.*, *Thermutis*, *Lempholemma*, *Thyrea*, *Tichocyphus* and *Watsoniomyces*. Most species have pynoascocarps (no

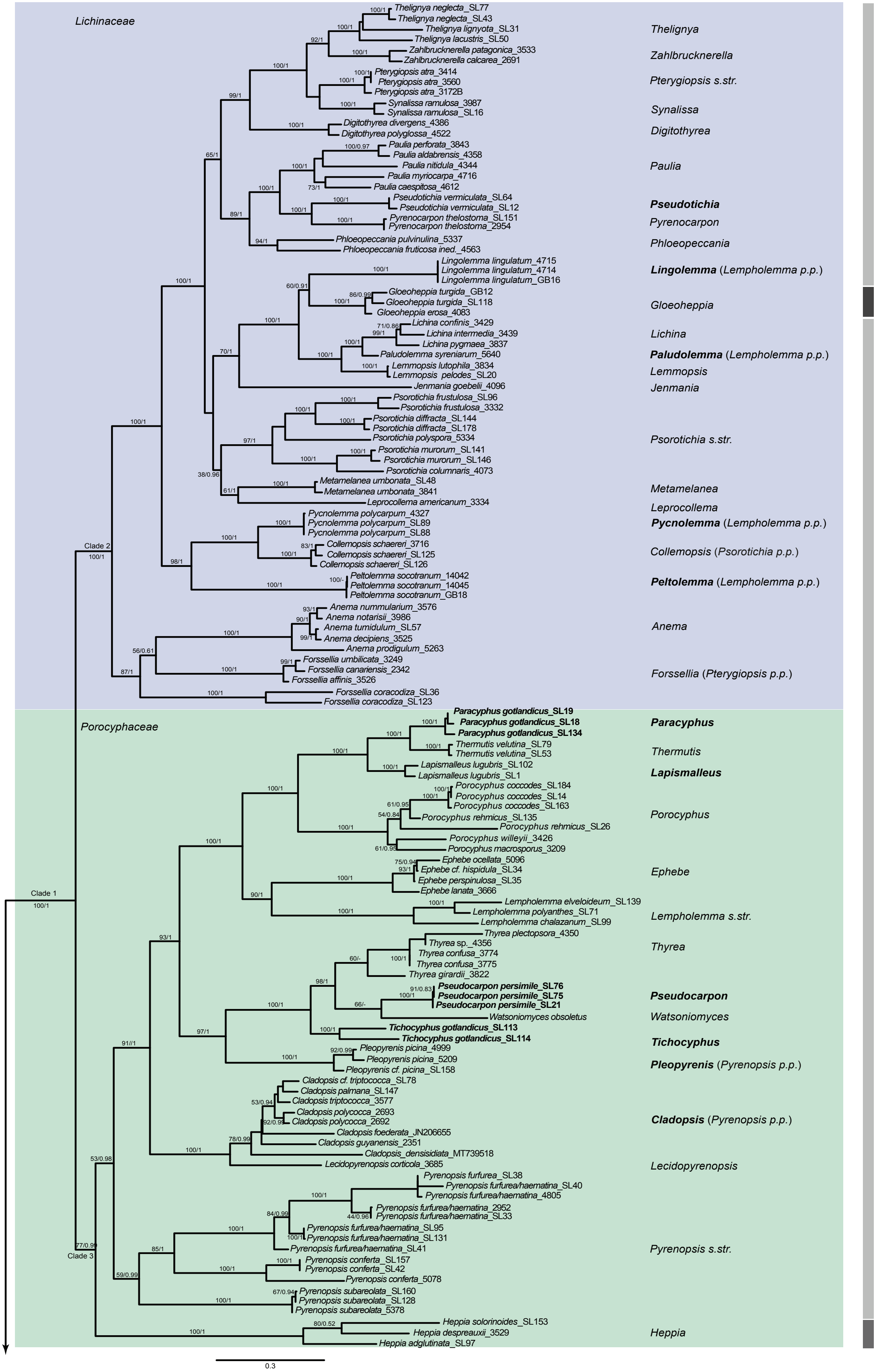

Fig. 4. Best tree from Maximum Likelihood (ML) with values from ML bootstrap followed by Posterior Probabilities from Bayesian analyses. New genera and species are depicted in bold. Previous family classifications are depicted in the tree with a lateral bar with increasing grey tones indicating *Lichinaceae* < *Peltulaceae* < *Heppiaceae* < *Gloeoheppiaceae*.

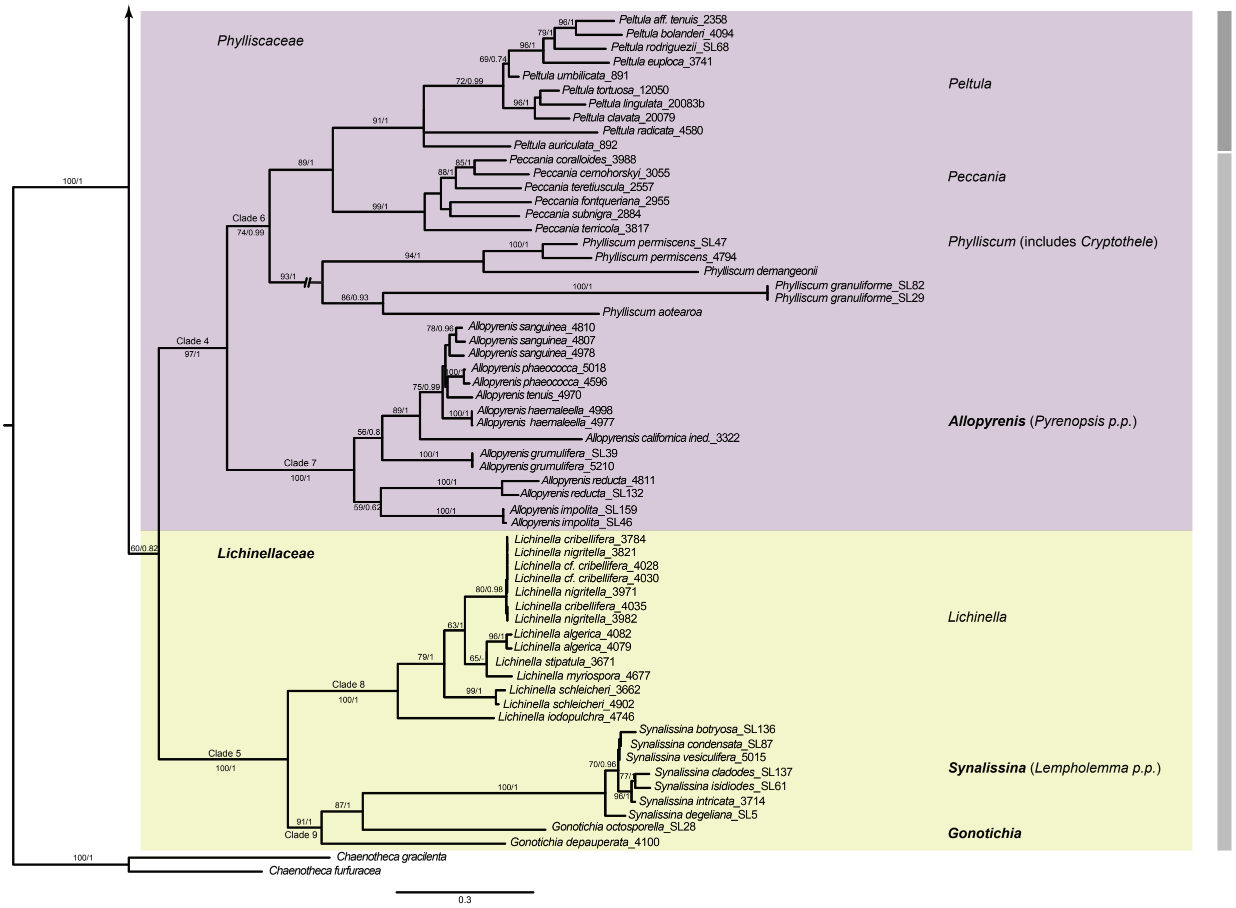

Fig. 4. (Continued).

thallinocarps are present), showing at least two changes to typical apothecia and have variable asci (unitunicate-rostrate, *Peccania* and *Lichina* types). All growth forms are present and polysporous asci have evolved at least twice. Clade 4 (*Phylliscaceae*) includes *Allopyrenis*, *Peccania*, *Peltula*, *Phyllisciella* and *Phylliscum*. The ancestral state for the ascoma development is reconstructed as pycnoascocarps although typical apothecia also occur. Unitunicate-rostrate, *Peccania*, *Phyllisciella* and *Phylliscum* type asci are present. Crustose is the ancestral state for the growth form which evolved to squamulose and fruticulose forms. Polysporous asci have evolved at least three times. Clade 5 (described here as *Lichinellaceae*) includes *Gonotichia*, *Lichinella* and *Synalissina*. The ancestral state for the ascoma development is reconstructed as thallinocarps which evolved once to typical apothecia. Only asci of *Peccania* and *Lichinella* types are present. Ancestor is crustose, but all growth forms except filamentous and endolithic are present. Polysporous asci have evolved once.

Main results from divergence time estimate analyses (Supplementary Fig. S1 show that the *Lichinomycetes* diversified around 138.29 Mya (range 114–208.95). Clade 1 diversified *ca*. 118.13 Mya (range 89.55–178.75). The families *Lichinaceae*, *Porocyphaceae* and *Phylliscaceae* diversified in similar dates (clade 2, median 104.18 (range 77.73–160.99); clade 3, median 110.86 (range 83.82–169.25) and clade 4, median 112.67 (range 85.93–172.74). *Lichinellaceae* is younger than the other three families (clade 5, median 89.72 (range 64.55–140.4)). Most genera diversified between 0.5 and 60 Mya but several groups are older, diversifying between 70 and 83 (*e.g. Pyrenopsis s. str.* and *Phylliscum*).

DISCUSSION

This phylogenetic framework together with the results of the ASR and SCM constitutes the basis for an improved taxonomy of *Lichinomycetes.* Topologies obtained with different algorithms were largely congruent making the delimitation of major lineages and clades more confident. However, ML BP values were generally lower than PP values, which has been related with a less susceptibility to strongly support a wrong phylogenetic hypothesis (Douady *et al*. 2003). Therefore, clades recognized in this study were determined by both Bayesian analysis and ML.

Despite our best effort to obtain a complete sequence data set for all the genes some of them are missing due to failure in the PCR amplification and contaminations. Although the relatively low amount of missing data does not significantly influence the reliability of the resulting phylogeny, this may explain differences in support obtained for the three single gene data sets (as differences in support for clades 3–5, or in *Forssellia*). The results show that the *RPB2* data set was more informative in terms of parsimony-informative characters for the inference of phylogenetic relationships, but the mtSSU data set resolved slightly better the deeper relationships.

The results constitute a significant improvement in terms of obtaining a robust topology with a broader data set and a higher resolution compared with the previous phylogeny of the *Lichinales* based on the 18S rDNA (Schultz & Büdel 2003).

Our findings show evidence for considerable non-monophyly of groups currently accepted at the family and genus levels. The phylogenetic relationships hardly support the current classification scheme based on morphological and anatomical data, and a substantial revision of generic boundaries is needed in order to circumscribe monophyletic groups.

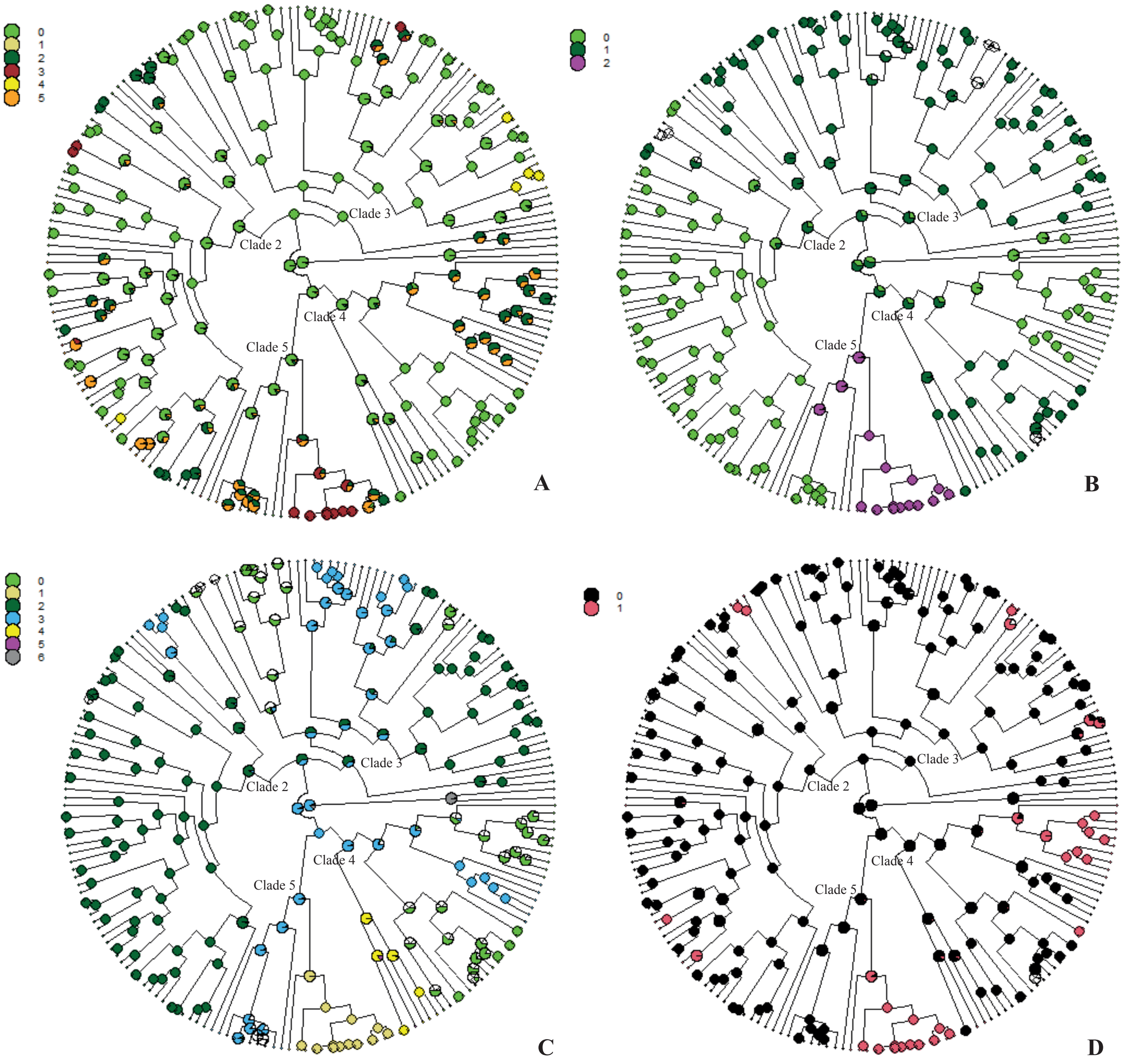

Fig. 5. Ancestral state reconstructions of selected morphological characters from stochastic mapping analyses. **A.** Growth form. 0: crustose, 1: endolithic, 2: squamulose, 3: foliose, 4: filamentose, 5: fruticulose. **B.** Ascoma development 0: typical apothecia, 1: pycnoascocarps, 2: thallinocarps. **C.** Type of asci. 0: unitunicate rostrate, 1: *Lichinella*, 2: *Lichina*, 3: *Peccania*, 4: *Phylliscum*, 5: *Phyllisciella*, 6: prototunicate. **D.** Spore number. 0: octosporous, 1: polysporous. For taxon names see Supplementary Fig. S2.

Families as previously delimited are not monophyletic and are here emended to include more genera thus avoiding the description of a high number of families. Extreme cases of polyphyly have been observed in crustose genera such as *Psorotichia* (distributed in five different clades), *Pterygiopsis* (distributed in three different clades), *Lempholemma* (distributed in six different clades) and *Pyrenopsis* (distributed in four different clades).

Taxonomic delimitations in challenging groups can benefit from phylogenetic comparative methods as they help to evaluate the convergent evolution of a given morphological character, thus enabling the discovery of traits useful for classifications. Thus, in this study, we investigated the evolution of selected traits to test for their suitability for generic delimitations (Bogarín *et al.* 2019). The SCM analysis shows that studied characters are either plesiomorphic or homoplastic. Thus, crustose forms are ancestral in the *Lichinomycetes* and most of the remaining growth forms have evolved from this form. Groups currently accepted as genera include mixed growth forms, thus showing that this character cannot be used for generic delimitation. Although the number of spores per ascus shows trends towards the presence of only one of the states, there are always exceptions, and is not constant in some genera, *e.g.* in *Allopyrenis*, *Ephebe*, *Forssellia* and *Phylliscum*. Ascoma development is quite constant within families and genera, but some exceptions are also observed. In the case of the type of asci, the high variability observed makes it difficult to assess the ancestral and derived states and their gains and losses. Other characters traditionally used for characterizing higher taxa in the *Lichinomycetes*, such as the type of photobiont, have resulted in polyphyletic groups. An example is the genus *Lempholemma*, characterized until now by the presence of *Nostoc* as photobiont. *Lempholemma* is here shown to be highly polyphyletic as it is distributed in six distant clades. However, until recently, photobiont identification has mostly been established based on morphology but studied in lichenized conditions and photobionts show a different morphology when lichenized (Schultz & Büdel 2002) having thus limitations in the identification (Büdel 1983). Recent studies have used photobiont cultures and a polyphasic approach in cyanobacteria identification revealing an unexpected high

Table 2. Synopsis of families with key characters.

Family	Clade	Cyanobiont	Ascus type	Ascoma development	Paraphyses	Conidia
Lichinaceae	2	coccoid (very rarely reddish) or filamentous	*Lichina* or *Peccania* types	typical apothecia, rarely pycnoascocarps	always present	small, ellipsoid or bacilliform
Porocyphaceae	3	coccoid (often reddish) or filamentous	unitunicate-rostrate, *Lichina* or *Peccania* types	pycnoascocarps, rarely typical apothecia	always present	small, ellipsoid, bacilliform or globose
Phylliscaceae	4	coccoid (reddish or yellowish brown)	unitunicate-rostrate, *Peccania*, *Phyllisciella* or *Phylliscum* types	typical apothecia or pycnoascocarps	present or not	small, ellipsoid, bacilliform or large, needle-like/filiform
Lichinellaceae fam. nov.	5	coccoid (not reddish) or *Nostoc*	*Lichinella* or *Peccania* types	thallinocarps or typical apothecia	present, but sometimes sparse	small, ellipsoid or bacilliform

diversity, and very few studies have used molecular data (Jung *et al.* 2021) showing some congruence/stability in photobiont composition within genera but also some cases of variability which demonstrates that further studies are needed using this approach.

Thus, we used a combination of several characters such as the ascoma development and the type of asci to delineate taxonomic groups in the *Lichinomycetes* (Table 2).

Current classification

Because the current classification of the Lichinomycete genera into three families *Lichinaceae*, *Gloeoheppiaceae* and *Peltulaceae* is highly incongruent with the phylogenetic relationships (Fig. 4), a new, fundamentally different classification at family level is needed. Main clades 2–5 are taken up at family level resulting in four families that are more balanced regarding species and genus numbers. Although synapomorphies are missing for all four families, it is possible to circumscribe them by certain sets of characters. Thus, using a combination of characters, their evolution and the phylogenetic relationships, we here propose a re-classification of the *Lichinomycetes* that will resolve some of the major issues outlined above.

The revised classification includes 11 new genera, five resurrected genera, and 54 new combinations distributed in 4 families (3 emended and 1 new). Three new species are also described: *Paracyphus gotlandicus*, *Pseudocarpon persimile* and *Tichocyphus gotlandicus.* New genera: *Allopyrenis*, *Gonotichia*, *Lapismalleus*, *Lingolemma*, *Paludolemma*, *Paracyphus*, *Peltolemma*, *Pseudocarpon*, *Pseudotichia*, *Pycnolemma*, *Tichocyphus*. New family: *Lichinellaceae*.

Lichinaceae Nyl., Mem. Soc. Sci. Nat. Cherbourg 2: 8. 1854. MycoBank MB 81718. Fig. 6.
Synonyms: *Psorotichiaceae* Körb., Parerga Lichenol.: 433. 1865. *inval. nom. nud*. MycoBank MB 81619.
Gloeoheppiaceae Henssen, Lichenologist 27: 266. 1995. MycoBank MB 81968.

Diagnosis: Species rich family of usually small-sized, blackish cyanolichens associating with single-celled cyanobacteria with yellowish brown, rarely with reddish purple gelatinous sheaths or with filamentous cyanobacteria (*Nostoc*, *Scytonema*, *Rivulariaceae*) and of mostly crustose, more rarely squamulose, foliose, fruticulose or filamentous (Fig. 6), but not endolithic growth form. *Thalli* predominantly homoiomerous, rarely corticate, heteromerous and dorsoventrally stratified thalli absent, filiform conidia or branched conidiophores absent. *Paraphyses* always present. *Asci* predominantly 8-spored, but polysporous ones occur as well. *Ascoma* development predominantly starting with ascogones formed freely below thallus surface or formed within a tangle of generative hyphae, pycnoascocarps rare, thallinocarps absent. Resembling *Porocyphaceae*, but ascomata typical apothecia and only rarely pycnoascocarps. Differing from *Phylliscaceae* in the absence of unitunicate-rostrate, *Phyllisciella* and *Phylliscum* type asci. Similar to *Lichinellaceae*, but differing in the absence of thallinocarps and *Lichinella* type asci.

Discriminating characters: Cyanobionts mostly unicellular with yellowish brown, rarely with reddish purple gelatinous sheaths, no unitunicate-rostrate, *Lichinella*, *Phyllisciella* or *Phylliscum* type asci, typical apothecia common, pycnoascocarps rare, no thallinocaps, no filiform or needle like conidia, no reddish brown blotchy coloured epihymenium, no hormocystangia, thallus homoiomerous and ecorticate, IF corticate THEN NOT resembling *Heppia*. Apothecia lecanorine or zeorine, not biatorine.

Description: Lichen-forming ascomycetes obligatory associating with various single-celled cyanobacteria with yellowish brown or rarely reddish-purple gelatinous sheaths or with filamentous cyanobacteria (*Nostoc*, *Scytonema*, *Rivulariaceae*). *Thalli* usually blackish and distinctly swelling when wet, rarely subgelatinous and rarely colour shades of olive or greyish pruinose. Growth forms diverse, ranging from crustose, crustose-effigurate, squamulose, squamulose-peltate, foliose, dwarf fruticose to filamentous, but not endolithic. Thalli fixed to substrate by rhizophyphae, tufts of rhizohyphae, an umbilicus, gelatinous basal layer or holdfast. Isidia sometimes formed, soralia very rare, hormocystangia absent. Thallus homoiomerous and ecorticate, rarely corticate, but if so, thallus not squamulose and dorsoventrally stratified. *Ascomata* predominantly typical apothecia developing from freely arising ascogones or ascogones formed in a tangle of generative hyphae or rarely pycnoascocarps, but never thallinocarps. *Apothecia* zeorine or lecanorine, but not biatorine. *Asci Lichina*, and *Peccania* types, thin-walled and predominantly releasing mature ascospores passively through apical ruptures, rarely by disintegration of the ascus wall when spores are mature. Unitunicate-rostrate, *Lichinella*, *Phyllisciella* or *Phylliscum* type asci absent, predominantly 8-spored, rarely polysporous. *Ascospores* simple, usually broadly ellipsoid, rarely (sub)globose or bean-shaped, walls usually thin, rarely distinctly

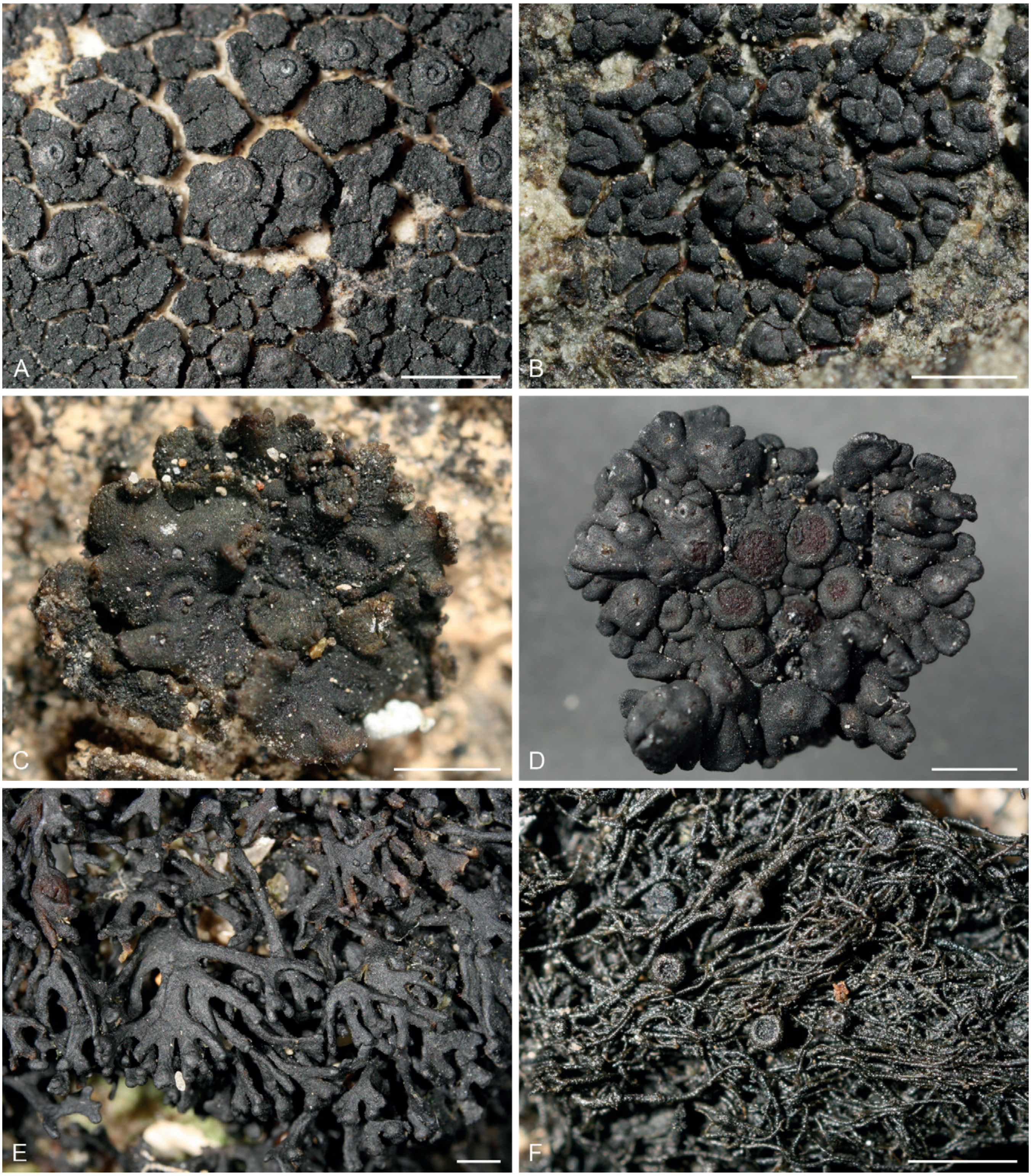

Fig. 6. Thallus growth forms in main clade 2 (*Lichinaceae s. str.*). **A.** *Metamelanea umbonata*, crustose, areoles angulate, thick with blackish, umbonate apothecia (Orange 15053). **B.** *Forssellia affinis*, crustose, margin effigurate, apothecia semi-immersed to sessile (Yoshi 100198). **C.** *Gloeoheppia erosa*, squamulose, margins coarsely sorediate, apothecia immersed to semi-immersed (Feuerer). **D.** *Anema nummularium*, squamulose, umbilicate-rosette shaped, pycnoascocarps at first punctiform and immersed, finally with widely opened, dark red discs (Marques 659). **E.** *Lichina pygmaea*, dwarf fruticose, branches palmate, flattened with globose pycnidia at tips (Schultz 17140). **F.** *Zahlbrucknerella patagonica*, filamentous, furcate, shape determined by *Scytonema* cyanobiont, apothecia lateral (Feuerer). Scale bars = 1 mm.

thickened. *Paraphyses* always present, sparingly to somewhat branched, thin or robust, usually distinctly septate, sometimes apically widened, rarely becoming (sub)moniliform. *Epihymenium* colourless, faintly yellowish to pale reddish or brownish, rarely emerald green, hymenium sometimes divided by intrusions of sterile excipular hyphae and apothecial disc then becoming umbonate or gyrose. *Conidiomata* pycnidia, immersed to slightly elevated, conidiophores simple, conidia formed terminally, simple, small ellipsoid or short bacilliform, rarely subglobose. *Distribution* cosmopolitan, but rare in dense forest habitats lacking exposed rock or soil crusts. On various rocks, sporadically or seasonally wetted and usually in well lit situations, rarely in intertidal coastal zones or amphibious to inundated along lake shores and river banks, also in biological soil crusts, one species on bark

(*Paludolemma syreniarum*). No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Main clade 2 contains the type of genus *Lichina*, *L. pygmaea*, and forms the *Lichinaceae*. The family includes the *Gloeoheppiaceae* and *Psorotichiaceae* (*nom. inval.*), but excludes *Heppiaceae* (Henssen 1995) that falls into main clade 3.

Contains the genera: *Anema*, *Collemopsis*, *Digitothyrea*, *Forssellia*, *Gloeoheppia*, *Gudelia* (likely close to *Gloeoheppia*), *Jenmania* (for *J. goebelii* only), *Lemmopsis* (incl. "*Psorotichia*" *lutophila*), *Leprocollema*, *Lichina*, *Lingolemma* (for "*Lempholemma*" *lingulatum*), *Metamelanea*, *Paludolemma* (for "*Lempholemma*" *syreniarum*), *Paulia*, *Peltolemma* (for "*Lempholemma*" *socotranum*), *Phloeopeccania*, *Pseudopaulia* (probably close to *Psorotichia*), *Pseudopeltula* (likely close to *Gloeoheppia*), *Pseudotichia*, *Psorotichia*, *Pterygiopsis s. str.*, *Pycnolemma* (for "*Lempholemma*" *polycarpum*), *Pyrenocarpon*, *Synalissa*, *Thelignya*, *Thermutis* and *Zahlbrucknerella*. Approx. 125 spp.

The placement of *Gudelia*, *Pseudopaulia* and *Pseudopeltula* is here inferred from their combination of morphological characters that show largest agreement with those of the *Lichinaceae* as circumscribed here, but remains to be verified by further molecular analyses.

Anema Nyl. *ex* Forssell, Beitr. Gloeolich.: 91. 1885. MycoBank MB 192. Fig. 6D.

Type species: *Anema decipiens* (A. Massal.) Forssell, Beitr. Gloeolich.: 92. 1885. MycoBank MB 376136.

Notes: according to Jørgensen & Santesson (1989), *Anema* was invalidly described by Nylander (*nom. inval*., Art. 38.1(a), Melbourne) and validated by Forssell in 1885. *Anema* was later conserved against *Omphalaria* (Jørgensen & Santesson 1989). The species of *Anema* included here all form a monophyletic group. The genus is characterized by having pycnoascocarps and squamulose, sometimes rosulate thalli (Fig. 6D) and *Peccania* type asci (Fig. 3F). At some point it was considered as part of the so-called complex *Anema*-*Thyrea*-*Peccania* (Henssen 1980) based on some similarities in the anatomy (Moreno & Egea 1992a). Our results do not support this complex as the cited genera are not genetically related.

Seven species are currently accepted: *Anema decipiens*, *A. nodulosum*, *A. notarisii* (by some authors considered to belong to *A. nummularium*), *A. nummularium*, *A. prodigulum*, *A. suffruticosum*, and *A. tumidulum*.

Collemopsis Nyl. *ex* Crombie, J. Bot., London 12: 332. 1874. MycoBank MB 1183. Fig. 7.

Type species: *Collemopsis schaereri* (A. Massal.) Cromb., J. Bot., London 12: 332. 1874. MycoBank MB 383561.

Description: *Thallus* blackish or dark brown, sometimes partly becoming greyish pruinose (Fig. 7A, B), gelatinous when wet, crustose, rarely with thick areoles becoming subsquamulose. Fastened to substrate by rhizohyphae. Thallus ecorticate, paraplectenchymatous, hyphae small-celled, forming a dense network (Fig. 7D, E); cyanobiont single-celled, with gelatinous sheaths yellowish brown, thin (Fig. 7D, E). *Apothecia* semi-immersed to sessile (Fig. 7A, B), zeorine with distinct thalline and only thin, often pale yellowish proper exciple (Fig. 7C, D), hymenium with septate *paraphyses*, KOH/Lugol+ blue, *asci Lichina* type, 8-spored, subhymenium and hypothecium often extending downwards as a short stipe (Fig. 7C). *Ascomata* developing from tangle of generative hyphae (Ellis 1981), but pycnoascocarps found in material studied here (Fig. 2G). *Pycnidia* immersed to slightly elevated, simple, conidiophores simple, pycnospores small ellipsoid, produced terminally. On usually calcareous or mineral rich, rarely acidic rock including artificial substrate such as mortar and brick, on inclined rock faces in well lit situations temporarily or occasionally moistened by seeping water, widespread in the northern hemisphere, from boreal to subtropical regions, old southern hemisphere reports are to be confirmed. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Nylander (1873: 17) first used this name in a footnote, with no formal description and thus created an invalid *nomen nudum*. Later, Crombie (1874: 332) described the genus briefly and included five crustose, though unrelated species: *C. schaereri*, *C. lecanopsides* (= *Porocyphus coccodes)*, *C. furfurella* (= *Porocyphus coccodes*), *C. oblongans* (= *Lemmopsis oblongans*), and *C. diffundens* (= *Porocyphus rehmicus*). Later, Jørgensen & Henssen (1990) lectotypified *Collemopsis* with *C. schaereri* and established the genus as a synonym of *Psorotichia*.

The results show *Psorotichia* divided into five distantly related clades (see further explanation in *Psorotichia s. str.*). Specimens of *C. schaereri* form a clade with members of *Pycnolemma* and *Peltolemma* (previously included in *Lempholemma*), having pycnoascocarps and typical apothecia. Although Ellis (1981) illustrates ascoma development as typical apothecia in *C. schaereri*, we have repeatedly found pycnoascocarps in the revised material but not in the lectotype. Thus, this character is dubious and has not been included in the ancestral reconstruction. Here we reinstate the genus *Collemopsis* and resurrect it from synonymy with *Psorotichia* for *P. scharereri* which we found is not related with the type of *Psorotichia* (*i.e. P. murorum*).

So far, a monotypic genus only containing the variable and widely distributed species *Collemopsis schaereri*. For detailed species descriptions see *e.g.* Jørgensen (2007), Smith *et al.* (2009), and Wirth *et al.* (2013).

Digitothyrea P.P. Moreno & Egea, Lichenologist 24(3): 216. 1992. MycoBank MB 25324. Fig. 1D.

Type species: *Digitothyrea rotundata* (Büdel *et al.*) Moreno & Egea, Lichenologist 24(3): 225. 1992. MycoBank MB 359100.

Notes: Moreno & Egea (1992b) pointed that the genus *Thyrea* included a heterogeneous grouping of species. One of the most important differences was the ascoma development, with pycnoascocarps in the type of *Thyrea* (*T. plectopsora*) and the foliose group (*T. girardii*, *T. pachyphylla*, *T. asahinae* and *T. latissima*) and typical apothecia found in digitate species (*T. divergens*, *T. polyglossa* and *T. rotundata*). Based on differences in morphology and ascoma ontogeny, Moreno & Egea (1992b) described the genus *Digitothyrea* and placed the later three species into it. Our results show the two genera as two distant clades. These are the genus *Thryrea* containing *T. confusa*, *T. plectopsora* and *T. girardii*, characterized by pycnoascocarps and having squamulose-peltate or foliose-umbilicate thalli, and *Digitothyrea*, formed by *D. divergens*, *D. polyglossa* (Fig. 1D) and *D. rotundata* with foliose-fruticose-peltate thalli and typical apothecia. The latter species (the type of *Digitothyrea*) has not been included in the tree and

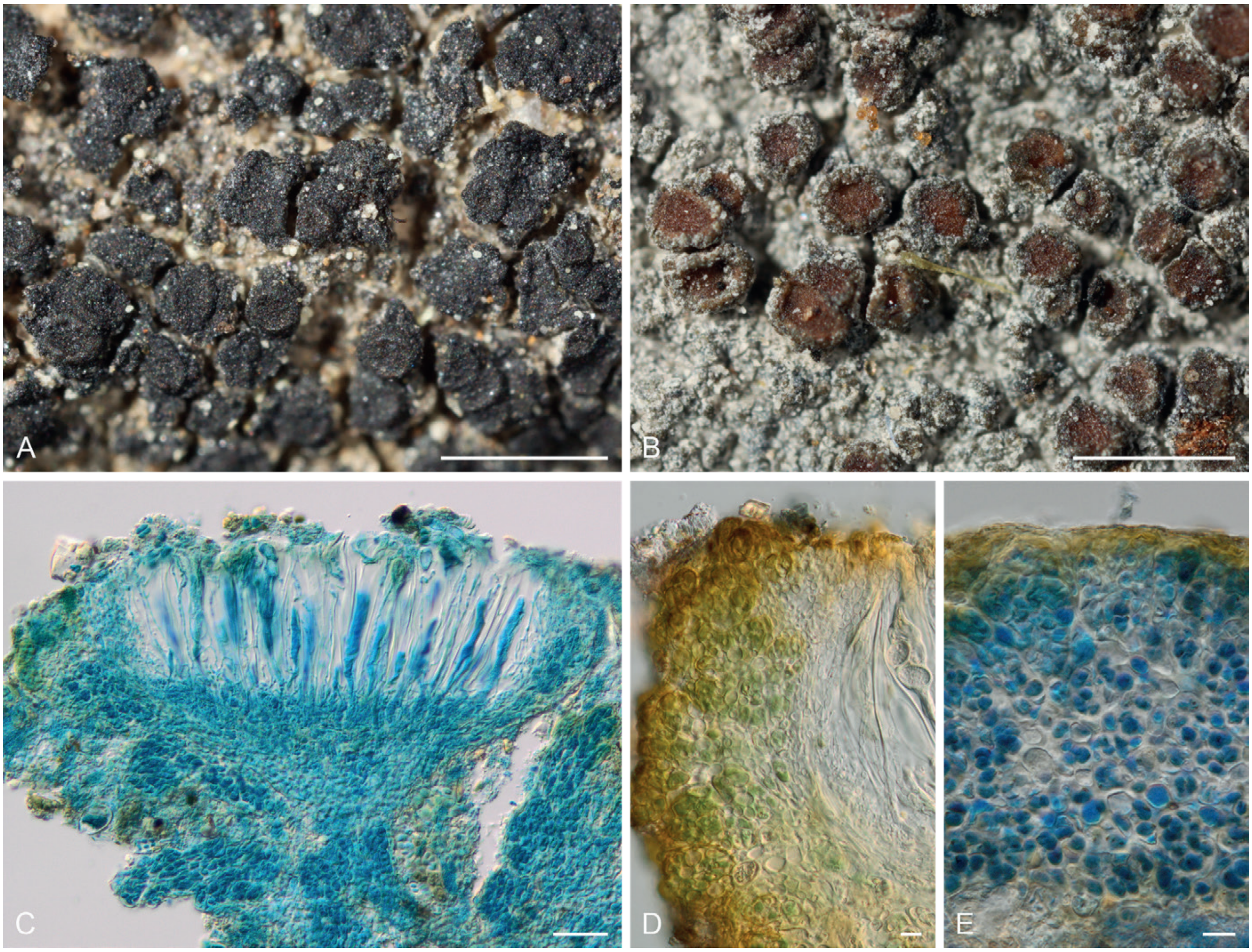

Fig. 7. *Collemopsis schaereri*. **A.** Thallus black, areoles with adnate apothecia (Schultz 08926b). **B.** Grey pruinose morphotype, apothecia with reddish brown, open discs (Teuber 1527). **C.** Apothecium with zeorine margin, subhymenium inversely cone shaped in LPCB (Massalongo Lich. Ital. 338, UPS lectotype). **D.** Zeorine apothecial margin (Schultz 03438). **E.** Paraplectenchymatous thallus anatomy in LPCB (Schultz 03440b). Scale bars: A, B = 1 mm; C = 25 µm; D, E = 10 µm.

the monophyly of the genus will have to be tested in subsequent studies.

The genus currently contains three species, but we are aware of undescribed taxa in Arabia: *Digitothyrea divergens*, *D. polyglossa*, and *D. rotundata*.

Forssellia Zahlbr., Nat. Pflanzenfam. 1(1*): 161. 1906. MycoBank MB 2006. Fig. 8.

Type species: *Forssellia affinis* (A. Massal.) Zahlbr., Nat. Pflanzenfam. 1(1*): 161. 1906. MycoBank MB 385035.

Description: *Thallus* blackish (brown), sometimes greyish pruinose (Fig. 8A–D), gelatinous when wet, crustose, sometimes effigurate (Fig. 8A), rarely small squamulose (Fig. 8C). Fastened to substrate by rhizohyphae, a basal gelatinous layer or small umbilicus, sometimes attachment point with purplish colour. Thallus ecorticate, paraplectenchymatous, hyphae ± distinctly fan shaped or vertically arranged (Fig. 8E, G), cyanobiont single-celled, gelatinous sheaths yellowish brown, rarely reddish (Fig. 8E, G). *Apothecia* semi-immersed to sessile (Fig. 8A, B, D), zeorine with distinct thalline and only thin proper exciple (Fig. 8G), hymenium with septate *paraphyses*, KOH/Lugol+ blue, *asci* prototunicate (*Lichina* type), 8-spored to polysporous, ascospores simple, hyaline, broad ellipsoid to globose, small (Fig. 8F). *Ascomata* are pycnoascocarps. *Pycnidia* immersed to slightly elevated, simple, conidiophores simple, pycnospores small ellipsoid, produced terminally. Usually on calcareous or mineral rich, rarely acidic, inclined rock in well lit situations temporarily or occasionally moistened by seeping water, also semi-aquatic along lake margins, mainly northern hemisphere, from boreal to subtropical regions. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: *Pterygiopsis sensu* Henssen is split in two clades: a clade formed by *Pterygiopsis s. str.* (*P. atra*), and a clade formed by *F. affinis*, *F. umbilicata* and *F. canariensis* (*i.e.* the *affinis* group; Fig. 8A–C, E–G) which is sister to another clade formed by *P. coracodiza* (Fig. 8D). These latter two formed a supported clade with *Anema*, but the relationships among them are not fully supported. As the relationship between the species of the *affinis* group and *Pterygiopsis concordatula* within this clade is not supported we carried out a monophyly test. The results showed that a clade containing all the species of *Pterygiopsis* with pycnoascocarps was not rejected and had a lower likelihood than the tree not supporting this relationship. Thus, the name *Forssellia* is reinstated for this group of species and a description of the genus is provided below. For comments on *Pterygiopsis s. str.* see there.

Four species are known: *F. affinis*, *F. canariensis* (new combination introduced below), *F. concordatula* (new combination introduced below), and *F. umbilicata* (syn. *Pterygiopsis umbilicata*),

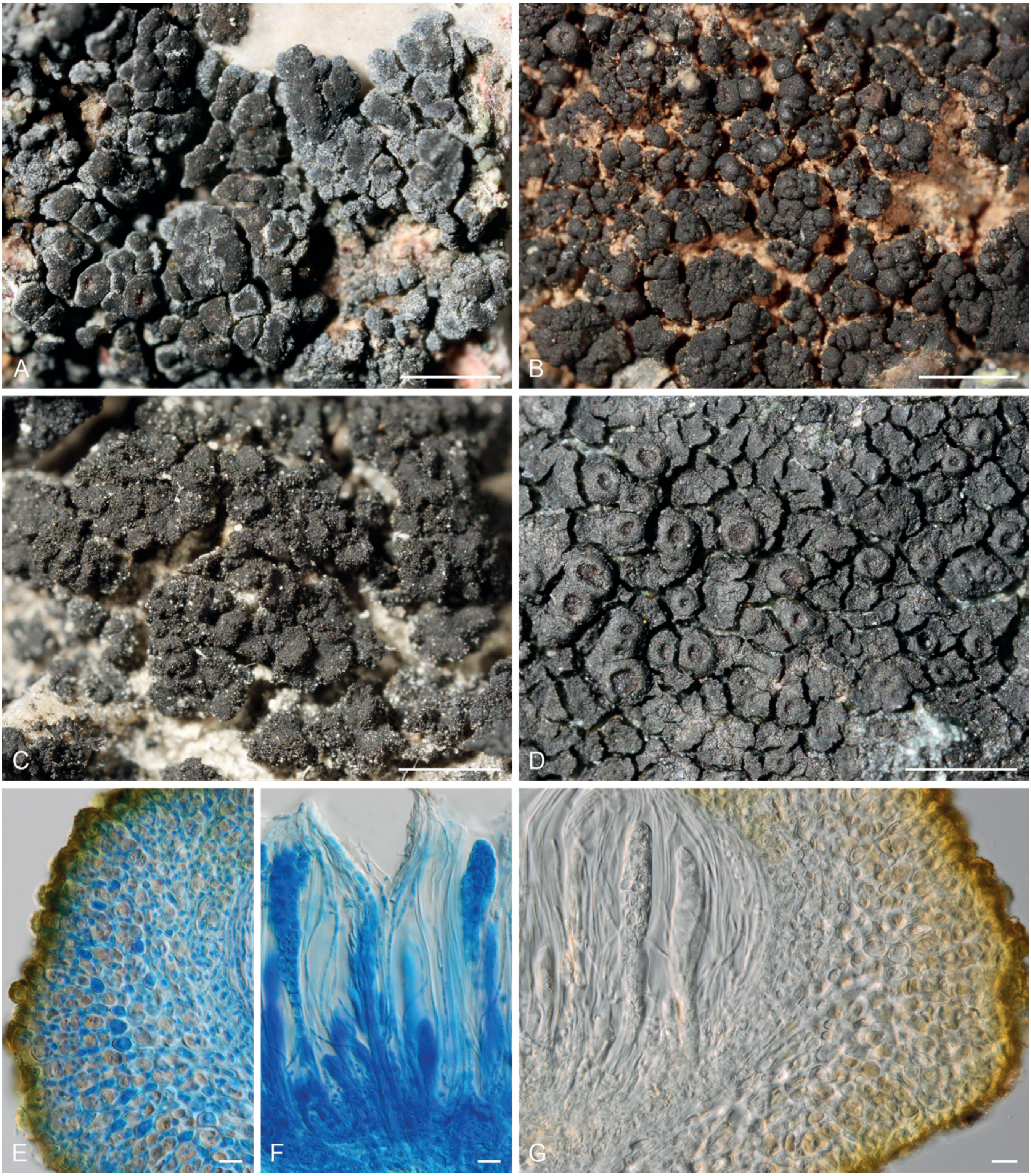

Fig. 8. A. *Forssellia affinis*, areoles thick, slightly effigurate and pruinose, apothecia adnate (Palice 4034). **B.** *Forssellia canariensis*, areoles subsquamlose, epruinose, apothecia sessile with constricted base (Ertz 16309). **C.** *Forssellia umbilicata*, squamules imbricate with coarsely sorediate margin (Schultz 08907a). **D.** *Forssellia concordatula*, morphotype of *"Pterygiopsis" coracodiza*, areoles angulate, apothecia adnate (Schultz 08572a). **E–G.** *Forssellia canariensis* (Ertz 16309). **E.** Paraplectenchymatous thallus anatomy with anticlinal hyphae in LPCB. **F.** Paraphyses and polysporous asci in LPCB. **G.** Polysporous ascus and thick thalline margin. Scale bars: A–D = 1 mm; E–G = 10 µm.

but unpublished sequence data indicate that there are undescribed taxa in Europe and Arabia. Judging from the description of the recently described *Pyrenopsis chejudoensis* (Kondratyuk *et al.* 2016), this species unlikely belongs to any of the pyrenopsoid genera treated here and might belong to *Forssellia* instead. The placement of other species still treated in *Pterygiopsis* (see there) should be evaluated further. For *Forssellia neglecta* see *Thelignya*.

New combinations in *Forssellia*:

Forssellia canariensis (Henssen) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852301.
Basionym: *Pterygiopsis canariensis* Henssen, Lich. Cyanoph. Fungi Saxic. Exsicc., Fasc. 2(nos 26–50) (Marburg): 8, no. 42. 1990.

Forssellia concordatula (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852302.
Basionym: *Pyrenopsis concordatula* Nyl., Flora, Regensburg 58: 440. 1875.
Synonyms: *Collemopsis coracodiza* Nyl., Flora, Regensburg 61(16): 241. 1878.
Pterygiopsis coracodiza (Nyl.) Henssen, Lichenologist 22(2): 143. 1990.

Gloeoheppia Gyeln., Feddes Repert. 38: 311. 1935. MycoBank MB 2082. Fig. 6C.

Type species: *Gloeoheppia turgida* (Ach.) Gyeln., Feddes Repert. 38: 312. 1935. MycoBank MB 119603.

Notes: *Gloeoheppia* and the related genera *Gudelia* and *Pseudopeltula* were placed in the family *Gloeoheppiaceae* in the *Lichinales* (Henssen 1995). The distinction of a different family containing *Gloeoheppia* is not supported by our phylogenetic analyses. *Gudelia* and *Pseudopeltula* are not included in the phylogenetic study, but they are included in this family due to morphology.

The species of *Gloeoheppia* included in the analysis form a monophyletic clade. The genus is characterized by having squamulose thalli (Fig. 6C) with typical apothecia and cerebriform pycnidia.

They form a clade with *Lichina*, *Lingolemma*, *Paludolemma syreniarum*, *Lemmopsis* and *Jenmannia*. This clade includes members sharing different characters. On the one hand, some species have a fruticose thallus as *Lichina* and *Jenmania* (Schultz & Büdel 2002) with species with the same ecology, as they are semi-aquatic, growing immersed in lakes or seashores. *Paludolemma syreniarum*, very close to *Lichina*, also shares this ecology as it grows in temporarily submerged trees. Within this clade there are two distantly related groups with *Nostoc* as photobiont: *Paludolemma syreniarum* and *Lingolemma lingulatum*. Both, *Lemmopsis* and *Gloeoheppia* are crustose and squamulose species growing in biological soil crusts in dry and disturbed habitats.

Currently we accept five species: *Gloeoheppia erosa*, *G. polyspora*, *G. rugosa*, *G. squamulosa*, and *G. turgida*. Unpublished data indicate that the variable species *G. turgida* is probably not monophyletic and we are further aware of an undescribed species occurring in South Arabia.

Gudelia Henssen, Lichenologist 27: 287. 1995. MycoBank MB 6190.

Type species: *Gudelia mexicana* Henssen, Lichenologist 27: 289. 1995. MycoBank MB 413135.

Notes: A monotypic genus not covered molecularly in this study. Originally placed by Henssen (1995) in the newly established *Gloeoheppiaceae*, this species seems to be reliably placed (based on morphology) in *Lichinaceae* as circumscribed here just like the genus *Gloeoheppia*.

Jenmania W. Wächt., Flora, Regensburg 84: 349. 1897. MycoBank MB 2531.

Type species: *Jenmania goebelii* W. Wächt., Flora, Regensburg 84: 349. 1897. MycoBank MB 387153.

Notes: Because only one sample was included, the monophyly of the genus could not be tested. According to Schultz & Büdel (2002), *Jenmania* is heterogeneous because the second species described in the genus, *J. osorioi*, may be closer to *Thyrea* than to the type, *J. goebelii.* Although both species share the same ecology as they are semi-aquatic on rocks, they differ in their ascoma ontogeny, cortex, number of spores and pycnidial shape. Additionally, there are other species of *Thyrea* growing along river margins (*T. asahinae*, *T. leptophylla*). See further details under the genus *Gloeoheppia.*

Lemmopsis (Vain.) Zahlbr., Nat. Pflamzenfam. 1(1*): 171. 1906. MycoBank MB 2732. Fig. 9.

Type species: *Lemmopsis arnoldiana* (Hepp) Zahlbr., Nat. Pflanzenfam. 1(1*): 171. 1906. MycoBank MB 393114.

Notes: *Lemmopsis pelodes* (Fig. 9C) is phylogenetically closely related with *Psorotichia lutophila* (Fig. 9D–G) and colonizes similar loamy soil habitats. The latter species clusters far outside *Psorotichia* and is thus much better accommodated in *Lemmopsis*. The type of the genus, *L. arnoldiana* (Fig. 9A, B), was not included in the present study due to the lack of reliable material, but very recently obtained nuITS sequences from specimens collected in Franconia (Germany) confirms its placement next to *L. pelodes* and *L. lutophila*.

It constitutes a small genus of four species growing as pioneers on calcareous rock and calciferous or loamy soils. The species taxonomy and generic placement of *Lemmopsis oblongans* so far only known from Britain must be clarified in subsequent studies.

New combination in *Lemmopsis*:

Lemmopsis lutophila (Arnold) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852303.
Basionym: *Psorotichia lutophila* Arnold, Ber. Bayer. Bot. Ges. 1: 129. 1891.

Leprocollema Vain., Acta Soc. Fauna Flora Fenn. 7(1): 232. 1890. MycoBank MB 2753. Fig. 10.

Type species: *Leprocollema americanum* Vain., Acta Soc. Fauna Flora Fenn. 7(1): 232. 1890. MycoBank MB 393286.

Notes: Only one sample has been included, thus the monophyly of the genus containing three species worldwide is not tested. In *L. americanum* the apothecial discs soon become umbonate, as it is the case in *Metamelanea* (*i.e. M. umbonata* and *M. melambola*), a clade with which it is closely related.

A very small, poorly known genus. *Leprocollema finkii* is probably conspecific with *L. americanum* (Fig. 10). We are aware of several tropical crustose *Lichinaceae* that might belong here.

Lichina C. Agardh, Syn. Alg. Scand.: xii, 9. 1817. MycoBank MB 2857. Figs 2A, 3G, 6E.

Type species: *Lichina pygmaea* (Lightf.) C. Agardh, Syn. Alg. Scand.: xii, 9. 1817. MycoBank MB 123156.

Emended description: Fruticose, blackish lichens (Fig. 6E) with filamentous cyanobionts (*Rivulariaceae*; Fig. 2A), branches cylindrical or flattened, palmately or (sub)dichotomously branched, distinctly corticate or not, with a compact central hyphal cord and fountain-like hyphal arrangement. *Apothecia* terminal or

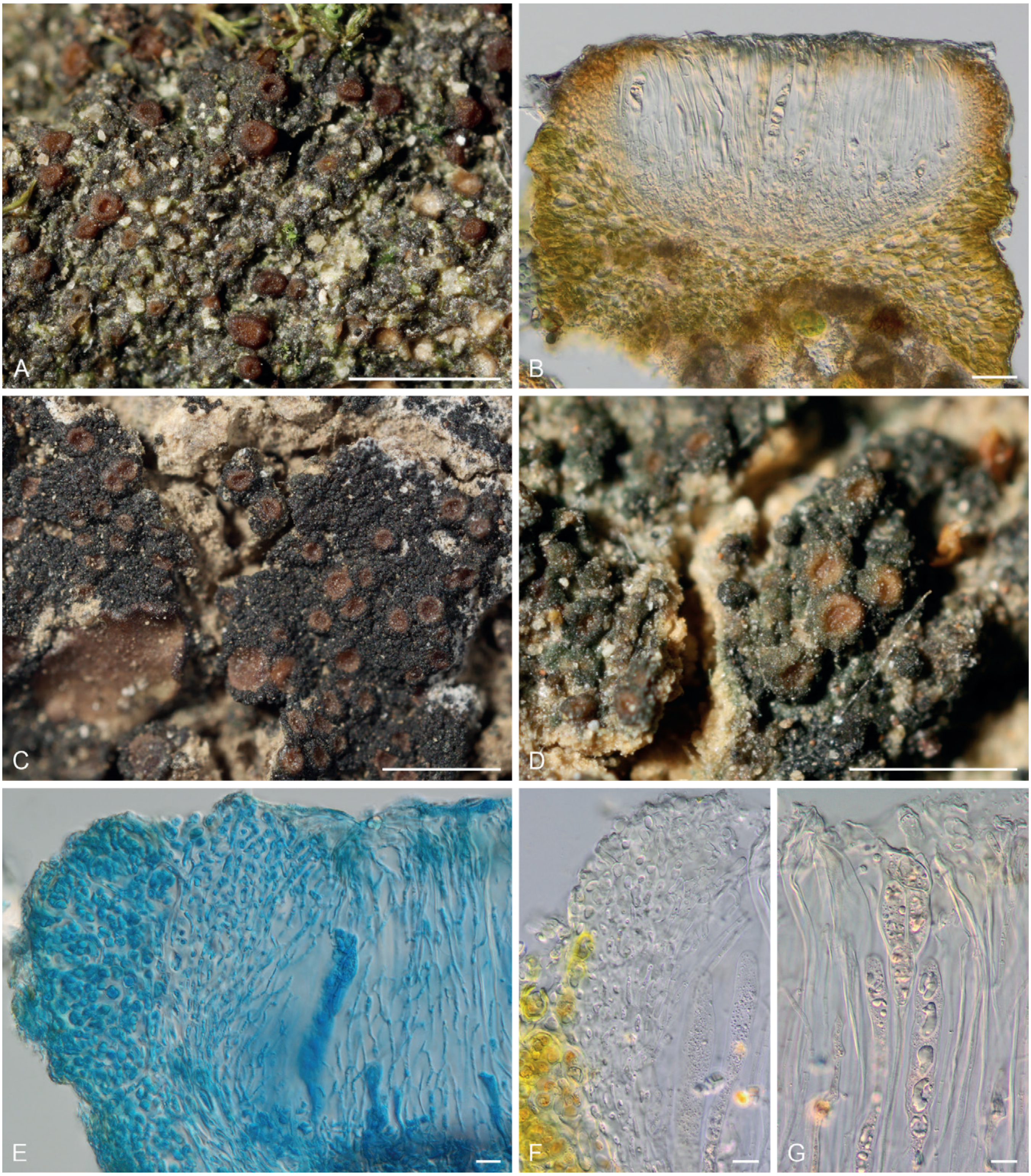

Fig. 9. A. *Lemmopsis arnoldiana*, apothecia with distinct, brick coloured proper margin (Schultz 03446). **B.** *Lemmopsis arnoldiana*, apothecia with very thick proper, and receding thalline margin (Schultz 03441a). **C.** *Lemmopsis pelodes*, apothecia immersed in thallus, proper exciple distinct (Groner 4528, HBG). **D.** *Lemmopsis lutophila*, apothecia semi immersed with distinct proper and thin thalline margin (Vezda, GZU). **E.** *Lemmopsis lutophila*, zeorine apothecial margin in LPCB (Arnold Lich. Monac. 74a, M holotype). **F.** *Lemmopsis lutophila*, distinct proper exciple in KOH. **G.** *Lemmopsis lutophila*, asci and paraphyses in KOH (Zimmermann). Scale bars: A, C, D = 1 mm; E = 25 µm; F, G = 10 µm.

subterminal, formed from a tangle of generative hyphae with ascogones (Fig. 2A), no *pycnoascocarps*, hymenium KOH/Lugol- or only faintly bluish, asci thin walled, often bulging and wall disintegrating at spore maturity (Fig. 3G) or opening by apical ruptures, *ascospores* simple, hyaline, ellipsoid to subglobose, wall often becoming thickened (Fig. 3G). On rocks in the intertidal zone of cold coasts, sea spray influenced maritime rocks or semi inundated on boulder beaches. On both hemispheres, but absent in the tropics. No secondary metabolites detected by TLC (Jørgensen 2007). However, other compounds have been detected by different methods in *Lichina pygmaea* as mycosporine serinol, L-glutamic acid, pygmeine and volatile sesquiterpenes (Roullier *et al.* 2010, Sanad *et al*. 2022).

Notes: Members of *Lichina* are split in two clades, with two non-marine species (*L. willeyi* and *L. macrospora*) closely related with a

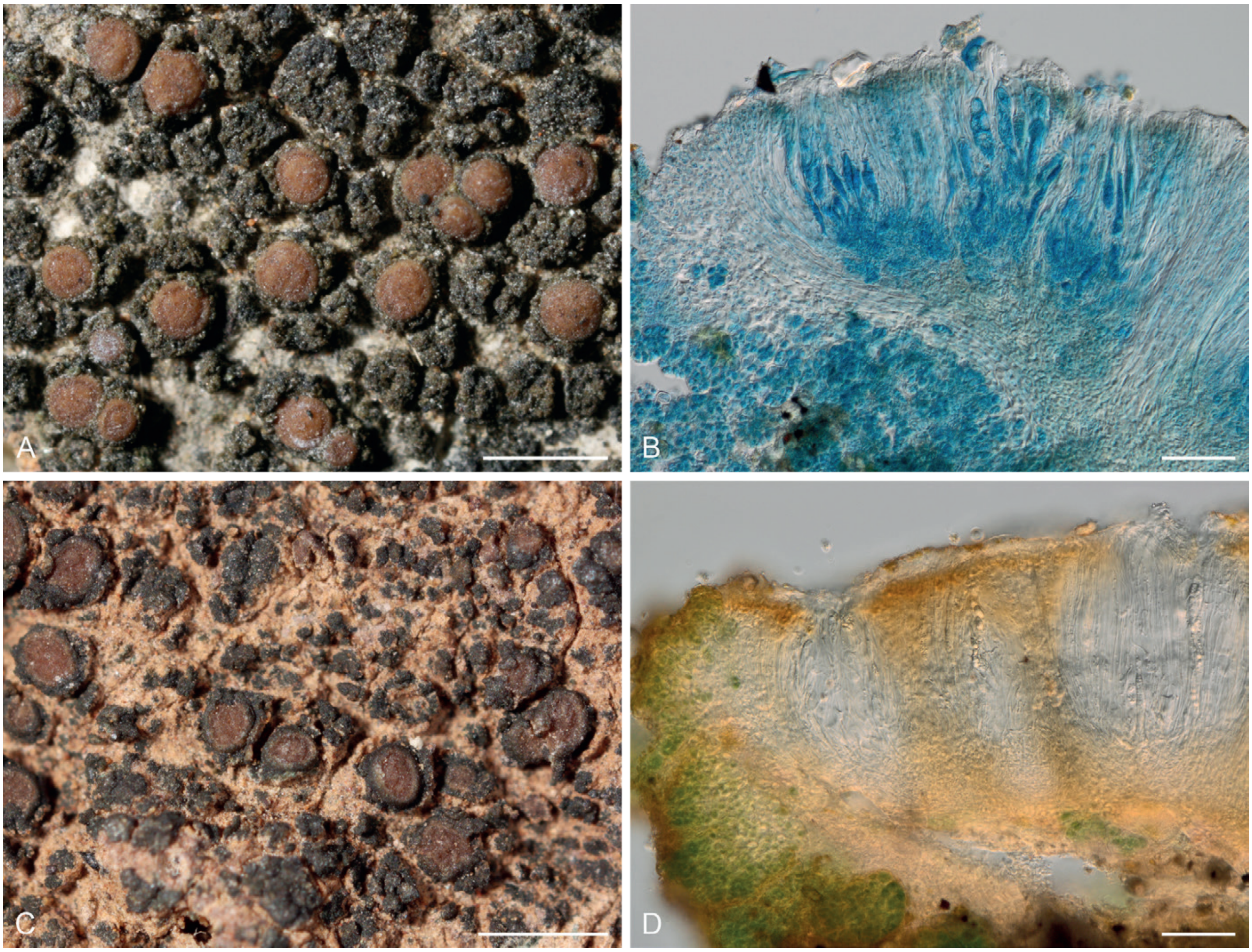

Fig. 10. *Leprocollema americanum*. **A.** apothecia with expanded, multiply umbonate discs, thalline margin receding (Vainio, TUR-VAIN11602, lectotype). **B.** Apothecial margin zeorine, becoming biatorine, hymenium divided by hyphal vertical bands into chambers in LPCB. **C.** Apothecia zeorine, discs multiply umbonate (van den Boom 36840). **D.** Zeorine apothecium, proper exciple distinct and apically reddish brown, hymenium divided into chambers (van den Boom 36843). Scale bars: A, C = 1 mm; B, D = 25 µm.

clade formed by *Porocyphus* members. The problematic delimitation of *Lichina* from *Porocyphus* was previously discussed by Henssen (1969a). These non-marine species were included in *Lichina* mainly by their fruticose thallus and the fountain-like arrangement of the internal hyphae, however, their apothecia originate from pycnidia (pycnoascocarps) as the rest of members of *Porocyphus* (and differently to marine species of *Lichina*). Additionally, other members of *Porocyphus* are also fruticose and the apothecia are even terminal on branches (*e.g. P. lichinelloides,* Henssen 1963a, p. 68, plate 16c) and some species also develop the multiaxial, fountain-like development as in *Lichina* (*e.g. P. kenmorense*). The habitat and ecology were at some point used to delimit *Lichina* from *Porocyphus* (Henssen, 1963a, p. 36.). Our results support these differences and thus, we restrict *Lichina* for marine species; the non-marine *Lichina* are included in *Porocyphus* as this genus also includes some semiaquatic and aquatic lichens growing at the margins of lakes or waterfalls or on boulders in streams and rivers or in rocks with running water.

Contains four species: *Lichina canariensis*, *L. confinis*, *L. intermedia*, and *L. pygmaea*.

Excluded from the genus: *L. antarctica*, *L. macrospora*, *L. rosulans*, *L. tasmanica*, and *L. willeyi*, all have a deviating type of ascoma development (pycnoascocarps), a tropical or subantarctic distribution and/or occur in non-marine habitats. Because of the close relationship with *Porocyphus*, and a striking similarity especially with dwarf fruticose species of that genus, *i.e. P. lichinelloides* and *P. dimorphus*, the pycnoascocarp forming species of *Lichina* are recombined into *Porocyphus* (see below).

Lingolemma M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852304. Fig. 11.

Etymology: *lingua* (Latin = tongue), because of the tonge shaped lobes in the thalli of the only species, *L. lingulatum*.

Type species: ***Lingolemma lingulatum*** (Tuck.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852305.
Basionym: *Omphalaria lingulata* Tuck., Proc. Amer. Acad. Arts 5: 384. 1862. MycoBank MB 396184.
Homotypic synonyms: Thyrea lingulata (Tuck.) Zahlbr., Cat. Lich. Univ. 2: 806. 1924. MycoBank MB 407576.
Lempholemma lingulatum (Tuck.) Henssen, Lich. Cyanoph. Exsicc. (Marburg): 3. 1969. MycoBank MB 345229.

Diagnosis: Genus of the *Lichinaceae*. *Thallus* squamulose-peltate with lingulate lobes (Fig. 11A). Resembling other squamulose-peltate species from dry, rocky habitats of the genera *Anema*, *Lichinella*, *Paulia*, *Peltula*, *Peccania*, *Thyrea* but differing in the *Nostoc* cyanobionts (Fig. 11B). Differing from *Peltolemma* (*socotranum*) in the much smaller, immersed *apothecia* and presence of a central

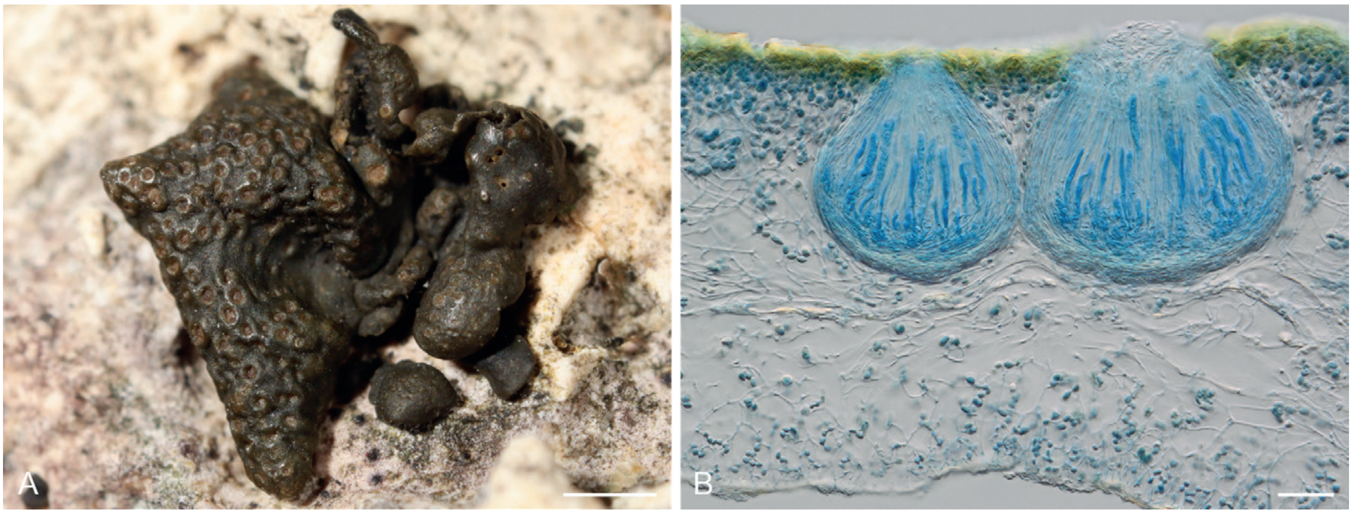

Fig. 11. *Lingolemma lingulatum* (Berger 25056a). **A.** Squamulose thallus with convex, lingulate lobules and numerous immersed apothecia. **B.** Anatomy with *Nostoc* cyanobionts, a thin central hyphal strand and two apothecia in LPCB. Scale bars: A = 1 mm; B = 25 µm.

hyphal strand. Differing from *Pycnolemma* (*polycarpum*) in the formation of typical apothecia (no pycnoascocarps) and in the central hyphal strand.

Description: *Thallus* squamulose-peltate divided into convex, tonge shaped lobes with revolute margins (Fig. 11A). Thallus ecorticate, reticulate hyphae surrounding *Nostoc* chains and forming a central strand (Fig. 11B). *Apothecia* immersed with punctiform discs (Fig. 11A), zeorine with thin proper exciple and shallow excipulum thallinum (Fig. 11B). Asci *Lichina* type, 8-spored, ascospores simple, hyaline, broad ellipsoid, 10–15 × 4.5–7 µm, hymenium KOH/Lugol+ blue. *Ascomata* formed from ascogones arising in a tangle of generative hyphae. Resembling *Peltolemma socotranum* which differs in thallus shape (squamules incised at margin and not tongue shaped), thallus anatomy (no central hyphal strand) and the larger, semi-sessile apothecia. Also resembling *Pycnolemma polycarpum* which differs in the deeply divided, more elongated and adpressed lobes and the presence of pycnoascocarps with a very thin proper exciple. Differing from all other squamulose-peltate species of the *Lichinomycetes* growing in dry, rocky habitats in tropical to subtropical regions (*Anema*, *Lichinella*, *Paulia*, *Peltula*, *Peccania*, *Thyrea*) in the *Nostoc* cyanobionts. Secondary metabolites detectable by TLC not tested.

Notes: See *Lempholemma* notes below and phylogenetic relationships and affinities with the *Lichina*-*Gloeoheppia* clade.

A single species, *Lingolemma lingulatum*, known from dry, coastal calcareous rocks in the Caribbean.

Metamelanea Henssen, Lichenologist 21: 102. 1989. MycoBank MB 25323. Fig. 6A.

Type species: *Metamelanea umbonata* Henssen, Lichenologist 21(2): 105. 1989. MycoBank MB 135895.

Description: See Henssen (1989) and Henssen & Jørgensen (1990).

Notes: Both genera, *Psorotichia* and *Metamelanea*, are closely related (supported by Bayesian analysis), sharing some characters such as the crustose growth form and the presence of typical apothecia. On the other hand, in *M. umbonata* (Fig. 6A) and *M. melambola* (not included in the study) the apothecial discs become distinctly umbonate and the hymenium is surrounded by a thick and distinctly coloured proper excipulum, features shared with the closely related *Leprocollema americanum*. Unpublished sequence data of the third species, *Metamelanea caesiella*, retrieved from material collected on Gotland (Sweden) indicate that this species also belongs here.

Paludolemma M. Schultz & M. Prieto, ***gen. nov*****.** MycoBank MB 852306.

Etymology: from *palus* (Lat. = swamp) because of the swampy habitat and *Lempholemma* because of the *Nostoc* cyanobiont.

Type species: ***Paludolemma syreniarum*** (C.J. Lewis & M. Schultz) M. Schultz & M. Prieto, ***comb. nov*****.** MycoBank MB 852307.
Basionym: *Lempholemma syreniarum* C.J. Lewis & M. Schultz, Bryologist 122: 424. 2019. MycoBank MB 832121.

Description: A detailed description of the only species is given in Lewis & Schultz (2019).

Diagnosis: Genus of the *Lichinaceae*. Resembles *Lemmopsis* in the crustose growth form and apothecia with soon receding thalline margin becoming almost biatorine but differing in having densely coiled chains of the *Nostoc*-like cyanobiont, and in the corticolous ecology. Differs from *Lempholemma* in the formation of the apothecia that develop from ascogones arising in a tangle of generative hyphae (no pycnoascocarps) and from *Synalissina* in the corticolous growth, *Lichina* type asci and the absence of hormocystangia. Pycnidia unknown. No secondary metabolites detected by TLC (Lewis & Schultz 2019).

Notes: This species occurs in swampy habitats and grows on the bark of deciduous tree bases that are seasonally flooded. Morphologically different to *Lichina* in the habit (crustose, granulose-areolate versus fruticose), in the photobiont (Nostocoid in *Paludolemma* and *Rivularia and Pleurocapsa* in *Lichina*; Chrismas *et al.* 2023), and the apothecia (open in *Paludolemma* and punctiform in *Lichina*). Based on all these differences and despite its genetical closeness to *Lichina* a new genus is described to accommodate this species.

Apart from this species, the only currently known corticolous *Lichinaceae* now are *Lecidopyrenopsis corticola* (from Thailand, Seychelles, Costa Rica, French Guyana), and *Leprocollema novocaledonianum* (from New Caledonia). The predominantly saxicolous genus *Peltula* (*Phylliscaceae)* also contains two species that grow on bark, *P. corticola* and *P. steppae*.

Paulia Fée, Linnaea 10: 471. 1836. MycoBank MB 3775.

Type species: *Paulia pullata* Fée, Linnaea 10: 471. 1836. MycoBank MB 399231.

Notes: The genus is morphologically very well circumscribed (Henssen 1986) and the five species included form a monophyletic group, sister to *Pseudotichia* and *Pyrenocarpon*. All these genera share the presence of typical apothecia, but differ in the thallus anatomy. The latter two include crustose species whereas *Paulia* species have rosette-shaped, peltate, squamulose-peltate and dwarf fruticose thalli.

Currently recognized species: *Paulia aldabrensis*, *P. caespitosa*, *P. cubana*, *P. gibbosa*, *P. glomerata*, *P. japonica*, *P. myriocarpa*, *P. nitidula*, *P. perforata*, (?) *P. pyrenoides*, *P. rhizophora*, *P. salevensis*, *P. schroederi*, *P. stipitata*, and *P. wrightii*.

Peltolemma M. Schultz & M. Prieto, ***gen. nov***. MycoBank MB 852308.

Etymology: Because of the squamulose-peltate thallus resembling many species of *Peltula* and the *Nostoc* cyanobionts similar to those of *Lempholemma*.

Type species: *Peltolemma socotranum* (M. Schultz) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852309.
Basionym: *Lempholemma socotranum* M. Schultz, Bibl. Lichenol. 86: 156. 2003. MycoBank MB 367264.

Diagnosis: Genus of the *Lichinaceae* resembling other squamulose-peltate species from dry, rocky habitats of the genera *Anema*, *Lichinella*, *Paulia*, *Peltula*, *Peccania*, *Thyrea*, but differing in the *Nostoc* cyanobionts. Differing from *Lingolemma* (*lingulatum*) in the bigger apothecia surrounded by a distinct thalline margin, the shortly incised lobes and the strictly homoiomerous thallus anatomy lacking a central hyphal strand. Differing from *Pycnolemma* (*polycarpum*) in the formation of typical apothecia (no pycnoascocarps), bigger apothecia surrounded by a distinct thalline margin and the shortly incised lobes.

Description: A detailed description of the species (and thus of the genus *Peltolemma*) is given in Schultz (2003). This description is expanded here for the type of ascoma development that now has been clarified: typical apothecia (no pycnoscocarps).

Notes: Its phylogenetic affinities are discussed in *Lempholemma*. A distinctive, squamulose-peltate lichen superficially resembling squamulose species of *Peltula* or *Thyrea* but containing *Nostoc* cyanobionts. So far only known from Socotra Island (Yemen).

Phloeopeccania J. Steiner, Denkschr. Österr. Akad. Wiss. Math.-Naturwiss. Kl. 71: 93. 1902. MycoBank MB 4004. Fig. 2B.

Type species: *Phloeopeccania pulvinulina* J. Steiner, Denkschr. - Österr. Akad. Wiss. Math.-Naturwiss. Kl. 71: 93. 1902. MycoBank MB 400337.

Notes: *Phloeopeccania* is a small monophyletic genus, characterized by crustose to squamulose and subfruticose thalli and typical apothecia. A mainly tropical-subtropical genus closely related with *Paulia* and comprising *P. anemoides*, *P. australiensis*, *P. hispanica*, and *P. pulvinulina* and 2–3 yet undescribed species.

Pseudopaulia M. Schultz, Mycotaxon 82: 446. 2002. MycoBank MB 28607.

Type species: *Pseudopaulia tessellata* M. Schultz, Mycotaxon 82: 446. 2002. MycoBank MB 380961.

Notes: Currently a monotypic genus. Attempts to sequence the type and other material collected on Socotra Island failed. However, there is a putatively undescribed, second species found in Oman, which is closely related with *Psorotichia* as circumscribed here (unpublished results). Both species share many anatomical similarities with *Psorotichia* and deviate only in the squamulose growth form. Subsequent analyses with a more complete set of genetic markers for at least the putatively undescribed taxon from Oman will help to answer the question if *Pseudopaulia* should be included in *Psorotichia*.

Pseudopeltula Henssen, Lichenologist 27: 279. 1995. MycoBank MB 6198.

Type species: *Pseudopeltula myriocarpa* Henssen, Lichenologist 27: 279. 1995. MycoBank MB 413984.

Notes: Attempts to sequence material of this genus established in the *Gloeoheppiaceae* failed. Based on available data (Henssen 1995, Büdel & Schultz 2011), we think that *Pseudopeltula* is well placed in the *Lichinaceae* and closely related to *Gloeoheppia*. It differs from the latter mostly in the distinctly divided hymenium.

Included species: *Pseudopeltula dicyanophora*, *P. heppioides*, *P. myriocarpa*, and *P. necrocorticata*.

Pseudotichia M. Schultz & M. Prieto, ***gen. nov***. MycoBank MB 852310. Fig. 12.

Etymology: Because of the general resemblance with *Psorotichia*.

Type species: ***Pseudotichia vermiculata*** (Nyl.) Schultz & M. Prieto, ***comb. nov***. MycoBank MB 852311.
Basionym: *Collemopsis vermiculata* Nyl., Flora, Regensburg 64: 529. 1881. MycoBank MB 383567.
Homotypic synonym: *Psorotichia vermiculata* (Nyl.) Forssell, Beitr. Gloeolich.: 73. 1885. MycoBank MB 517463.

Diagnosis: Genus of the *Lichinaceae*. Similar to *Psorotichia*, but differing in the cryptolecanorine apothecia surrounded by a shallow and indistinct thalline margin, the presence of a distinct proper exciple and uneven to umbonate apothecia discs caused by intrusions of sterile hyphal bands separating the hymenium into chambers, and the thick thallus areoles with cottony basal layer. Differs from *Pyrenocarpon* in the cryptolecanorine apothecia and dry, only occasionally seeping moist habitat. Resembles

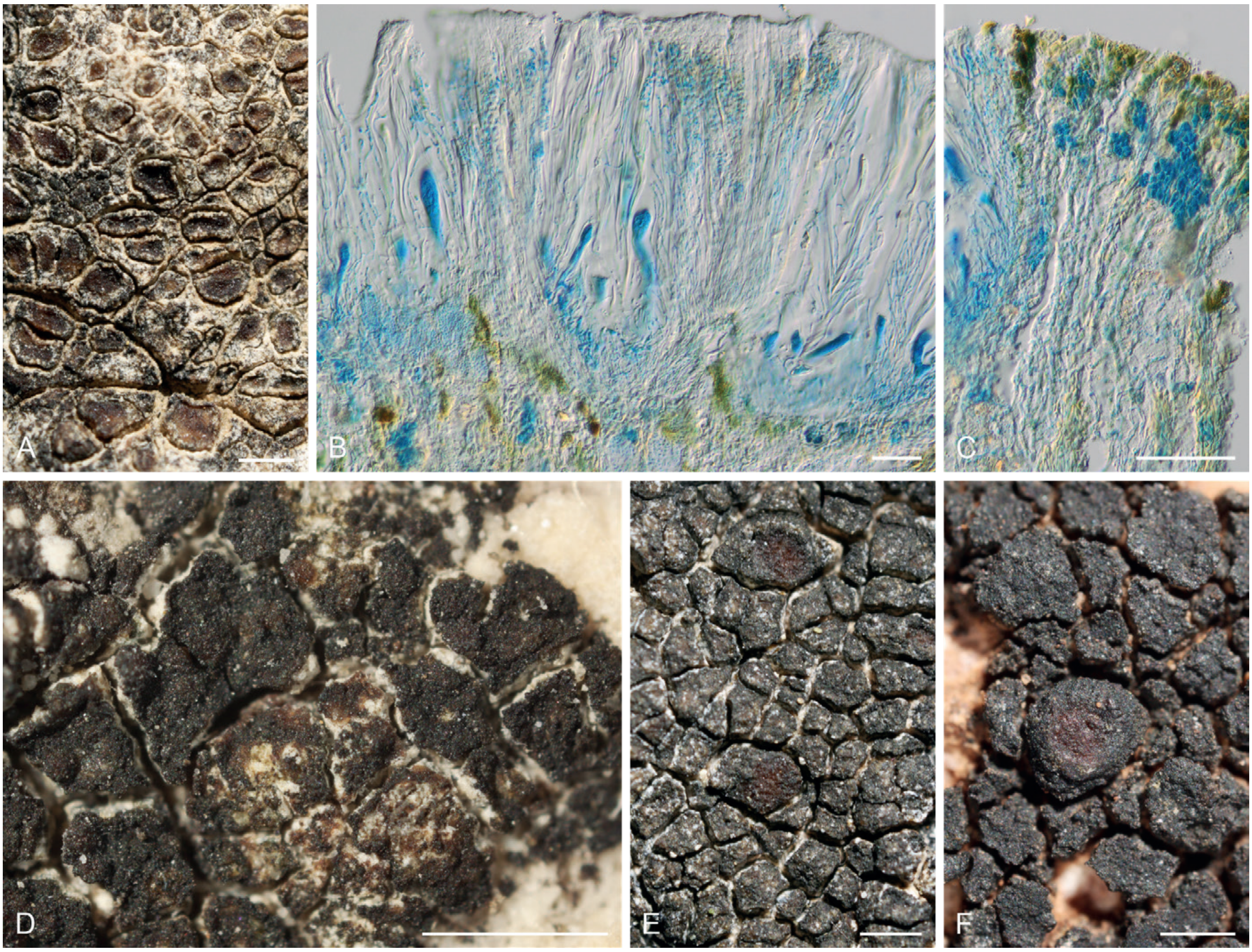

Fig. 12. *Pseudotichia vermiculata*. **A.** Thallus areoles angulate, becoming eroded, apothecia immersed (H-NYL42517, lectotype). **B.** Older hymenium divided by sterile hyphae in LPCB (H-NYL42517, lectotype). **C.** Section of thick areole, top paraplectenchymatous, vertical hyphae forming thick medulla below in LPCB (H-NYL42517, lectotype). **D.** Thick, blackish thallus areoles becoming superficially eroded (Lojka 4, B, isolectotype). **E.** Thick, angulate areoles with two large apothecia, discs multiply umbonate (Palice 14422). **F.** Thick thallus areoles with slightly elevated, large apothecium (Prieto SMP52B). Scale bars: A, D–F = 1 mm; B, C = 25 µm.

Lapismalleus and *Metamelanea* in the thick areoles and thallus anatomy with mostly vertical hyphae, but differs in the less distinctly umbonate apothecial discs and pale colouration of the proper exciple. It differs from *Collemopsis* and *Porocyphus* by the multiple divided hymenium caused by intrusions of sterile hyphae and cottony basal attachment layer.

Description: *Thallus* blackish, dark brownish or with a dirty grey tinge when surface erodes (Fig. 12A, D–F), crustose-areolate, areoles 0.4–1 mm, angulate, ± plane, surface rough, 0.75–1(1.5) mm thick (Fig. 12C), attached by robust rhizohyphae forming a cottony basal layer. Thallus ecorticate, homoiomerous, anatomy ± paraplectenchymatous forming an irregular network around single-celled cyanobionts, hyphae in apical thallus parts indistinct, becoming vertical and loose (Fig. 12C), 5–6 × 2–3 µm with thickened, gelatinous wall, dying towards the cottony base, often incorporating mineral particles and colonies of associated microorganisms, cyanobiont a coccoid cyanobacterium, cells tightly packed, ± globose, 6.5–11 µm with gelatinous sheaths, 3.5–6 µm without sheath, gelatinous sheath thin, yellowish brown at outer thallus parts, colourless inside. *Apothecia* cryptolecanorine, up to 0.8 mm, disc roundish or somewhat distorted, dark reddish brown, concave to ± plane, rough and becoming multiple umbonate (Fig. 12A, E, F), thalline margin reduced to the remnants of surrounding areole (Fig. 12A, C, E, F), flat and very indistinct, 42–75 µm thick, exipulum proprium well developed (Fig. 12C), apically widened and 50–110 µm thick, laterally 50–95 µm, pale reddish or brownish, hymenium 150–185 µm high, becoming multiple divided by intrusions of sterile hyphae (Fig. 12B) that cause the rough, multiple umbonate appearance of the apothecial discs, partial hymenia 65–110 µm wide, *paraphyses* distinct, septate, becoming loose, branched and anastomosing and then well contrasting with the excipular hyphae, 5.5–6 × 1.5–2 µm, apical cells somewhat enlarged and submoniliform, 5–6.5 × 3–3.5 µm, KOH/Lugol+ blue, asci *Lichina* type, 8-spored, *ascospores* simple, hyaline, ellipsoid to broad ellipsoid, 12–20 × 6–10 µm, old spores with very thick walls often oversized and sometimes (sub)globose. *Ascomata* develop from ascogones arising in a tangle of generative hyphae. Pycnidia not observed in the type material studied so far (Lojka 4, H-NYL42517, B600129465). Known from western Romania (original collection), other reports should be checked critically, but likely occurring in suitable sites elsewhere in (southern) Europe. On exposed limestone moistened by seeping water. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: The genus is introduced to accommodate *Psorotichia vermiculata* as it forms another separate clade distantly related to *Psorotichia s. str*. In fact, the species differs considerably from characteristic species of *Psorotichia*, mostly by the cryptolecanorine apothecial discs with rough to somewhat umbonate discs and the multiple divided hymenium caused by intrusions of sterile hyphae. Particularly similar to *Lapismalleus lugubris* as well as *Metamelanea melambola* and *M. umbonata*, but differing in the much paler colouration of the apothecia and excipular structures.

Psorotichia A. Massal., Framm. Lichenogr.: 15. 1855. MycoBank MB 4531. Figs 2D, 3H, 13.

Type species: *Psorotichia murorum* A. Massal., Framm. Lichenogr.: 15. 1855. MycoBank MB 402888.

Description: *Thallus* crustose, granulose to distinctly areolate (Fig. 13A–C, E), rarely minutely fruticulose, with exclusively single-celled cyanobionts, thallus homoiomerous, anatomy paraplectenchymatous with a dense and compact network of short hyphae with ± isodiametric cells and small-celled cyanobionts with very narrow, yellowish brown gelatinous sheaths (Fig. 13D, F). *Ascomata* formed from ± spheroid tangle of generative hyphae with ascogones and trichogynes (Fig. 2D), never pycnoascocarps. *Apothecia* with a thick, sometimes bulging thalline margin, discs usually sunken or concave, reddish or dark yellowish brown, not conspicuously black (Fig. 13A–F), excipulum propium rudimentary or absent (Fig. 13D, F), epihymenium yellowish or reddish brown, hymenium usually KOH/Lugol+ blue, paraphyses straight, distinctly septate (Fig. 13D, F), terminal cells slightly widened to submoniliform, subhymenium often extending downwards into a short stipe (Fig. 13F), asci *Lichina*-type, ascospores 8 (Fig. 3H), rarely polysporous. *Pycnidia* immersed or slightly elevated in small thallus warts, wall pale, conidia simple, short ellipsoid or bacilliform, produced terminally on simple conidiophores. Widely distributed on both hemispheres with preference for warm-temperate to semi-arid regions. On calcareous or otherwise mineral-rich rock in inclined rock faces sporadically or seasonally moistened by seeping water but in exposed situations. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: *Psorotichia* in the traditional, very wide circumscription, is characterized by having typical, lecanorine apothecia and crustose thalli but the results show the studied species as belonging to five clades, an extreme case of polyphyly:

Psorotichia s. str. The *sensu stricto* clade includes the type (*P. murorum*) together with *P. columnaris*, *P. diffracta* and *P. frustulosa*. The first three species are very similar (Moreno & Egea 1994), the fourth one fits to them very well, but it was initially considered to represent fertile *Metamelanea caesiella* because of greyish pruinose thallus. However, it falls clearly outside that genus. *Psorotichia polyspora* was described from Venezuela and it is also known from Brazil. It deviates in the polysporous asci and faintly yellowish hymenial reaction with Lugol. For the time being, it seems well placed in the much narrower genus *Psorotichia* as circumscribed above, but subsequent studies will have to test the relationship of *P. polyspora* and several other tropical species. Based on ongoing morphological studies of type material planned to be published elsewhere, we estimate that only 12–15 out of more than 60 species currently accepted in *Psorotichia* fall within this genus in our narrow concept. Species of *Psorotichia* with a vivid emerald green epihymenium and/or blackish umbonate apothecial discs belong to *Thelignya* (see there). Other species morphologically clearly falling outside *Psorotichia* will be treated in an upcoming publication (Schultz in prep.).

-*Collemopsis* (including *C. schaereri*).
-*Pseudotichia* (including *P. vermiculata*).
-*Lapismalleus* (including *L. lugubris*).
-*Lemmopsis* (including *L. pelodes* and *L. lutophila*).

We have been unable to solve the question if the enigmatic *Thelochroa montinii* belongs to *Psorotichia s. str.* or not. If so, no problems emerge because this species would generally fit into *Psorotichia* even in the much narrower circumscription adopted here. If not, the species is in need of a new genus, because *Thelochroa* is based on *Verrucaria flotowiana*, the type of the slightly older genus *Pyrenocarpon* and it seems unlikely that *Pyrenocarpon thelostoma* and *Thelochroa montinii* can be accommodated in the same genus.

Pterygiopsis Vain., Acta Soc. Fauna Flora fenn. 7(1): 238. 1890. MycoBank MB 4540. Fig. 1A.

Type species: *Pterygiopsis atra* Vain., Acta Soc. Fauna Flora fenn. 7(1): 238. 1890. MycoBank MB 402923.

Description: Genus of the *Lichinaceae*, thallus blackish or dark brownish, rarely greyish pruinose, crustose, often distinctly effigurate (Fig. 1A), sometimes small-squamulose with somewhat lobate margins, often attached by a gelatinous basal layer. *Thallus* ecorticate, anatomy paraplectenchymatous, often with fan shaped hyphal arrangement, cyanobiont a coccoid cyanobacterium with yellowish brown gelatinous sheaths. *Apothecia* lecanorine or zeorine with prominent thalline margin, proper exciple rudimentary, thin or distinct, *asci* prototunicate, *Lichina* type, 8-spored, *paraphyses* septate, apical cells somewhat widened, hymenium KOH/IKI- or weakly blue. Resembling *Forssellia*, but differing in the absence of pycnoascocarps and the presence of typical apothecia. *Pycnidia* small, immersed, conidiophores simple, *conidia* bacilliform to short ellipsoid. Distribution (sub)tropical, mostly in the southern hemisphere, usually on acidic, rarely calcareous rock, along drainage channels, semi-amphibious along river margins or on steep, seeping moist rock faces. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Originally a monotypic genus, *Pterygiopsis* was subsequently expanded (Henssen 1963a, 1980, 1990a, Henssen *et al.* 1985, Henssen & Jørgensen 1990, Schultz *et al.* 2000, Schultz 2004, 2006, Oliveira Junior *et al.* 2020) containing *ca*. 20 species that differ in ascoma ontogeny and number of ascospores. This indicates that *Pterygiopsis* in its previous circumscription was a heterogeneous assemblage. The eight species covered by this study are represented in four clades. The clade containing the type species (*P. atra*) is relatively close to a clade formed by *P. neglecta*, *P. lacustris* and *Thelignya lignyota* and thus the former two are combined in *Thelignya* (see below). A recently described sterile species, *P. densisidiata* (Oliveira Junior *et al.* 2020) and *P. guyanensis* fall within *Cladopsis* and are recombined accordingly (see there). Four species of the *affinis* group proved to be closely related, and we place them in the reinstated genus *Forssellia* (see above).

Pterygiopsis atra is closely related with *Synalissa* forming a clade with *Zahlbrucknerella* and *Thelignya*, all of them with typical apothecia. Most of these species (except *S. ramulosa*) are found on wet rocks, some of them growing submerged.

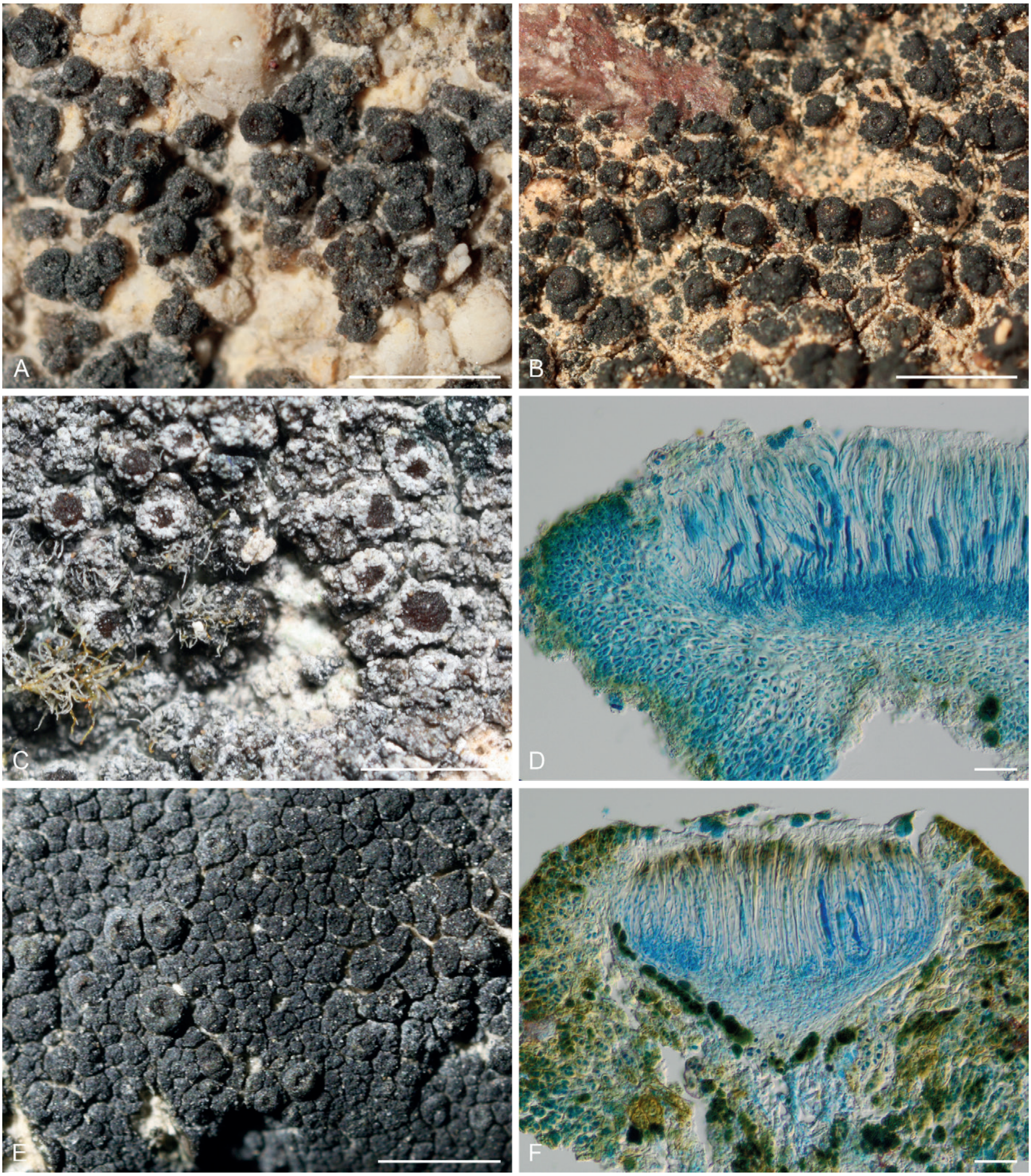

Fig. 13. A. *Psorotichia murorum*, granulose crustose thallus with indistinct areoles and grouped apothecia (Massalongo Lich. Ital. 300, M, isolectotype). **B.** *Psorotichia columnaris*, apothecia distinctly sessile, thalline margin bulging (Feuerer). **C.** *Psorotichia diffracta*, thallus pruinose, apothecia adnate with finally expanded discs (Groner 4157). **D.** Apothecium with thick, paraplectenchymatous thallus margin, hymenium with straight, septate paraphyses and juvenile asci in LPCB (Claudel & Harmand Lich. Gall. 485, B). **E.** *Psorotichia frustulosa*, thallus areolate, somewhat pruinose, apothecia with concave discs and thick thallus margin (Palice 12703). **F.** Apothecium with thick thalline margin and inversely cone shaped subhymenium (Prieto SL96). Scale bars: A–C, E = 1 mm; D, F = 25 µm.

Pterygiopsis s. l. comprises:

-*Pterygiopsis s. str.* (including *P. atra*).

-*Forssellia* (including *P. affinis*, *P. canariensis*, *P. concordatula* and *P. umbilicata*).

-*Thelignya* (including *T. neglecta* and *T. lacustris*).

Among the species not included in the phylogenetic analysis, we assume that those forming pycnoascocarps should be excluded and might be better accommodated in *Forssellia* (*P. australiensis*, *P. cava*, *P. convoluta*). *Pterygiopsis somaliensis* and its var. *pallidolobata* are known in sterile state only, but according to the rather detailed description of the thallus anatomy most likely belong to *Peltula*. The remaining taxa of *Pterygiopsis s. str.* are (sub) tropical species from the southern hemisphere with the exception of *P. pulchra* described from the Dhofar Mountains in Yemen (Schultz

2004). Attempts to sequence type and other material collected later in Oman failed. Because the presence of typical apothecia, it is retained in *Pterygiopsis s. str*. just like *P. convexa*, *P. foliacea*, *P. melanophthalma*, *P. mutabilis* and *P. submersa*.

Pycnolemma M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852312.

Etymology: The name points to the type of ascoma (pycnoascocarps) and the resemblance with *Lempholemma* (*Nostoc* cyanobiont).

Type species: ***Pycnolemma polycarpum*** (M. Schultz) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852313.
Basionym: *Lempholemma polycarpum* M. Schultz, Lichenologist 37(3): 231 2005. MycoBank MB 342442.

Diagnosis: Genus of the *Lichinaceae*. Thallus umbilicate-lobate, rosette shaped with radiating lobes. Resembling other peltate and rosette shaped species from dry, rocky habitats of the genera *Anema*, *Lichinella*, *Paulia*, *Peltula*, *Peccania*, *Thyrea* but differing in the *Nostoc* cyanobionts. Differing from *Lingolemma* (*lingulatum*) in the elongated and furcate lobes and the strictly homoiomerous thallus anatomy lacking a central hyphal strand. Differing from *Peltolemma* (*socotranum*) in the formation of pycnoascocarps, the smaller apothecia with punctiform discs surrounded by an indistinct thalline margin and the elongated and furcate lobes.

Description: A detailed description of the only species is given in Schultz (2005).

Notes: Phylogenetic affinities are discussed in *Lempholemma*. The only species, *Pycnolemma polycarpum*, is known from Yemen, Oman, Aldabra, Madagascar and Puerto Rico (Schultz & Aptroot 2008).

Pyrenocarpon Trevis., Riv. Accad. di Padova: 49. 1855. MycoBank MB 4583. Fig. 14.

Type species: *Pyrenocarpon flotowianum* (Hepp) Trevis. 1855. MycoBank MB 403004.
Synonym: *Pyrenocarpon thelostoma* (Ach. *ex* J. Harriman) Coppins & Aptroot, Lichenologist 40(5): 372. 2008. MycoBank MB 539628.

Notes: Currently a monotypic genus of the *Lichinaceae* characterized by crustose-areolate thalli with typical apothecia, eventually exposing a reddish-brown disc and with a wide pale proper exciple. While growth form and thallus anatomy are similar to *Psorotichia*, the presence of a distinct proper exciple and apothecia with umbonate discs is shared with its closest relative, *Pseudotichia vermiculata*, but also with *Metamelanea*, *Leprocollema* and *Paracyphus*, the latter clustering in main clade 3 and thus belonging to *Porocyphaceae*. *Pseudocarpon persimile* is strikingly similar in external appearance (Fig. 28) and ecology but differs in thallus anatomy (robust hyphae forming a very dense network) and ascoma ontogeny (pycnoascocarps). *Pyrenocarpon flotowianum* grows on seeping moist or semi-aquatic calcareous or siliceous rocks, *e.g.* along river margins. The phylogenetic placement in our tree is based on North American material from the shore of Lake Michigan, Illinois (HBG-015213; Fig. 14) with seasonal inundation. The application of this name still remains somewhat vague as there is much confusion around the identity of *Pyrenocarpon flotowianum* and *P. thelostoma*. A detailed discussion was provided by Ellis (1981) based on European material. In the possible case that *Pyrenocarpon thelostoma* is not the same as *P. flotowianum*, the relationship with the new genus *Pseudotichia* established here for *Psorotichia vermiculata* should be evaluated in detail. In any case, genus *Pyrenocarpon* is typified with *Verrucaria flotowiana*. A possible synonym of *Pyrenocarpon thelostoma* is *Pyrenopsis fuscoatra* described from Montgomery Co., Indiana, "on limestone in low, open, moist fields" (Fink & Fuson 1918). It is a psorotichioid lichen which has nothing in common with *Pyrenopsis s. l.*

Synalissa Fr., Syst. Orb. Veg. 1: 297. 1825. MycoBank MB 5323. Fig. 3K.

Type species: *Synalissa ramulosa* (Hoffm.) Fries, Syst. Orb. Veg. 1: 297. 1825. MycoBank MB 406704.
Synonym: *Synalissa symphorea* (Ach.) Nyl., Actes Soc. Linn. Bordeaux 21: 264. 1857. MycoBank MB 406708.

Notes: We have only included one species, but unpublished data indicate that other members of the genus are closely related (*e.g. S. austroafricana*, *S. lichinella*, and *S. mattogrossensis*). Early authors focusing on either growth form or type of photobiont had much difficulty to separate *Synalissa* from *Peccania* (likewise fruticose

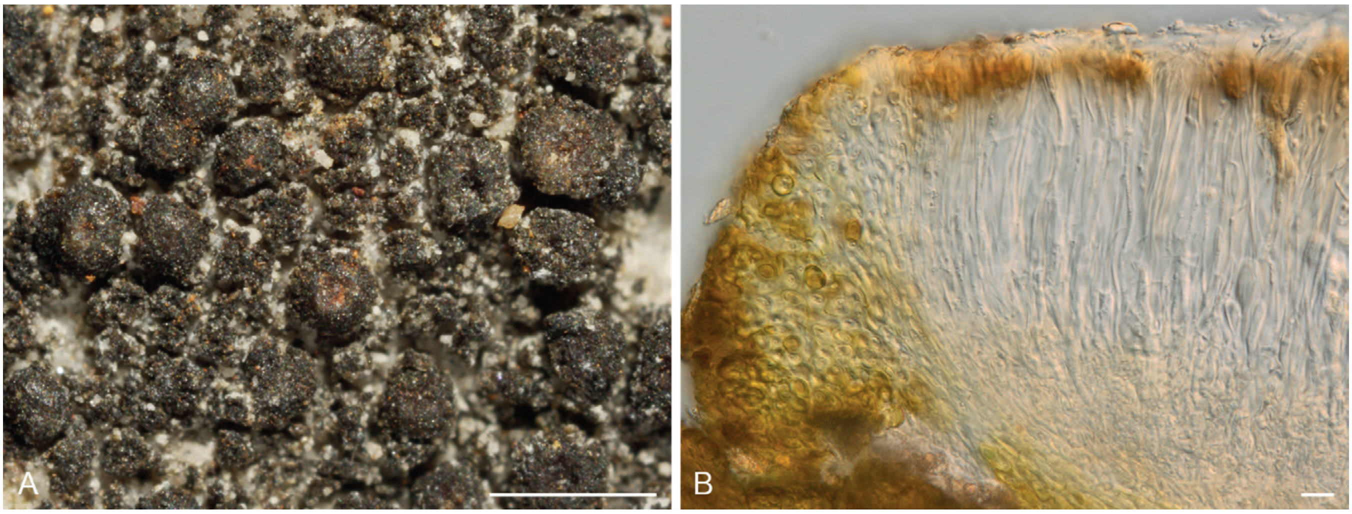

Fig. 14. *Pyrenocarpon thelostoma* (Hyerczyk 2400). **A.** Hemispherical apothecium with narrow discs resembling fish eyes. **B.** Zeorine apothecial margin with distinct thalline and proper margin in KOH. Scale bars: A = 0.5 mm; B = 10 µm.

but different cyanobiont) and *Pyrenopsis* (same cyanobiont but different crustose growth form); however, these three groups are not closely related. As it has been shown here, growth form (crustose *vs* fruticose) and type of photobiont (gloeocapsoid *vs* xanthocapsoid) alone are not suitable characters for delineating monophyletic entities at genus level.

Thelignya A. Massal., Framm. Lichenogr.: 18. 1855. MycoBank MB 5428. Fig. 15.

Type species: *Thelignya fuliginea* (Wahlenb.) A. Massal., Framm. Lichenogr.: 18. 1855. MycoBank MB 407111.
Synonym: *Thelignya lignyota* (Wahlenb.) P.M. Jørg. & Henssen, Lichenologist 22: 145. 1990. MycoBank MB 125711.

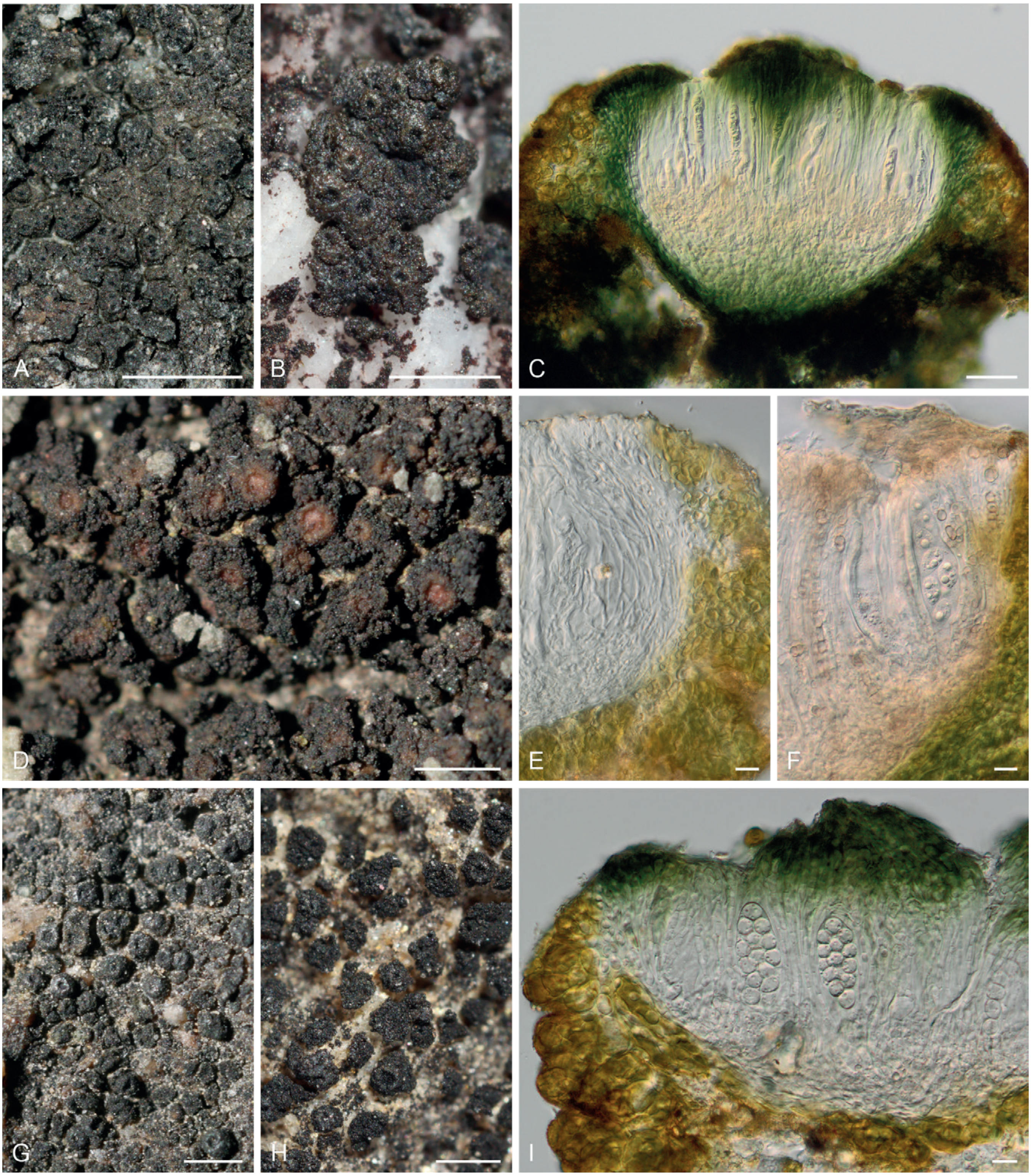

Fig. 15. A. *Thelignya lacustris*, thallus rimose areolate with immersed, black apothecia (Gilbert). **B.** *Thelignya lignyota*, thallus squamule with numerous immersed, black apothecia (Schultz 16867). **C.** Apothecium with distinct green colouration of exciple and central umbo (Prieto Pirineos 51). **D.** *Thelignya neglecta*, (semi-)immersed apothecia in granulose areoles with brownish, umbonate discs (Schultz 07143b, epitype). **E.** Zeorine apothecial margin, proper exciple pale, paraphyses lax (Schultz 07226, epitype). **F.** Ascus with simple ascospores in small hymenial chamber surrounded by robust excipular hyphae, with unknown lichenicolous fungus (Malíček & Kulíková 7316). **G.** *Thelignya arnoldii*, thallus crustose with sessile apothecia, discs black (Arnold, W1913-5405, holotype). **H.** Flat thallus areoles with semi immersed to sessile apothecia and black discs (Schultz 08933). **I.** Hymenium with polysporous asci, upper part of proper exciple and central umbo distinctly greenish (Schultz 08933). Scale bars: A = 1 mm; B, D, G, H = 0.5 mm; C = 25 µm; E, F, I = 10 µm.

Emended description: Thallus crustose, uniformly thin, granulose, areolate (Fig. 15A, D, G, H) or subsquamulose (Fig. 15B), fixed to substrate by a basal gelatinous layer, rhizohyphae or minute stalk, cyanobionts *Rivulariaceae* with usually much bent and split filaments, basal heterocytes often difficult to discern or with single-celled cyanobionts with thin, yellowish brown gelatinous sheaths, thallus homoiomerous, anatomy ± paraplectenchymatous or with an irregular, ± dense network of short celled hyphae with ± isodiametric cells. *Apothecia* with shallow or prominent thallus margin and distinct proper exciple (Fig. 15C, E, I), discs usually sunken or concave, often narrow (Fig. 15A, B) but becoming distinctly umbonate when fully developed (Fig. 15C, D, I), conspicuously black and emerald green in section (Fig. 15C, I) and then N+ blue or reddish to yellowish brown or pale (Fig. 15E, F), epihymenium blue green or yellowish or reddish brown, hymenium KOH/Lugol-, yellowish or reddish but not distinctly blue, *paraphyses* septate, straight or ± irregular, branched and anastomosing, terminal cells slightly widened, *asci Lichina* type, ascospores 8 or 16, subhymenium/hypothecium roundish at the base. *Ascomata* formed from ± spheroid tangle of generative hyphae with ascogones and trichogynes, no pycnoascocarps. *Pycnidia* immersed or slightly elevated in small thallus warts, globose, wall pale, but apically often emerald green, conidia simple, short ellipsoid, subglobose or bacilliform, produced terminally on simple conidiophores. Widely distributed in the northern hemisphere with preference for cool to cold, high montane to alpine sites, but also along lowland river banks, often semi-aquatic but also submerged in clear water lakes. On siliceous rocks, also on mineral rich rocks. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Species of *Thelignya* form a clade consisting of *T. lignyota*, the type of the genus, and two species of *Pterygiopsis*. All these share the presence of typical apothecia, crustose thalli and a similar ecology, as all the species grow on (temporarily) submerged rocks. The type specimen of *Pterygiopsis neglecta* was collected in 1904 on the shores of the Elbe River in Hamburg, Germany. Its identity long remained a mystery until it was described by Erichsen (1940) as *Forssellia neglecta*. Thüs & Schultz (2009) suggested that *Forssellia neglecta* was a “forgotten taxon” and provisionally placed it into *Pterygiopsis* because *Forssellia* was considered a synonym of that genus by Henssen (1980). The authors were hesitant to formally make the combination because of severe problems with the generic delimitation of the genus *Pterygiopsis*. Therefore, it remained not validly published, but it is listed in the checklist of lichens and lichenicolous fungi in Germany (Wirth *et al.* 2011, Printzen *et al.* 2022) as *P. neglecta*. The genus description is emended to include *Pterygiopsis lacustris* and *P. neglecta* which are shown here to be closely related to *Thelignya lignyota*.

New combination in *Thelignya*:

Thelignya arnoldii (Frauenf.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852314.
Basionym: *Psorotichia arnoldii* Frauenf., in Arnold, Verh. K. K. Zool.-Bot. Ges. Wien 14: 462. 1864, in footnote. MycoBank MB 402841.
Homotypic synonym: *Psorotichia tiroliensis* Zahlbr., Cat. lich. univ. 2: 798. 1924, *nom. superfl*. MycoBank MB 615322.
Synonym: *Psorotichia taurica* (Nyl.) Vain., Termeszetr. Füzetek 22: 312. 1899. MycoBank MB 541806.

Notes: A distinctive species with complicated synonymy. Following Printzen *et al.* (2022), the names introduced by Frauenfeld in an editorial note at the end of Arnold (1864) are validly published. Thus, *Psorotichia arnoldii* is the earliest available name. “*Psorotichia arnoldii* Körb.” cited in MycoBank does not exist (or acutally refers to *Psorotichia arnoldiana* (Hepp *ex* Arnold) Körb, =*Lemmopsis arnoldiana* (Hepp *ex* Arnold) Zahlbr.) and anyhow would not be potentially conflicting as the species is excluded from *Psorotichia* here.

Thelignya lacustris (P.M. Jørg. & R. Sant.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852315.
Basionym: *Pterygiopsis lacustris* P.M. Jørg. & R. Sant., Lichenologist 22(3): 214. 1990. MycoBank MB 128013.

Thelignya neglecta (Erichsen) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852316.
Basionym: *Forssellia neglecta* Erichsen, Ann. Mycol. 38: 313. 1940. MycoBank MB 366244.
Homotypic synonym: *Pterygiopsis neglecta* (Erichsen) Thüs & M. Schultz, *comb. prov.*, *nom. inval*. MycoBank MB 658995.

Type: Germany, Hamburg, Vierlande, am Kalksteinschutz des Elbdeiches bei Warwisch, 9 June 1904, *C.F.E. Erichsen* (***holotype***-HBG1000025).

Additional specimens studied: **Germany**, Hamburg, Nienstedten, Teufelsbrück, periodically flushed slag stones of bank of river Elbe just below bus stop “Teufelsbrück”, 0 m a.s.l., 53.547222°N, 9.864167°E, 29 Apr. 2013, *M. Schultz*, 07226 (**epitype**-HBG-025110, designated here); Schleswig-Holstein, Wedel, Willkomm-Höft, amphibious on slack stones on the bank of river Elbe, *Staurothele frustulenta* belt, 1 m a.s.l., 53.568363°N, 9.702954°E, 21 Apr. 2008, *M. Schultz*, 07143b (HBG-015559); Wedel, 150 m E of Willkomm-Höft, amphibious on slack stones on the bank of river Elbe, *Staurothele frustulenta* belt, 1 m a.s.l., 53.568043°N, 9.704639E, 21 Apr. 2008, *M. Schultz*, 07144 (HBG-015600).

Thelignya obtenebrans (Nyl.) M. Schultz, ***comb. nov.*** MycoBank MB 852317.
Basionym: *Collemopsis obtenebrans* Nyl., Flora 68: 39. 1885. MycoBank MB 383554.
Homotypic synonym: *Psorotichia obtenebrans* (Nyl.) Forssell, Beitr. Gloeolich.: 77. 1885. MycoBank MB 476317.
Synonyms: *Psorotichia incrustans* Arnold, in Flagey, Rev. Mycol. 17: 114. 1895 and Flagey, Lichenes Algerienses no. 302 (not *Thrombium incrustan*s Wallr.). MycoBank MB 402877.
Psorotichia numidella sensu Flagey, Rev. Mycol. 17: 114. 1895 and Flagey, Lichenes Algerienses no. 301 (not *Psorotichia numidella* (Nyl.) Forssell).
Psorotichia numidella var. *flageyana* J. Steiner, Sitzungsber. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Cl. 107, Abt. 1: 109. 1898. MycoBank MB 541128.

Thermutopsis Henssen, Lichenologist 22: 254. 1990. MycoBank MB 25467.

Type species: *Thermutopsis jamesii* Henssen, Lichenologist 22: 254. 1990. MycoBank MB 127827.

Notes: Not treated in the phylogenetic analysis. An enigmatic genus and species only known from Antigua where it grows on coastal calcareous rocks. Henssen (1990b) described the ascoma as thallinocarps, but in our opinion they have little in common with the thallinocarps of *Lichinella* or *Gonotichia*. There are also differences in the type of paraphyses (pointed tips) that according to Henssen resemble those of the *Coccocarpiaceae* (*Peltigerales*, *Lecanoromycetes*), a distantly related family of cyanolichens. We consider the placement of *Thermutopsis* in the *Lichinomycetes* to be dubious but the genus is kept in the family *Lichinaceae* mostly because of the filamentous cyanobionts.

Zahlbrucknerella Herre, J. Wash. Acad. Sci 2: 384. 1912. MycoBank MB 5863. Fig. 6F.

Type species: *Zahlbrucknerella calcarea* (Herre) Zahlbr., Cat. lich. univ. 2: 762. 1924. MycoBank MB 10083.

Notes: Species have filamentous thalli (Fig. 6F) containing *Scytonema* cyanobionts and produce typical apothecia. The genus was monographed by Henssen (1977). It is phylogenetically related with crustose species from *Thelignya*, sharing the presence of typical apothecia and a similar ecology. In many aspects it is a parallel genus to *Ephebe* which differs in the *Stigonema* cyanobionts and formation of pycnoascocarps. It includes ten species worldwide: *Z. africana*, *Z. calcarea*, *Z. californica*, *Z. compacta*, *Z. fabispora*, *Z. indica*, *Z. maritima*, *Z. marionensis*, *Z. maxima*, and *Z. patagonica*. The identity of *Z. granitica* described from Argentina and its var. *crispa* described from Ethiopia remains dubious.

Lichinellaceae M. Prieto & M. Schultz. ***fam. nov.*** MycoBank MB 852318. Figs 1F, 16.

Diagnosis: Small sized family of cyanolichens exclusively associating with single-celled cyanobacteria (never with reddish/purplish sheaths) OR with *Nostoc* (but no other filamentous cyanobacteria). *Thalli* predominantly squamulose, but also crustose, foliose or fruticulose, but never long filamentous or endolithic. Thalli homoiomerous, never truly corticated, never sorediate but isidia or isidia-like outgrowths occur. IF containing *Nostoc* THEN often with hormocystangia. *Ascomata* typical apothecia with 8-spored, *Peccania* type asci OR thallinocarps with much reduced excipular structures and polysporous, *Lichinella* type *asci*, rarely octosporous and IF so THEN hymenium staining reddish with KOH/Lugol. *Conidia* small ellipsoid or short bacilliform, but never filiform or acicular, conidiophores always simple.

Discriminating characters: No single-celled cyanobionts with reddish/purplish sheaths, no filamentous cyanobionts other than *Nostoc* and IF so THEN no pycnoascocarps, asci *Peccania* type, thalli often with hormocystangia and species usually extra tropical, thallus never truly corticate, no unitunicate-rostrate asci, asci either *Lichinella* or *Peccania* type, conidia never filiform or acicular, conidiophores always simple, thallus never with true soralia, never corticolous.

Description: Lichen-forming ascomycetes of blackish colour, rarely greyish pruinose (Fig. 16) and obligatory associating with single-celled cyanobacteria with yellowish brown gelatinous sheaths OR filamentous cyanobacterium *Nostoc*. Growth forms diverse, ranging from crustose, squamulose, squamulose-peltate, foliose to dwarf-fruticose (Figs 1F, 16), but not long filamentous or endolithic. *Thalli* fixed by rhizohyphae, tufts of rhizohyphae or a central umbilicus. True soralia absent, isidia present in some species, hormocystangia formed in some *Nostoc* containing species. Thallus anatomy homoiomerous, ecorticate, hyphal irregularly reticulate, in some species forming a central strand or special fountain-like hyphal systems. *Ascomata* of two types: the species with single-celled cyanobionts have thallinocarps with reduced excipular and hymenial structures (Fig. 2H–L) and predominantly polysporous, *Lichinella* type asci (Fig. 3D) and wine red Iodine reaction turning blue. Ascomata of species with *Nostoc* cyanobionts are formed from ascogones in a tangle of generative hyphae and hymenium with bluish Iodine reaction, true paraphyses and a usually thin proper exciple, asci 8-spored, *Peccania* type. *Conidiomata* pycnidia, immersed to slightly elevated, conidiophores always simple, *conidia* produced terminally, small ellipsoid or short bacilliform, never filiform. Distribution mostly in the northern hemisphere but *Lichinella* extending into dry regions in the southern hemisphere. On bare, often calcareous, volcanic or mineral rich rocks, occasionally or seasonally wetted in well lit or steep and somewhat shaded situations, also in biological soil crusts, never corticolous. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: The novel family *Lichinellaceae* is established for main clade 5 to accommodate the thallinocarp forming genera *Lichinella* (incl. *Gonohymenia*, *Thallinocarpon*, and *Rechingeria*) and *Gonotichia* (*gen. nov.*) as well as the reestablished genus *Synalissina* for non-thallinocarpous, lempholemmatoid species that cannot be placed in *Lempholemma s. str.* or any other of the *Nostoc*-containing genera which all fall within *Lichinaceae*. There is no synapomorphy supporting clade 5, but a distinction from the other three families is possible by exclusion of certain sets of characters that assign a given lichen to one of the other families.

Included genera: *Edwardiella*, *Gonotichia*, *Lichinella* (incl. *Gonohymenia*, *Rechingeria*, and *Thallinocarpon*), *Synalissina*; approx. 50 spp.

Edwardiella Henssen, Lichenologist 18: 51. 1986. MycoBank MB 6003.

Type species: *Edwardiella mirabilis* Henssen, Lichenologist 18: 52. 1986. MycoBank MB 104233.

Notes: An enigmatic, monotypic genus from the Subantarctic not included in our phylogeny. The species forms thallinocarpous fruiting bodies. However, these thallinocarps seem to differ from those of *Lichinella* and therefore, we assume this species is close to *Gonotichia*.

Gonotichia M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852319. Figs 16F, 17.

Etymology: *Gonotichia* is selected to stress the partial similarities with both *Psorotichia* (crustose growth) and *Gonohymenia* (thallinocarpous ascomata).

Type species: *Gonotichia octosporella* (Lettau) M. Schultz & M. Prieto (syn. *Gonohymenia octosporella* Lettau)

Diagnosis: Genus of the *Lichinellaceae* resembling *Psorotichia*, but differing in the thallinocarpous ascomata. Related to *Synalissina*, but deviating in the coccoid cyanobionts and presence of thallinocarpous ascomata. Differing from *Lichinella* in the octosporous, *Peccania* type asci and only very patchy presence of cyanobacteria on the hymenium.

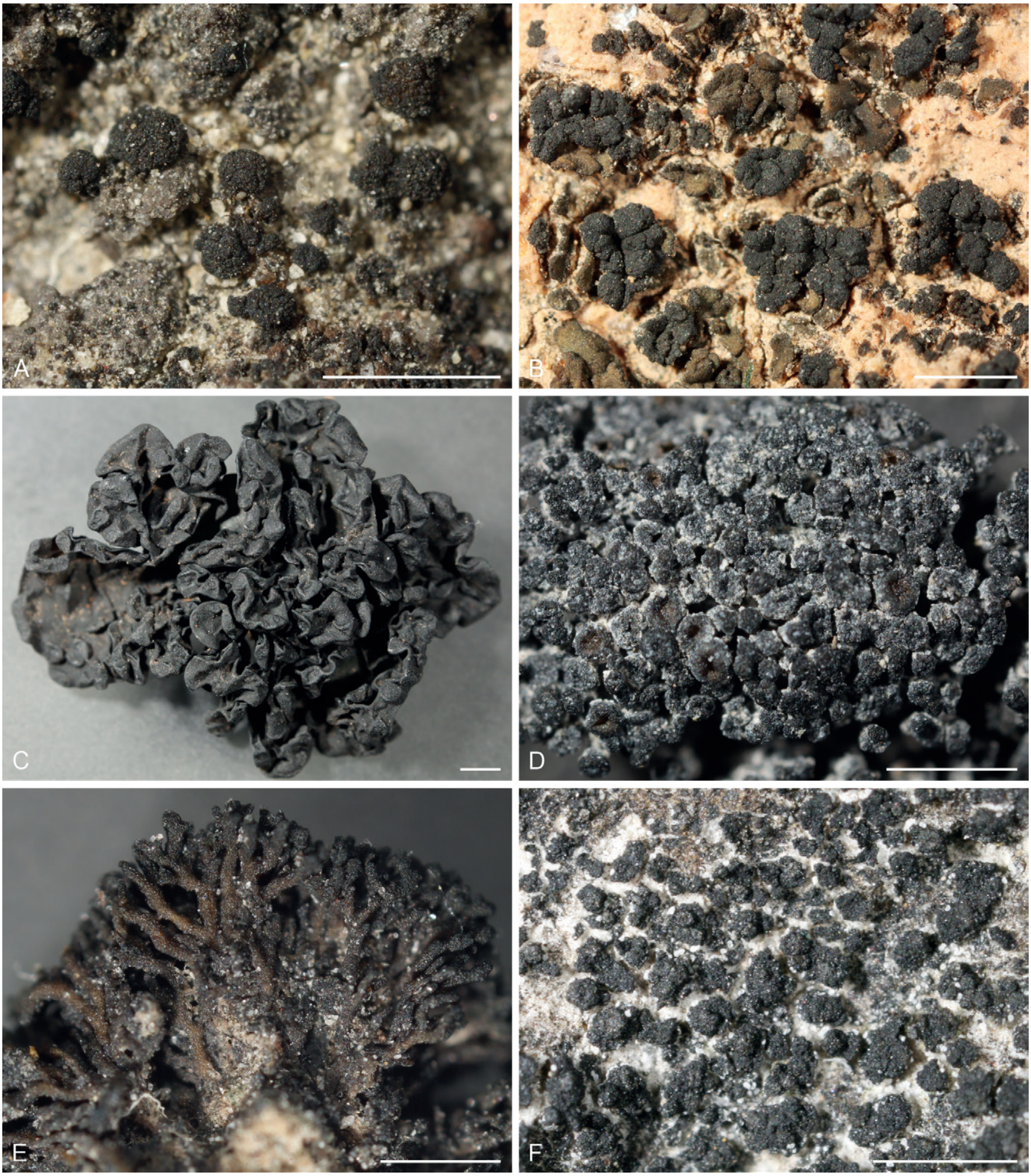

Fig. 16. Thallus growth forms in main clade 5 (*Lichinellaceae*). **A.** *Lichinella myriospora*, crustose, areoles fully occupied by mature thallinocarps (Palice 15858). **B.** *Lichinella algerica*, squamules becoming convex and ascending, thallinocarps inconspicuous submarginal swellings (Feuerer). **C.** *Lichinella cribellifera*, foliose, lobes rounded, margin down rolled, surface folded (Ertz 16312). **D.** *Synalissina condensata*, squamules bluish grey pruinose, stout, erect and densely aggregated, tips with small apothecia and concave discs (Groner 4014). **E.** *Synalissina vesiculifera*, lower surface of fruticulose cushion, branches cylindrical, furcate (Rosentreter 18798). **F.** *Gonotichia octosporella*, crustose, areoles irregular, some with thallinocarps resembling gall like swelling (Schultz 05576b). Scale bars = 1 mm.

Description: *Thallus* blackish, crustose-areolate to minutely squamulose, areoles/squamules thin or swollen when containing thallinocarps (Figs 16F, 17A, B, E, F), attached by rhizohyphae. Thallus ecorticate, homoiomerous, anatomy ± paraplectenchymatous forming an irregular network around single-celled cyanobionts with yellowish brown gelatinous sheaths (Fig. 17C, D). *Ascomata* develop from free ascogones, as indistinct thallinocarps ± hidden in swollen thallus areoles/squamules, thalline margin flat and indistinct, exipulum proprium absent, hymenium shallow, 60–65 µm high, covered by sparse patches of sterile thalline plectenchyma/cyanobiont colonies (Fig. 17C, D), paraphyses septate, becoming branched and anastomosing, KOH/Lugol+ blue, asci prototunicate with amyloid outer cap (*Peccania* type), 8-spored, ascospores simple, small, broad ellipsoid,

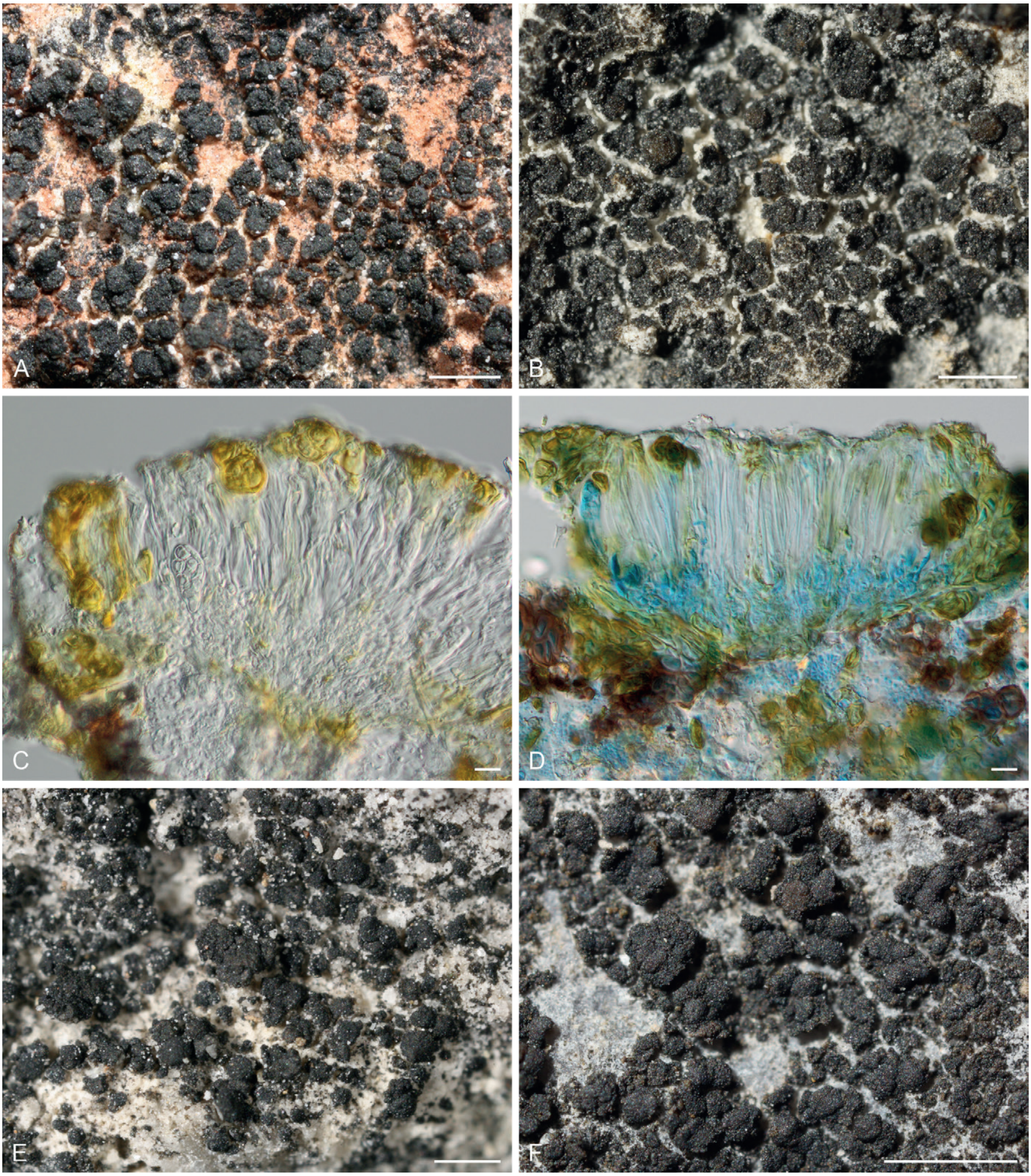

Fig. 17. *Gonotichia octosporella*. **A.** Areoles with small, gall like thallinocarps (Prieto SL28). **B.** Areoles with slightly lifted margins and some thallinocarps (Prieto SMP137). **C.** Mature thallinocarp with scattered patches of sterile thallus on the hymenium and 8-spored ascus (Lettau, B, holotype). **D.** Thallinocarp with patches of sterile thallus on hymenium in LPCB (Prieto SL28). *Gonotichia depauperata*. **E.** Irregularly areolate thallus with convex, roundish thallinocarps (Nadvorník, PRM-634147, syntype). **F.** Thallus areoles of variable size, large areoles filled by thallinocarps (Schultz 08299). Scale bars: A, B, E, F = 0.5 mm; C, D = 10 µm.

sometimes bean-shaped. *Pycnidia* not observed. No secondary metabolites detectable by TLC reported in the literature and not tested.

New combinations in *Gonotichia*:

Gonotichia depauperata (Servít) M. Schultz & M. Prieto, ***comb. et stat. nov.*** MycoBank MB 852320.
Basionym: *Gonohymenia myriospora* var. *depauperata* Servít, Věstn. Král. České Společn. Nauk Tř. Mat.-Přír. 2, 12: 7. 1937. MycoBank MB 438020.

Gonotichia octosporella (Lettau) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852321.
Basionym: *Gonohymenia octosporella* Lettau, Repert. Spec. Nov. Regni Veg. Beih. 119(5): 269. 1942. MycoBank MB 366299.

Notes: A new genus described here as the type of *Gonohymenia* (*G. algerica*) is placed within *Lichinella*. Sample SL28 matches the holotype of *Gonohymenia octosporella* very well. It shows the same rather unique iodine staining pattern in the hymenium with a yellowish reddish colouration which slowly turns into a distinct blue. Close to SL28 (S) is sample 4100 (HBG-015060), which is best referred to as *Gonohymenia myriospora* var. *depauperata*. *Gonohymenia myriospora* is clustering within *Lichinella*, and thus the variety *Gonohymenia myriospora* var. *depauperata* is elevated here to species level. Although both species do not form a monophyletic group, we think the best option is to keep them together for the time being in the new genus *Gonotichia*.

Lichinella Nyl., Bull. Soc. linn. Normandie, sér. 2, 6(2): 301. 1872. MycoBank MB 2858. Figs 1F, 2H–L, 3D, 16A–C.

Type species: *Lichinella stipatula* Nyl., Bull. Soc. linn. Normandie, sér. 2, 6(2): 301. 1872. MycoBank MB 394645.
Synonyms: *Gonohymenia* J. Steiner, Verh. zool.-bot. Ges. Wien 52: 484. 1902. MycoBank MB 2113. *Type species*: *Gonohymenia algerica* J. Steiner, Verh. zool.-bot. Ges. Wien 52: 485. 1902. MycoBank MB 385199.
Rechingeria Servít, Ann. Naturhist. Mus. Wien 46: 80. 1931 (”1932/33”). MycoBank MB 4659. *Type species*: *Rechingeria cribellifera* (Nyl.) Servít, Ann. Naturhist. Mus. Wien 46: 80. 1931 (“1932/33”). MycoBank MB 403877.
Thallinocarpon E. Dahl, Meddel. Grønland 150(2): 42. 1950. MycoBank MB 5389. *Type species*: *Thallinocarpon pulvinatum* E. Dahl, Meddel. Grønland 150(2): 42. 1950. MycoBank MB 370615.

Notes: Currently, the genus *Lichinella* includes dwarf-fruticose as well as foliose-fruticose, squamulose-peltate and crustose species. The various external growth forms are accompanied by a wide array of hyphal arrangement types. Thus, the anatomy is either homoiomerous (paraplectenchymatous or densely reticulate) in the crustose to small squamulose species or heteromerous with a loose or compact, sometimes distinctly fountain-like central, hyphal strand in the squamulose lobate, foliose and fruticulose species. On the other hand, the type of ascoma and asci is a constant character separating the genus from other members of the *Lichinellaceae* and *Lichinomycetes* in general. The so called thallinocarps (Henssen 1963a, 1980) are characterised by a continuous or discontinuous layer of sterile thallus plectenchyma covering the hymenium. The hymenium itself may be continuous or interrupted by sterile plectenchyma or merely consist of a few asci and paraphyses dispersed in the upper thallus portions (see Henssen 1963a, 1980, Henssen *et al.* 1985, Moreno & Egea 1992c, Schultz *et al.* 2000, Schultz & Büdel 2002, Schultz 2005, Fig. 2I–L). Further characteristics include irregularly shaped asci which contain 16–32, small ascospores (Fig. 3D) and the reddish brown or wine-red reaction of the hymenium with iodine turning blue (Figs 2J, 3D). No secondary metabolites detected by TLC (Jørgensen 2007).

The same ascomata are found in the genus *Gonohymenia* (Henssen 1980, 1986, Lange 1958). Based on the striking similarities in the thallinocarpous ascomata as well as some ascus characteristics, Moreno & Egea (1992c) suggested the synonymy of *Gonohymenia* with *Lichinella*. Thus, they accepted a very high morphological and anatomical variability in a more broadly circumscribed genus *Lichinella*. This new concept has not been uniformly accepted by lichenologists and *Gonohymenia* is still used in new species descriptions (Makryi 1992), big floras and checklists (Wirth *et al.* 2013, Printzen *et al.* 2022). However, Jørgensen (2007) reestablished the genus *Thallinocarpon*, arguing that the type of *Thallinocarpon* was wrongly included in *Gonohymenia* even it was not closely related with the type of *Gonohymenia* (*G. algerica*). Thus, within *Thallinocarpon* he included *T. nigritellum* and *T. pulvinatum*. Although we did not include the type of *Thallinocarpon* in the phylogenetic analysis, the results show *T. nigritellum* mixed with species of *Gonohymenia* and *Lichinella*. Likewise, our results show that *L. cribellifera*, the type of the genus *Rechingeria*, falls among *Lichinella s. str.*, *Gonohymenia* and *Thallinocarpon*. Thus, based on these results, we synonymize under *Lichinella* the genus *Rechingeria* as well as *Thallinocarpon* and *Gonohymenia* as already proposed by Moreno & Egea (1992c). The high morphological intraspecific variability found, as in the case of *L. iodopulchra*, results in enormous difficulties in species recognition (Moreno & Egea 1991). This is supported by our phylogenetic results as the genetic variability does not reflect the morphology. Further studies should be carried out including more samples and additional molecular markers.

A difficult, medium sized genus of almost 30 species occurring worldwide with preference for warm-temperate to arid-tropical regions and growing on temporarily moistened rock as well as in biological soil crusts. According to the description by Golubkova (1970), *Gonohymenia reophila* could be related to *Gonotichia*.

New combinations in *Lichinella*:

Lichinella baicalensis (Makryi) M. Schultz, ***comb. nov.*** MycoBank MB 852322.
Basionym: *Gonohymenia baicalensis* Makryi, Nov. Sist. Nizsh. Rast. 28: 113. 1992. MycoBank MB 361418.

Lichinella etoshica (Brusse) M. Schultz, ***comb. nov.*** MycoBank MB 852323.
Basionym: *Gonohymenia etoshica* Brusse, Bothalia 17: 35. 1987. MycoBank MB 130529.

Note: A species from the *L. algerica* complex.

Lichinella lusitanica (Henssen) M. Schultz, ***comb. nov.*** MycoBank MB 852324.
Basionym: *Gonohymenia lusitanica* Henssen, Lich. Cyanoph. Fungi Saxic. Exsic., Fasc. 2(nos 26–50) (Marburg): 7, no. 39. 1990. MycoBank MB 126776.

Note: A crustose species very close to *L. myriospora*.

Lichinella pulvinata (E. Dahl) M. Schultz, ***comb. nov.*** MycoBank MB 852325.
Basionym: *Thallinocarpon pulvinatum* E. Dahl, Meddel. Grønland 150: 42. 1950. MycoBank MB 370615.

Notes: A large, Nordic species from the *L. nigritella* complex not to be confused with *L. iodopulchra* and *Thyrea confusa*, which have a more southern, thermophilic distribution in Europe.

Lichinella schleicheri (Hepp) M. Schultz, ***comb. nov.*** MycoBank MB 852326.
Basionym: *Omphalaria pulvinata* var. *schleicheri* Hepp, Flecht. Eur. 3, Fasc. 12: pl. 74, no. 659. 1860. MycoBank MB 373750.
Homotypic synonym: *Gonohymenia schleicheri* (Hepp) Henssen, Lichenologist 22: 141. 1990. MycoBank MB 125699.

Note: A species ± intermediate between *L. nigritella* and *L. iodopulchra*, but differing mostly in the finely granulose texture of lobe surface.

Lichinella terrestris (Makryi) M. Schultz, ***comb. nov.*** MycoBank MB 852327.
Basionym: *Gonohymenia terrestris* Makryi, Nov. Sist. Nizsh. Rast. 28: 115. 1992. MycoBank MB 361419.

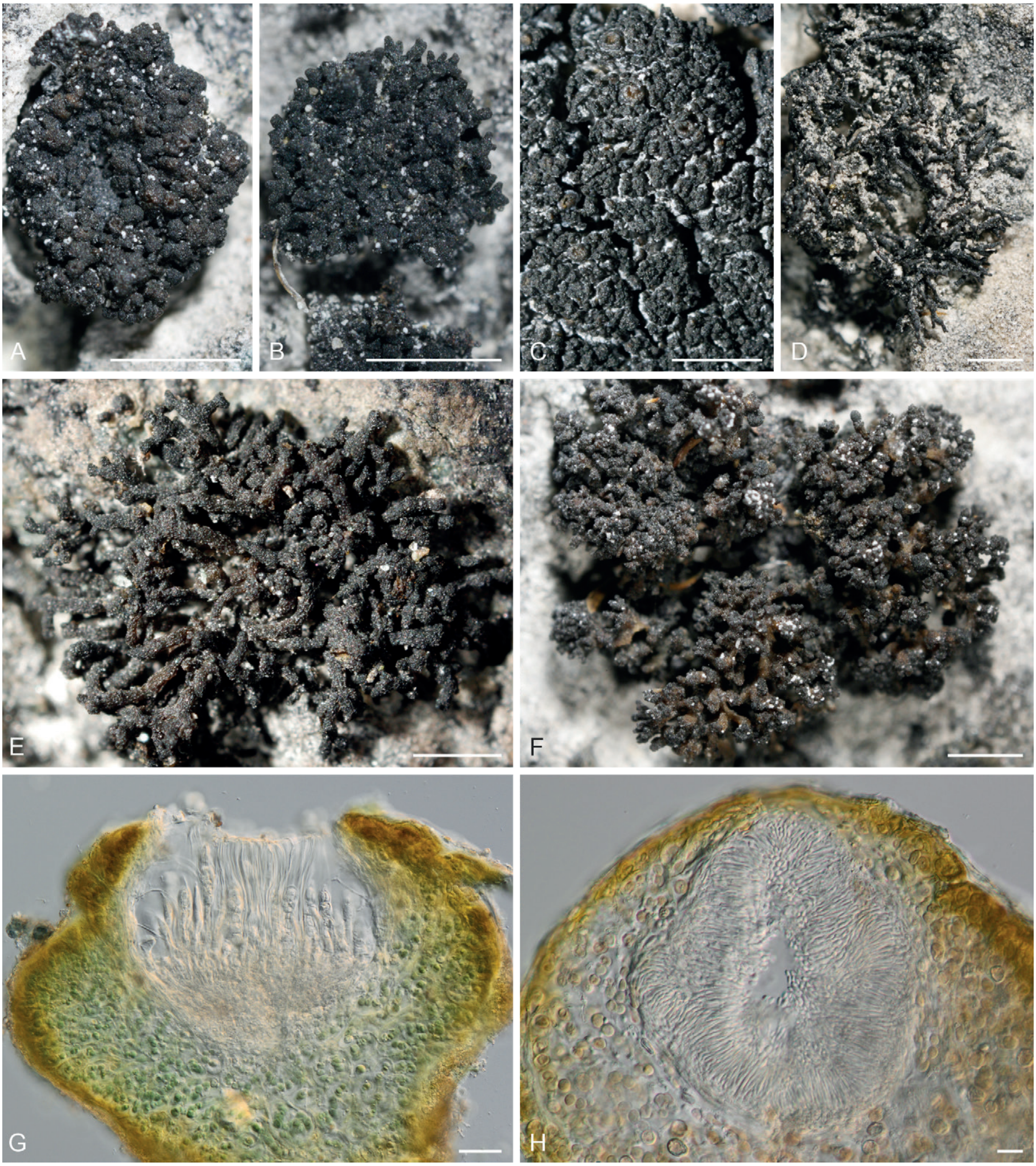

Fig. 18. A. *Synalissina botryosa*, thallus button like with some emptied hormocystangia (Schultz 05517a). **B.** *Synalissina isidiodes*, thallus with minute, isidioid outgrowths (Schultz 05517b). **C.** *Synalissina condensata*, densely aggregated, erect squamules, basally pruinose, small apothecia at tips (Schultz 08216a). **D.** *Synalissina intricata*, much elongated, intricately furcate branches (Schultz 08148c). **E.** *Synalissina cladodes*, branches shortly furcate, somewhat bent, surface striate (Schultz 08779). **F.** *Synalissina degeliana*, tufted, caespitosely branched lobes with coarsely granulose tips (Schultz 05544a). **G.** *Synalissina botryosa*, apothecium in lobe tip with thick thalline margin and rudimentary proper exciple (Schultz 08406a). **H.** *Synalissina vesiculifera*, pycnidium hidden in lobe tip with small, simple pycnospores (Rosentreter 18798). For *Synalissina condensata* and *S. vesiculifera* see also Fig. 16 D, E. Scale bars: A–F = 1 mm; G = 25 µm; H = 10 µm.

Note: According to the original description by Makryi (1992), this species must be assigned to *Lichinella*.

Synalissina Nyl., in Hue, Rev. Bot. Bull. Mens. 4: 349. 1886. MycoBank MB 5324. Figs 16D, E, 18.

Type species: *Synalissina intricata* (Arnold) Nyl., in Hue, Rev. Bot. Bull. Mens. 4, 1885–1886: 349. 1886. MycoBank MB 406713.
Synonym: *Physma* sect. *Collemella* (Tuck.) Zahlbr., in Engler & Prantl, Nat. Pflanzenfam. 1(1*): 171. 1906. *Type species*: *Physma cladodes* (Tuck.) "Zahlbr.", in Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1(1*): 171. 1906. (= *Synalissina cladodes* (Tuck.) M. Schultz & M. Prieto, present study). MycoBank MB 400887.

Diagnosis: Genus of the *Lichinellaceae* with *Nostoc* cyanobionts resembling *Lempholemma*, but apothecia always formed from ascogones arising in a tangle of generative hyphae, *Peccania* type asci, formation of hormocystangia in some species and exclusive occurrence on rock.

Description: *Thallus* blackish, sometimes greyish pruinose, small foliose to small squamulose-peltate or dwarf fruticose (Figs 16D, E, 18A–F), sometimes with terminal hormocystangia, rarely isidiate or phyllidiate, with *Nostoc* cyanobionts (Fig. 18G, H) and distinctly swelling when wet, fastened to substrate by rhizohyphae or a small umbilicus. Thallus ecorticate, homoiomerous, delicate hyphae forming a loose reticulum around chains of *Nostoc* cyanobiont, haustoria finger-like. *Apothecia* small, sessile or stalked on tips of delicate, upright branches (Fig. 18C), zeorine with thick thalline exciple and pale, thin proper exciple (Fig. 18G), hymenium with septate paraphyses, KOH/Lugol+ blue, *asci Peccania* type, 8-spored, *ascospores* simple. *Ascomata* develop from ascogones arising in a spheroid tangle of generative hyphae. *Pycnidia* immersed to slightly elevated, simple, conidiophores simple, pycnospores produced terminally, small bacilliform to ellipsoid (Fig. 18H). Early colonizers of calcareous or mineral rich rocks, on exposed to steep and somewhat shaded rock faces, also in temporary moist situations. Widely distributed in boreal to warm temperate regions in the northern hemisphere. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: The genus *Synalissina* is reinstated for the *Lempholemma botryosum* group to which *L. intricatum* belongs. It is characterized by typical apothecia and a diverse thallus morphology: dwarf-fruticose, squamulose-peltate, squamulose-subfruticose.

New combinations and species of *Synalissina* verified so far:

Synalissina botryosa (A. Massal.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852328.
Basionym: *Arnoldia botryosa* A. Massal., Miscell. Lichenol.: 20. 1856. MycoBank MB 376279.
Homotypic synonym: *Lempholemma botryosum* (A. Massal.) Zahlbr., Cat. lich. univ. 3: 20. 1924. MycoBank MB 393119.

Synalissina cladodes (Tuck.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852329.
Basionym: *Collema cladodes* Tuck., Gen. lich. (Amherst): 89. 1872. MycoBank MB 383207.
Homotypic synonym: *Lempholemma cladodes* (Tuck.) Zahlbr., Cat. lich. univ. 3: 23. 1924. MycoBank MB 393124.

Synalissina condensata (Arnold) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852331.
Basionym: *Plectopsora botryosa* var. *condensata* Arnold, Verh. K. K. Zool.-Bot. Ges. Wien 19: 655. 1869. MycoBank MB 123189.
Homotypic synonym: *Lempholemma condensatum* (Arnold) Zahlbr., Cat. lich. univ. 3: 20. 1924. MycoBank MB 393126.

Synalissina degeliana (P.M. Jørg.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852332.
Basionym: *Lempholemma degelianum* P.M. Jørg., Graphis Scripta 9(1): 5. 1998. MycoBank MB 474060.

Synalissina dispansa (H. Magn.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852333.
Basionym: *Lempholemma dispansum* H. Magn., Bot. Not.: 302. 1939. MycoBank MB 367807.

Synalissina intricata (Arnold) Nyl., in Hue, Rev. Bot. Bull. Mens. 4, 1885–1886: 349. 1886. MycoBank MB 406713.
Homotypic synonym: *Lempholemma intricatum* (Arnold) Zahlbr., Cat. Lich. Univ. 3: 22. 1924. MycoBank MB 393135.

Synalissina intricatissima (J. Steiner) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852334.
Basionym: *Physma intricatissimum* J. Steiner, Ann. K. K. Naturhist. Hofmus. Wien 23: 113. 1909. MycoBank MB 400897.
Homotypic synonym: *Lempholemma intricatissimum* (J. Steiner) Zahlbr., Cat. lich. univ. 3: 22. 1924. MycoBank MB 393134.

Note: Perhaps only a small, sterile form of *S. intricata*.

Synalissina isidiodes (Nyl. *ex* Arnold) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852335.
Basionym: *Collema isidiodes* Nyl. *ex* Arnold, Flora 53: 232. 1870. MycoBank MB 383306.
Homotypic synonym: *Lempholemma isidiodes* (Nyl. *ex* Arnold) H. Magn., Bot. Not.: 303. 1939. MycoBank MB 367808.

Notes: Epithet often incorrectly cited as "*isidioides*". Very closely related to *S. botryosa*.

Synalissina vesiculifera (Henssen) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852336.
Basionym: *Lempholemma vesiculiferum* Henssen, Lichenologist 4: 99. 1969. MycoBank MB 345231.

Phylliscaceae Th. Fr., Nova Acta Regiae Soc. Sci. Upsal. 3: 288. 1860. MycoBank MB 81158. Figs 1C, 19.
Synonym: *Peltulaceae* Büdel (in Eriksson & Hawksw.), Systema Ascom. 5: 149. 1986. MycoBank MB 81121.

Diagnosis: Small or medium sized family of cyanolichens exclusively associating with single-celled cyanobacteria. Thalli predominantly crustose to squamulose, also foliose or fruticulose, but never filamentous or endolithic. IF thallus truly heteromerous and corticate THEN asci unitunicate-rostrate and polysporous. IF thallus homoiomerous and ecorticate THEN asci *Peccania* type, conidia filiform and ascomata arising from freely formed, coiled ascogones OR asci either unitunicate-rostrate (but sometimes indistinctly so), thick walled or *Phylliscum* type AND ascomata always pycnoascocarps, paraphyses present or not and conidia filiform or small ellipsoid.

Fig. 19. Thallus growth forms in main clade 4 (*Phylliscaceae*). **A.** *Allopyrenis sanguinea*, crustose, areoles irregular, granulose, pycnoascocarps small with thick thalline margin narrow, concave disc (Schultz 16954a). **B.** *Phylliscum aotearoa*, crustose-squamulose, margin slightly effigurate, pycnoascocarps numerous, semi-immersed to adnate, discs narrow (Kantvilas 113-16). **C.** *Peccania cernohorskyi*, squamulose, margin becoming lobulate, center isidiate (Candan 22). **D.** *Phylliscum demangeonii*, squamulose, umbilicate-rosette shaped, pycnoascocarps remaining immersed and with pin hole discs (Schultz 16868). **E.** *Peccania coralloides*, foliose, lobes conspicuously grey pruinose and the marginal apothecia (TARI-3677). **F.** *Peltula tortuosa*, subfruticose with tufted, contorted lobes (Büdel 24058). Scale bars = 1 mm.

Discriminating characters: No filamentous cyanobionts, no filamentous or endolithic thalli, no thallinocarps and asci either unitunicate-rostrate, *Peccania*, *Phyllisciella*, *Phylliscum* types, but never *Lichina* or *Lichinella* ascus types.

Description: Lichen-forming ascomycetes obligatory and exclusively associating with single-celled cyanobacteria. *Thallus* blackish (Fig. 19C), shades of olive (Figs 1C, 19F) or dark reddish(brown) (Figs 19A, B, D, 20A–D), usually epruinose, rarely (bluish)grey pruinose (Fig. 19E) or appearing greyish due to presence of epinecral layer. Thallus growth diverse, ranging from crustose (Figs 19A, 20A–D), crustose- and squamulose-effigurate (Fig. 19B, D), squamulose-peltate (Fig. 1C), foliose to dwarf-fruticose (Fig. 19E, F), but never filamentous or endolithic. Thallus fixed by rhizohyphae, tufts of rhizohyphae, a central umbilicus, gelatinous basal layer or holdfast. Soralia and isidia present only in few species (Figs 1C, 19C), hormocystangia absent. Thallus anatomy heteromerous and truly corticate OR homoiomerous and ecorticate. *Ascomata* typical apothecia (Fig. 19E) or pycnoascocarps (Fig. 20E, F), in *Phylliscum* and allies perithecioid (Fig. 19B, D), but never thallinocarps. *Asci* unitunicate-rostrate (but sometimes indistinctly so; Fig. 3A), *Peccania*, *Phyllisciella* or *Phylliscum* types, asci often polysporous, but also 8-spored (Fig. 3E, L, M). *Apothecia* lecanorine, rarely zeorine, never biatorine. Epihymenium usually pale yellowish to reddish or brownish, rarely with conspicuous dark reddish brown blotches in *Peccania* or colourless, paraphyses usually present, rarely absent and then with periphysoids around the punctiform disc of perithecioid apothecia. *Conidiomata* pycnidia, conidiophores simple or branched in *Peccania*, conidia formed terminally, small ellipsoid, short bacilliform or needle-like and long-filiform, bent or sigmoid in *Peccania*. Cosmopolitan, but most diverse in warm-temperate to (semi)arid tropical regions (esp. *Peccania* and *Peltula*) and in cool-temperate, humid regions (esp. *Allopyrenis* and *Phylliscum*). On all rocky substrata, often on sporadically or periodically wetted, but well-lit rock surfaces, rarely semi-amphibious, common also in biological soil crusts, rarely on bark. No secondary metabolites reported except for myeloconone D_1 and D_2 found in *Peltula langei* (Büdel & Elix 1997).

Notes: Main clade 4 contains the genera *Cryptothele*, *Peccania*, *Peltula*, *Phylliscum* (excluding *macrocarpum* group), *Phyllisciella* and the "*Pyrenopsis" haemaleella*/*sanguinea* group (*Allopyrenis*), a diverse clade for which the names *Peltulaceae* and *Phylliscaceae* are available, with *Phylliscaceae* being the oldest. There is no synapomorphy supporting the family, but within the clade there are certain sets of characters not found in any of the other three families.

Included genera: *Allopyrenis* ("*Pyrenopsis" haemeleella*/*sanguinea* group), *Peccania*, *Peltula* (incl. *Neoheppia*, *Phyllopeltula*), *Phylliscidium* (likely belonging here), *Phyllisciella* and *Phylliscum* (incl. *Cryptothele*); approx. 100 spp.

Allopyrenis M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852337. Figs 19A, 20.

Etymology: from *allo-* (Greek = other or another), because of the resemblance with *Pyrenopsis*.

Type species: *Allopyrenis sanguinea* (Anzi) M. Schultz & M. Prieto

Diagnosis: Belonging to *Phylliscaceae*. Closely resembling *Cladopsis*, *Pleopyrenis* and *Pyrenopsis*. Differing from *Cladopsis* in the presence of unitunicate-rostrate asci with distinct, strongly amyloid apical dome. Differing from *Pleopyrenis* in the absence of polysporous asci (except *A. grumulifera* which, however, has broader asci), more robust, often (sub)moniliform paraphyses and usually a less compact thallus anatomy with larger cyanobiont cells and more distinct hyphae (except *A. grumulifera* and *A. haemaleella* with compact anatomy, small cyanobionts and delicate hyphae). Differing from *Pyrenopsis* in lacking, or at most rudimentary proper exciple (present in *Pyrenopsis furfurea*, thin in *P. haematina*, but likewise absent or only rudimentary in *P. subareolata* and *P. conferta*).

Description: *Thallus* crustose, granulose, areolate to subsquamulose, dark reddish black (Figs 19A, 20A–D), often attached to the substrate by thin gelatinous basal layer. Thallus anatomy homoiomerous, ecorticate, hyphae forming a dense network around cyanobiont cells, hyphal cells isodiametric or elongated, usually distinct, sometimes inconspicuous, photobiont a gloeocapsoid cyanobacterium with reddish, layered gelatinous sheaths (Fig. 20E, F), attacked by finger like fungal haustoria. *Apothecia* usually small, often perithecioid with narrow, usually slightly concave discs, rarely expanded, dark reddish brown to blackish, semi immersed to sessile, lecanorine with persisting, smooth, sometimes bulging thalline margin, proper exciple lacking, epithecium usually pale reddish brown, rarely colourless, subhymenium with rounded base, hymenium KOH/IKI+ deep blue, *paraphyses* distinct, often robust, usually straight, rarely bent, often becoming (sub)moniliform with distinctly expanded terminal cells, *asci* clavate, sometimes broadly clavate, unitunicate-rostrate, with distinct KOH/IKI+ blue apical dome and distinct outer gelatinous cap (Fig. 20E, F), 8-spored, polysporous only *A. grumulifera*, *ascospores* simple, hyaline, broad ellipsoid, small. *Ascoma* ontogeny with ascogones formed beneath pycnidia (pycnoascocarps). *Pycnidia* usually ± pyriform, *conidiophores* simple, *conidia* produced terminally, small ellipsoid to short bacilliform. Widely distributed in the northern hemisphere in boreal to (high) montane regions, growing on wet acidic, usually mineral rich rock temporarily indundated along clear water creeks or inclined rock faces moistened from seeping water in usually clear situations. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Species previously described in *Pyrenopsis* have been divided in four genera (see *Pyrenopsis*). All species included in *Allopyrenis* share unitunicate-rostrate asci with 8 spores, except for the polysporous *A. grumulifera*. In *A. haemaleella* and *A. grumulifera* the amyloid apical dome is similarly distinct as in *e.g. Pyrenopsis fuscatula* and *P. furfurea*, whereas it may be somewhat less apparent in *A. sanguinea* and allies. However, there are no asci with a uniform wall such as in *Cladopsis*. Because there is no generic name available, we have described the new genus *Allopyrenis*. The genus *Allopyrenis* and the only distantly related *Pyrenopsis* in its much narrower sense presented here constitute an unexpected, striking case of parallel evolution (within the *Lichinomycetes)* of lichens associating with gloeocapsoid cyanobionts adapted to exposed, moist, rocky substrates in mountainous and boreal-subarctic regions across the northern hemisphere.

This clade is comprised of closely related species such as *Pyrenopsis haemaleella*, the Central European *P. sanguinea* and the putatively very closely related, variable North American *P. phaeococca*, the Scandinavian *P. reducta*, the polysporous Scandinavian *P. grumulifera*, and the North American *"Phylliscum" tenue*. The latter is a member of the *Phylliscum macrosporum* group that is certainly not close to the core of *Phylliscum* and that can conveniently be placed in *Allopyrenis* despite its subsquamulose growth form. The Scandinavian *P. impolita* is probably identical with *P. sanguinea*.

New combinations in *Allopyrenis*:

Allopyrenis grumulifera (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852338.
Basionym: *Pyrenopsis grumulifera* Nyl., Lich. Scand.: 26. 1861. MycoBank MB 403077.

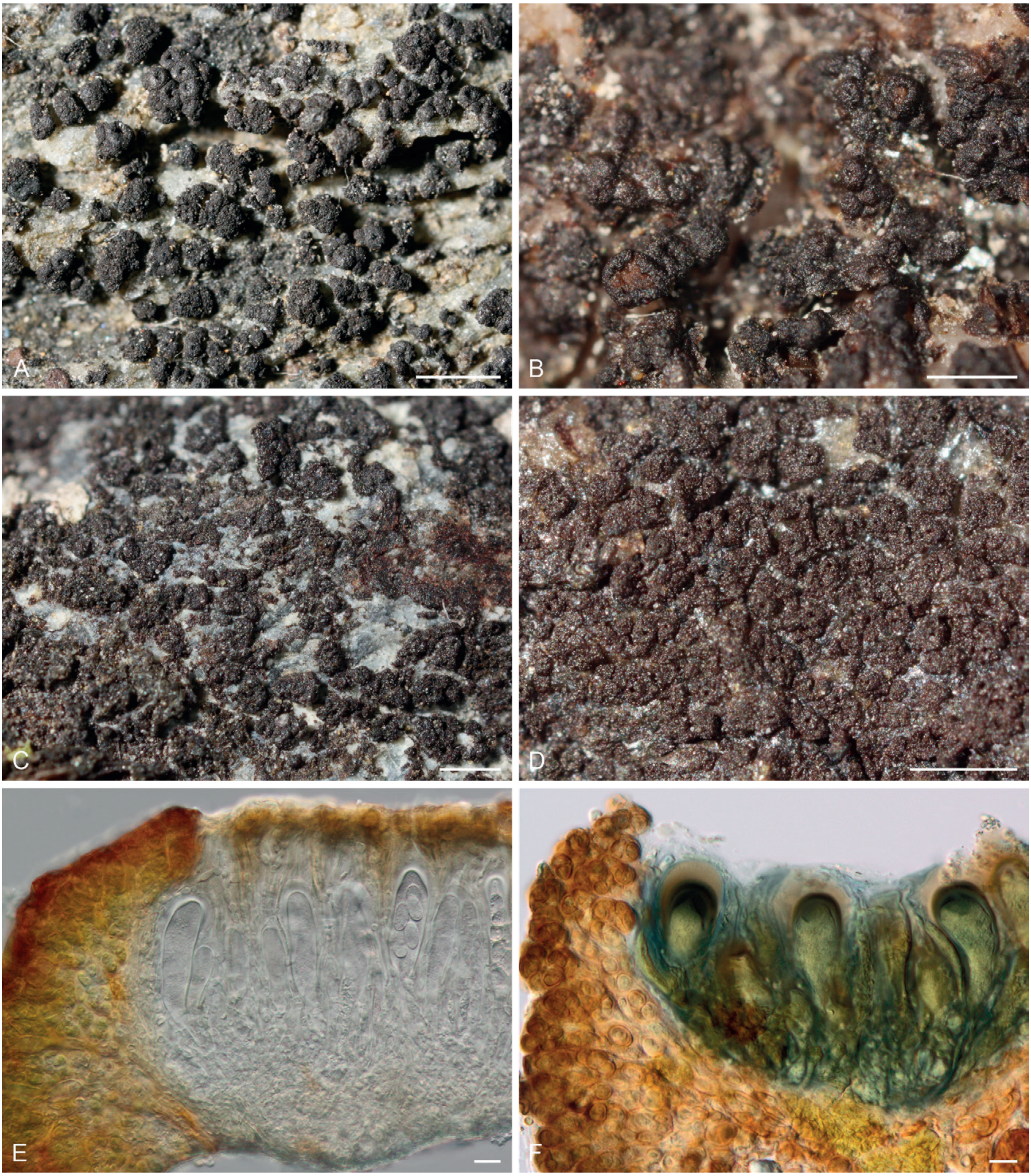

Fig. 20. A. *Allopyrenis sanguinea*, areoles thick, slightly granulose, apothecia semi immersed to sessile and almost globose, discs narrow, later somewhat opened, thalline margin thick (Anzi Lich. Rar. Langob. 474, W2009-00156, type). **B.** *Allopyrenis haemaleella*, thallus areoles thin, smooth, apothecia sessile with open discs and surrounded by thin, elevated thalline margin (Schultz 05594). **C.** *Allopyrenis reducta*, thallus areoles small granulose, very thin, apothecia very small (Schultz 16950). **D.** *Allopyrenis grumulifera*, thallus very thin, granulose, apothecia very small with discs remaining punctiform (Prieto SL39). **E.** *Allopyrenis haemaleella*, lecanorine apothecium, thick-walled asci (Schultz 05595). **F.** *Allopyrenis grumulifera*, lecanorine apothecium lacking proper exciple, clavate asci with distinct gelatinous cap and apical thickening in KOH/Lugol (Malmgren, H-NYL42947, holotype). Scale bars: A–D = 0.5 mm; E, F = 10 µm.

Allopyrenis haemaleella (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852340.
Basionym: *Euopsis haemaleella* Nyl., Flora, Regensburg 60: 457. 1877. MycoBank MB 403079.
Homotypic synonym: *Pyrenopsis haemaleella* (Nyl.) Blomberg & Forssell, Enum. Pl. Scand.: 110. 1880. MycoBank MB 403079.

Allopyrenis impolita (Th. Fr.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852341.
Basionym: *Pyrenopsis subareolata* var. *impolita* Th. Fr., Bot. Not.: 57. 1866. MycoBank MB 403084.
Homotypic synonym: *Pyrenopsis impolita* (Th. Fr.) Forssell, Beitr. Gloeolich.: 48. 1885. MycoBank MB 403084.

Allopyrenis phaeococca (Tuck.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852342.
Basionym: *Synalissa phaeococca* Tuck., Gen. lich.: 80. 1872. MycoBank MB 406699.
Homotypic synonym: *Pyrenopsis phaeococca* (Tuck.) Tuck., Syn. N. Amer. Lich. 1: 136. 1882. MycoBank MB 403105.

Allopyrenis reducta (Th. Fr.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852343.
Basionym: Pyrenopsis reducta Th. Fr., Bot. Not.: 57. 1866. MycoBank MB 403114.

Allopyrenis sanguinea (Anzi) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852344.
Basionym: *Pyrenopsis sanguinea* Anzi, Atti Soc. Ital. Sci. Nat. 9: 241. 1866. MycoBank MB 403120.

Allopyrenis tenuis (Henssen) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852345.
Basionym: *Phylliscum tenue* Henssen, Svensk Bot. Tidskr. 57: 152. 1963. MycoBank MB 345608.

Notes: A small squamulose species described from North America. Initially placed by Henssen (1963b) in the *Phylliscum macrosporum* group, but sequence data indicate that it falls into the *Pyrenopsis sanguinea* complex for which the genus *Allopyrenis* is established.

Peccania A. Massal. *ex* Arnold, Flora 41: 93. 1858. MycoBank MB 3779. Fig. 19C, E.

Type species: *Peccania coralloides* (A. Massal.) A. Massal. Atti Reale Ist. Veneto Sci. Lett. Arti, ser. 3, 5: 335. 1860. MycoBank MB 399233.

Notes: *Nom. cons*., see Art. 14 (Turland *et al.* 2018). Squamulose-peltate to dwarf fruticose thalli with typical apothecia arising from free ascogones (Fig. 2C), *Peccania* type asci (*sensu* Moreno & Egea 1991; Fig. 3E) and long, filiform conidia. It constitutes the sister clade of *Peltula*, the latter characterized by typical apothecia with ascogones formed in a tangle of generative hyphae, unitunicate rostrate, polysporous asci (Fig. 3A) as well as a heteromerous, corticate thallus. *Peccania* is a medium sized genus of 13–14 species occurring worldwide in warm temperate to (semi) arid subtropical regions on calcareous or volcanic rocks as well as in biological soil crusts.

Peltula Nyl., Ann. Sci. Nat., Bot. 20: 316. 1853. MycoBank MB 3803. Figs 1C, 19F.

Type species: *Peltula radicata* Nyl., Ann. Sci. Nat., Bot. 20: 316. 1853. MycoBank MB 399380.

Notes: A species rich, monophyletic genus (Kauff *et al.* 2018) closely related with *Peccania* (see notes above). Occurring worldwide in warm temperate to tropical regions on various rocky substrates as well as in biological soil crusts.

Phylliscidium Forssell, Beitr. Gloeolich.: 58. 1885. MycoBank MB 4055.

Type species: *Phylliscidium monophyllum* (Kremp.) Forssell, Beitr. Gloeolich.: 58. 1885.

Notes: An enigmatic monotypic, tropical genus not treated in the phylogenetic analysis, but according to characteristics described in Henssen (1980) and Henssen & Büdel (1984) it may be related to *Phylliscum* and *Phyllisciella*. It seems to fit best in *Phylliscaceae* especially because of the thick-walled asci.

Phyllisciella Henssen, in Henssen & Büdel, Beih. Nova Hedwigia 79: 382. 1984. MycoBank MB 25658, Figs 3M, 19B.

Type species: *Phyllisciella marionensis* Henssen, in Henssen & Büdel, Beih. Nova Hedwigia 79: 385. 1984. MycoBank MB 107547.

Notes: The only species included in our phylogeny, *Phyllisciella aotearoa*, groups with *Cryptothele granuliformis*, though on long branches, and both form the sister clade of *Phylliscum demangeonii* and *Cryptothele permiscens*. While the species of *Cryptothele* share several key characters with *Phylliscum demangeonii, Phyllisciella aotearoa* deviates clearly in the ascus type (Fig. 3 L, M). Given that *Phyllisciella* is anatomically different from *Phylliscum* and that the type is not included in the analyses, we prefer to keep *Phyllisciella* as a distinct genus for the time being, although based on the phylogenetic results *Phyllisciella aotearoa* is combined in *Phylliscum*.

Phylliscum Nyl., Mém. Soc. Imp. Sci. Nat. Cherbourg 3: 166. 1855. MycoBank MB 4056. Figs 19D, 21.

Type species: *Phylliscum demangeonii* (Moug. & Mont.) Nyl., Mém. Soc. Imp. Sci. Nat. Cherbourg 3: 166. 1855. MycoBank MB 400407.
Synonym: *Cryptothele* Th. Fr., Bot. Notiser: 59. 1866. MycoBank MB 1337. *Type species*: *Cryptothele permiscens* (Nyl.) Th. Fr., Bot. Notiser 1866: 59. 1866. MycoBank MB 383943.

Notes: *Cryptothele* species (Fig. 21A–D) do not form a monophyletic group and are mixed with *Phylliscum*. The similarities of both genera: pycnoascocarps and *Phylliscum* type (thin-walled, pointed tip) asci, paraphyses lacking, apothecial disc punctiform (perithecioid), living in moist, acidic rocks support merging the two genera whose species otherwise differ only in the general growth form. *Cryptothele granuliforme* (Fig. 21D) was already included in *Phylliscum* by Nylander (1881) which indicates that the various similarities mentioned above were already seen by early authors. This clade has very long branches, probably related with missing data of the *mcm7* and *RPB2* genetic markers.

The genus *Phylliscum* as adopted here excludes the species of the *macrosporum* group (Henssen 1963b). These differ from the type, *P. demangeonii* (Figs 19D, 21E), and its allies such as *P. japonicum* (Fig. 21F) in the presence of distinct paraphyses, apothecia with finally open discs, asci with broadly rounded tips and short pycnospores. Thus, they resemble species of *Pyrenopsis* that we transfer here to *Allopyrenis* and *Cladopsis* differing only in the squamulose thallus habit, a character unsuitable for generic circumscription as shown here for other genera such as *Psorotichia*.

Because of the 2-celled ascospores and blackish exciple of the perithecia type ascomata, the species *Cryptothele africana* likely belongs to *Collemopsidium*. *Cryptothele iocarpa* has already been recombined into *Collemopsidium iocarpum* by Nylander (1881). According to Henssen (1980), the type material is a mixture with the description based on the perithecia and 2-celled ascospores of a *Didymella* species growing on colonies of cyanobacteria.

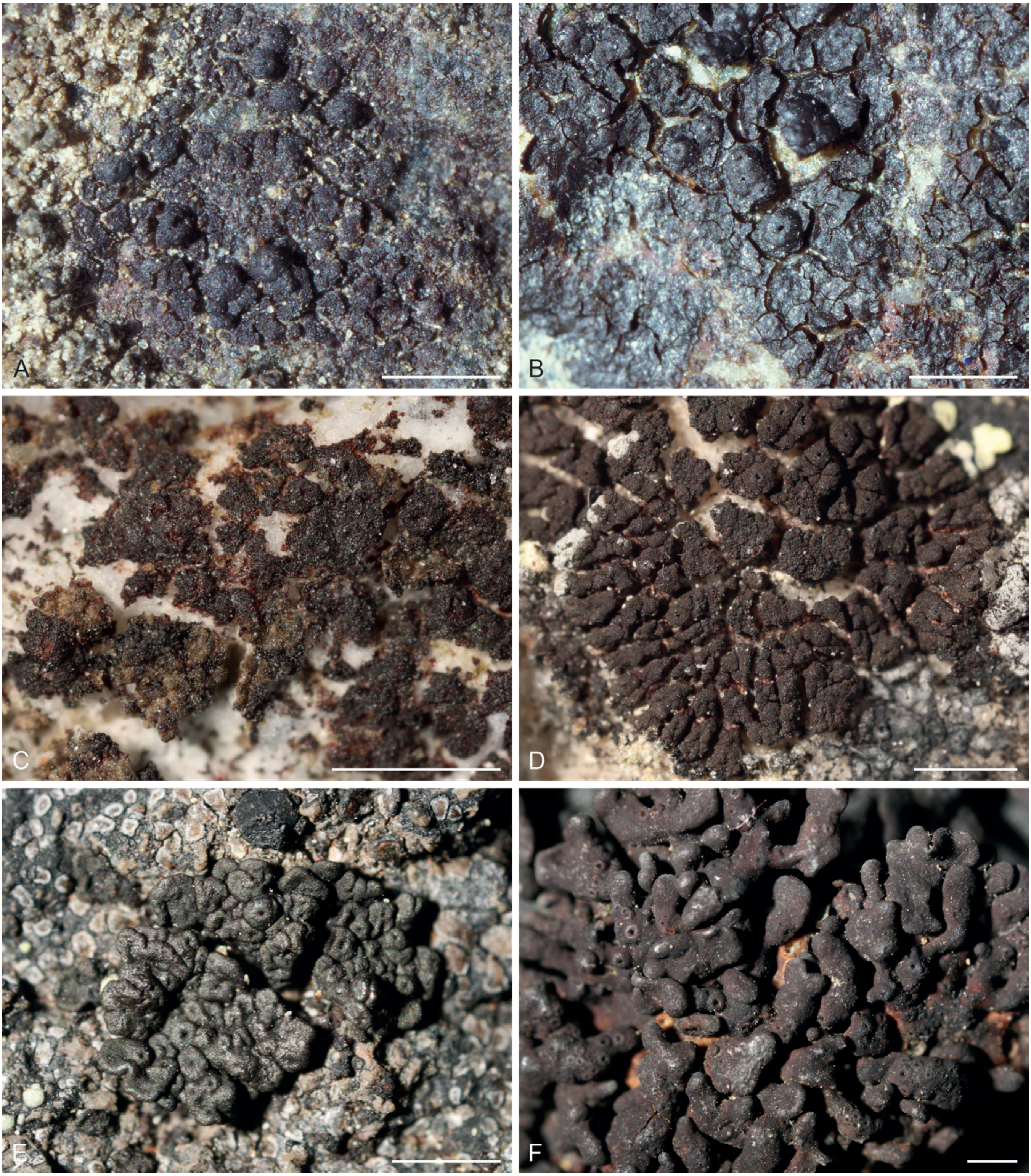

Fig. 21. A. *Phylliscum neglectum*, thallus very thin with hemispherical apothecia (Blomberg, B600132196). **B.** *Phylliscum rhodostictum*, thallus areolate, perithecioid apothecia semi-immersed (Øvstedal, BG L-34197). **C.** *Phylliscum permiscens*, thallus with minute, inconspicuous apothecia (Schultz 16877). **D.** *Phylliscum granuliforme*, thallus effigurate, apothecia semi-immersed (Lewis 1303). **E.** *Phylliscum demangeonii*, thallus rosulate, apothecia semi-immersed (Schultz 16386). **F.** *Phylliscum japonicum*, thallus lobate, apothecia (semi-)immersed (Ogata 519, W1927-373, holotype). Scale bars = 1 mm.

New combinations in *Phylliscum*:

Phylliscum aotearoa (Henssen & B. Bartlett) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852543.
Basionym: *Phyllisciella aotearoa* Henssen & B. Bartlett, Beih. Nova Hedwigia 79: 382. 1984. MycoBank MB 107546.

Phylliscum cylindrophorum (Vain.) M. Schultz, ***comb. nov.*** MycoBank MB 852346.
Basionym: *Pyrenopsis cylindrophora* Vain., Acta Soc. Fauna Flora fenn. 7(1): 241. 1890. MycoBank MB 403063.
Homotypic synonym: *Cryptothele cylindrophora* (Vain.) Henssen, Ber. dt. bot. Ges. 92: 485. 1980. MycoBank MB 114386.

Phylliscum laatokkaense (Vain.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852347.
Basionym: *Malmgrenia laatokkaënsis* Vain., in Räsänen, Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo" 12: 126. 1939. MycoBank MB 269708.

Phylliscum neglectum (Henssen) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852348.
Basionym: *Cryptothele neglecta* Henssen, Ber. dt. bot. Ges. 92: 486. 1980. MycoBank MB 114395.

Phylliscum permiscens (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852349.
Basionym: *Pyrenopsis permiscens* Nyl., Lich. Scand.: 288. 1861. MycoBank MB 403103.

Phylliscum rhodostictum (Taylor) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852350.
Basionym: *Verrucaria rhodosticta* Taylor, London J. Bot. 6: 154. 1847. MycoBank MB 409660.
Homotypic synonym: *Cryptothele rhodosticta* (Taylor) Henssen, Lichenologist 22: 140. 1990. MycoBank MB 125694.

Porocyphaceae Körb., Syst. lich. germ.: 425. 1855. MycoBank MB 81212. Figs 1B, C, E, 22.
Synonyms: *Heppiaceae* Zahlbr., Nat. Pflanzenfam. 1(1*): 176. 1906. MycoBank MB 80853.
Ephebaceae Th. Fr., Nova Acta Reg. Soc. Scient. upsal. ser. 3, 3: 289. 1860. MycoBank MB 80744.
Pyrenopsidaceae Th. Fr., Nova Acta Reg. Soc. Scient. upsal. ser. 3, 3: 289. 1860. MycoBank MB 81319.

Diagnosis: Species rich family of usually small-sized, blackish cyanolichens associating with single-celled cyanobacteria with yellowish brown or reddish purple, gelatinous sheaths or with various filamentous cyanobacteria (*Nostoc*, *Scytonema*, *Stigonema*, *Rivulariaceae*) and of mostly crustose, more rarely squamulose, foliose, fruticulose or filamentous and rarely endolithic growth form. *Thalli* predominantly homoiomerous, rarely corticate and truly heteromerous with dorsoventrally stratified thalli, *paraphyses* always present, *asci* predominantly 8-spored, but polysporous ones occur as well, asci prototunicate, *Lichina* and *Peccania* types but also unitunicate-rostrate, *ascoma* development predominantly starting with ascogones formed beneath pycnidia (pycnoascocarps), rarely starting from ascogones formed in a tangle of generative hyphae, conidiophores simple, conidia small. Resembling *Lichinaceae*, but ascomata predominantly pycnoascocarps. Differing from *Phylliscaceae* in the absence of unitunicate-rostrate asci AND corticate, heteromerous thalli as well as absence of *Phyllisciella* and *Phylliscum* type asci and absence of filiform conidia and branched conidiophores and paraphyses always present. Differing from *Lichinellaceae* in the absence of thallinocarps and *Lichinella* type asci.

Discriminating characters: Cyanobionts diverse, *Stigonema* photobiont and endolithic growth form not present in any of the other families, ascomata predominantly pycnoascocarps. IF asci unitunicate-rostrate THEN thallus not truly corticate and dorsoventrally stratified. Ascomata with distinct, often thickened proper exciple at least if photobiont is unicellular and not with reddish or purple gelatinous sheaths.

Description: Lichen-forming ascomycetes obligatory associating with various single-celled or filamentous cyanobacteria (*Nostoc*, *Scytonema*, *Stigonema*, *Rivulariaceae*). Thalli usually blackish (Figs 1E, 22A, C, E) and distinctly swelling when wet, rarely subgelatinous and colour olivaceous, rarely greyish pruinose (Fig. 22D), rarely whitish (*Heppia solorinoides*). Growth forms very diverse ranging from variously crustose (Figs 22A, B, 23A, C), crustose-effigurate (Fig. 23D), squamulose (Fig. 23B), squamulose-peltate (Fig. 22C), foliose (Fig. 22D), dwarf fruticose (Fig. 22F), filamentous (Figs 1E, 22E) to endolithic (Fig. 1B). Thalli fixed to substrate by rhizophyphae, tufts of rhizohyphae, an umbilicus or gelatinous holdfasts. Isidia rare (Fig. 23D), soralia very rare (*Heppia conchiloba*), two species with tiny, translucent, spike-likes hairs (*Heppia echinulata*, *H. trichophora*), hormocystangia absent. Thallus homoiomerous and ecorticate, rarely corticate and dorsoventrally stratified (*Heppia*). Ascomata predominantly pycnoascocarps, *i.e.* developing from ascogones formed beneath pycnidia (Figs 2E, F, 23E), rarely apothecia formed from ascogones in a tangle of generative hyphae (*e.g.* *Heppia*), thallinocarps absent. Apothecia zeorine, lecanorine or biatorine, proper exciple well developed or absent, disc open or narrow and then appearing perithecioid, rarely umbonate. Asci prototunicate with *Lichina* and *Peccania* types (Fig. 23F, G), thin walled and predominantly releasing mature ascospores passively through apical ruptures or asci unitunicate-rostrate with distinct amyloid apical dome and active ascospore discharge through rostrum (Fig. 3B), predominantly 8-spored, rarely polysporous. Ascospores simple, usually broadly ellipsoid, rarely (sub)globose or bean shaped, walls usually thin, rarely distinctly thickened. Paraphyses always present. Epihymenium colourless, faintly yellowish to pale reddish or brownish. Conidiomata pycnidia, immersed to slightly elevated, conidiophores simple, conidia formed terminally, simple, small ellipsoid or short bacilliform, rarely globose. Distribution cosmopolitan, but rare in dense forest habitats lacking exposed rock or soil crusts. On various rocks, sporadically or seasonally wetted and usually in well lit situations or amphibious to inundated, also in biological soil crusts, but rarely on bark. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Main clade 3 contains the bulk of the pyrenopsoid lichens including the core of genus *Pyrenopsis*. It further contains well known genera *Heppia*, *Ephebe*, *Lempholemma s. str.* and *Porocyphus* for all of which families have been established. The oldest one is *Porocyphaceae* for the sole genus *Porocyphus* (Körber 1855). However, *Porocyphaceae* has not been taken up by later authors and the genus *Porocyphus* was included in the *Ephebaceae* (Zahlbruckner 1906–1907, 1926). Other genera included in this family are *Cladopsis*, *Lapismalleus*, *Paracyphus*, *Pleopyrenis*, *Pseudocarpon*, *Thermutis*, *Thyrea*, *Tichocyphus* and *Watsoniomyces*.

Included genera: *Calotrichopsis* (likely close to *Ephebe*), *Cladopsis* ("*Pyrenopsis" triptococca* and allies), *Ephebe*, *Gyrocollema* (incl. *Ginzbergerella*; likely close to *Porocyphus*/*Watsoniomyces* or "*Psorotichia*" *obpallescens*), *Heppia*, *Lapismalleus* (for *"Psorotichia" lugubris*), *Lecidopyrenopsis*, *Lempholemma*, *Paracyphus* (for *P. gotlandicus*), *Pleopyrenis* (for "*Pyrenopsis" picina*), *Porocyphus* (incl. "*Lichina" willeyi* group), *Pseudocarpon* (for *P. persimile*), *Pseudoheppia* (probably close to *Porocyphus*), *Pyrenopsis*, *Stromatella*, *Thermutis*, *Thyrea*, *Tichocyphus* (for *T. gotlandicus*), *Watsoniomyces*. Approx. 125 spp.

Fig. 22. Thallus growth forms in main clade 3 (*Porocyphaceae*). **A.** *Lempholemma chalazanum*, crustose, film-like thin to somewhat lobate at margin and numerous laminal apothecia (Feuerer). **B.** *Pyrenopsis conferta*, crustose, granules becoming coralloid with terminal, globose apothecia (van den Boom 26043). **C.** *Thyrea plectopsora*, squamulose, margin incised forming lobules (Schultz 18162a). **D.** *Thyrea girardii*, foliose, divided into few broadly rounded, conspicuously bluish grey pruinose lobes (Urbanavichus 0905071a). **E.** *Thermutis velutina*, filamentous, branches furcate, shape determined by *Scytonema* cyanobiont, biatorine apothecia lateral (Lich. Fenn. 51b, W1903-638). **F.** *Porocyphus willeyi*, dwarf-fruticose, branches furcate with terminal apothecia (Beeching). For endolithic growth see *Watsoniomyces obsoletus* in Fig. 1B. Scale bars = 1 mm.

Placement of *Calotrichopsis*, *Gyrocollema*, *Pseudoheppia* and *Stromatella* is inferred from the sets of morphological characters that show largest agreement with those of the *Porocyphaceae* as circumscribed here, but remains to be verified by subsequent molecular analyses.

Calotrichopsis Vain, Acta Soc. Fauna Flora fenn. 7(1): 243. 1890. MycoBank MB 763.

Type species: *Calotrichopsis insignis* Vain., Acta Soc. Fauna Flora fenn. 7(1): 243. 1890. MycoBank MB 381860.

Notes: Not included in the phylogenetic analysis, but well placed in *Porocyphaceae* because of the filamentous cyanobionts and presence of pycnoascocarps. Close to *Ephebe* but differing in the type of filamentous cyanobiont (Henssen 1963a).

Three species: *Calotrichopsis filiformis*, *C. granulosa*, and *C. insignis*. *Calotrichopsis rivae* is an unlichenized cyanobacterium of the *Nostocaceae* (Henssen 1963a).

Cladopsis Nyl., Rev. Bot. Bull. Mens.: 345. 1885. MycoBank MB 1081. Fig. 23.

Type species: *Cladopsis triptococca* (Nyl.) Nyl., in Hue, Rev. Bot. 4: 347. 1886. *Pyrenopsis triptococcus* is selected as lectotype of *Pyrenopsis* subgen. *Cladopsis* (syn. *Cladopsis*).

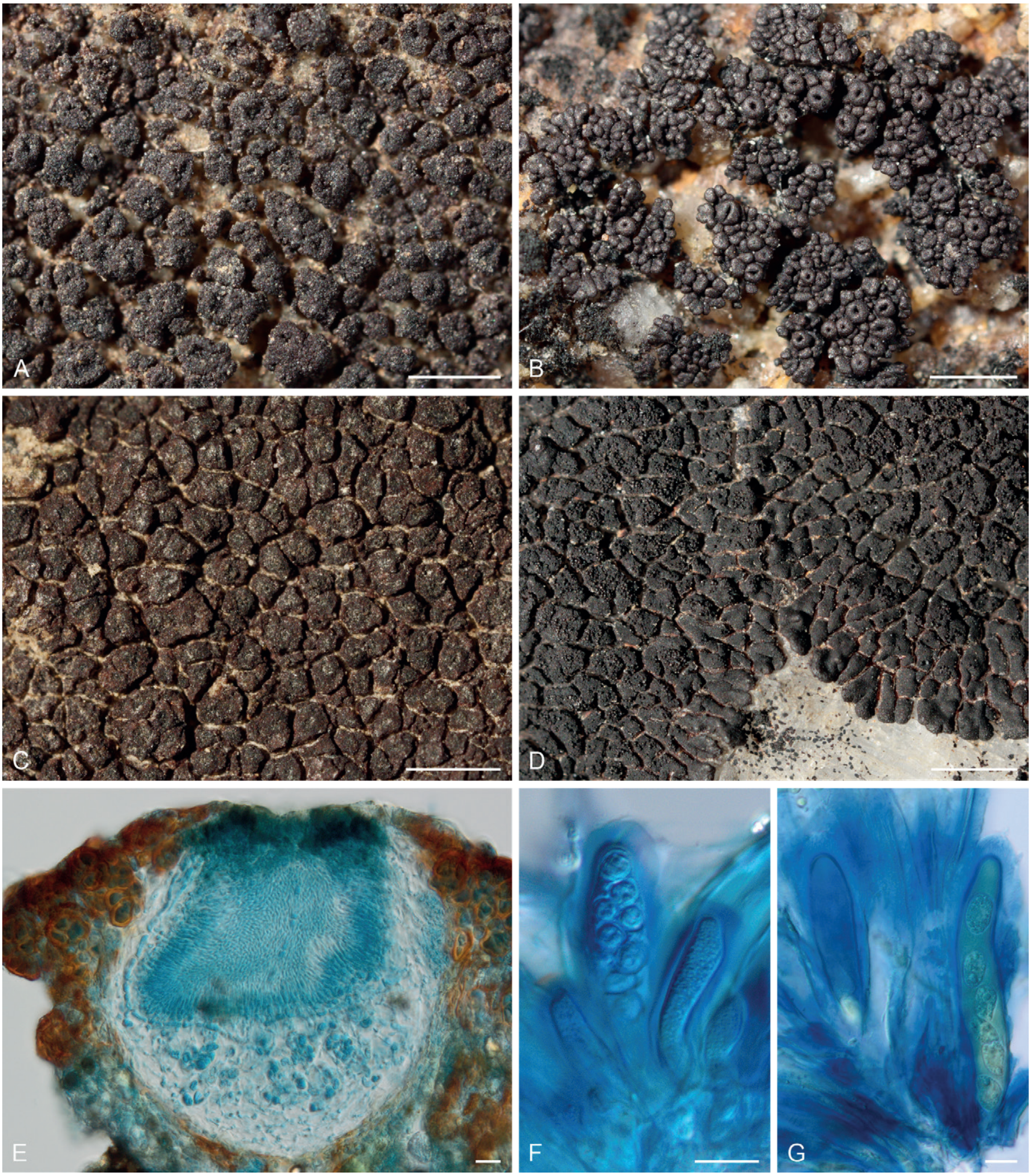

Fig. 23. A. *Cladopsis triptococca*, thallus areoles granulose, apothecia with thick thalline margin and concave discs (Marques 928). **B.** *Cladopsis polycocca*, areoles abundantly fertile, becoming subquamulose (Beeching 3152). **C.** *Cladopsis palmana*, thallus areoles angulate, plane to slightly convex, apothecia small, discs punctiform to sunken (Feuerer). **D.** *Cladopsis guyanensis*, crustose, areoles angulate and effigurate at margin, isidiate towards the center (Schultz 20004). **E.** *Cladopsis portoricensis*, pycnidium with tangle of generative hyphae, ascogones and trichogynes beneath in LPCB (Fink 690, MICH, isosyntype). **F.** *Cladopsis polycocca*, juvenile and mature ascus lacking apical thickening but covered by distinct gelatinous cap in KOH/Lugol (Feuerer). **G.** *Cladopsis triptococca*, two thin-walled asci with distinct outer gelatinous cap in KOH/Lugol (Schultz 16587a). Scale bars: A–D = 1 mm; E–G = 10 µm.

Description: *Thallus* crustose, small granulose, granulose-coralloid, areolate to subsquamulose, sometimes effigurate and/or isidiate, dark reddish brown to blackish (Fig. 23A–D), often attached to the substrate by a gelatinous basal layer. Thallus anatomy homoiomerous, ecorticate, hyphae usually forming a dense network around relatively large cyanobiont cells, rarely appearing compact and almost paraplectenchymatous (*C. polycocca*) or with air filled spaces (*C. foederata*), hyphal cells isodiametric or elongated, usually distinct, photobiont a gloeocapsoid cyanobacterium with reddish, layered gelatinous sheaths (Fig. 23E), attacked by finger like fungal haustoria, cells relatively large. *Apothecia* small and perithecioid with narrow, usually slightly concave discs (Fig. 23A–C), or discs expanded, dark reddish or brownish, sometimes black, rarely umbonate (*C. olivacea*), semi immersed, sessile, adnate with broad base or constricted at base, rarely stalked, lecanorine with persisting, smooth, sometimes bulging thalline margin, proper exciple lacking or rudimentary, rarely well developed (*C. olivacea*), epithecium pale reddish or olivaceous brown, subhymenium/hypothecium with rounded base or short inversely conical, hymenium KOH/IKI+ deep blue, paraphyses robust, usually straight, rarely bent, usually sparsely branched and anastomosing, often becoming (sub)moniliform with distinctly expanded terminal cells, asci usually narrow clavate, prototunicate with gelatinous outer cap (*Pyrenopsis* type *sensu* Moreno and Egea 1991, =*Peccania* type here; Fig. 23F, G), outer wall/hymenial gelatine KOH/IKI+ deeply blue, but no distinct apical dome, rarely inner wall at tip amyloid, 8-spored, *ascospores* simple, hyaline, usually broad ellipsoid, rarely globose, small, sometimes with thick walls. *Ascoma* ontogeny with ascogones formed beneath pycnidia (pycnoascocarps; Fig. 23E). *Pycnidia* (sub)globose or broad pyriform, conidiophores simple, conidia produced terminally, small ellipsoid to short bacilliform. Chiefly tropical but extending into warm temperate regions, apparently lacking in cold regions, growing on acidic or volcanic, usually mineral rich rock in inclined rock faces moistened from seeping water, usually in exposed situations. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: *Pyrenopsis triptococca, P. foederata, P. polycocca* form a distinct clade that is recognized as a genus by reestablishing *Cladopsis* (currently a synonym of *Pyrenopsis*). This group is closely related with *Lecidopyrenopsis corticola* which is easily distinguished from these lichens by the (almost) biatorine apothecia and corticolous growth (Henssen 1980). The genus is characterized by *Peccania* type ascus and pycnoascocarps. Includes Mediterranean species (*P. triptococca*, *P. palmana*) and species from tropical humid sites (*P. polycocca*, *Pterygiopsis guyanensis*), growing on siliceous rocks, seeping moist or shaded (*Pterygiopsis densisidiata*). Also include some sterile species previously placed in *Pterygiopsis* (*P. guyanensis* and *P. densisidiata*).

New combinations in *Cladopsis*:

Based on morphological inspection of type material the following species of *Pyrenopsis s. l.* best fit here: *P. antillarum*, *P. australiensis*, *P. brasiliensis*, *P. carassensis*, *P. monilifera*, *P. negans*, *P. olivacea*, *P. portoricensis*, and *P. robustula*.

Cladopsis densisidiata (Aptroot *et al.*) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852351.
Basionym: *Pterygiopsis densisidiata* Aptroot *et al.*, Bryologist 123: 628. 2020. MycoBank MB 836255.

Cladopsis foederata (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852352.
Basionym: *Pyrenopsis foederata* Nyl., Bull. Soc. linn. Normandie, sér. 2, 6: 297. 1872. MycoBank MB 403068.

Cladopsis guyanensis (M. Schultz *et al.*) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852353.
Basionym: *Pterygiopsis guyanensis* M. Schultz *et al.*, Pl. Biol. 2: 489. 2000. MycoBank MB 474428.

Cladopsis palmana (J. Steiner) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852354.
Basionym: *Pyrenopsis palmana* J. Steiner, Oesterr. Bot. Z. 54: 333. 1904. MycoBank MB 403100.

Cladopsis polycocca (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852355.
Basionym: *Synalissa polycocca* Nyl., Syn. meth. lich. (Parisiis) 1(1): 96. 1858. MycoBank MB 406703.
Homotypic synonym: *Pyrenopsis polycocca* (Nyl.) Tuck., Syn. N. Amer. lich. 1: 136. 1882. MycoBank MB 403111.

Ephebe Fr., Syst. orb. veg. (Lundae) 1: 256. 1825. MycoBank MB 1845. Fig. 1E.

Type species: *Ephebe lanata* (L.) Vain. 1888, Meddeland. Soc. Fauna Flora fenn. 14: 20. 1888. MycoBank MB 119172.

Notes: The genus is monophyletic. It is characterized by filamentous branched thalli with *Stigonema* cyanobionts, pycnoascocarps, asci with 8 or 16 spores and *Lichina* type asci.

Included taxa: *Ephebe americana*, *E. brasiliensis*, *E. epheboides*, *E. fruticosa*, *E. hispidula*, *E. japonica*, *E. lanata*, *E. multispora*, *E. ocellata*, *E. orthogonia*, *E. perspinulosa*, *E. solida*, *E. solida f. lesquereuxii*, and *E. tasmanica*.

Gyrocollema Vain., Mycologia 21: 37. 1929. MycoBank MB 2182.

Type species: *Gyrocollema scyphuliferum* Vain., Mycologia 21: 36. 1929. MycoBank MB 386509.

Notes: Originally a monotypic genus described from Puerto Rico, and later expanded with the inclusion of *Ginzbergerella rupestrina*, likewise a monotypic genus described from Italy and only known from the type collection. Both species share an endolithic growth of the thallus, a fact overlooked by Díaz-Escandón *et al.* (2021) when they established the new genus *Watsoniomyces* for an enigmatic, endolithic cyanolichen known for many years from Great Britain. *Psorotichia obpallescens* is yet another endolithic species described from Romania. Not treated in the phylogenetic analysis because attempts to sequence *G. scyphuliferum* failed. Because of the endolithic growth form and biatorine apothecia we consider that it is best placed in *Porocyphaceae*, probably close to *Porocyphus* and *Watsoniomyces*.

Heppia Nägeli *ex* A. Massal., Geneac. Lich.: 7. 1854. MycoBank MB 2296.

Type species: *Heppia adglutinata* A. Massal., Geneac. Lich.: 8. 1854. MycoBank MB 386732.

Notes: The species of *Heppia* included in the analysis form a monophyletic clade. We assume that the remaining species of that genus as circumscribed by Henssen (1994) cluster here as well. They are characterized by having typical apothecia and squamulose thalli. The genus *Heppia* is similar to *Peltula*, from which it is phylogentically distantly related, and from which it can be distinguished by the spore number and ascus structure (*i.e.* 8 spores and *Lichina*-type asci in *Heppia* and 16–128 spores and unitunicate-rostrate asci in *Peltula*).

Included species: *Heppia adglutinata*, *H. arenacea*, *H. conchiloba*, *H. despreauxii*, *H. echinulata*, *H. lutosa*, *H. solorinoides*, and *H. trichophora*.

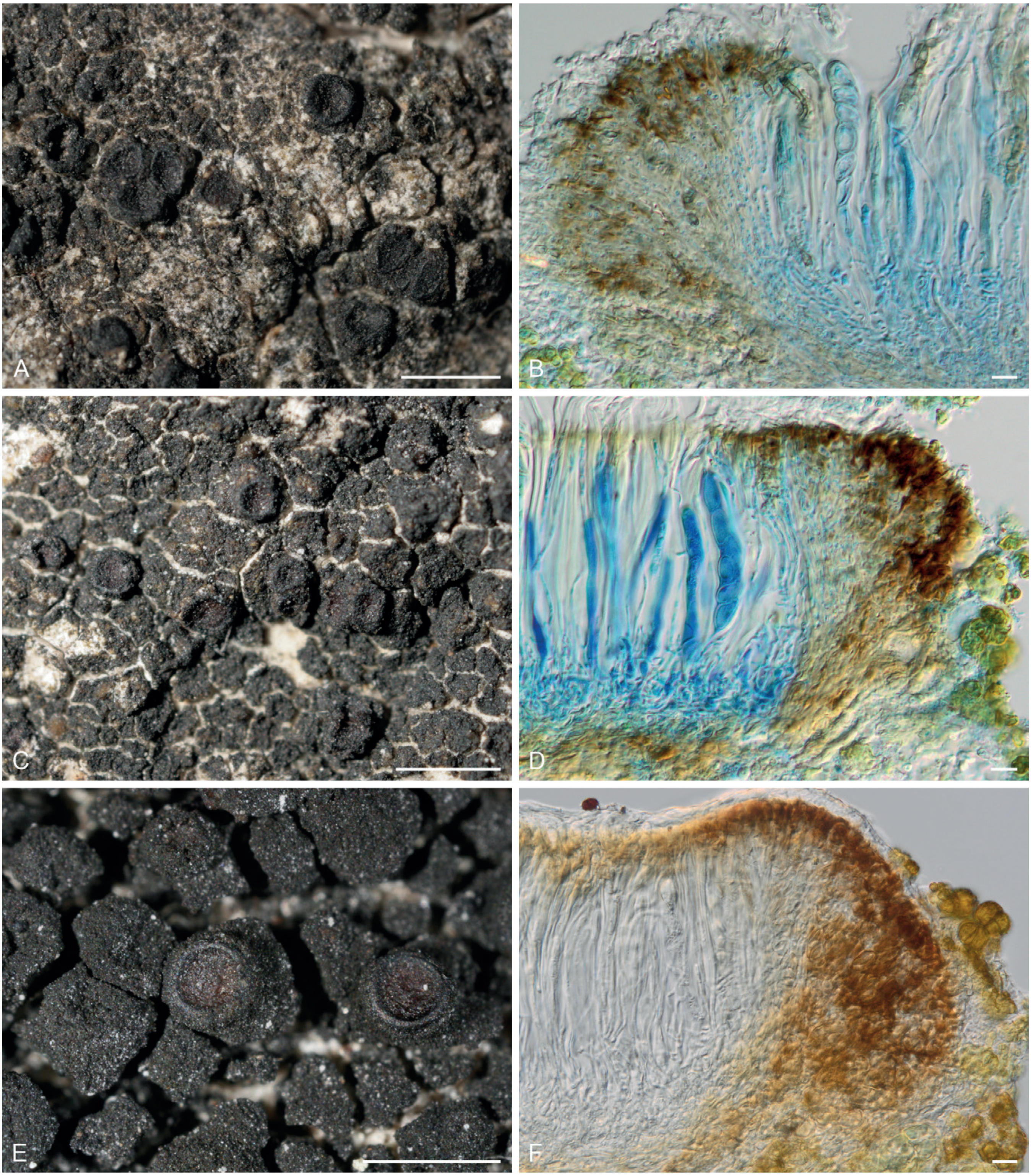

Fig. 24. *Lapismalleus lugubris*. **A.** Areoles becoming eroded, apothecia almost lecideine (Hepp Lich. Eur. 728, M0140086, topotype). **B.** Apothecium with thick, brownish proper exciple and simple ascospores in LPCB (Arnold 6, M0140087, syntype). **C.** Thallus black, areoles thin with whitish base, apothecia almost lecideine (*Psorotichia lugubris* f. *atrata* Arnold 40, M0140084, type). **D.** Apothecium with thick, brownish proper exciple, indistinct thalline margin and simple ascospores in LPCB (*Psorotichia lugubris* f. *atrata* Arnold 40, M0140084, type). **E.** Areoles thick, irregularly polygonal, apothecia (semi)immersed with widely opened discs surrounded by thin, blackish proper exciple, thalline margin indistinct (Schultz 05566). **F.** Apothecium with thick, brownish proper exciple, indistinct thalline margin (Schultz 05559). Scale bars: A, C, E = 1 mm; B, D, F = 10 µm.

Lapismalleus M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852357. Fig. 24.

Etymology: Combined from *lapis* (Lat. = stone) and *malleus* (Lat. = hammer), a transliteration of the name of Christian Stenhammar (1783–1863) who is commemorated in *Stenhammara* Flot. *ex* Körb. (for nomenclatural notes see below).
Type species: *Lapismalleus lugubris* (A. Massal.) M. Schultz & M. Prieto

Diagnosis: Genus of the *Porocyphaceae* with crustose thallus and immersed blackish apothecia surrounded by a shallow thalline and distinct, blackish proper margin. Resembling *Psorotichia*, but differing in the presence of a well developed, apically distinctly widened, dark coloured excipulum proprium and in the paraplectenchymatous thallus anatomy with ± vertically arranged, robust hyphae that become loose towards the base creating a cottony basal layer on the substrate surface. Resembles *Pseudotichia* in thallus growth form and anatomy, but differing in the distinct, blackish coloured proper exciple and reddish black apothecial disc.

Description: *Thallus* blackish, crustose, areoles thick (Fig. 24E), but surface sometimes eroded (Fig. 24A), becoming cottony towards the base. Thallus ecorticate, anatomy compact paraplectenchymatous with single-celled cyanobionts having yellowish brown gelatinous sheaths, hyphae robust, in ± distinct vertical rows, becoming loose and cottony towards the base of areoles and substrate surface. *Apothecia* zeorine with apically distinctly widened, reddish brown proper exciple and shallow, inconspicuous excipulum thallinum (Fig. 24B, D, F), discs dark reddish, brownish to almost black (Fig. 24A, C, E), finally widely opened and becoming somewhat to distinctly umbonate, hymenium with septate *paraphyses*, KOH/Lugol+ blue, *asci Lichina* type, 8-spored, ascospores simple, hyaline, broad ellipsoid (Fig. 24B, D). *Ascomata* develop from ascogones arising in a tangle of generative hyphae. *Pycnidia* ± pyriform, simple, wall becoming involuted, pycnospores short bacilliform. On inclined, well lit, seeping moist calcareous rock, also seasonally in shallow rock pools in alvar areas, so far only known from Central to Northern Europe. No secondary metabolites detectable by TLC reported in the literature and not tested.

Notes: Because *Psorotichia lugubris* is distantly related with *Psorotichia s. str.* (type species *P. murorum*) and could not be accommodated in any other genus of the *Lichinomycetes*, the new genus *Lapismalleus* is erected here.

According to Hertel (1967: 125), Massalongo (1856: 40) tentatively placed his new species *Stenhammara lugubris* ("*Stenhammera lugubris*" =*Psorotichia lugubris*) into *Stenhammara* Flot. *ex* Körb., a genus established shortly before by Körber (1855: 221) for an entirely unrelated lecideoid lichen, *Lecidea turgida* (=*Stenhammarella turgida*, *Lecideaceae*). However, Körber's genus is an invalid later homonym of the plant genus *Steenhammera* (=*Mertensia* Roth *nom. cons.*, *Boraginaceae*) and Hertel (1967: 124) therefore used *Stenhammarella* as a substitute name.

New combination in *Lapismalleus*:

Lapismalleus lugubris (A. Massal.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852358.
Basionym: *Stenhammara lugubris* A. Massal., Misc. Lichenol.: 40. 1856.
Homotypic synonym: *Psorotichia lugubris* (A. Massal.) Arnold, Flora 68: 218. 1885. MycoBank MB 402882.
Synonyms: *Stenhammara lugubris f. atrata* Arnold, Flora 43: 71. 1860.
Psorotichia lugubris f. atrata (Arnold) Arnold, Flora 68: 218. 1885.

Description: For a description of the species, see Prieto *et al.* (2015) and Wirth *et al.* (2013). Characterized by having a thick, crustose-areolate thallus which is black to dark olive brown. The surface of aged areoles is often being partially eroded exposing the pale, cottony lower surface of the thallus. The apothecial disc is blackish to reddish brown surrounded by a thin, pale brown proper exciple which is apically distinctly thickened and dark brown coloured. Typical apothecia.

Lecidopyrenopsis Vain., Hedwigia 46: 172. 1907. MycoBank MB 2701.

Type species: *Lecidopyrenopsis corticola* Vain., Hedwigia 46: 172. 1907. MycoBank MB 393008.

Notes: A monotypic genus and species clustering basal to those species of *Pyrenopsis s. l.* that are transferred here to *Cladopsis* (see there). *Lecidopyrenopsis corticola* deviates from all *Cladopsis* species in the presence of biatorine apothecia and a peculiar hyphal collar surrounding the coralloid thallus granules. One of the few corticolous members of the *Lichinomycetes,* pantropic.

Lempholemma Körb., Syst. lich. germ.: 400. 1855. MycoBank MB 2733. Fig. 22A.

Type species: *Lempholemma compactum* (Wallr.) Körb., Syst. lich. germ. (Breslau): 401. 1855. MycoBank MB 393125 (=*Lempholemma polyanthes* (Bernh.) Malme, Lich. Suec. Exsicc.: no. 883. 1924. MycoBank MB 342449).

Synonyms: *Arnoldia* A. Massal., Flora 39: 214. 1856. *nom. illeg. non Arnoldia* Cass. 1824 (*Compositae*) *nec Arnoldia* Blume 1826 (*Cunoniaceae*). *Type species*: *Arnoldia cyathodes* A. Massal., Flora, Regensburg 39: 214. 1856. (= *Lempholemma elveloideum* (Ach.) Zahlbr., Cat. lich. univ. 3: 21. 1924[1925].).
Plectopsora A. Massal., Atti Reale Ist. Veneto Sci., ser. 3, 5: 336. 1860). *Type species*: *Plectopsora cyathodes* (A. Massal.) Körb., Parerga lichenol. (Breslau) 5: 432. 1865. (= *Lempholemma elveloideum* (Ach.) Zahlbr., Cat. lich. univ. 3: 21. 1924[1925].).
Collema sect. *Arnoldiella* Vain., Étude lich. Brésil 1: 234. 1891). *Type species*: *Collema minutulum* (Bornet) Vain., Acta Soc. Fauna Flora fenn. 7(no. 1): 234. 1890. (= *Lempholemma minutulum* (Bornet) Zahlbr., Cat. lich. univ. 3: 12. 1924[1925].).

Emended description: Genus of the *Porocyphaceae*. *Thallus* blackish, minutely granulose, filmy subfoliose (Fig. 22A) to squamulose-peltate, with *Nostoc* cyanobionts and distinctly swelling when wet due to delicate, loose hyphae embedded in massive gelatine, fastened to substrate by rhizohyphae or a small umbilicus. Thallus ecorticate, homoiomerous, thin hyphae forming a loose reticulum around *Nostoc* chains. *Apothecia* immersed to semi-immersed (Fig. 22A), rarely sessile, zeorine with thick thalline exciple and pale, thin proper exciple, hymenium with septate *paraphyses*, KOH/Lugol+ blue, *asci Lichina* type, 8-spored, ascospores simple, ellipsoid, sometimes guttulate. *Ascomata* develop from ascogones arising beneath pycnidia (pycnoascocarps). *Pycnidia* immersed to slightly elevated, simple, conidiophores simple, pycnospores produced terminally, small bacilliform. On calcareous, loamy soils, over mosses on calcareous rocks or directly on calcareous rocks, in exposed to somewhat shaded, rarely moist situations. Widely distributed in boreal to warm temperate regions in the northern hemisphere, also known from Tasmania (*L. polyanthes*). No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: The phylogenetic results show that *Lempholemma* is split in six distantly related clades, resulting thus in six different genera. The genus *Lempholemma s. l.* in the traditional sense contains approximately 40 species worldwide (Lumbsch *et al.* 2011), characterized by the presence of *Nostoc* photobionts. However, several authors previously noticed its heterogeneity (Henssen 1969b, Jørgensen 2007). Henssen described two major pathways of ascocarp development in the genus (Henssen 1969b). Muscicolous and soil dwelling species such as *L. chalazanum* and *L. polyanthes* possess pycnoascocarps, whereas the strictly saxicolous members of the *L. botryosum* group produce ascomata from a tangle of generative hyphae just like the unrelated saxicolous *L. lingulatum* (=*Lingolemma*). In another unrelated, saxicolous species, *L. socotranum* (=*Peltolemma*), the typical apothecia are formed from freely arising ascogones. However, pycnoascocarps are also found in saxicolous species, *e.g. L. elveloideum* and the unrelated *L. polycarpum* (= *Pycnolemma*). Based on the phylogenetic results we here describe four genera and reinstated the genus *Synalissina* to accommodate the species previously included in *Lempholemma*. All these clades are not closely related except *Peltolemma* and *Pycnolemma* that form a clade together with *Collemopsis*.

-***Lempholemma s. str.*** includes at current state of knowledge: *L. polyanthes* (the type of the genus), *L. chalazanum* and *L. eleveloideum*. *Lempholemma minutulum* and *L. segregatum* fall here as well (unpublished ITS data). The species are crustose-subfoliose, minutely granulose to subsquamulose and grow on solid or over mosses, whereas the latter is squamulose-peltate and grows on rock. They all have pycnoascocarps.

-***Paludolemma gen. nov.*** (for *P. syreniarum*): crustose, granulose-areolate thalli with typical apothecia, on bark.

-***Lingolemma gen. nov.*** (for *L. lingulatum*): squamulose peltate thalli, central hyphal strand and with typical apothecia, on rock.

-***Peltolemma gen. nov.*** (for *L. socotranum*): squamulose peltate thallus, homomerous throughout, with typical apothecia, on rock.

-***Pycnolemma gen. nov.*** (for *L. polycarpum*): divided foliose-peltate thalli, no distinct central hyphal strand, with pycnoascocarps, on rock.

-***Synalissina*** reinstated: dwarf-fruticose, squamulose-peltate, squamulose-subfruticose thalli, homoiomerous throughout, with typical apothecia, *Peccania* type asci and hormocystangia.

New combination in *Lempholemma*:

Lempholemma segregatum (Nyl.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852359.
Basionym: *Collemopsis segregata* Nyl., in Hasse, Lich. S. Calif.: 6. 1898. MycoBank MB 383562.
Homotypic synonym: *Psorotichia segregata* (Nyl.) Hasse, Contr. U. S. Natl. Herb. 17: 68. 1913. MycoBank MB 476320.

Notes: This species was considered by Schultz (2007) to be just a dwarfish form of *L. chalazanum*. However, according to unpublished sequence data based on western North American material it falls into the type clade, but is genetically distinct from *L. chalazanum* and the other species of *Lempholemma s. str*.

Paracyphus M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB: 852361. Fig. 25.

Etymology: Similar to *Porocyphus*.

Type species: ***Paracyphus gotlandicus*** M. Schultz & M. Prieto, ***sp. nov.*** MycoBank MB 852362.

Etymology: Species found in Gotland (Sweden).

Diagnosis: Belonging to *Porocyphaceae*. Crustose to subsquamulose, blackish cyanolichens resembling *Porocyphus* and *Lapismalleus*, but differing from the former in the eventually umbonate apothecial discs and from the latter in the formation of pycnoascocarps. Deviating from both these genera in the ascus walls covered by compact outer gelatinous coat that stains deeply blue in Lugol solution after pretreatment with KOH.

Typus: **Sweden**, Gotland, 10 km SE of Läbro, between Smöjen and Sudergårde, 34V 376861, 640291, 15 m a.s.l., alvar area, 10 Jul. 2013, *M. Prieto & M. Schultz*, SL 19 [**holotype** M. Prieto SMP137 (S)].

Description: *Thallus* crustose, areolate to subsquamulose, areoles irregularly angulose (Fig. 25A–C), 125–200 µm thick, but sometimes distinctly thickened due to pronounced vertical growth, surface epruinose, uneven to warty, dull, affixed to the substrate by pale, robust rhizohyphae that sometimes form a ± compact, gelatinous basal holdfast. Thallus anatomy uniformly compact paraplectenchymatous (Fig. 25D–G) with indistinct hyphae, cells isodiametric to slightly elongated, angulate, 4.5–6 × 2–2.5 µm, cyanobiont a filamentous cyanobacterium with split chains and basal heterocyte (*Rivulariaceae*), trichomes up to 35 µm long, but soon much contorted and cells appearing ± coccoid especially in the thallus margin, 4–6 µm in size, with gelatinous sheath 7.5–10 µm, sheath yellowish brown, thin. *Apothecia* roundish, semi immersed to sessile with constricted base (Fig. 25A–D), zeorine, thalline margin distinctly developed, 40–60 µm thick but receding with age, proper exciple pale, 11.5–15 µm thick, apically reddish brown and distinctly widened, 20–60 µm thick (Fig. 25E–G), in fully mature apothecia exposed as a thin, yellowish brown ring well contrasting with the blackish thalline margin (Fig. 25B, C), disc dark reddish brown, slightly concave to finally plane and becoming umbonate, epihymenium hyaline to pale reddish brown, hymenium hyaline, up to 150 µm high, KOH/IKI+ distinctly blue, *paraphyses* distinct, ±straight to rather loose and somewhat bent, branched and anastomosing, thin, 1–1.5 µm thick, terminal cells hardly widened, *ca*. 1.5 µm thick, *asci* (sub)cylindrical to very narrow clavate with attenuate base, 70–96 × 9–12 µm, wall thin but with compact outer, gelatinous coat that stains deeply blue in Lugol's solution after pretreatment with KOH (Fig. 25H–J), ± *Lichina* type, uniseriate, ascospores hyaline, thin walled, simple, but sometimes with plasmatic bridges and then appearing 2-celled, broad ellipsoid to subglobose, 8.5–14.5 × 5–9.5 µm (Fig. 25H, I), subhymenium and hypothecium with roundish base, pycnoascocarps, ascogones formed beneath pycnidia. *Pycnidia* immersed, ellipsoid, *ca*. 120 × 90 µm, conidia ellipsoid, 2.5 × 1.5 µm, terminally formed on simple conidiophores. Grows on calcareous rocks on margins of shallow pools in alvar areas. So far only known from Gotland (Sweden, SL 18, 19, 134). Secondary metabolites detectable by TLC not tested.

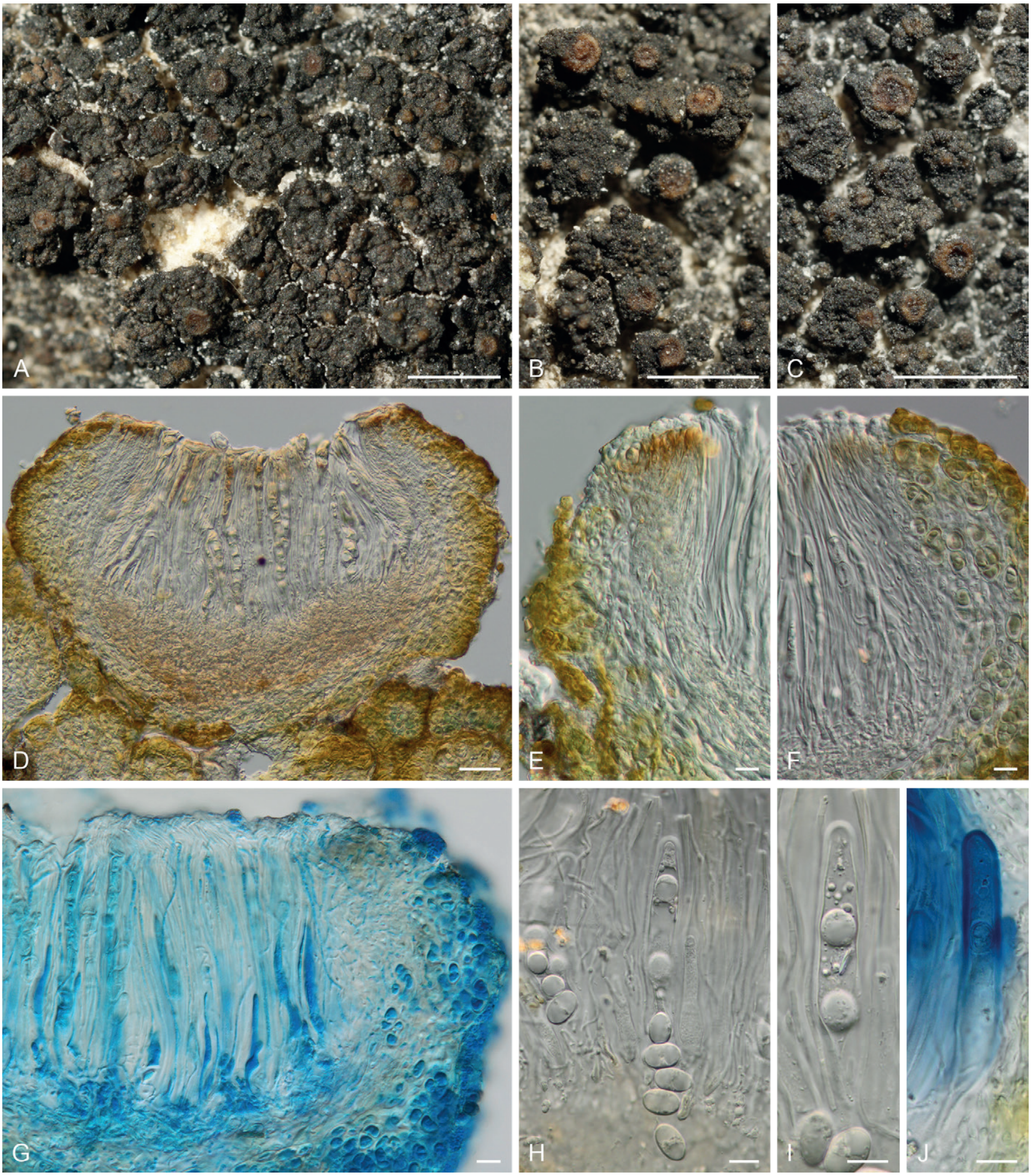

Fig. 25. *Paracyphus gotlandicus*. **A.** Irregularly shaped, thick thallus areoles with numerous apothecia (Prieto SL19, holotype). **B.** Thick thallus areoles with coarsely warty surface, mature apothecia adnate with pale brownish excipulum proprium and reddish brown, finally umbonate discs (Schultz 05554, paratype). **C.** Juvenile apothecia emerging in thallus warts in the center, mature apothecia with distinct proper and receding thalline margin at the top and bottom right (Schultz 05553, paratype). **D.** Apothecium with zeorine margin, asci and paraphyses (Prieto SL134, paratype). **E.** Margin of old apothecium, proper exciple pale, only at the top reddish brown, thalline margin receding (Prieto SL19, holotype). **F.** Margin of younger apothecium with less distinct proper exciple and thalline margin still well developed. **G.** Mature apothecium with zeorine margin, asci and paraphyses in LPCB (Schultz 05554, paratype). **H.** Tip of ascus and released ascospores in KOH (Prieto SL134, paratype). **I.** Ascus with uniformly thickened walls and septate paraphyses in KOH. **J.** Ascus wall uniformly thickened and thick outer coast staining deeply blue in KOH/Lugol (Prieto SL19, holotype). Scale bars: A–C = 1 mm; D = 25 µm; E–J = 10 µm.

Additional specimens examined: **Sweden,** Gotland, Kyrgatmyr 2.5 km S of Ar, alvar-like area, on loose stones in exposed, slightly depressed rock surfaces, limestone, 57.891706°N, 18.960581°E, 22 m a.s.l., 9 Jul. 2013, *M. Schultz & M. Prieto*, Schultz 05553 & Schultz 05554 (**paratypes** HBG-015551 and HBG-015552).

Notes: The new species forms a clade with *Thermutis* (filamentous thalli with pycnoascocarps) and *Lapismalleus* (crustose thallus with typical apothecia) forming a sister clade to *Porocyphus* (crustose with pycnoascocarps). A porocyphoid lichen at first glance much resembling growth forms of *Porocyphus rehmicus* and *P. coccodes*, but differing in the eventually umbonate apothecial discs and the peculiar asci that appear rather thick walled, but in fact have a thin, not bulging wall covered by a compact outer coat that stains deeply blue in Lugol's solution after pretreatment with KOH. Despite intensive search, we have been unable to match this peculiar lichen with any porocyphoid species of the *Lichinaceae* known from Europe.

Pleopyrenis Clem., Gen. fung.: 174. 1909. MycoBank MB 4223. Fig. 26.

Type species: *Pleopyrenis picina* (Nyl.) Clem., Gen. fung.: 174. 1909. MycoBank MB 401637.

Diagnosis: Genus of the *Porocyphaceae* resembling *Allopyrenis*, *Cladopsis* and *Pyrenopsis* in the gloeocapsoid cyanobionts with reddish sheaths, but differing in the very thin, filmy thallus with immersed, perithecioid apothecia with punctiform discs. Asci polysporous, clavate with distinct amyloid apical dome.

Description: *Thallus* thin, crustose, continuous film like, rimose to (incompletely) areolate, dark reddish black (Fig. 26A, B), areoles flat, angulose, 0.12–0.5 mm, to 125 µm thick, attached to the substrate by thin gelatinous basal layer. Thallus anatomy homoiomerous, ecorticate, hyphae forming a delicate network around cyanobiont cells, hyphal cells ± isodiametric, angulate, 3–4 µm, photobiont a gloeocapsoid cyanobacterium with reddish gelatinous sheaths, cells globose, single or paired, 5.5–8.5 µm with sheath, 3–6.5 µm without sheath, sheath 1–1.5 µm thick, cyanobiont packets arranged in ± vertically orientated, attacked by finger like fungal haustoria. *Apothecia* numerous, very small, perithecioid (Fig. 26A, B), immersed to semi immersed, (0.16–)0.2–0.24(–0.28) mm, lecanorine with persisting, smooth and shallow thalline margin, 65–73 µm, proper exciple lacking, discs punctiform, usually slightly concave, dark reddish brown, epithecium pale reddish brown or colourless, subhymenium with rounded base, hymenium 85–100 µm high, KOH/IKI+ deep blue (Fig. 26D, E), paraphyses distinct, at first ± straight, later becoming reticulate, branched and anastomosing, cells elongate, *ca*. 4 × 1 µm, apical cells somewhat widened, but not becoming moniliform, 3.5–5 × 2–3.5 µm, *asci* clavate, (55–)58–72.5 × 10–16.5 µm, unitunicate-rostrate, with distinct KOH/IKI+ blue apical dome and distinct outer gelatinous cap (Fig. 26C–E), polysporous (24–)32(–64), ascospores simple, hyaline, broad ellipsoid, small, 4.5–7 × 2.5–4.5 µm. *Ascoma* ontogeny with ascogones formed beneath pycnidia (pycnoascocarps). *Pycnidia* broadly pyriform, at first 40 × 50 µm, conidiophores simple, conidia produced terminally, small ellipsoid, 3 × 1.5 µm. Widely distributed in continental Europe (Pyrenees,

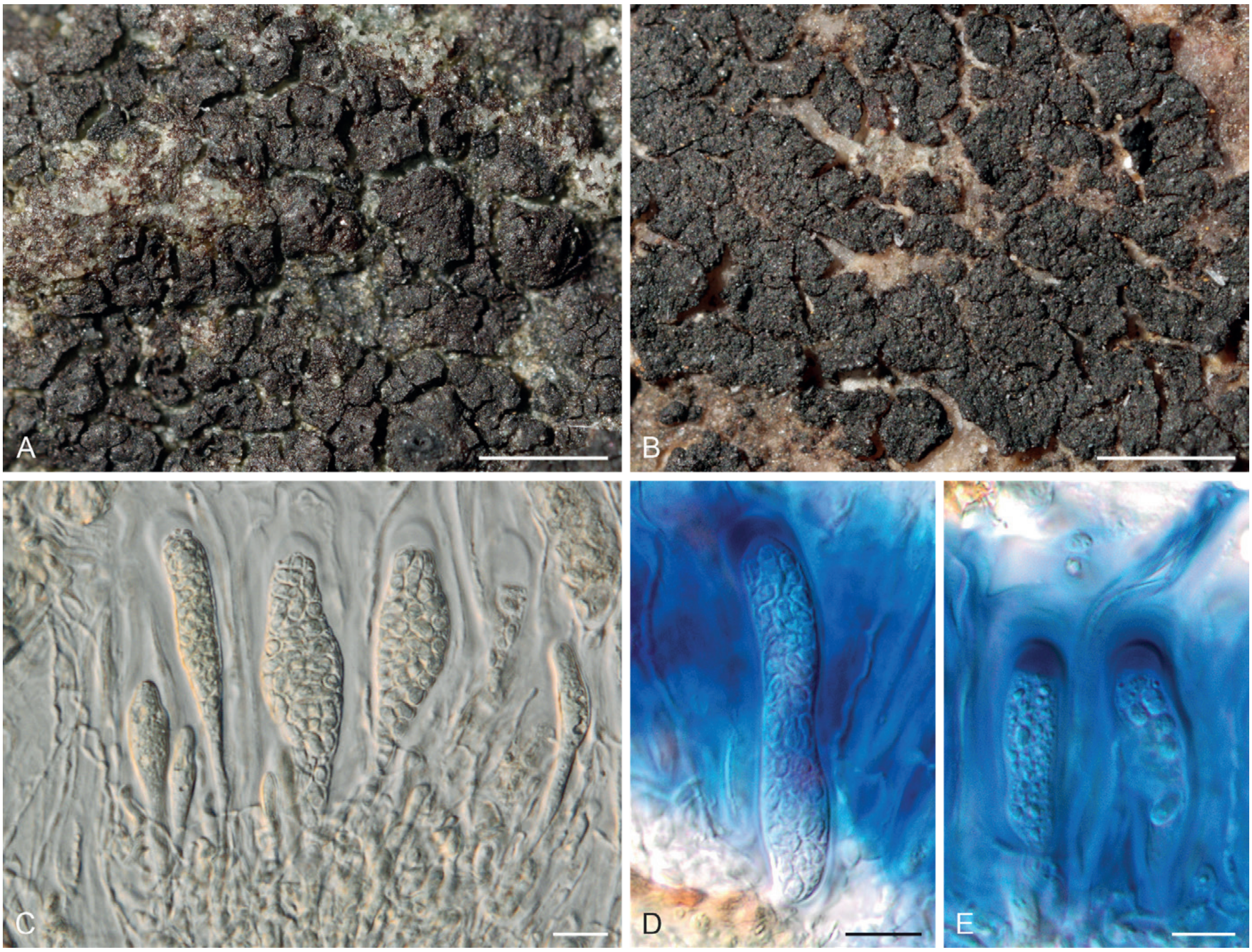

Fig. 26. *Pleopyrenis picina*. **A.** Thallus thin, areolate, apothecia (semi-)immersed, discs remaining very narrow (Schultz 08573). **B.** Thallus thin, continuous to rimose (Wirth 1832). **C.** Polysporous asci with distinct apical wall thickening in KOH (Schultz 08609). **D.** Ascus with amyloid tip in KOH/Lugol (Schultz 08573). **E.** Two immature asci with amyloid tips and an emptied ascus between them with stretched rostrum in KOH/Lugol (Schultz 08609). Scale bars: A, B = 1 mm; C–E = 10 µm.

Black Forest, northern Alps, Ore Mountains, Giant Mountains), growing on wet acidic rock, *e.g.* temporarily or seasonally inundated along clear water creeks or inclined rock faces moistened from seeping water in usually clear situations. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Our material clustered outside genus *Pyrenopsis* as redefined by us here, comprising *P. subareolata*, *P. conferta* and the *P. furfurea/haematina* complex. *Cladopsis* is reestablished for *P. triptococca* and allied, mostly (sub)tropical species unrelated with the members of the *P. sanguina* complex for which we establish another generic segregate here, *Allopyrenis*. Surprisingly, *Pleopyrenis picina* was not closely related with *Allopyrenis grumulifera* with which it shares the unitunicate rostrate, polysporous asci. When Clements (1909) established *Pleopyrenis* as a genus separate from *Pyrenopsis*, he provided a rudimentary diagnosis ("*Pyrenopsis polyspora*") and selected *Pyrenopsis picina* as type. It remains unclear if Clements was aware of other polysporous species in *Pyrenopsis*, *i.e. P. grumulifera* and *P. pleiobola*. The type material of the latter two species is extremely scarce. While *P. grumulifera* seems to be sufficiently distinct from *Pleopyrenis picina* (apothecia eventually more distinctly sessile and asci broader), the taxonomic status of *Pyrenopsis pleiobola* remains unclear. Henssen initially annotated the lectotype (H-NYL41318) as identical with *P. grumulifera*, but later changed her annotation to keep the two species as distinct. We are not aware of more differences among them beyond the number and shape of ascospores cited in the literature (*e.g.* Ozenda & Clauzade 1970, Clauzade & Roux 1985). There is also confusion about the actual spore number in *P. grumulifera*: polysporous according to Nylander (1861), octosporous according to Nylander (1867). We have sequenced material formally fitting *P. grumulifera*, but differing in the ascospore number. However, we found the number of ascospores to be fixed within the samples studied. Therefore, we believe that there are two different species involved; however, both fall within *Allopyrenis*. Here, we included only the polysporous form and treat this as the true *P. grumulifera* and in accordance with the current usage of this name. The situation, however, is additionally complicated by the original material of *P. picina* that we have traced so far. According to Nylander (1857) it consists of three elements: "*Tortulas* et alios muscos obducens, prope Parisios et a Dno Lenormand ad Vire observata" plus the material of "*Collema pulposum* var. *diffracto-areolatum* Schaer." that he cited in synonymy. The material deposited in H-NYL42522 has nothing to do with *P. picina* as currently understood (*e.g.* by Thüs & Schultz 2009, Wirth *et al.* 2013, Ozenda & Clauzade 1970, Clauzade & Roux 1985) and does not even represent a lichen (annotated by A. Henssen "nur Algenüberzug gesehen", *i.e.* only algal cover seen, which we confirm here). "*Collema pulposum* var. *diffacto-areolatum* Schaer." is referred by Degelius (1954) to *Collema*, resp. *Echylium tenax*. We have seen H-NYL41996 and likewise found a lichen of the *Enchylium tenax* group. So far, we did not locate the material collected by Lenormand in Vire. In order to fix the current usage of the name *Pyrenopsis picina* we intend to select Schultz 08627 (HBG-015205) as epitype for this crustose, pyrenopsoid lichen with polysporous asci growing on wet, acidic rocks. Because it clearly falls outside *Pyrenopsis* even in its reduced circumscription established here, we reinstate genus *Pleopyrenis*.

Porocyphus Körb., Syst. lich. germ.: 425. 1855. MycoBank MB 4342. Fig. 27.

Type species: *Porocyphus coccodes* Flot. *ex* Körb., Syst. lich. germ.: 425. 1855. MycoBank MB 402349.

Description: A medium sized genus in its expanded circumscription. Thalli crustose, areolate, granulose-coralloid (Fig. 27A, D), placodioid to dwarf-fruticose (Fig. 27E, G), ecorticate, usually with fountain-like (Fig. 27F) or fan-shaped hyphal systems and filamentous cyanobionts (Fig. 27B, F, H) with basal heterocyte, sometimes threads much contorted and split, apothecia ± globose, usually with sunken discs, pycnoascocarps (Fig. 2E), asci *Lichina* type (large, wall very thin, with thin amyloid outer coat, often bulging when spores mature; Fig. 27B, H). Distributed worldwide, often in wet habitats, but also on steep rock faces moistened by seeping water. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: Species of non-marine *Lichina* belong to this clade. As both groups share characters pycnoascocarps, *Lichina* type asci, *Rivulariaceae* as photobiont and the anatomy densely reticulate and ecorticate, non-marine *Lichina* species are included in *Porocyphus*. *Included species*: *Porocyphus antarcticus*, *P. coccodes*, *P. dimorphus*, *P. effiguratus*, *P. kalbarrensis*, *P. kenmorensis*, *P. leptogiella* (to *P. rehmicus*?), *P. lichinelloides*, *P. macrosporus*, *P. minutissimus*, *P. rehmicus*, *P. rosulans*, *P. ruttneri*, *P. tasmanicus*, and *P. willeyi*.

New combinations in *Porocyphus*:

Porocyphus antarcticus (Cromb.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852364.
Basionym: *Lichina antarctica* Cromb., J. Bot., Lond. 14: 21. 1876. MycoBank MB 394636.

Notes: Not included in the phylogenetic analysis, but best placed in *Porocyphus* because of pycnoascocarps, ecorticate thallus lacking a compact central hyphal cord and the rocky habitat not directly under the influence of sea water, all characters requiring exclusion from the *Lichina pygmaea* group.

Porocyphus macrosporus (Henssen *et al.*) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852365.
Basionym: *Lichina macrospora* Henssen *et al.*, Mycotaxon 22: 171. 1985. MycoBank MB 105483.

Porocyphus minutissimus (Henssen) M. Schultz, ***comb. nov.*** MycoBank MB 852366.
Basionym: *Lichina minutissima* Henssen, Lichenologist 5: 449. 1973. MycoBank MB 342494.

Notes: A member of the *Lichina willeyi* group not included in the phylogenetic analysis, but best placed in *Porocyphus* because of pycnoascocarps, ecorticate thallus lacking a compact central hyphal cord and non-marine habitat.

Porocyphus rosulans (Henssen) M. Schultz, ***comb. nov.*** MycoBank MB 852367.
Basionym: *Lichina rosulans* Henssen, Lichenologist 4: 95. 1969. MycoBank MB 345262.

Notes: A member of the *Lichina willeyi* group not treated in our analysis, but best placed in *Porocyphus* because of pycnoascocarps, ecorticate thallus lacking a compact central hyphal cord and non-marine habitat.

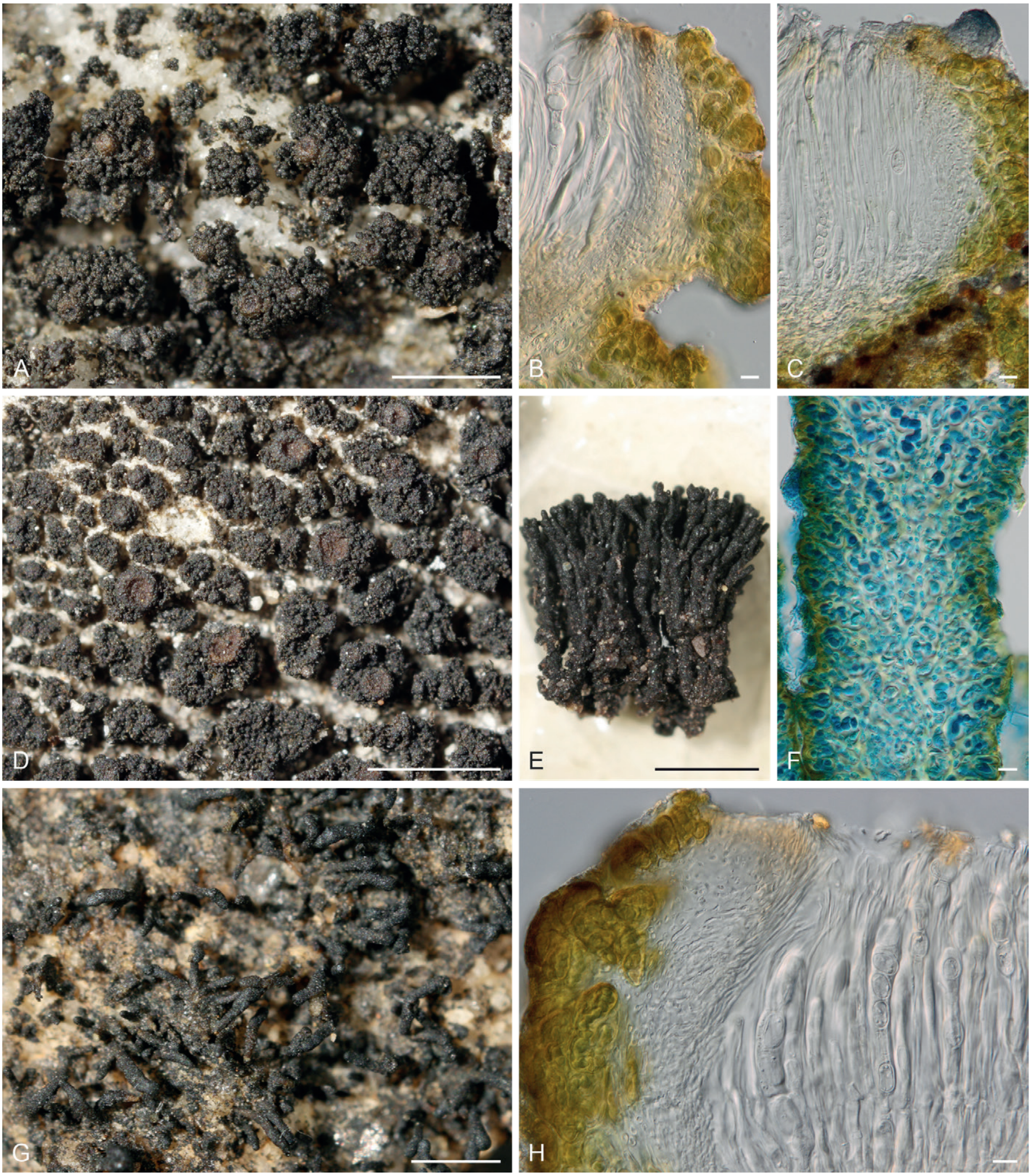

Fig. 27. A. *Porocyphus coccodes*, irregular, thick areoles with small, almost globose apothecia (Schultz 08895a). **B.** Zeorine apothecial margin with equally thick thalline and proper exciple, thin walled ascus with ascospores (Schultz 16918c). **C.** *Porocyphus rehmicus*, zeorine apothecial margin, slender paraphyses and ascospores (Schultz 03471a). **D.** Areoles with rough surface and adnate apothecia (Schultz 03456). **E.** *Porocyphus antarcticus*, fragment of areole composed of erect branchlets with terminal pycnoascocarps (Eaton, BM000022209, holotype). **F.** Hyphae reticulate and fountain like surrounding Rivulariaceae cyanobiont in LPCB (for pycnoascocarp see Fig. 2E). **G.** *Porocyphus macrosporus*, thallus fruticulose with terminal pycnoascocarps (Ertz 12986). **H.** Mature apothecium (pycnoascocarp) with zeorine margin, thin walled, *Lichina* type asci and ascospores (Büdel & Wessels 14312a). Scale bars: A, D, E, G = 1 mm; B, C, F, H = 10 µm.

Porocyphus tasmanicus (Henssen) M. Schultz, ***comb. nov.*** MycoBank MB 852368.
Basionym: *Lichina tasmanica* Henssen, Lichenologist 4: 94. 1969. MycoBank MB 345263.

Notes: A member of the *Lichina willeyi* group not included in the phylogenetic analysis, but best placed in *Porocyphus* because of pycnoascocarps, ecorticate thallus lacking a compact central hyphal cord and non-marine habitat.

Porocyphus willeyi (Tuck.) M. Schultz & M. Prieto, ***comb. nov.*** MycoBank MB 852369.
Basionym: Lichina confinis * *willeyi* Tuck., Syn. N. Amer. Lich. (Boston) 1: 133. 1882. MycoBank MB 324020.

Homotypic synonym: *Lichina willeyi* (Tuck.) Henssen, Lichenologist 4: 90. 1969. MycoBank MB 345264.

Notes: The placement of *Lichina microcarpa* described from Cayenne remains to be clarified, but from the original description and the non-marine, tropical habitat it seems very unlikely that this species will stay in *Lichina s. str.* and a placement in *Porocyphus* in its expanded circumscription employed here seems more plausible.

Pseudocarpon M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852370. Fig. 28.

Type species: ***Pseudocarpon persimile*** M. Schultz & M. Prieto, ***sp. nov.*** MycoBank MB 852371.

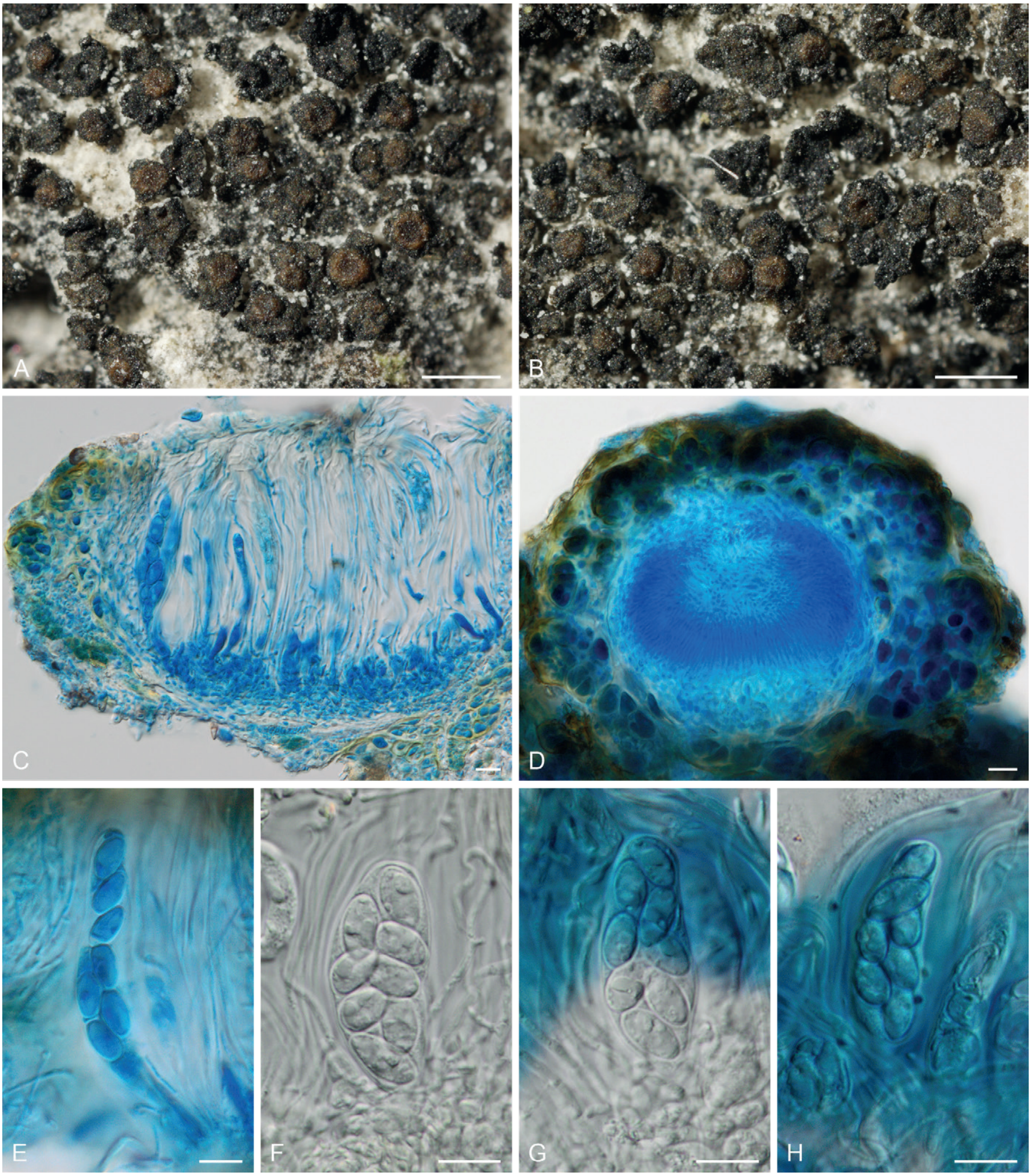

Fig. 28. *Pseudocarpon persimile*. **A, B.** Thallus small areolate, thin, apothecia at first hemispherical, later sessile, discs narrow, plane to slightly concave and resembling fish eyes (Schultz 05557, holotype). **C.** Section of mature apothecium showing zeorine margin, asci and paraphyses, hypothecium roundish lacking a stipe in LPCB (Prieto SL76, paratype). **D.** Ascogones in tangle of generative hyphae beneath a pycnidium in LPCB (Groner 4588). **E.** Mature ascus with ellipsoid spores in LPCB (Prieto SL76, paratype). **F.** Thin-walled ascus with spores in KOH (Schultz 05557, holotype). **G, H.** Ascospore walls staining blue in KOH/Lugol, ascus wall not amyloid. Scale bars: A, B = 0.5 mm; C–H = 10 µm.

Etymology: Because of the striking external similarity with *Pyrenocarpon thelostoma*.

Diagnosis: Belonging to the *Porocyphaceae*, resembling *Paracyphus*, *Porocyphus* and *Pyrenocarpon*. Differing from the latter in the thallus anatomy with larger, coccoid cyanobionts and more robust hyphae forming a dense reticulate network (not small celled paraplectenchymatous with very delicate hyphae), in the presence of pycnoascocarps (ascomata not forming from spheroid tangle of generative hyphae) and in the plane apothecial discs (not becoming umbonate in mature apothecia). Differing from *Porocyphus* in the coccoid cyanobiont (not short, often coiled filamentous) and in the hemispherical apothecia with narrow, plane discs (not globose with narrow, concave discs). Differing from *Paracyphus* in the much lower hymenium and smaller asci of *Lichina* type (no thick, pale grey outer layer that stains conspicuously deep blue in Lugol's solution).

Typus: **Sweden***,* Gotland, Kyrgatmyr 2.5 km S of Ar, alvar-like area, on exposed rock surfaces, limestone, 57.889894°N, 18.966220°E, 22 m a.s.l., 9 Jul. 2013, *M. Schultz & M. Prieto*, Schultz 05557 (**holotype** HBG-015208).

Description: *Thallus* forming very small, scattered patches among other lichens, blackish, crustose, granulose to small areolate (Fig. 28A, B), areoles very thin, 0.12–0.2 mm in size, attached to the substrate by robust rhizohyphae sometimes forming a ± distinct gelatinous basal layer. Thallus anatomy homoiomerous, ecorticate, hyphae forming a dense network around cyanobiont cells (Fig. 28C, D), hyphal cells distinct, angulate, short, 4.5–6.5 × 2–2.5 µm, photobiont a coccoid cyanobacterium, cells globose to somewhat applanate, 5.5–11 µm with sheath, 3–6.5 µm without sheath, 1–2 cells in distinct gelatinous sheath, 1.5–2.5 µm thick, yellowish brown, cyanobiont surrounded by hyphae with finger like haustoria. *Apothecia* numerous, 1 per areole, rarely 2, hemispherical to finally broad and sessile, 0.2–0.4 mm, zeorine (Fig. 28C) with persisting, smooth and shallow thalline margin, 14–38.5 µm thick and distinct, pale proper margin composed of conglutinate hyphae, laterally and towards the base 5.5–9.5 µm, apically reddish brown and distinctly widened, 16–38.5 µm thick, discs ± plane, not distinctly concave, not umbonate, dark reddish brown, epithecium pale reddish brown, subhymenium 12.5–19 µm high, hymenium translucent, 75–90 µm high, KOH/IKI+ blue, *paraphyses* straight, robust, distinctly septate, cells 4.5–7.5 × 1.5–2 µm, apical cells widened, 2.5–4 µm thick, moderately branched and anastomosing, *asci* narrow clavate to obclavate with attenuate base, 43–52 × 8–9 µm thin-walled, *Lichina* type, wall KOH/IKI-, but with bluish outer gelatinous coat (Fig. 28F–H), subbiseriate, 8-spored, *ascospores* simple, hyaline, 7.5–11.5 × 4–6.5 µm, wall amyloid (Fig. 28G, H). *Ascoma* ontogeny with ascogones formed beneath pycnidia (pycnoascocarps); Fig. 28D, pycnidial wall soon thickened and serving as a proper exciple, conidiophores likewise soon disappearing and whole pycnidium rapidly transformed into an apothecium. *Pycnidia* broadly pyriform, 85–95 µm, conidiophores simple, *conidia* produced terminally, small ellipsoid, 2.5–3.5 × 1 µm. Widely distributed in Europe (Gotland, Switzerland, perhaps also in Bavaria and in Mallorca) and growing on calcareous rocks along river banks as well as shallow rock pools and getting temporarily or seasonally inundated. Secondary metabolites detectable by TLC not tested.

Additional specimens examined: **Sweden**, Gotland, Fallet, shooting area, E of Tingstadträske, S of road 148, E of Tingstade, 57.737951ºN, 18.656655ºE, 44 m a.s.l., 10 Jul. 2013, *M. Schultz & M. Prieto*, SMP142 (**paratype** SL21); Gotland, between Smöjen and Sudergårde, 10 km SE of Läbro, 57.739605ºN, 18.937290ºE, 15 m a.s.l., alvar area, 10 Jul. 2013, *M. Schultz & M. Prieto*, SMP134B (**paratype** SL76).

Notes: Three samples from Gotland with hemispherical apothecia resembling fish eyes included in the phylogenetic analysis are superficially very similar to *Pyrenocarpon thelostoma*. They could also be mistaken for juvenile *Lemmopsis arnoldiana* (but apothecia soon becoming biatorine with brick coloured proper margin), *Paracyphus* (but apothecia more sessile, discs eventually expanded and becoming umbonate, asci with thick, conspicuous grey outer layer that stains deeply blue in Lugol's solution) or even *Porocyphus* (but apothecia globose, photobiont a cyanobacterium with short, often much split and twisted threads of the *Rivulariaceae*). However, the samples cluster next to *Watsoniomyces* and did not fall together with closely related *Porocyphus* or *Paracyphus*. Surprisingly, they are only distantly related with *Pyrenocarpon* and *Lemmopsis*. Intensive search for a described candidate species failed and *Pseudocarpon* is established as a new, monotypic genus for *P. persimile*. On Gotland, the new species occurs in the same sites as *Paracyphus gotlandicus*, and the two species can easily be mistaken. The latter, however, has larger, thicker areoles of irregular shape, more sessile, larger apothecia with more expanded discs, a distinctly higher hymenium and different, larger asci (see above). Material exhibiting the same haplotype as the Gotland samples have been collected on the bank of River Rhine in Basel, Switzerland (Groner 4588, HBG). Evidently closely related collections come from Munich on concrete along the bank of River Isar (Feuerer, HBG) as well as shallow rock pools in NE Mallorca (Schultz 17154b, HBG). However, more material is needed to better understand the species boundaries. Herbarium specimens of *Pyrenocarpon thelostoma* and its synonym *P. flotowianum* should be checked for thallus anatomy in order to identify more material belonging to *Pseudocarpon persimile*.

Pseudoheppia Zahlbr., Ann. Mycol. 1: 356. 1903. MycoBank MB 4440.

Type species: *Pseudoheppia schuleri* Zahlbr., Ann. Mycol. 1: 356. 1903. MycoBank MB 402468.

Notes: Not included in the phylogenetic analysis. An enigmatic genus and species of uncertain affinity. Gylenik (1935: 310) placed it into *Porocyphus*, though with hesitation ("einstweilen"). According to Schultz (2014), close to *Psorotichia obpallescens*, a species that clearly falls outside *Psorotichia* as circumscribed here.

Pyrenopsis (Nyl.) Nyl., Syn. meth. lich. (Parisiis) 1(1): 97. 1858. MycoBank MB 4601. Figs 22B, 29.

Type species: *Pyrenopsis fuscatula* Nyl., Mém. Soc. Imp. Sci. Nat. Cherbourg 5: 143. 1858. MycoBank MB 403073.

Description: *Thallus* crustose, granulose, areolate to subsquamulose (Fig. 29A, C, H), rarely coralloid (Fig. 22B), dark reddish brown to blackish, often attached to the substrate by gelatinous basal layer. Thallus anatomy homoiomerous, ecorticate, hyphae forming a dense network around cyanobiont cells (Fig. 29B) or paraplectenchymatous (Fig. 29D), hyphal cells isodiametric or elongated, usually distinct, sometimes inconspicuous, photobiont a gloeocapsoid cyanobacterium with reddish, layered gelatinous sheaths, surrounded by finger like fungal haustoria, cells relatively

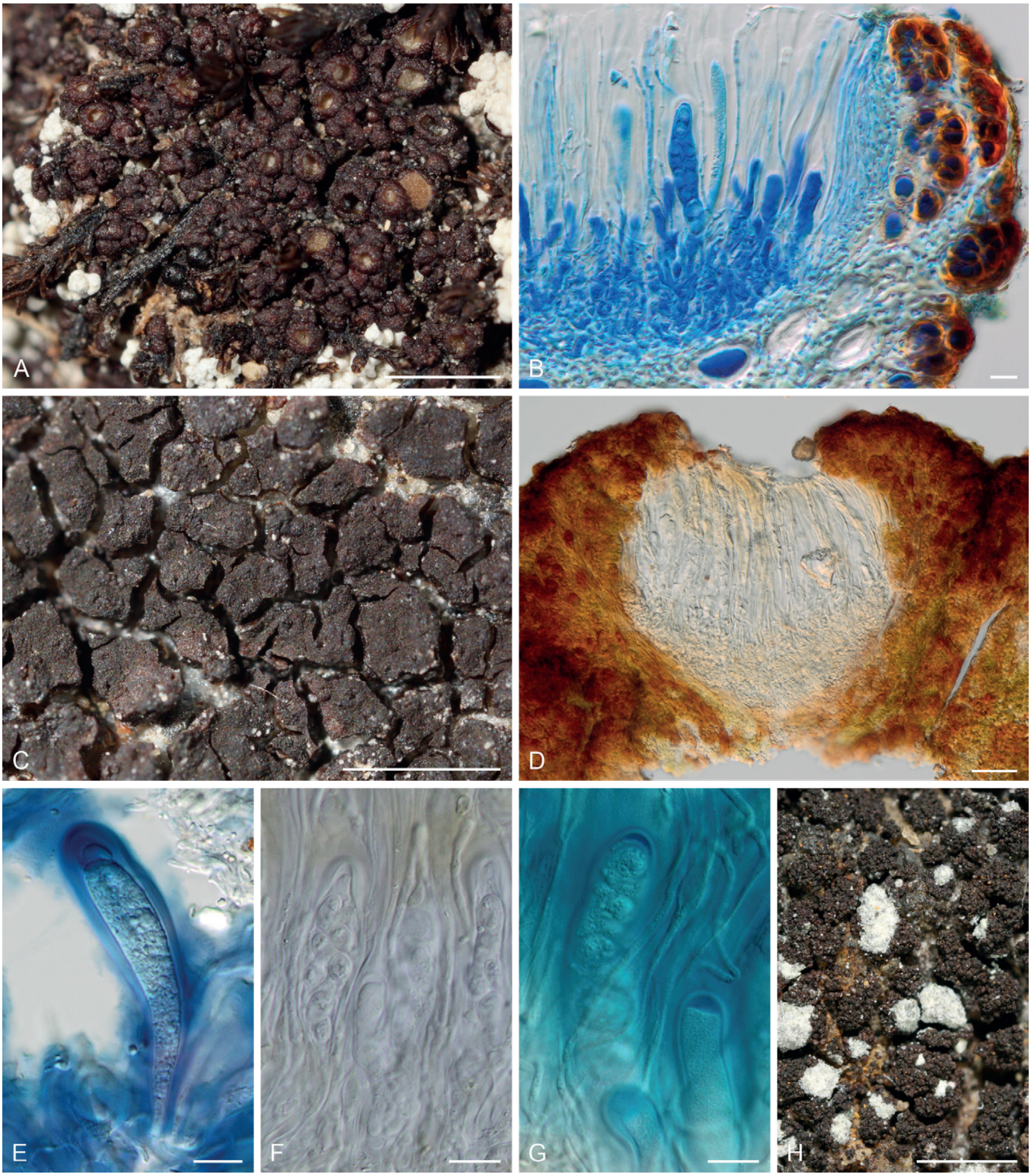

Fig. 29. A. *Pyrenopsis furfurea*, juvenile to mature apothecia, hymenia partly fallen off (Schultz 16925). **B.** Ascus with ascospores appearing 2-celled due to plasmatic bridges, thalline margin thick, proper margin thin in LPCB (Jones, H-NYL42916, lectotype). **C.** *Pyrenopsis subareolata*, thallus areoles angulate, plane to slightly convex, apothecia remaining immersed and discs punctiform (Westberg, S). **D.** Immersed apothecium, thallus anatomy compact paraplectenchymatous (Halda 17352). **E.** Ascus with distinct amyloid tip and outer gelatinous cap in KOH/Lugol (Halda 17352). **F.** *Pyrenopsis fuscatula*, ascus with thickened apex, simple ascospores in KOH (Holmes, BM00073226). **G.** *Pyrenopsis conferta*, asci with amyloid tip in KOH/Lugol (Prieto SL42). **H.** *Pyrenopsis haematina*, sterile thallus with coralloid-granulose areoles partly overgrowing other crustose lichens (Prieto SMP249). Scale bars: A, C, H = 1 mm; B, E–G = 10 µm; D = 25 µm.

large or very small. *Apothecia* small and perithecioid with narrow, usually slightly concave discs (Fig. 29C, D), or discs becoming expanded (Fig. 29A), dark reddish or brownish, sometimes blackish, usually semi immersed to sessile, rarely stalked (Fig. 22B), lecanorine with persisting, smooth, sometimes bulging thalline margin, proper exciple lacking (Fig. 29D) or thin and inconspicuous (Fig. 29B), epithecium pale reddish brown or colourless, subhymenium/hypothecium with rounded base or short inversely conical, hymenium KOH/IKI+ deep blue, paraphyses robust, usually straight, rarely bent, usually sparsely branched and anastomosing, often becoming (sub)moniliform with distinctly expanded terminal cells, *asci* usually narrow clavate, unitunicate-rostrate, with distinct

KOH/IKI+ blue apical dome and distinct outer gelatinous cap (Fig. 29E–G), 8-spored, ascospores simple, hyaline, broad ellipsoid, small. *Ascoma* ontogeny with ascogones formed beneath pycnidia (pycnoascocarps). *Pycnidia* subglobose to pyriform, conidiophores simple, conidia produced terminally, small ellipsoid to short bacilliform. Widely distributed in the northern hemisphere in boreal-arctic to (high) montane regions, growing on wet acidic, usually mineral rich rocks along clear water creeks or inclined rock faces moistened from seeping water, usually in well lit situations, rarely on mineral soil and debris in exposed, arctic-alpine meadows. No secondary metabolites detected by TLC (Jørgensen 2007).

Notes: The genus *Pyrenopsis* is characterized by having crustose areolate thalli, pycnoascocarp type ascoma, lecanorine apothecia lacking a distinct true exciple, and gloeocapsoid photobionts with reddish sheaths. The phylogenetic results show that *Pyrenopsis* is highly polyphyletic with the species scattered across four clades showing that the genus has subsequently become a large container for unrelated species. Our results also show that unitunicate-rostrate asci and polysporous asci have evolved several times in the *Lichinomycetes.* The species are distributed in four distantly related clades belonging to two families. These clades are:

-***Allopyrenis*** (*A. haemaleella*, *A. phaeococca*, *A. sanguinea*, *A. reducta*, *A. impolita*, *A. grumulifera*). These are all northern hemisphere species occurring in montane to alpine, boreal to arctic regions and represent characteristic species of *Pyrenopsis s. l.* They possess unitunicate-rostrate, narrowly clavate asci (distinct amyloid dome and outer cap) asci with eight spores, except *A. grumulifera* with broadly clavate asci and 32(–64) spores. For details on distinction from *Pyrenopsis s. str.* see above.

-***Cladopsis*** (*C. triptococa*, *C. foederata*, *C. polycocca*, *C. guyanensis*, *C. palmana*). Tropical to subtropical species, some of them reaching warm-temperate regions, *Peccania* type asci lacking a distinct, amyloid apical dome. Also includes *Pterygiopsis densisidiata*. For details see above.

-***Pleopyrenis*** (*P. picina*). Very similar Nordic species *P. picina* and *A. grumulifera* both having rostrate, polysporous asci are unrelated. The latter belongs to the *haemaleella*/*sanguinea* group for which the new genus *Allopyrenis* in the *Phylliscaceae* is erected (see there).

-***Pyrenopsis*** *s. str.* (*P. conferta*, *P. furfurea*, *P. fuscatula*, *P. haematina*, *P. subareolata*). These species cluster together in main clade 3 and are not closely related with the other species that possess rostrate asci, clustering in main clade 4 (*Phylliscaceae*). As the results show, this type of ascus has evolved independently in different groups. *Pyrenopsis subareolata* is similar to *P. fuscatula* (*e.g.* compact thallus anatomy) and considered to be very closely related, if not identical. Due to lack of material, we have not sequenced the type of the genus *Pyrenopsis* (*i.e. P. fuscatula*), but we are confident to have identified the type clade of *Pyrenopsis* with the closely related *P. subareolata*. This allows to retain the name *Pyrenopsis* for a set of known and widely distributed, characteristic species such as *P. furfurea*, *P. haematina* and *P. subareolata*. The species *P. haematina* and *P. furfurea* seem to constitute a complex which needs to be resolved based on larger amount of material (Schultz *et al.* in prep).

Stromatella Henssen, Lichenologist 21: 111. 1989. MycoBank MB 25344.

Type species: *Stromatella bermudana* (Riddle) Henssen, Lichenologist 21: 112. 1989. MycoBank MB 135897.

Notes: A monotypic, crustose genus not included in the phylogenetic analysis because attempts to sequence material from Bermuda repeatedly failed. The ascoma primordials are described to be stromatic, but pycnoascocarps have been reported as well (Henssen 1989), an observation which is confirmed here. Based on the available data, we think this genus is better placed in *Porocyphaceae*. The earlier rhodophyte genus *Stromatella* (Kormann & Sahling 1985) is invalid.

Thermutis Fr., Systema Orbis Vegetabilis 1: 302. 1825. MycoBank MB 5447. Fig. 22E.

Type species: *Thermutis velutina* (Ach.) Flot., Linnaea 23: 170. 1850. MycoBank MB 407527.

Notes: A monotypic genus and species having filamentous thalli with *Scytonema* cyanobionts surrounded by hyphal collar and pycnoascocarps with biatorine margin. It is phylogenetically related to crustose species with pycnoascocarps (*Paracyphus*) and typical apothecia (*Lapismalleus lugubris*).

Thyrea A. Massal., Sched. Crit. Lich. Exsicc. (Veronae): 75. 1856. MycoBank MB 5462. Fig. 22C, D.

Type species: *Thyrea plectopsora* A. Massal., Sched. Crit. Lich. Exsicc. (Veronae): 75. 1856. MycoBank MB 407586.

Notes: See notes under *Digitothyrea*. Type material of *Thyrea plicatissima* is sterile (Moreno & Egea 1992a), therefore its position cannot be inferred from morphology alone. The placement of tropical species *T. leptophylla*, *T. porphyrella* and recently described *T. pulverulenta* (Kitaura *et al.* 2023) in this genus seems plausible based on available data. Both species, *Pseudocarpon persimile* and *Watsoniomyces obsoletus*, form a clade with *Thyrea*, containing *T. confusa*, *T. plectopsora* and *T. girardii*, characterized by pycnoascocarps and having squamulose-peltate or foliose-umbilicate thalli. *Watsoniomyces obsoletus* has been recently included in the *Lichinomycetes* and is characterized by having an endolithic thallus, growing on chalk pebbles in disturbed habitats (Díaz-Escandón *et al.* 2021). The authors were not able to ascertain which of the three ascoma ontogeny it has, but it is suspected to be thallinocarpic. Based on material studied by us (material from M. Powell) we can at least exclude thallinocarps, but could not find ascoma initials that would allow to distinguish between pathways leading to pycnoascocarps or typical apothecia.

Jenmania osorioi shares several features with *Thyrea* (squamulose to foliose growth form, ecorticate thallus with a central hyphal strand, pycnoascocarps), whereas the type *J. goebelii* differs in the distinctly corticate thallus and formation of typical apothecia originating from a tangle of generative hyphae. While Henssen (1963a, b, 1969b, 1980) accepted genera with species that deviate in the ascoma formation, our phylogeny shows that species of *Lempholemma*, *Lichina* and *Pterygiopsis* differing in the ascoma ontogeny are not closely related. We also confirm the placement of those species of *Thyrea* that do not form pycnoascocarps into the new genus *Digitothyrea* proposed by Moreno & Egea (1992b) based on morphological evidence. Our attempts to sequence material of *J. osorioi* failed, but because the species shares many more features with *Thyrea* than with *Jenmania* – especially the ascoma ontogeny type – we propose to recombine it into the former genus.

New combination in *Thyrea*:

Thyrea osorioi (Henssen) M. Schultz, ***comb. nov.*** MycoBank MB 852372.
Basionym: *Jenmania osorioi* Henssen, Lichenologist 5: 447. 1973. MycoBank MB 342351.

Tichocyphus M. Schultz & M. Prieto, ***gen. nov.*** MycoBank MB 852373. Fig. 30.

Etymology: Highlights the resemblance with *Psorotichia* in the crustose thallus shape and with *Porocyphus* in the concave discs of the apothecia.

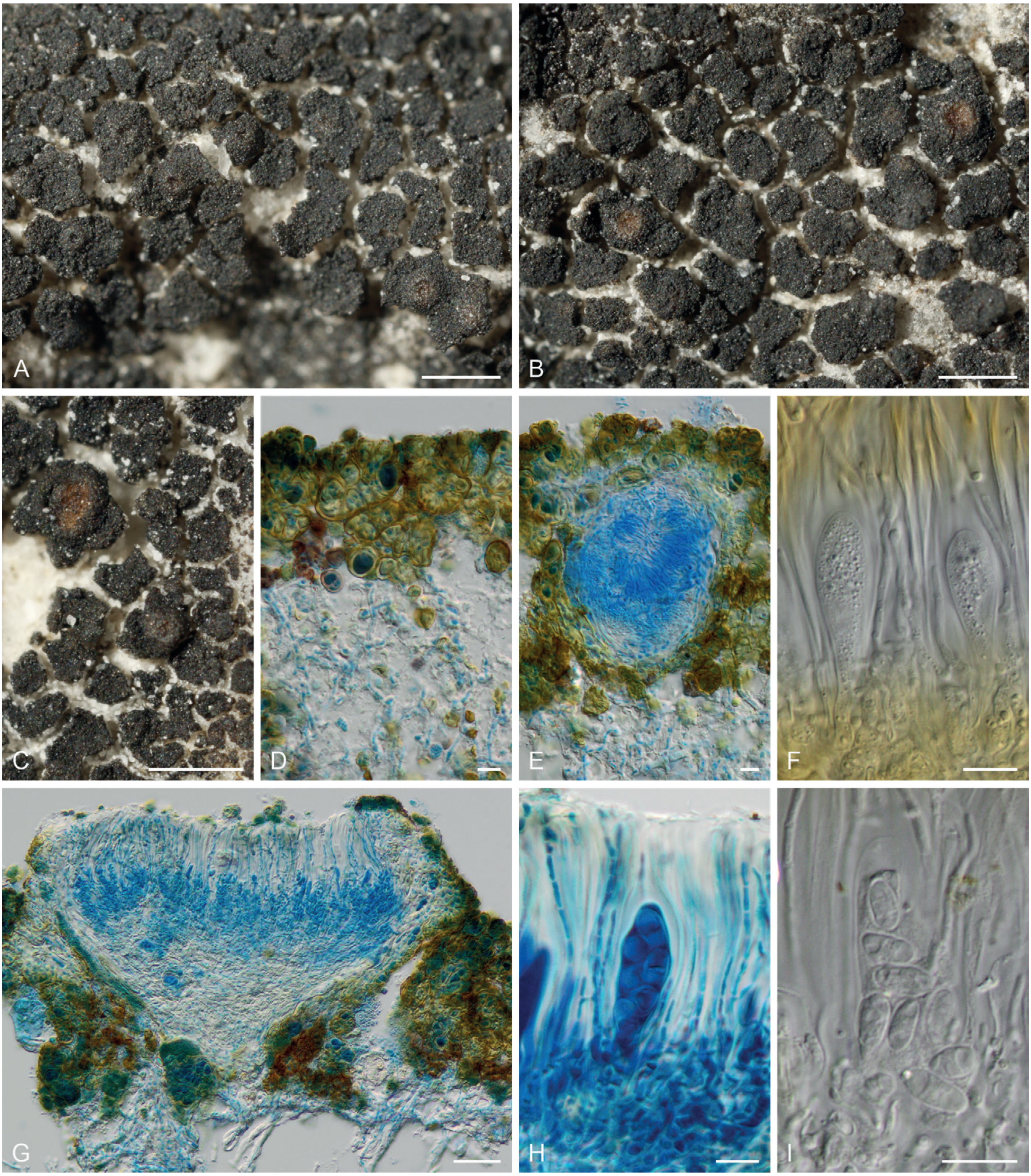

Fig. 30. *Tichocyphus gotlandicus*. **A.** Thallus areoles angulate with finely granulose surface texture, mature apothecia with pale brownish discs (Schultz 05538b, holotype). **B.** Juvenile, semi-immersed apothecia with narrow, concave discs (Schultz 05534, paratype). **C.** Mature apothecium top left with thalline margin and juvenile apothecium center right with still indistinct thalline margin and narrow, concave disc (Schultz 055569, paratype). **D.** Thallus compact paraplectenchymatous in upper part and loose hyphal reticulum towards the base in LPCB (Schultz 05538b, holotype). **E.** Marginal section of pycnidium with small conidia released and tangle of generative hyphae formed at the base of pycnidial cavity as earliest stage of ascoma development in LPCB. **F.** Juvenile, thin-walled asci in KOH. **G.** Section of mature apothecium with low thalline margin and rather distinct, pale excipulum proprium, subhymenium and hypothecium extending downwards as a stipe in LPCB (Schultz 055569, paratype). **H.** Section of hymenium, clavate asci with ascospores and septate, sparsely branched paraphyses in LPCB (Schultz 05538b, holotype). **I.** Simple, ellipsoid ascospores in KOH. Scale bars: A–C = 0.5 mm; D–F, H, I = 10 µm; G = 25 µm.

Type species: ***Tichocyphus gotlandicus*** M. Schultz & M. Prieto, ***sp. nov.*** MycoBank MB 852374.

Diagnosis: Belonging to the *Porocyphaceae*. Crustose areolate to subsquamulose, blackish cyanolichen with areoles ± distinctly divided into a compact paraplectenchymatous upper layer containing the cyanobionts and the loose basal layer with robust reticulate hyphae. Resembling *Porocyphus*, *Psorotichia* and *Thelignya* but differing from the former in the (semi)immersed apothecia, from the latter two in the formation of pycnoascocarps and from *Thelignya* in the coccoid cyanobionts. Deviating from all these genera in the *Peccania* type asci and formation of a medulla or basal layer devoid of cyanobiont cells.

Typus: **Sweden**, Gotland, Skarphagen 2 km SW of Ireviken and Ire, alvar-like area just S of road, on exposed rock surface, limestone, 57.822871°N, 18575295°E, 35 m a.s.l., 9 Jul. 2013, *M. Schultz & M. Prieto*, Schultz 05538b (**holotype** HBG-015244).

Description: *Thallus* deeply black, crustose, areolate, areoles sharply angulate (Fig. 30A–C), regularly increasing in size from 0.12 mm at the thallus margin to up to 0.72 mm in the thallus center, thin to thickened, 150–250 µm, sharply angulate, plane or with slightly lifted margins and then resembling tiny squamules, surface with very finely roughened texture, dull to slightly glossy, affixed to the substrate by rhizohyphae. Thallus ecorticate with two, ± distinctly separated layers (Fig. 30D, E, G), upper layer dark coloured, 42–100(–120) µm high, compact paraplectenchymatous with dense network of small, short celled hyphae surrounding the photobionts, cells 2.5–4 × 1.5–2.5 µm, lower layer pale, 100–170 µm high, a loose network of irregular, somewhat elongated, robust hyphae and devoid of photobiont cells forming a medulla, hyphal cells thick walled, 4.5–6 × 2–4 µm, cyanobiont a coccoid cyanobacterium, cells ± globose, arranged in irregular colonies forming packets, surrounded by a thin, yellowish brown gelatinous sheath, 5.5–10.5 µm with sheath, 3.5–7 µm without sheath, accessory cyanobacteria and other microorganisms repeatedly observed. *Apothecia* small, 0.12–0.24 mm, 1(–2) per areole, roundish, at first immersed, becoming semi immersed, finally adnate with broad base but only slightly elevated above the areole surface (Fig. 30A–C), zeorine with thin and shallow, sometimes indistinct thalline margin , 40–45 µm thick and a distinct, pale proper exciple, laterally and basally 6.5–11.5 µm thick, apically distinctly widened and 35–75 µm thick (Fig. 30G), disc dark reddish brown, at first punctiform becoming slightly expanded, concave, not umbonate, epihymenium pale yellowish brown to almost colourless, hymenium hyaline, 71.5–81.5 µm high, KOH/IKI+ distinctly blue, *paraphyses* distinct, straight, septate, somewhat branched and anastomosing towards the tips, 4.5–7 × 1–1.5 µm, terminal cells somewhat widened, 5–7 × 2.5–3.5 µm, *asci* clavate (Fig. 30F, H), short to somewhat elongated, 40–50 × 8.5–12 µm, wall thin but with compact outer, gelatinous coat that stains deeply blue in Lugol's solution after pretreatment with KOH, *Peccania* type, 8-spored, subbiseriate, *ascospores* simple, hyaline, broad ellipsoid (Fig. 30H, I), thin walled but becoming somewhat thickened with age, 7–11.5 × 5–7 µm, subhymenium and hypothecium extending downwards as a short, broad stipe (Fig. 30G), pycnoascocarps, ascogones formed beneath pycnidia (Figs 2F, 30E). *Pycnidia* immersed, broad elliposoid, at first 60–67.5 × 50–51.5 µm, becoming enlarged when ascogones are formed, 125 × 75 µm, *conidia* small, ellipsoid to short bacilliform, 2.5–3 × 1 µm, terminally formed on simple conidiophores. Grows on calcareous rocks along margins of shallow pools in alvar areas. So far only known from Gotland (Sweden). Secondary metabolites detectable by TLC not tested.

Additional specimens studied: **Sweden**, Gotland, Skarphagen 2 km SW of Ireviken and Ire, alvar-like area just S of road, on exposed rock surface, limestone, 57.822871°N, 18575295°E, 35 m a.s.l., 9 Jul. 2013, *M. Schultz & M. Prieto*, Schultz 05534 (**paratype** HBG-015553); Gotland, 11 km E of Lärbro, 1 km S of Kyllaj, coastal cliff area, on exposed rock surface, limestone, 57.740689°N, 18.949482°E, 3 m a.s.l., 10 Jul. 2013, *M. Schultz & M. Prieto* (**paratype** Schultz 05569 (S)).

Notes: Phylogenetically related with a clade composed of *Thyrea* and *Pseudocarpon persimile* (both pycnoascocarps) as well as *Watsoniomyces* (unknown ascoma ontogeny type, but not thallinocarps). A peculiar lichen that was only rarely found in fertile condition. The external growth form resembles species of *Psorotichia* (black areolate crust) but also *Thelignya lignyota* (small, semi-immersed apothecia) especially when the fertile areoles become subsquamulose. However, differing from both in the formation of pycnoascocarps and evidently more closely related with *Porocyphus*.

Watsoniomyces D. Hawksw., M. Powell & T. Sprib., Fungal Biol. 125: 501. 2021. MycoBank MB 558104. Fig. 1B.

Type species: *Watsoniomyces obsoletus* (Nyl.) M. Powell & T. Sprib., Fungal Biol. 125(7): 501. 2021. MycoBank MB 558105.

Notes: A new genus recently established for an enigmatic, endolithic lichen that has been shown to fall into *Lichinomycetes.* In the phylogenetic analysis it is closest to *Thyrea* and *Pseudocarpon*, but also related with the *Porocyphus*-*Ephebe*-*Lempholemma* clade.

Genera excluded from *Lichinomycetes*

Finkia is excluded from the *Lichinomycetes* based on type material studies. Its identity will be dealt with elsewhere.

Harpidium and *Euopsis* are evidently closely related, and Hafellner (1984) established the family *Harpidiaceae* for them. However, based on unpublished data and preliminary results from Amo *et al.*, both genera fall outside the *Lichinomycetes.* This is in contrast to Henssen *et al.* (1987), who did not accept *Harpidiaceae* and put *Harpidium* and *Euopsis* into *Lichinaceae* (*Lichinales*). Their placement among lineages basal to the *Lecanoro*- and *Eurotiomycetes* is currently under study.

Epiphloea was considered a member of the *Heppiaceae* by Jørgensen (2007). Schultz *et al.* (2015) showed that the two species included in *Epiphloea* belong to *Collemataceae* instead, falling into *Leptogium* as circumscribed by Otálora *et al.* (2013).

Lichinodium was considered a member of the *Ephebaceae* and included in *Lichinaceae* by Henssen (1963a). Prieto *et al.* (2019) revealed that *Lichinodium* is the only lichen forming lineage within *Leotiomycetes* and it is currently classified in the family *Lichinodiaceae*.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

REFERENCES

Arnold F (1864). Lichenen aus dem südöstlichen Tirol, gesammelt von L. Molendo. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* **14**: 459–462.

Altekar G, Dwarkadas S, Huelsenbeck JP, *et al.* (2004). Parallel Metropolis-coupled Markov chain Monte Carlo for Bayesian phylogenetic inference. *Bioinformatics* **20**: 407–415.

Ayres DL, Darling A, Zwickl DJ, *et al.* (2012). BEAGLE: an application programming interface and high-performance computing library for statistical phylogenetics. *Systematic Biology* **61**: 170–173.

Beimforde C, Feldberg K, Nylinder S, *et al.* (2014). Estimating the phanerozoic history of the *Ascomycota* lineages: combining fossil and molecular data. *Molecular Phylogenetics and Evolution* **77**: 307–319.

Bogarín D, Pérez-Escobar OA, Karremans AP, *et al.* (2019). Phylogenetic comparative methods improve the selection of characters for generic delimitations in a hyperdiverse Neotropical orchid clade. *Scientific Reports* **9**: 15098.

Bubrick P (1978). *Studies on the phycobionts of desert cyanolichens: Parts I and II.* Ph.D. dissertation, Florida State University, USA.

Büdel B (1982). *Phycobionten der Lichinaceen.* Dissertation, Philips Universität, Marburg, Germany.

Büdel B (1983). *Chroococcidiopsis* (*Cyanophyceae*), a phycobiont in the lichen family *Lichinaceae*. *Phycologia* **22**: 367–375.

Büdel B (1985). Blue-green phycobionts in the lichen family *Lichinaceae*. *Archiv für Hydrobiologie*, *Supplement* **71**: 355–357.

Büdel B (1987). Taxonomy and biology of the lichen genus *Peltula* Nyl. *Bibliotheca Lichenologica* **25**: 209–217.

Büdel B, Elix JA (1997). *Peltula langei* Büdel *et* Elix *spec. nov.* from Australia, with remarks on its chemistry and the ascoma of *Peltula clavata* (Krempelh.) Wetm. *Bibliotheca Lichenologica* **67**: 3–9.

Büdel B, Henssen A (1983). *Chroococcidiopsis* (*Cyanophyceae*), a phycobiont in the lichen family *Lichinaceae*. *Phycologia* **22**: 367–375.

Büdel B, Schultz M (2011). *Pseudopeltula necrocorticata sp. nova*, a new species in the cyanolichen order *Lichinales* with an unusual thallus morphology. *Bibliotheca Lichenologica* **106**: 15–20.

Büdel B, Darienko T, Deutschewitz K, *et al.* (2009). South African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microbial Ecology* **57**: 229–247.

Castresana J (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**: 540–552.

Clauzade G, Roux C (1985). Likenoj de Okcidenta Eŭropo. Illustrita determinlibro. *Bulletin de la Société Botanique du Centre-Ouest, Nouvelle Série - Numéro Spécial* **7**: 1–893.

Clements FE (1909). *The Genera of Fungi*, 1st edn. The HW Wilson Company, USA.

Chrismas N, Tindall-Jones B, Jenkins H, *et al.* (2024). Metatranscriptomics reveals diversity of symbiotic interaction and mechanisms of carbon exchange in the marine cyanolichen *Lichina pygmaea*. *New Phytologist* **241**: 2243–2257.

Crombie (1874). Revision of the British Collemacei. *Journal of Botany* **12**: 330–337.

Degelius G (1954). The lichen genus *Collema* in Europe. *Symbolae Botanicae Upsaliensis* **20**: 1–499.

Díaz-Escandón D, Hawksworth DL, Powell M, *et al.* (2021). The British chalk specialist *Lecidea lichenicola* auct. revealed as a new genus of *Lichinomycetes*. *Fungal Biology* **125**: 495–504.

Díaz-Escandón D, Tagirdzhanova G, Vanderpool G, *et al.* (2022). Genome-level analyses resolve an ancient lineage of symbiotic ascomycetes. *Current Biology* **32**: 5209–5218.

Douady CJ, Delsuc F, Boucher Y, *et al.* (2003). Comparison of Bayesian and maximum likelihood bootstrap measures of phylogenetic reliability. *Molecular Biology and Evolution* **20**: 248–254.

Drummond AJ, Suchard MA, Xie D, *et al.* (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29**: 1969–1973.

Ellis LT (1981). A revision and review of *Lemmopsis* and some related species. *The Lichenologist* **13**: 123–139.

Erichsen CFE (1940). Lichenologische Beiträge III. *Annales Mycologici* **38**: 303–331.

Eriksson OE (1981). The families of bitunicate *Ascomycetes*. *Opera Botanica* **60**: 1–209.

Eriksson OE (2000). Notes on ascomycete systematics Nos 2940–3127. *Myconet* **5**: 1–35.

Eriksson OE, Hawksworth DL (1998). Outline of the ascomycetes-1998. *Systema Ascomycetum* **16**: 83–301.

Fink B, Fuson SC (1918). Ascomycetes new to the Flora of Indiana. *Proceedings of Indiana Academy of Science* **1918**: 264–275.

Forssell KBJ (1885). *Beiträge zur Kenntniss der Anatomie und Systematik der Gloeolichenen*. Stockholm, Sweden.

Golubkova A (1970). De stationibus primis generis *Gonohymenia* Steiner in URSS. *Novitates Systematicae Plantarum on Vascularium* **7**: 266–273.

Gyelnik V (1935). De familia Heppiacearum, II. *Feddes Repertorium specierum novarum regni vegetabilis* **38**: 307–313.

Hafellner J (1984). Studien in Richtung einer natürlicheren Gliederung der Sammelfamilien *Lecanoraceae* und *Lecideaceae*. *Beihefte Nova Hedwigia* **79**: 241–371.

Henssen A (1963a). Eine Revision der Flechtenfamilien *Lichinaceae* und *Ephebaceae*. *Symbolae Botanicae Upsaliensis* **18**: 1–123.

Henssen A (1963b). Drei neue Arten der Flechtengattung *Phylliscum*. *Svensk Botanisk Tidskrift* **57**: 145–160.

Henssen A (1969a). Three non-marine species of the genus *Lichina*. *The Lichenologist* **4**: 88–98.

Henssen A (1969b). An interesting new species of *Lempholemma* from Canada. *The Lichenologist* **4**: 99–104.

Henssen A (1977). The genus *Zahlbrucknerella*. *The Lichenologist* **9**: 17–46.

Henssen A (1980"1979"). Problematik der Gattungsbergrenzung bei den Lichinaceen. *Berichte der Deutschen Botanischen Gesellschaft* **92**: 483–506.

Henssen A (1986). The genus *Paulia* (*Lichinaceae*). *The Lichenologist* **18**: 201–229.

Henssen A (1989). *Metamelanea* and *Stromatella*, new genera of *Lichinaceae*. *The Lichenologist* **21**: 101–118.

Henssen A (1990a). *Lichenes Cyanophili et Fungi Saxicolae Exsiccati ausgegeben von Aino Henssen. Fasc. II, Nos. 26-50.* Fachbereich Biologie der Philipps-Universität, Marburg, Germany.

Henssen A (1990b). *Thermutopsis jamesii*, a new member of the *Lichinaceae* from Antigua. *The Lichenologist* **22**: 253–259.

Henssen A (1994). Contribution to the morphology and species delimitation in *Heppia sensu stricto* (lichenized *Ascomycotina*). *Acta Botanica Fennica* **150**: 57–73.

Henssen A (1995). The new lichen family *Gloeoheppiaceae* and its genera *Gloeoheppia*, *Pseudopeltula* and *Gudelia* (*Lichinales*). *The Lichenologist* **27**: 261–290.

Henssen A, Büdel B (1984). *Phyllisciella*, a new genus of the *Lichinaceae*. *Beihefte Nova Hedwigia* **79**: 381–398.

Henssen A, Büdel B (1986). No.115. *Lichinales* Henssen and Büdel *ordo nov*. In: *Notes on ascomycete systematics, nos. 1–224* (Eriksson OE, Hawksworth DL, eds). *Systema Ascomycetum* **5**: 138.

Henssen A, Büdel B, Titze A (1987). *Euopsis* and *Harpidium*, genera of the *Lichinaceae* (Lichenes) with rostrate asci. *Botanica Acta* **101**: 49–55.

Henssen A, Büdel B, Wessels D (1985). New or interesting members of the *Lichinaceae* from southern Africa I. Species from northern and eastern Transvaal. *Mycotaxon* **22**: 169–195.

Henssen A, Jahns HM (1974). *Lichenes. Eine Einführung in die Flechtenkunde*. Georg Thieme Verlag, Stuttgart, Germany.

Henssen A, Jørgensen PM (1990). New combinations and synonyms in the *Lichinaceae*. *The Lichenologist* **22**: 137–147.

Hertel H (1967). Revision einiger calciphiler Formenkreise der Flechtengattung *Lecidea*. *Beihefte Nova Hedwigia* **24**: 1–155.

Huelsenbeck JP, Ronquist F (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **17**: 754–755.

Jaklitsch WM, Baral HO, Lücking R, Lumbsch HT (2016). *Ascomycota*. In: *Syllabus of Plant Families – Adolf Engler's Syllabus der Pflanzenfamilien* (Frey W, ed). Borntraeger, Stuttgart, Germany: 1–322.

Janex-Favre MC (1967). L'ontogénie et l'organisation des ascocarpes des *Lichina*, et la position systématique de ces lichens. *Bulletin de la Société Botanique de France* **114**: 145–162.

Jørgensen PM (2007) *Lichinales*. In: *Nordic Lichen Flora. Volume 3. Cyanolichens* (Ahti T, Jørgensen PM, Kristinsson H, *et al.*, eds). Nordic Lichen Society, Uddevalla, Sweden: 46–76.

Jørgensen PM, Santesson R (1989). Proposal to conserve *Anema* Nylander ex Forssell against *Omphalaria* Massalongo (Lichenes). *Taxon* **38**: 303–304.

Jørgensen PM, Henssen A (1990). Proposal to conserve *Pyrenopsis* (Nyl.) Nyl., and nomenclatural comments on some related genera (lichenized fungi). *Taxon* **39**: 343–348.

Jung P, Brust K, Schultz M, *et al.* (2021). Opening the Gap: rare lichens with rare cyanobionts – unexpected cyanobiont diversity in cyanobacterial lichens of the order *Lichinales*. *Frontiers in Microbiology* **12**: 728378.

Katoh K, Toh H (2008). Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* **9**: 286–298.

Kauff F, Bachran A, Schultz M, *et al.* (2018). Molecular data favours a monogeneric *Peltulaceae* (*Lichinomycetes*). *The Lichenologist* **50**: 313–327.

Kitaura MJ, Scur MC, Lorenz AP (2023). A new species of *Thyrea* (*Lichinales*: *Lichinaceae*) from the Brazilian central-west region. *Anales de Biología* **45**: 43–51.

Körber, GW (1855). *Systema Lichenum Germaniae*. Breslau.

Kondratyuk SY, Lokös L, Halda JP, *et al.* (2016). New and noteworthy lichen-forming and lichenicolous fungi 4. *Acta Botanica Hungarica* **58**: 75–136.

Kornmann P, Sahling HP (1985). Erythropeltidaceen (*Bangiophyceae*, *Rhodophyta*) von Helgoland. *Helgoländer Meeresuntersuchungen* **39**: 213–236.

Lanfear R, Frandsen PB, Wright AM, *et al.* (2017). PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34**: 772–773.

Lange OL (1958). Einige neue *Gonohymenia*-Art (Lichenes) aus Mauretanien und ihre Stellung innerhalb der Gattung. *Berichte der Deutschen Botanischen Gesellschaft* **71**: 293–303.

Larsson A (2014). AliView: A fast and lightweight alignment viewer and editor for large datasets. *Bioinformatics* **30**: 3276–3278.

Lewis JC, Schultz M (2019). *Lempholemma syreniarum* (*Lichinaceae*), a new species from Ontario, Canada. *The Bryologist* **122**: 423–429.

Liu YJ, Whelen S, Hall BD (1999). Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. *Molecular Biology and Evolution* **16**: 1799–1808.

Lücking R, Hodkinson BP, Leavitt SD (2016). The 2016 classification of lichenized fungi in the *Ascomycota* and *Basidiomycota* – Approaching one thousand genera. *The Bryologist* **119**: 361–416.

Lumbsch HT, Ahti T, Altermann S, *et al.* (2011). One hundred new species of lichenized fungi: a signature of undiscovered global diversity. *Phytotaxa* **18**: 1–127.

Lutzoni F, Wagner P, Reeb V, Zoller S (2000). Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. *Systematic Biology* **49**: 628–651.

Maddison WP, Maddison DR (2019). Mesquite: a modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org

Makryi TV (1992). Species duae novae *Gonohymeniae* Steiner e regionibus Mari Baicalensi adjacentibus. *Novosti Sistematiki Nizshikh Rastenii* **28**: 112–118.

Massalongo AB (1856). *Miscellanea lichenologica*. Verona-Milano, Italy.

Miller MA, Pfeiffer W, Schwartz T (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans, LA, pp 1–8.

Moreno PP, Egea JM (1991). *Biología y taxonomía de la familia Lichinaceae, con especial referencia a las especies del S.E. Español y Norte de África.* Universidad de Murcia, Secretariado de Publicaciones, Spain.

Moreno PP, Egea JM (1992a). Estudios sobre el complejo *Anema-Thyrea-Peccania* en el sureste de la Península Ibérica y norte de Africa. *Acta Botanica Barcinonensia* **41**: 1–66.

Moreno PP, Egea JM (1992b). *Digitothyrea*, a new genus in the family *Lichinaceae*. *The Lichenologist* **24**: 215–228.

Moreno PP, Egea JM (1992c). El género *Lichinella* Nyl. en el sureste de España y norte de Africa. *Cryptogamie. Bryologie, lichenologie* **13**: 237–259.

Moreno PP, Egea JM (1994). El género *Psorotichia* y especies próximas en el sureste de España y norte de Africa. *Bulletin de la Société linnéenne de Provence* **45**: 291–308.

Nguyen LT, Schmidt HA, von Haeseler A, *et al.* (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* **32**: 268–274.

Nylander W (1857). Prodromus lichenographicae Galliae et Algeriae. *Actes de la Société Linnéenne de Bordeaux* **21**: 249–267.

Nylander W (1861). *Lichenes Scandinaviae (sive Prodromus Lichengraphiae Scandinaviae)*. Helsinki, Finland.

Nylander W (1867). Addenda nova ad Lichenographiam europaeam. Continuatio secta. *Flora* **50**: 369–374.

Nylander W (1873) Addenda nova ad Lichenographiam europaeam. Continuatio quinta decima. *Flora* **56**: 17–23.

Nylander W (1881) Addenda nova ad Lichenographiam europaeam. Continuatio quinta et tricesima. *Flora* **64**: 2–8.

Oliveira Junior I de, Aptroot A, Cavalcante JG, *et al.* (2020). Two further new lichen species from the Atlantic rain forest remnant Pedra Talhada (Alagoas, Brazil), with a list of species. *The Bryologist* **123**: 617–632.

Otálora M, Aragón G, Martínez I, Wedin M (2013). Cardinal characters on a slippery slope - A re-evaluation of phylogeny, character evolution, and evolutionary rates in the jelly lichens (*Collemataceae s. str.*). *Molecular and Phylogenetic Evolution* **68**: 185–198.

Ozenda P, Clauzade G (1970). *Les Lichens. Étude Biologique et Flore Illustrée*. Paris Masson, France.

Prieto M, Baloch E, Tehler A, *et al.* (2013). Mazaedium evolution in the *Ascomycota* (*Fungi*) and the classification of mazaediate groups of formerly unclear relationship. *Cladistics* **29**: 296–308.

Prieto M, Schultz M, Olariaga I, *et al.* (2019). *Lichinodium* is a new lichenized lineage in the *Leotiomycetes*. *Fungal Diversity* **94**: 23–39.

Prieto M, Wedin M (2013). Dating the diversification of the major lineages of *Ascomycota* (*Fungi*). *PLoS ONE* **8**: e65576.

Prieto M, Wedin M (2017). Phylogeny, taxonomy and diversification events in the *Caliciaceae*. *Fungal Diversity* **82**: 221–238.

Prieto M, Westberg M, Schultz, M (2015). New records of *Lichinomycetes* in Sweden and the Nordic countries. *Herzogia* **28**: 142–152.

Printzen C, von Brackel W, Bültmann H, *et al.* (2022). Lichens, lichenicolous and allied fungi of Germany – a revised checklist. *Herzogia* **35**: 193–393.

Rambaut A, Drummond AJ (2007). Tracer v1.4. http://beast.bio.ed.ac.uk/Tracer

Revell LJ (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.

Ronquist F, Huelsenbeck JP (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Ronquist F, Teslenko M, van der Mark P, *et al.* (2012). MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Systematic Biology* **61**: 539–542.

Roullier C, Chollet-Krugler M, van de Weghe P, *et al.* (2010). A novel aryl-hydrazide from the marine lichen *Lichina pygmaea*: isolation, synthesis of derivatives, and cytotoxicity assays. *Bioorganic and Medicinal Chemistry Letters* **20**: 4582–4586.

Sanad H, Belattmania Z, Nafis A, *et al.* (2022). Chemical composition and *in vitro* antioxidant and antimicrobial activities of the marine cyanolichen *Lichina pygmaea* volatile compounds. *Marine Drugs* **20**: 169.

Sanders WB, Masumoto H (2021). Lichen algae: the photosynthetic partners in lichen symbioses. *The Lichenologist* **53**: 347–393.

Schoch CL, Sung G-H, López-Giráldez F, *et al.* (2009). The *Ascomycota* tree of life: a phylum wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Systematic Biology* **58**: 224–239.

Schmitt I, Crespo A, Divakar PK, *et al.* (2009). New primers for promising single-copy genes in fungal phylogenetics and systematics. *Persoonia* **23**: 35–40.

Schultz M (2003). *Lempholemma socotranum*, a new species of the *Lichinaceae* from Socotra (Yemen, Indian Ocean). *Bibliotheca Lichenologica* **86**: 155–159.

Schultz M (2004). *Pterygiopsis pulchra*, a remarkable new species of the *Lichinaceae* from south-eastern Yemen. *Bibliotheca Lichenologica* **88**: 555–560.

Schultz M (2005). An overview of *Lichinella* in the southwestern United States and northwestern Mexico, and the new species *Lichinella granulosa*. *The Bryologist* **108**: 567–590.

Schultz M (2006). *Pterygiopsis cava* and *P. mutabilis* (*Lichinaceae*), two new species from southwestern United States and northwestern Mexico. *The Bryologist* **109**: 68–79.

Schultz M (2007). On the identity of *Anema dodgei*, *Psorotichia segregata* and *Psorotichia squamulosa*, three misunderstood cyanolichens from the southwestern United States. *The Bryologist* **110**: 286–294.

Schultz M (2014). Significant type collections of *Lichinaceae* and allied lichenized ascomycetes in the herbaria of the Natural History Museum, Vienna (W) and the Institute of Botany, Vienna University (WU). *Annalen des Naturhistorischen Museums in Wien. Serie B, Für Botanik und Zoologie* **116**: 207–246.

Schultz M, Aptroot A (2008). Notes on poorly known, small cyanobacterial lichens from predominantly wet tropical to subtropical regions. *Sauteria* **15**: 433–458.

Schultz M, Arendholz W-R, Büdel B (2001). Origin and evolution of the lichenized Ascomycete order *Lichinales*: monophyly and systematic relationships inferred from ascus, fruiting body and SSU rDNA evolution. *Plant Biology* **3**: 116–123.

Schultz M, Büdel B (2002). Key to the genera of the *Lichinaceae*. *The Lichenologist* **34**: 39–62.

Schultz M, Büdel B (2003). On the systematic position of the genus *Heppia* in the *Lichinales*. *The Lichenologist* **35**: 151–156.

Schultz M, Porembski S, Büdel B (2000). Diversity of rock-inhabiting cyanobacterial lichens: Studies on granite inselbergs along the Orinoco and in Guyana. *Plant Biology* **2**: 482–495.

Schultz M, Wedin M, Diel H, *et al.* (2015). *Epiphloea* belongs to *Collemataceae* (*Lecanoromycetes*, lichenized *Ascomycota*). *The Lichenologist* **47**: 369–378.

Shimodaira H (2002) An approximately unbiased test of phylogenetic tree selection. *Systematic Biology* **51**: 492–508.

Smith CW, Aptroot A, Coppins BJ, *et al.* (2009). *The Lichens of Great Britain and Ireland*. 2nd ed. The British Lichen Society, London, UK.

Spatafora J, Sung Gi-Ho, Johnson D, *et al.* (2006). A five-gene phylogeny of *Pezizomycotina*. *Mycologia* **98**: 1018–1028.

Stamatakis A (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1131.

Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* **56**: 564–577.

Tehler A (1996). Systematics, phylogeny and classification. In: *Lichen Biology* (Nash TH III, ed). Cambridge University Press, Cambridge: 217–239.

Thüs H, Schultz M (2009). *Fungi: Lichens Pt. 1 (Süßwasserflora Von Mitteleuropa / Freshwater Flora of Central Europe)*. Spektrum Akademischer Verlag, Heidelberg, Germany.

Turland NJ, Wiersema JH, Barrie FR, *et al.* (eds) (2018). *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017.* Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.

Voglmayr H, Fournier J, Jaklitsch WM (2019). Two new classes of *Ascomycota*: *Xylobotryomycetes* and *Candelariomycetes*. *Persoonia* **42**: 36–49.

Wijayawardene NN, Hyde KD, Al-Ani LKT, *et al.* (2020). Outline of Fungi and fungus-like taxa. *Mycosphere* **11**: 1060–1456.

Wirth V, Hauck M, von Brackel W, *et al.* (2011). Rote Liste und Artenverzeichnis der Flechten und flechtenbewohnenden Pilze Deutschlands. *Naturschutz und Biologische Vielfalt* **70**: 7–122.

Wirth, V, Hauck M, Schultz M (2013). *Die Flechten Deutschlands, Band 2.* Ulmer, Stuttgart, Germany.

Yang Q, Cheng X, Zhang T, *et al.* (2022). Five new species of the lichen-forming fungal genus *Peltula* from China. *Journal of Fungi* **8**: 134.

Zahlbruckner A (1906–1907). Lichenes (Flechten). B. Spezieller Teil. In: *Die Natürlichen Pflanzenfamilien 1(1*)* (Engler A, Prantl K, eds). Engelmann, Leipzig, Germany.

Zahlbruckner A (1926). Lichenes (Flechten). B. Spezieller Teil. In: *Die Natürlichen Pflanzenfamilien 1(1*), ed. 2* (Engler A, Prantl K, eds). Engelmann, Leipzig, Germany.

Zoller S, Scheidegger C, Sperisen C (1999). PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *The Lichenologist* **31**: 511–516.

Supplementary Material: https://studiesinmycology.org/

Table S1. Coding of selected characters used for ASR and SCM analysis.
Table S2. Ancestral state reconstruction of selected characters. Support is given as ML proportional likelihoods. Equivocal results are indicated with -.
Fig. S1. Maximum clade credibility chronogram resulting from the dating analysis. 95 % credibility intervals of divergence time estimates are showed.
Fig. S2. Ancestral state reconstruction scheme with taxon names.