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Gibbosporina, a new genus for foliose and tripartite, Palaeotropic *Pannariaceae* species previously assigned to *Psoroma*

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Abstract: Reports of '*Psoroma sphinctrinum*' from Palaeotropical areas are shown to represent instead species of the genus *Gibbosporina*, which is described here as new to science. This genus is superficially similar to tripartite, austral *Pannaria* species, such as the species now referred to as *Pannaria sphinctrina* (Mont.) Tuck. ex Hue. A phylogram based on an analysis of the nuclear large subunit rDNA (LSU) locus shows that *Gibbosporina* is instead a clade in a *Pannariaceae* branch referred to as the '*Physma* group', a most unexpected addition to *Pannariaceae* dealt with by several previous studies. Genera assigned to this group have very contrasting general appearances. However, this diverse group shares distinctly ring-like thalline excipular margins; strongly amyloid internal ascus structures; well-developed perispores which have irregular gibbae and/or nodulose or acuminate apical extensions, but not verrucae; lacks TLC-detectable secondary compounds and have tropical distributions. *Gibbosporina* is the only tripartite genus in the group, with distinct, nodulose, placodioid, mini-fruticose to mini-foliose cephalodia with a high diversity of *Nostoc* cyanobionts. The cyanomorphs can apparently exist independently in some cases, although the apothecia on such cephalodia on a specimen from Réunion were unexpectedly found to belong to the chloromorph. The genus and related genera forming the '*Physma* group' are probably evolutionarily old, and their weak affinity to the remaining part of *Pannariaceae*, concentrated in the Southern Hemisphere, is discussed. The genus includes 13 known species, and the generitype is *Gibbosporina boninensis* from the Japanese Ogasawara Islands, originally described as *Psoroma boninense* and recombined here. The following 12 species are described here as new to science, seven of them with molecular support in an LSU and ITS-based phylogram: *Gibbosporina acuminata* (Australia, the Philippines), *G. amphorella* (New Caledonia), *G. bifrons* (Malaysia, New Caledonia, the Philippines, Solomon Islands), *G. didyma* (Mauritius, Réunion), *G. elixii* (Australia), *G. leptospora* (Australia, Papua New Guinea), *G. nitida* (Australia, Papua New Guinea, the Philippines), *G. mascarena* (Mauritius, Réunion, Sri Lanka), *G. papillospora* (the Philippines), *G. phyllidiata* (Solomon Islands), *G. sphaerospora* (Australia, Indonesia, Malaysia, the Philippines, Samoa, and with *Psoroma sphinctrinum* var. *endoxanthellum* as a new synonym), and *G. thamnophora* (Australia and the Philippines). Except for the phyllidiate *G. phyllidiata* and for *G. thamnophora* which has cephalodia adapted for vegetative propagation, the species are all primarily fertile. A key for determining the species is provided.

Key words: biogeography, lichens, new taxa, *Nostoc*, photosymbiodemes, phylogeny, taxonomy

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Introduction

The introduction of molecular methods into the taxonomy of *Pannariaceae* has resulted in many surprising consequences. Ekman & Jørgensen (2002) showed that parts of the genera *Moelleropsis*, *Degelia* and *Fuscopannaria* did not belong to this family. Wedin *et al.* (2007, 2011) described the new families *Massalongiaceae* and *Vahliellaceae* with members previously placed within *Pannariaceae*, although Muggia *et al.* (2011) showed that *Polychidium* was heterogeneous, and they retransferred members of the

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reinstated genus *Leptogidium* from *Massalongaceae* to *Pannariaceae*. The new family *Koerberiaceae* described by Spribille & Muggia (2013) also includes ex-members of *Pannariaceae*. However, the family has also increased by the inclusion of genera previously belonging to *Collemataceae*. Wedin *et al.* (2009) showed that the genera *Leciophysma*, *Physma*, *Ramalodium* and *Staurolemma*, all with non-septate spores, have a phylogenetic position in *Pannariaceae* in spite of a strong gross morphological resemblance to *Collemataceae*. This conclusion was also subsequently reached independently by Otálora *et al.* (2010) in the case of *Physma* and *Staurolemma*. They also indicated that the genera *Homothecium* and *Leightoniella* might deserve a similar revised family affiliation; genera which still have not been studied genetically.

Two new phylogenetic studies on the family (Ekman *et al.* 2014; Magain & Sérusiaux 2014) confirmed the affiliation of the ex-*Collemataceae* genera and presented topologies of the family, both with two major, well-supported clades. One of these, the '*Parmeliella* s. str. clade', was well supported in both studies, and actually represents a still unrecognized family of its own, according to Spribille & Muggia (2013). The remaining samples of *Pannariaceae* were subdivided into three subgroups by both Ekman *et al.* (2014) and Magain & Sérusiaux (2014), including a subgroup with *Fuscopannaria* and neighbouring genera, defined in a similar way in both studies. The other subgroups were classified differently, a fact which can be partly attributed to the sequencing of different genes and taxa and partly to different major topics defined for the studies. *Psoroma* is a key genus in the process of redefining generic limits within *Pannariaceae*. It is now defined as species resembling its generitype *P. hypnorum* (Vahl) S. F. Gray, but was previously interpreted in a wider sense, including most tripartite species within the family. Several squamulose species have been transferred to the new genera *Joergensenia*, *Psorophorus*, and *Xanthopsoroma*, described with molecular support (Passo *et al.* 2008; Elvebakk *et al.* 2010). The austral foliose species have been transferred to *Pannaria*, for example by Jørgensen (2001) and Elvebakk & Galloway (2003). However, there are also foliose, tripartite species reported from many Paleotropical areas. *Psoroma sphinctrinum* (Mont.) Nyl. was reported from 'Insula Borbonia' (= Réunion), Mauritius and 'Promontorio Bonæ Spei' (in South Africa) by Nylander (1859). *Psoroma sphinctrinum* has now been shown to be a panaustral *Pannaria* species, known as *Pannaria sphinctrina* (Nyl.) Tuck. ex Hue (Elvebakk 2007, 2011). The only tripartite and foliose *Pannariaceae* species described exclusively from Palaeotropical areas is *Psoroma boninense* Kurok. from the Bonin Islands (= Ogasawara Gunto Islands) by Kurokawa (1969), in addition to *Pannaria lobulifera* Elvebakk, described from New Caledonia (Elvebakk 2007).

The first aim of the present study is to revise Paleotropical material of '*Psoroma*', which instead represents an undescribed genus, very distinct from *Pannaria*, as already indicated by Elvebakk (2007). During our initial studies of this group, we had the impression that this new tropical, ex-*Psoroma* genus included one or two widespread species, because the samples from widely separate geographical areas were found to be quite similar, except for cephalodium and spore morphology. However, we now conclude that the genus has a relatively high number of geographically differentiated species differing in several characters.

The previous transfer of tropical ex-*Collemataceae* genera to *Pannariaceae* by Wedin *et al.* (2009) and Otálora *et al.* (2010) has now been supported in the case of *Physma* by the new phylogenies presented by Magain & Sérusiaux (2014) and Ekman *et al.* (2014). The former study presented a separate '*Physma* group' represented by 20 sequences, 18 of these in a well-defined clade with species of *Physma*, *Parmeliella* s. lat. (now *Lepidocollema*) and a single 'tripartite *Pannaria*' sample from Réunion. The latter appeared to represent the undescribed genus which is the subject of the present study. Surprisingly, their '*Physma* group' included, although with low support,

two sequences of the very different genus *Xanthopsoroma*, which was a sister group to the remaining sequences. Ekman *et al.* (2014) included four sequences of *Physma* and *Parmeliella*, the latter transferred to the redefined genus *Lepidocollema*, in a well-supported branch, nested within the *Psoroma* clade ('Clade 2c').

The second objective of the present study is to examine the new genus phylogenetically, both for possible molecular support for some of the newly described species, and for affiliation with other genera of *Pannariaceae* in the present phylogeny as well as in the recently published phylogenies of the family.

Material and Methods

Taxon sampling and identification

Herbarium material used in this study is housed in ABL, BG, BM, CBG, PC, E, H, IRD, L, O, REU, S, TNS, TROM, TUR and UPS. A total of 119 samples were examined. In microscope sections, iodine reactions were tested by adding IKI to mounts pretreated with KOH (Orange *et al.* 2001). Perispore structures were studied in water mounts and restricted to spores liberated from the asci. Ascospore morphology was studied in detail by drawing detailed sketches of *c.* 880 ascospores from almost all collections, except for several samples of one species from the Solomon Islands housed at BM, where time did not permit this. The illustrations presented here aim to depict the variation in shape and size of ascospores within and between the species studied here (Fig. 7). Thin-layer chromatography of acetone extracts followed standard procedures and used solvents A and C (Culberson 1972; Orange *et al.* 2001). Nomenclature of ascospore structure follows Nordin (1997). Some of the type collections were also analyzed by HPLC following the procedure used by Bjerke *et al.* (2002).

Specimens, DNA extraction, and sequencing

Twenty-seven specimens including 19 samples of seven species of *Gibbosporina,* five samples comprising three *Physma* species, and three samples representing two *Lepidocollema* species, were newly sequenced for this study (Table 1). Successful sequencing included seven holotypes. Complete *Gibbosporina* voucher information is found where these samples are cited in the present paper. Reference sequences were selected to represent the major phylogenetic lineages of *Pannariaceae* recently published by Magain & Sérusiaux (2014) and Ekman *et al.* (2014), with clade names in the phylogram following those used by the former. Information on the previously published sequences included in Fig. 9 can be found in the tables of Elvebakk *et al.* (2010), Magain & Sérusiaux (2014) and Ekman *et al.* (2014). *Peltigera scabrosella* was included to root the tree. The freeze-dried lichen materials were ground using TissueLyser (Qiagen, Hilden, Germany) after freezing in liquid nitrogen, and genomic DNAs were extracted using FastDNA™ SPIN Kit for Soil (MP Biomedical, Santa Ana, California) according to the manufacturer's instructions. To determine phylogenetic relationships among lichenized fungi, amplification and sequencing of the ITS1, 5.8S, ITS2, and partial large subunit rDNA (LSU) were conducted using the ITS1F, ITS4, LR0R, and LR5 primers, following the procedures described in a previous study (Elvebakk *et al.* 2010). Sequences were deposited in the GenBank database under the accession numbers KM 887867–887893.

Phylogenetic analyses

Sequence alignment of ITS1, 5.8S, ITS2 and partial LSU was conducted by the program ClustalX (Larkin *et al.* 2007) and manually adjusted. Ambiguously aligned sites were excluded from the phylogenetic analyses. Phylogenetic trees were inferred from the datasets by neighbour-joining (NJ), maximum parsimony (MP), maximum likelihood (ML), and Bayesian analyses. The NJ tree was reconstructed using MEGA6 (Tamura *et al.* 2013) under Kimura's 2-parameter model (Kimura 1980). The MP tree was obtained using the Tree-Bisection-Regrafting (TBR) algorithm of MEGA6 with search level 5, in which the initial trees were obtained by the random addition of sequences (1000 replicates). The ML tree was searched for by using PhyML ver 3.1 (Guindon & Gascuel 2003) with the GTR + I + G evolutionary model (Lanave *et al.* 1984) and the search options of best tree topology finding by branch swapping of NNIs and SPRs, random addition of sequences (100 replicates), and parameter estimation for proportion of invariant and transition/transversion ratio. The Bayesian tree was searched for by MrBayes ver. 3.2 (Ronquist *et al.* 2012) with the GTR + I + G evolutionary model. Two parallel Markov chain Monte Carlo (MCMC) runs were performed, each with three heated chains and one cold chain, and the temperature parameter set to 0·1. Every 100th tree was sampled from 2 000 000 generations of analysis, and a consensus tree was calculated after discarding the first 25% trees as burn-in. The default search conditions were used for other options. The DNA evolutionary model was selected by AIC calculation implemented in jModelTest 2 (Darriba *et al.* 2012). Robustness of phylogenetic lineages was tested by posterior probability of Bayesian analysis and conservation in NJ, MP, and ML analyses. As the ITS sequences were hardly alignable among remotely related genera, phylogenetic relationships among genera of *Pannariaceae* were calculated based on LSU sequences only, and phylogenetic relationships among species of *Gibbosporina* were calculated based on combined sequences of ITS1, 5.8S, ITS2, and partial LSU.

TABLE 1. *Newly sequenced specimens in this phylogenetic study with locality information and GenBank accession number.*

Species and reference numbers	Locality and voucher information	GenBank Acc. No.
Gibbosporina amphorella Elvebakk & Hong		
NK-143	New Caledonia, 10 km NE of Nouméa, 8 Dec. 2005, *A. Elvebakk* 05:715 (TROM)	KM887882
NK-144	New Caledonia, 10 km NE of Nouméa, 8 Dec. 2005, *A. Elvebakk* 05:706 (TROM; S)	KM887883
NK-145	New Caledonia, 10 km NE of Nouméa, 8 Dec. 2005, *A. Elvebakk* 05:717 (PC—holotypus)	KM887884
NK-146	New Caledonia, 10 km NE of Nouméa, 8 Dec. 2005, *A. Elvebakk* 05:718 (IRD; PC; TROM; UPS)	KM887885
G. bifrons Elvebakk, Hong & P. M. Jørg.		
NK-166	New Caledonia, 10 km NE of Nouméa, 4 Dec. 2005, *A. Elvebakk* 05:614 (PC—holotypus)	KM887878
G. didyma Elvebakk, Hong & P. M. Jørg.		
NK-265	Réunion, *c.* 0·5 km E of the E end of Grand Étang, 17 Oct. 2011, *A. Elvebakk* 11:042(a) (PC—holotypus)	KM887875
NK-266	Réunion, *c.* 0·5 km E of the E end of Grand Étang, 17 Oct. 2011, *A. Elvebakk* 11:042(b) (PC—holotypus)	KM887876
G. elixii Elvebakk, Hong & P. M. Jørg.		
NK-172	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39884 (CANB—holotypus)	KM887879
G. mascarena Elvebakk, Hong & P. M. Jørg.		
NK-263	Réunion, *c.* 0·5 km E of the E end of Grand Étang, 17 Oct. 2011, *A. Elvebakk* 11:056 (PC—holotypus)	KM887880
NK-264	Réunion, *c.* 0·5 km E of the E end of Grand Étang, 17 Oct. 2011, *A. Elvebakk* 11:041 (TROM)	KM887881
G. nitida Elvebakk, Hong & P. M. Jørg.		
NK-154	Australia, Queensland, Wooroonooran National Park, 31 July 2006, *J. A. Elix* 39757 (CANB; BRI)	KM887886
NK-155	Australia, Queensland, Wooroonooran National Park, 31 July 2006, *J. A. Elix* 39757 (CANB; BRI)	KM887888
NK-170	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39886 (CANB; BRI)	KM887887
NK-171	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39883 (CANB—holotypus)	KM887889
NK-173	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39885 (CANB; BRI)	KM887890
NK-174	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39882 (CANB; BRI)	KM887891
NK-178	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 39880 (CANB; BRI)	KM887892
NK-179	Australia, Queensland, Mossman Gorge National Park, 1 Aug. 2006, *J. A. Elix* 398817 (CANB; BRI)	KM887893
G. sphaerospora Elvebakk & Hong		
NK-175	Australia, Queensland, Millaa Millaa Falls, 29 July 2006, *J. A. Elix* 39319 (CANB—holotypus)	KM887877
Lepidocollema brisbanense (C. Knight) P. M. Jørg.		
NK-253	New Caledonia SE, Prony, 2 Dec. 1995, *A. Elvebakk* 05:559 (TROM)	KM887867
L. stylophorum (Vain.) P. M. Jørg.		
NK-272	Réunion, below Mare Longue Nature Reserve, 24 Oct. 2011, *A. Elvebakk* 11:100 (TROM)	KM887868
NK-274	Réunion, below Mare Longue Nature Reserve, 24 Oct. 2011, *A. Elvebakk* 11:093 (TROM)	KM887869
Physma byrsaeum (Ach.) Tuck.		
NK-273	Réunion, below Mare Longue Nature Reserve, 24 Oct. 2011, *A. Elvebakk* 11:096 (TROM)	KM887874
P. radians Vain.		
NK-180	Seychelles, Mahé, Morne Seychelleois National Park, 10 Oct. 2008, *F. Schumm* 14658 & *J.-P. Frahm* (TROM)	KM887870
NK-268	Réunion, below Mare Longue Nature Reserve, 24 Oct. 2011, *A. Elvebakk* 11:095 (TROM)	KM887872
NK-270	Réunion, below Mare Longue Nature Reserve, 24 Oct. 2011, *A. Elvebakk* 11:097 (TROM)	KM887873
Physma sp.		
NK-162	New Caledonia, 10 km NE of Nouméa, 8 Dec. 2005, *A. Elvebakk* 05:694 (TROM)	KM887871

Results

Taxonomy

Gibbosporina Elvebakk, Hong & P. M. Jørg. gen. nov.

MycoBank No.: MB 811978

Pannariae similis, sed sine acidis lichenosis, apotheciis amylodeis asci tholis et perisporis gibbis tumescentibus praeditis; photobionte maiore viridi et cephalodiis cyanobionticis bene evolutis instructo.

Typus generis: *Gibbospora boninensis* (Kurok.) Elvebakk & P. M. Jørg.

(Figs 1–8)

Thallus foliose, pale greyish green when fresh, brown on old herbarium specimens, forming extensive, adpressed patches, partly developing distinct prothalli. *Upper cortex* distinct, forming a smooth, sometimes glossy upper surface; *lower cortex* lacking, but lower surface hyphae denser, running parallel to the lower surface.

Ascomata common, as large and substipitate apothecia with distinct, crenate thalline margins obscuring proper margins; *discs* reddish brown to orange-brown, dark brown on old, dry specimens. *Hymenium* colourless, IKI+ persistently deep blue, with paraphyses consisting of simple, septate hyphae which are apically thickened with external yellowish brown pigmentation. *Asci* clavate, apically with amyloid tube structures, 8-spored with simple, colourless, ellipsoid proper spores, surrounded by swelling, asymmetric and gibbose perispores.

Conidiomata rare, of protruding, black pycnidia of *Sticta*-type, producing bacilliform conidia 0·5–1·0 × 2–4 µm, laterally or terminally on short-celled conidiophores.

Major photobiont green, myrmecioid, but with *Nostoc*-containing laminal cephalodia which can be squamulose to nodulose, placodioid, mini-fruticose or mini-foliose, occasionally free-living with own rhizohyphae, but not yet observed completely independent with own cyanobiont apothecia.

Secondary chemistry. No acetone-soluble compounds detected by TLC and HPLC analysis.

Etymology. From Latin 'gibbus' (= 'with hump-like swellings'), which in combination with 'spora' refers to the unusual gibbose form of the perispores in most of the species.

Distribution and ecology. Corticolous in lowland and montane tropical and subtropical forests from central parts of the Pacific through SE Asia and NE Australia to Sri Lanka and Madagascar.

Gibbosporina acuminata Elvebakk sp. nov.

MycoBank No.: MB 811979

Gibbosporinae boninensi similis sed lobis impolitis vel debile nitidis, cephalodiis placodiodeis, adpressique, sporis angustioribus.

Typus: Australia, Queensland, Zillie Falls, 12 km by road NE of Millaa Millaa, 17°28'29"S, 145°39'22'E, 705 m elev., remnant rainforest near falls, on fallen tree, 29 July 2006, *J. A. Elix* 39509 (CANB 00783313—holotypus; BRI—isotypus).

(Figs 1A, 4A & 7A)

Thallus of chloromorph 5–15 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 160–200 µm thick, 0·8–1·5 mm broad, discrete and flat to weakly concave in peripheral parts, gradually becoming coalescent and convex, and often with small, geotropically oriented lobules in central parts of the thallus. *Upper surface* glabrous but weakly tomentose on young parts of lobes, matt to weakly glossy, fresh specimens bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry, old herbarium specimens either ochraceous or dark brown. *Upper cortex* 30–40 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 30–35 µm thick; *photobiont* myrmecioid, cells 3–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 80–120 µm thick, lowermost part brownly pigmented;

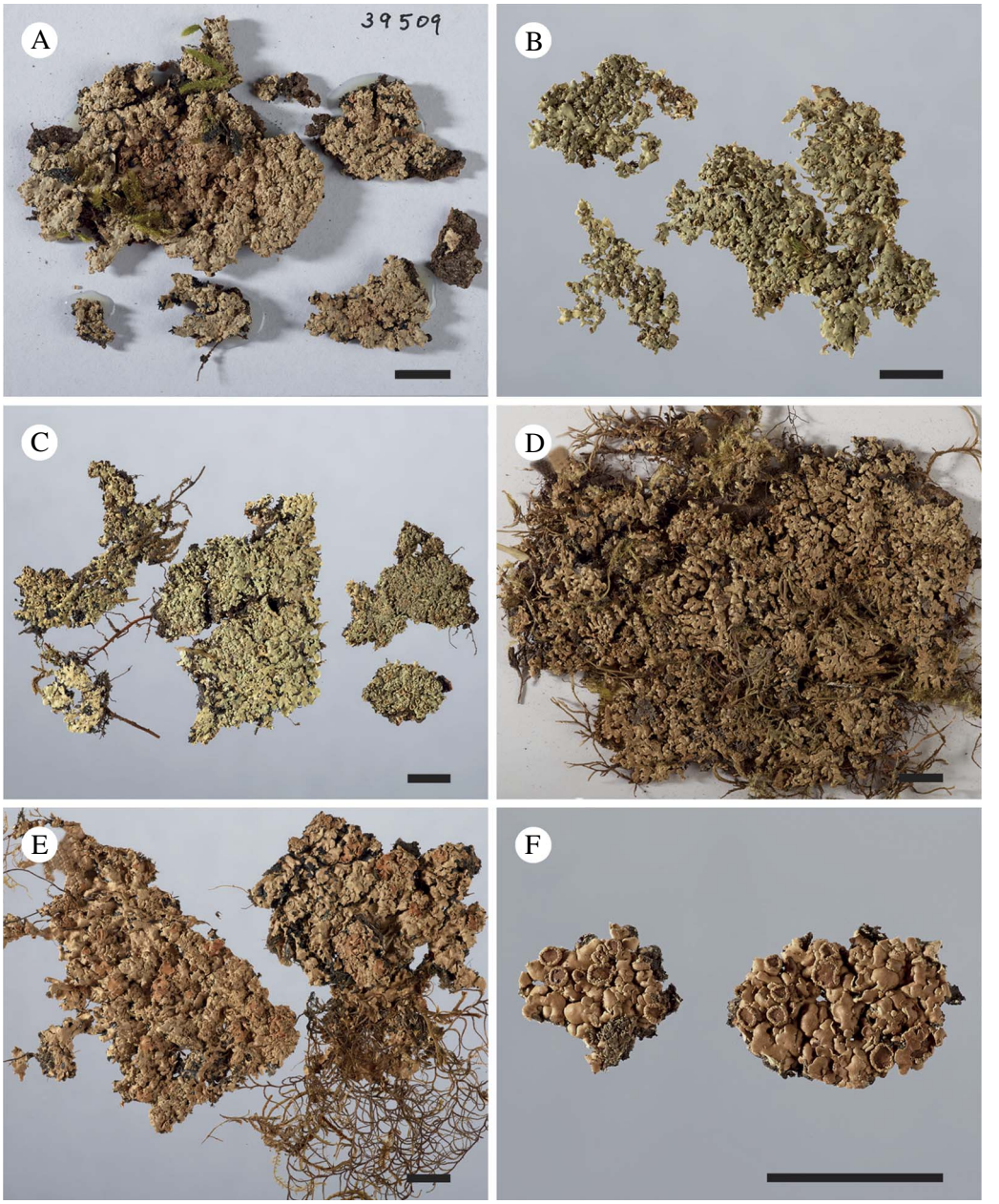

FIG. 1. *Gibbosporina* species, habitus. A, *G. acuminata* (holotype); B, *G. amphorella* (holotype); C, *G. bifrons* (holotype centre), IRD isotype specimen top left, remaining specimens from isotype at TROM; D, *G. bifrons* (*Coppins* 5440 *et al.*) from Malaysia; E, *G. bifrons* (*Hill* 9744) from Solomon Islands; F, *G. boninensis*, (*Knight*, PC 0012753); G, *G. didyma* (holotype); H, *G. elixii* (holotype). Scales = 1 cm.

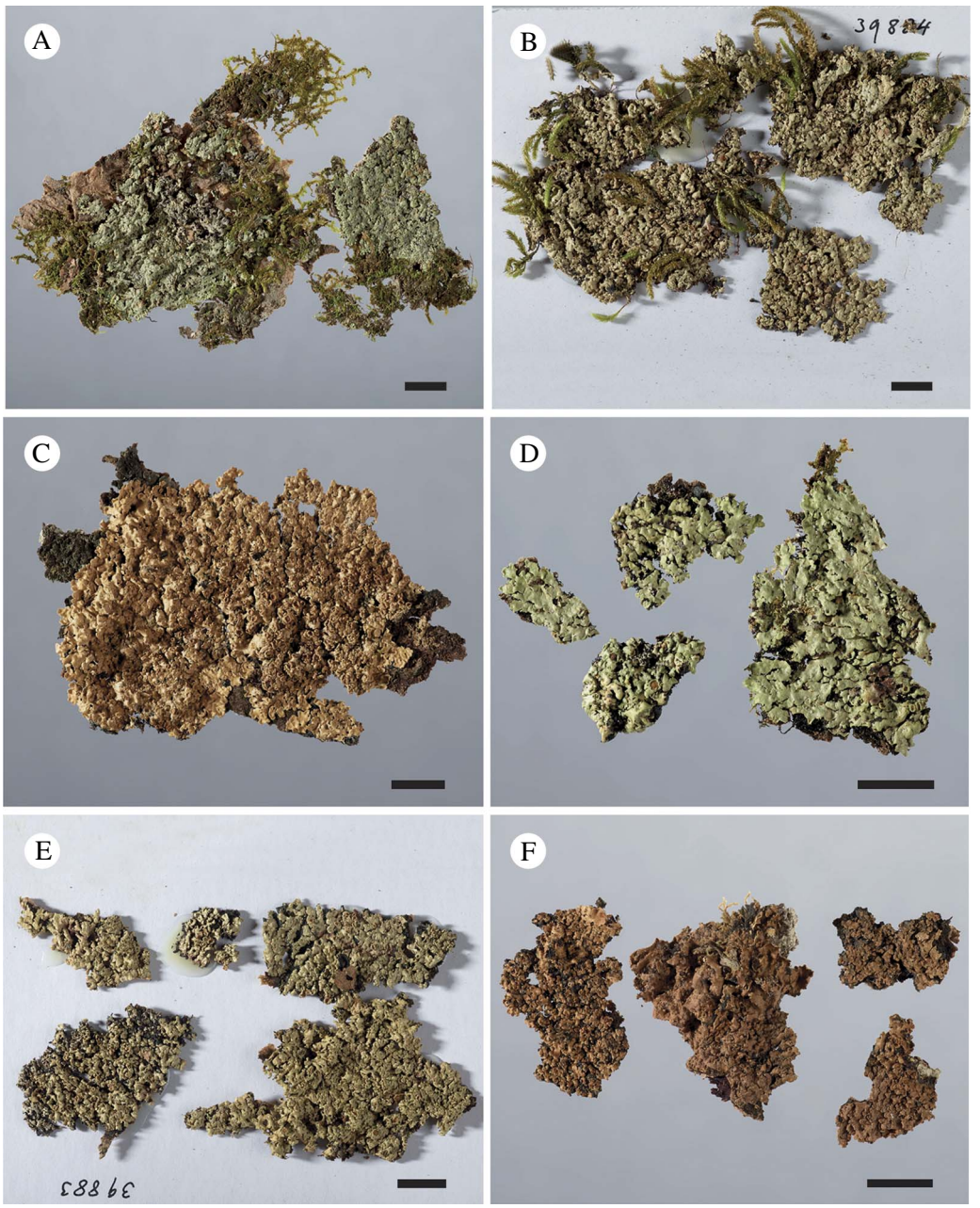

FIG. 2. *Gibbosporina* species, habitus. A, *G. didyma* (holotype); B, *G. elixii* (holotype); C, *G. leptospora* (holotype); D, *G. mascarena* (holotype); E, *G. nitida* (holotype); F, *G. nitida* (*Weber & McVean*, S L-50422). Scales = 1 cm.

rhizines marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes, placodioid both when young and mature, very rarely

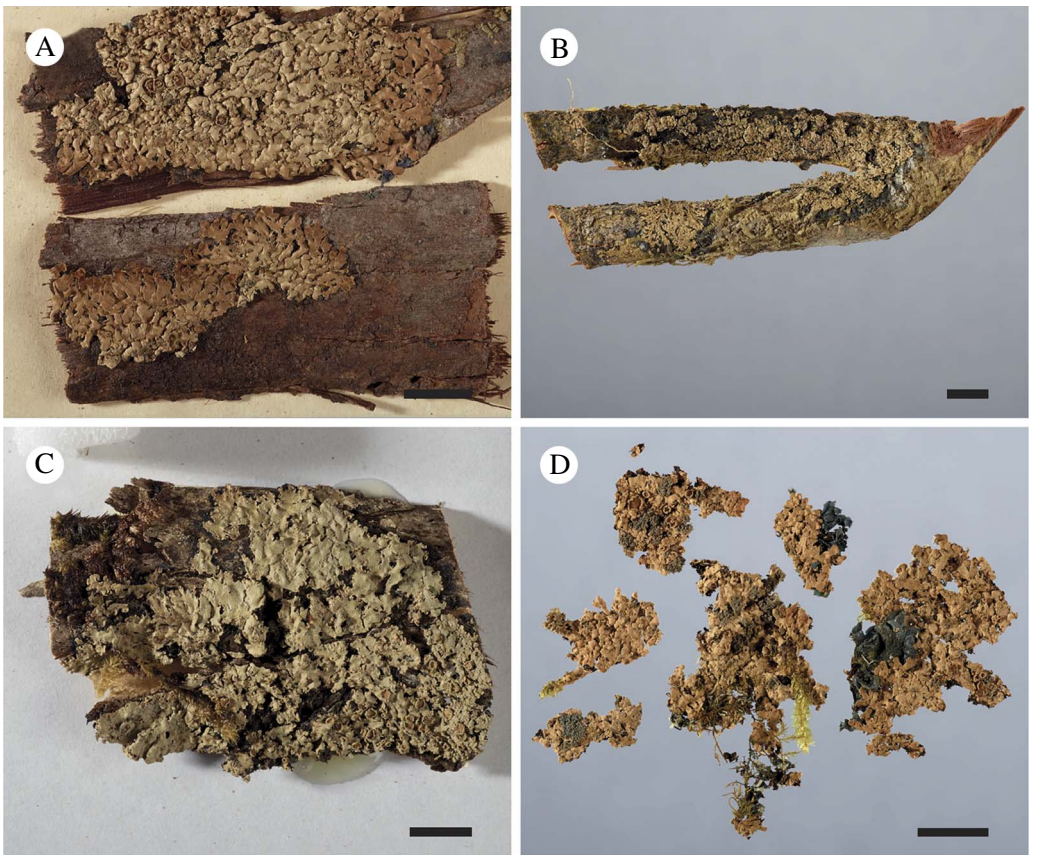

FIG. 3. *Gibbosporina* species, habitus. A, *G. papillospora* (holotype); B, *G. phyllidiata*, (holotype); C, *G. sphaerospora* (holotype); D, *G. thamnophora* (holotype). Scales: = 1 cm.

subfoliose and weakly ascending and rhizinate, surface smooth and with radiating furrows, 1–2 mm diam., with subdichotomously and weakly branching lobes, 0·2–0·3 mm wide, weakly convex. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–7 × 4–8 µm large, globose to short-ellipsoid, dark brownish green to greyish violet cells, blue-green on some older samples, organized within 20–50 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–4·0 mm diam.; *disc* orange-brown; *thalline excipulum* 0·15–0·30 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 11–17 × 7·5–11·0 µm; *perispores* 13–22 × 11–18 µm, walls 0·5–1·5 µm thick in addition to irregular gibbae, some bullate, others up to 6 µm tall, acuminate and sometimes asymmetrically oriented.

Pycnidia not seen.

Chemistry. No TLC - detectable compounds found.

Etymology. The specific epithet *acuminate*, from the Latin 'acumen' (= sharp point),

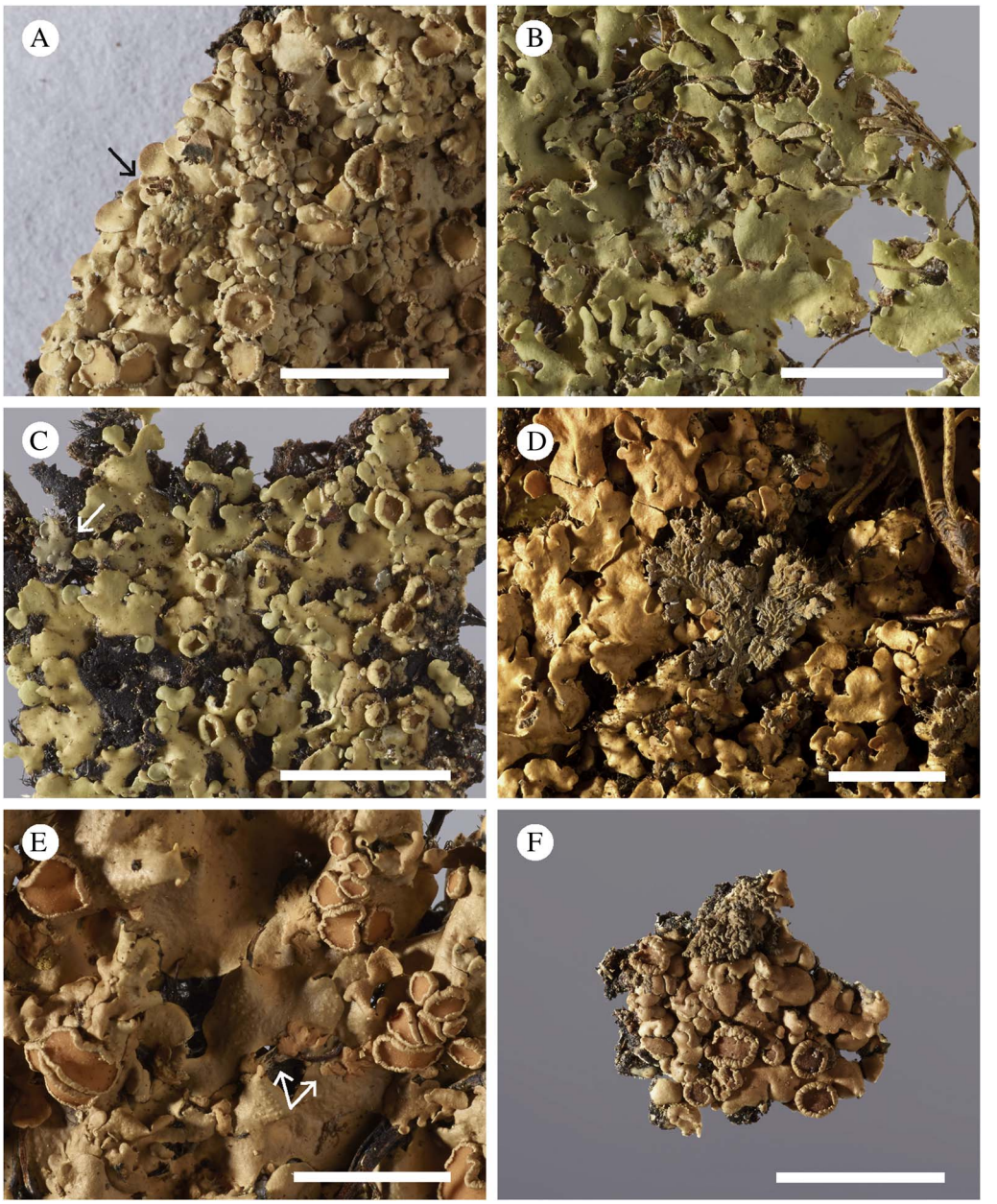

FIG. 4. *Gibbosporina* species, cephalodia. A, *Gibbosporina acuminata* (holotype); B, *G. amphorella* (holotype); C, *G. bifrons* (isotype at IRD); D, *G. bifrons* (*Coppins* 5440 *et al.*) from Malaysia; E, *G. bifrons* (*Hill* 9744) from the Solomon Islands; F, *G. boninensis* (*Knight*, PC 0012753). Scales = 0·5 cm.

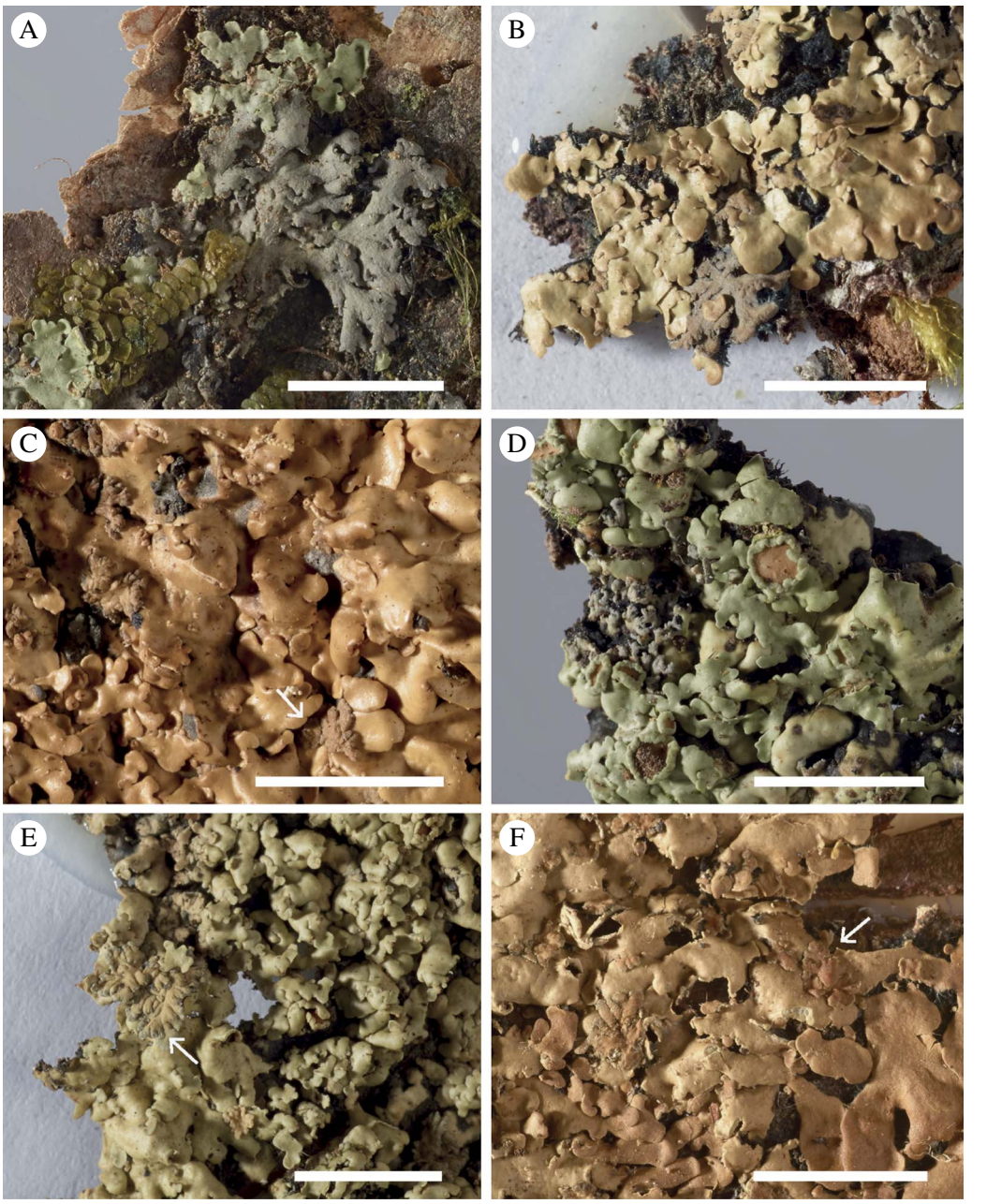

FIG. 5. *Gibbosporina* species, cephalodia. A, *G. didyma* (holotype). B, *G. elixii* (*Elix* 38759, CANB); C, *G. leptospora* (holotype); D, *G. mascarena* (holotype); E, *G. nitida* (holotype); F, *G. papillospora* (holotype). Scales: = 0·5 cm.

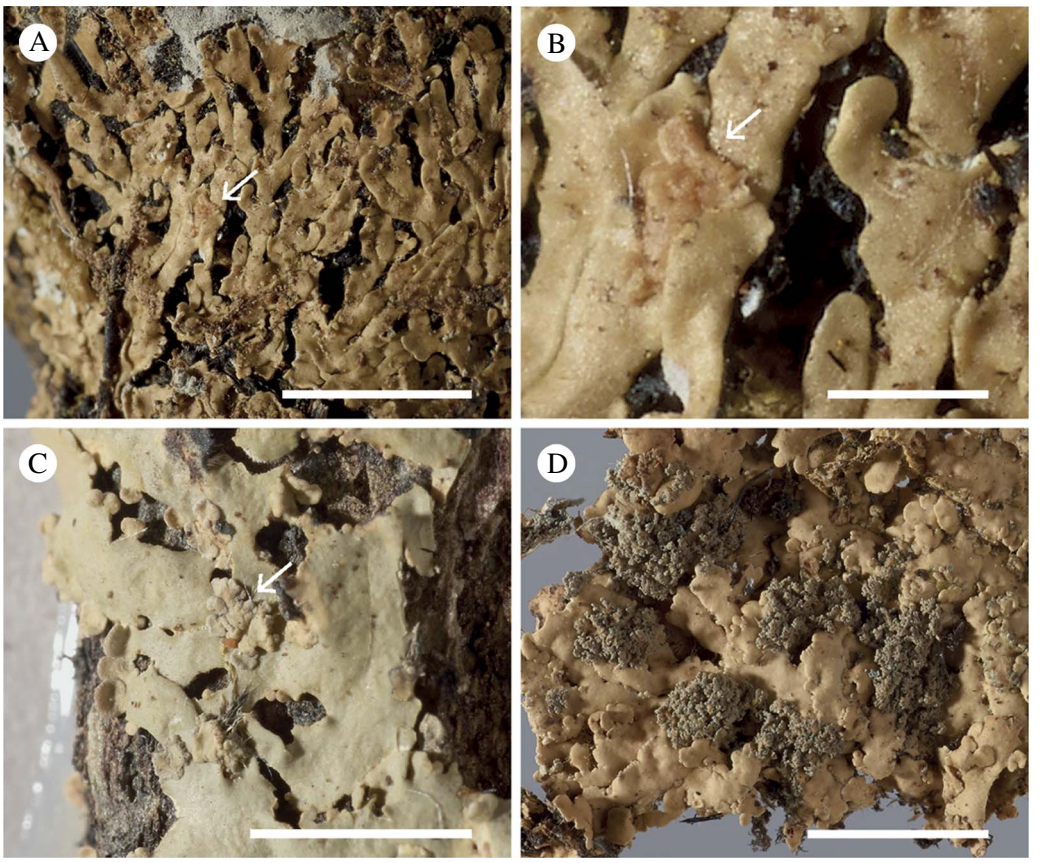

FIG. 6. *Gibbosporina* species, cephalodia. A & B, *G. phyllidiata* (holotype); C, *G. sphaerospora* (holotype); D, *G. thamnophora* (holotype). Scales: A, C & D = 0·5 cm; B = 0·1 cm.

refers to the distinctly spiked gibbae of the perispores.

Distribution and ecology. Known from tropical forests in Australia and the Philippines.

Major characteristics. A species with thick lobes, matt to weakly glossy, and without conspicuous pycnidia. Perispores are intermediately thick, but some have strongly acuminate gibbae, often slightly asymmetrical, resembling fins of ray fish in outline. Cephalodia are small and inconspicuous and remain placodioid.

Additional specimens examined (paratypes). **Australia:** *Queensland*: Millaa Millaa Falls, 4 km S of Millaa Millaa, 17°29'44"S, 145°36'41"E, 750 m, remnant rainforest, on fallen branches, 2006, *J. A. Elix* 39320 (CANB 00783312); Credition State Forest, 20 km SSW of Finch Hatton, 21°19'S, 148°33'E, 840 m, in rainforest dominated by *Syzygium* and *Argyrodendron trifoliatum*, on canopy of *Argyrodendron*, 1986, *J. A. Elix* 21050 & *H. Streimann* (H; B, not seen); Boonjie State Forest, 22 km SE of Yungaburra, 17°24'S, 145°45'E, 600 m, logged rainforest on flats, crown of medium-sized *Endiandra* sp. nov., 1983, *H. Streimann* 27603A (H; CANB & B, not seen).—**The Philippines:** *Luzon*: Province of Rizal, Antipolo, on tree, 1917, *M. Ramos & G. Edano* as *Vainio* 11990 (TUR 012395); Bataan Province, Mt. Mariveles, 1905, *E. D. Merrill* 3977(A) as *Vainio* 11987 (TUR 011310), 3968 as *Vainio* 11992 (TUR 12412), 3968 as *Vainio* 11992b (TUR 12416); 1000 m, trunks of trees, 1904, *E. D. Merrill* 3684 (S L31696; TUR 011317, as *Vainio* 11976); Province of Laguna, vi–viii 1915, *R. C. McGregor* as *Vainio* 11989 (TUR 012408); Island of Polillo, viii 1909, *C. B. Robinson* as *Vainio* 11991 (TUR 12418).

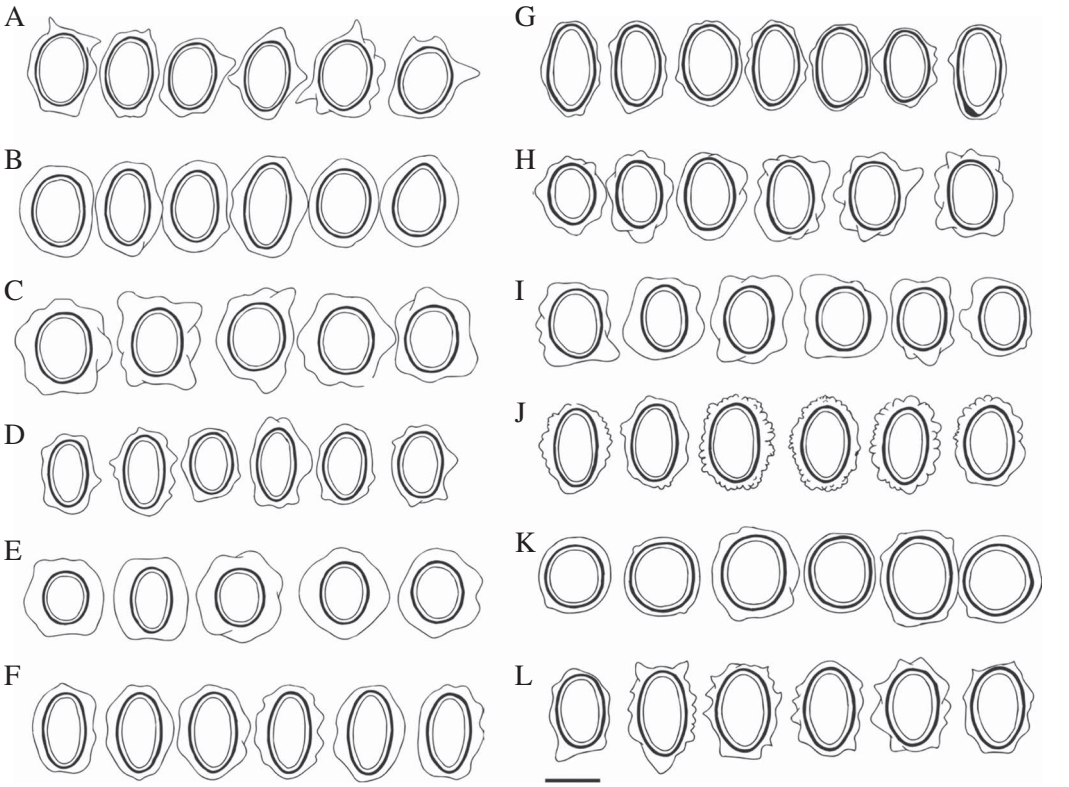

FIG. 7. *Gibbosporina* species, ascospores. A, *G. acuminata*; B, *G. amphorella*; C, *G. bifrons*; D, *G. boninensis*; E, *G. didyma*; F, *G. elixii*; G, *G. leptospora*; H, *G. mascarena*; I, *G. nitida*; J, *G. papillospora*; K, *G. sphaerospora*; L, *G. thamnophora*. Scales: = 10 μm.

Mindanao: Bukidnon Subprovince, Tangculan and vicinity, *M. Ramos & G. Edaño*, Bureau of Science no. 38378 (H).

Gibbosporina amphorella Elvebakk & Hong sp. nov.

MycoBank No.: MB 811980

Gibbosporinae boninensi similis sed lobis impolitis, pycnidiis conspicuis, urcelatisque, perisporis sporarum aequatis et gibbis leviter evolutis instructis.

Typus: New Caledonia, 10 km NE of Nouméa, W slope of Monts des Koghis, *c.* 0·8 km E of Auberge, along path to Les Sommets, 350 m after its bifurcation with the path to Belvedère, 22°10'S, 166°31'E, 685 m, 10–20 thalli on a 15 cm thick trunk of a smooth-barked palm in a semi-shaded forest, 8 December 2005, *A. Elvebakk* 05:717 (PC—holotypus, sequenced as KM887884; BM, IRD, TROM—isotypi).

(Figs 1B, 4B, 7B, 8A–C)

Thallus of chloromorph 5–30 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 120–160 μm thick, 0·8–1·5 mm broad, discrete and flat in peripheral parts, gradually becoming coalescent and convex, centrally forming mats of ascending and geotropically oriented lobules. *Upper surface* glabrous and matt, fresh specimens bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry, 10 year-old herbarium specimens immediately become dark brown after application of water. *Upper cortex* 25–35 μm thick, plectenchymatous, lumina up to 15 × 10 μm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous,

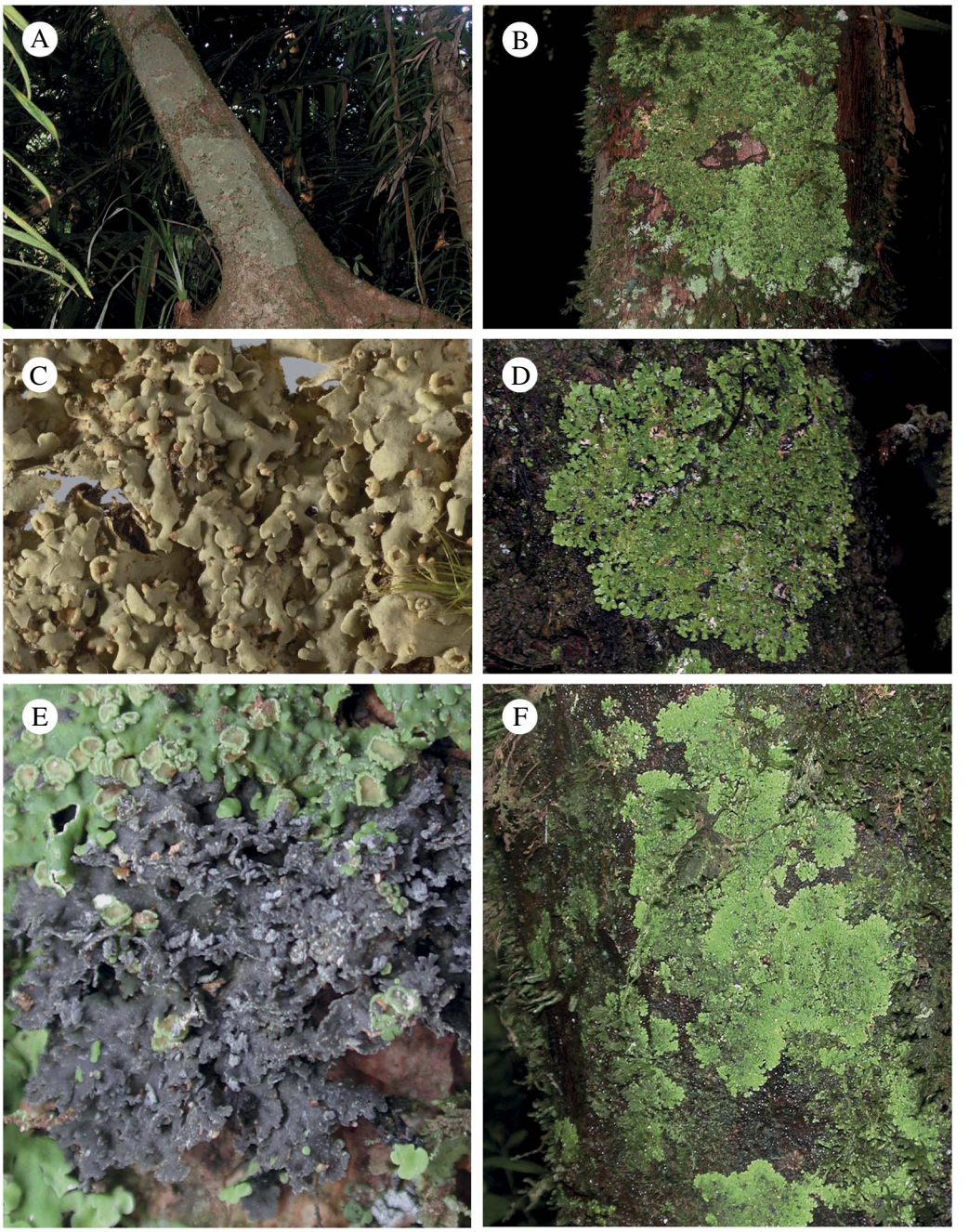

FIG. 8. *Gibbosporina amphorella* (holotype, *Elvebakk* 05:718). A and B *in situ* New Caledonia; C, pycnidia; D *Gibbosporina bifrons* holotype, *in situ* New Caledonia; E, *Gibbosporina didyma* (holotype) cephalodia carrying chlorobiont apothecia. Photographed when hydrated immediately after collection in Réunion; F, *Gibbosporina mascarena in situ* Réunion (*Elvebakk* 11:041).

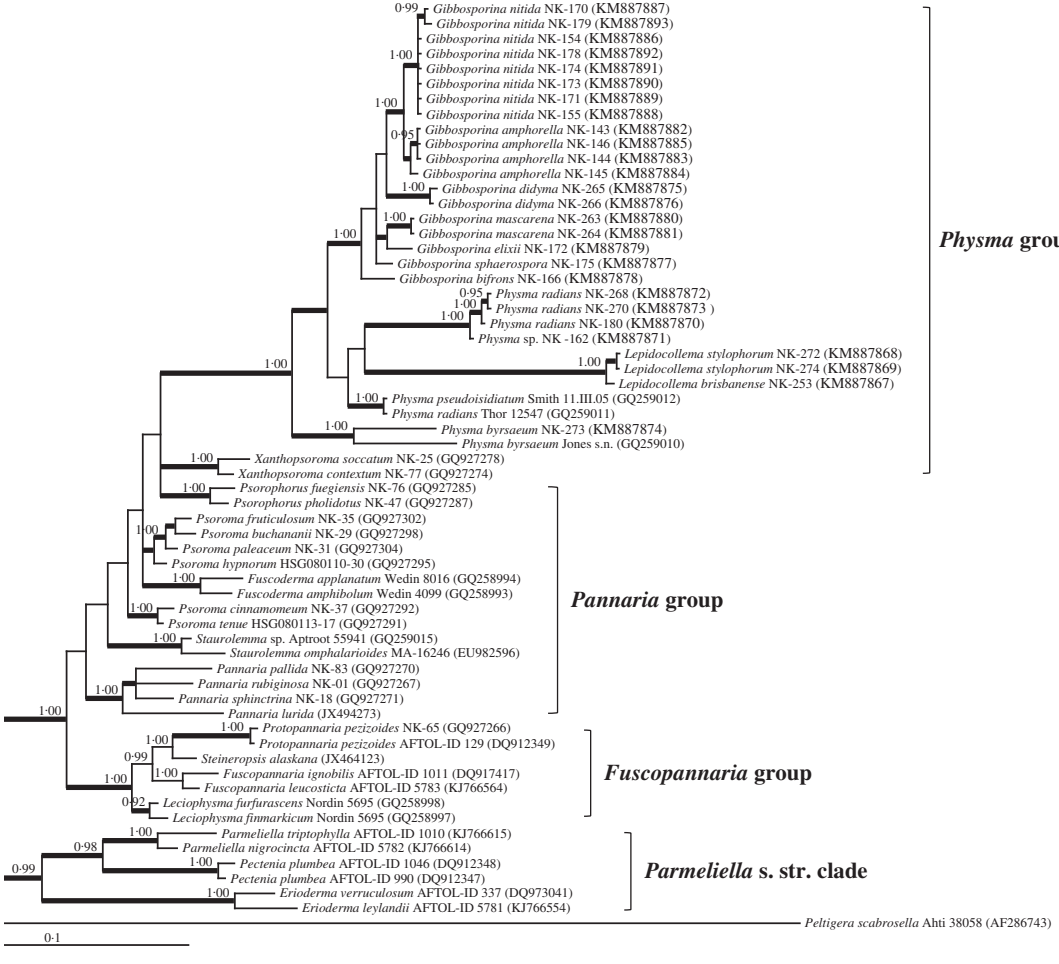

FIG. 9. Bayesian phylogenetic tree of *Gibbosporina* and representative clades of *Pannariaceae* inferred by MrBayes ver. 3.2 under a GTR + I + G model based on LSU sequences. Branches that were maintained in NJ, MP, and ML trees are indicated by thick lines. Bayesian posterior probabilities are indicated when the values were greater than 0·9. Clades are labelled as indicated in Magain & Sérusiaux (2014).

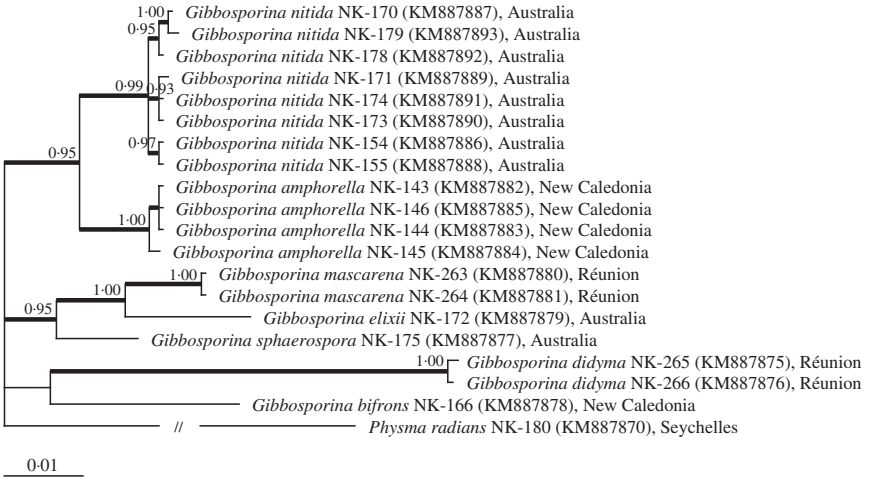

FIG. 10. Bayesian phylogenetic tree of the genus *Gibbosporina* with *Physma radians* as outgroup taxon. The tree was calculated by MrBayes ver. 3.2 under a GTR + I + G model based on ITS1, 5.8S, ITS2, and LSU sequences. Branches that were maintained in NJ, MP, and ML trees are indicated by thick lines. Bayesian posterior probabilities are indicated when the values were greater than 0·9.

lower cortex absent. *Algal layer* 25–35 µm thick; *photobiont* myrmecioid, cells small (3–7 µm) or large (6·0–12·5 µm), globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 60–90 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as conspicuous cephalodia, pale grey when dry, formed on chlorobiont lobes, placodioid when young, becoming mini-foliose, often as weakly ascending fan-shaped lobe systems, 2–4 mm diam., lobes smooth, subdichotomously and densely branched, 0·2–0·3 mm wide, strongly convex, mostly erhizinate. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–6 × 4–7 µm large, globose to short-ellipsoid, dark brownish green to greyish violet cells, organized within 20–80 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–5·0 mm diam., when large with irregular and wavy margins; *disc* orange-brown; *thalline excipulum* 0·15–0·25 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 50–80 µm thick; *algal layer* extending below the hypothecium and 50–80 µm thick; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–80 × 15–20 µm. *Proper ascospores* colourless, simple, ellipsoid, 12·5–19·0 × 7·5–10·0 µm; *perispores* 13–23 × 12–16 µm, walls 2–3 µm thick, even, sometimes with a few low and wide gibbae.

Pycnidia very common, brown and conspicuous, swollen and urn-shaped, 0·2 × 0·2 mm, mostly marginal, sometimes laminal, occasionally even developed on cephalodia. *conidia* bacilliform, 2·5–4·0 × 1 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. The specific epithet *amphorella*, from the Latin 'amphora' (= urn) and '-ella' (a diminuitive suffix), refers to the small, urn-shaped pycnidia.

Distribution and ecology. Known only from a small area in a subtropical forest, around 700 m, in New Caledonia.

Major characteristics. A species with matt, rather thin lobes, and easily recognized by the numerous, conspicuous urn-shaped pycnidia, mainly along the margins, producing conidia larger than in most other species. Proper spores are narrow and short-ellipsoid, whereas perispores are thick and even, with few low and wide gibbae. Cephalodia mini-fruticose with narrow, strongly convex, erhizinate and fan-shaped lobes.

Additional specimens studied (paratypes). **New Caledonia:** 10 km NE of Nouméa, W slope of Monts des Koghis, *c.* 0·8 km E of Auberge, along path to Les Sommets, 250 m after its bifurcation with the path to Belvedère, 22°10'S, 166°31'E, 700 m, on unknown tree trunk in a semi-shaded forest, 2005, *A. Elvebakk* 05:706 (TROM; S); 400 m after its bifurcation with the path to Belvedère, 680 m, many 20–30 cm large specimens on the stooping trunk of a *Montrouziera cauliflora* tree, 3–4 m above the ground in semi-shaded forest, *A. Elvebakk* 05:718 (IRD; TROM; PC; UPS); 690 m, on *Montrouzeria*, *A. Elvebakk* 05:715 (TROM).

Gibbosporina bifrons Elvebakk, Hong & P. M. Jørg. sp. nov.

MycoBank No.: MB 811982

Gibbosporinae boninensi similis sed cephalodeis rhizinophoris latiusque lobatis, perisporis crassissimis magisque gibbosis, plerumque cyanobiontibus distincte catenatis, pycnidiis parvis fuscis distinctisque.

Typus: New Caledonia, 10 km NE of Nouméa, W slope of Monts des Koghis, *c.* 0·8 km E of Auberge, near Belvedère, 22°10'S, 166°31'E, 750 m, two 10 cm-large thalli on the trunk of an unidentified small-leaved tree, 4 December 2005, *A. Elvebakk* 05:614 (PC—holotypus, sequenced as KM887878; IRD, TROM—isotypi) .

(Figs 1C–E, 4C–E, 7C, 8D)

Thallus of chlorobiont 5–20 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous often with a distinct black prothallus; *lobes* subdichotomously divided, 120–150 µm thick, 0·8–2·0 mm broad, flat to convex, discrete and elongate when muscicolous, shorter and often imbricate when corticolous. *Upper surface* glabrous and glossy or weakly glossy, fresh specimens bright green with contrasting blue-green cephalodia when moist, light greenish grey when dry, old herbarium specimens ochraceous brown. *Upper cortex* 20–30 µm thick, plectenchymatous, lumina up to 10 × 15 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous with ochraceous pigmentation on old herbarium specimens, no lower cortex present. *Algal layer* 15–25 µm thick; *photobiont* myrmecioid, cells 4·5–8·5 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 60–80 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise blackish, 0·5–1·5 mm long, simple or in bundles.

Cyanomorph as cephalodia, pale grey when dry, grey to dark brown on old herbarium specimens, formed on chlorobiont lobes or on the adjacent prothallus, placodioid when young, then becoming foliose, 2–12 mm diam., with 0·3–0·7 mm broad, subdichotomously branched lobes, becoming semi-erect and loosening from the chlorobiont substratum on its lower side, developing numerous rhizomorphs, in a few cases becoming apparently independent, although only immediately outside of the visible prothallus zone. In a few cases the cyanobiont has captured green algal cells and formed small chlorobiont lobules on the cephalodia. *Upper surface* smooth with radiating furrows to strongly areolate-ridged when dry, becoming smooth when moist. *Cortex* like in the chlorobiont, in some cases only 10–15 µm thick. *Cyanobiont Nostoc*, obviously of various strains, 3–6 × 4–7 µm diam., some with intensely violet-mauve cells in distinct chains, filling out most of the medulla within medullary compartments resulting in strongly gelatinous cephalodia, others greyish blue and small (2–4 × 3–5 µm diam.) or dark brownish violet and large (3–6 × 3–7 µm diam.), with cells in loose chain systems, sometimes the cyanobiont layer only occupying ¼ of the medulla, and occasionally as brownish violet cells in glomeruli without obvious visible chain structures.

Apothecia sessile, laminal, 1–5 mm diam., when large with irregular and wavy margins; *disc* orange to reddish brown; *thalline excipulum* circular or strongly sinuous on old apothecia,

0·1–0·3 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 30–50 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with internal, apical, amyloid tube structures, 50–70 ×10–15 µm in size. *Proper ascospores* colourless, simple, ellipsoid, 12–18 × 9–12 µm; *perispores* 17–23 × 13–20 µm, 1·0–5·5 µm thick, strongly and asymmetrically gibbose when mounted in water, gibbae up to 5 µm tall, obtuse.

Pycnidia common, small (0·05 mm), marginal, brown to blackish, bud-shaped, rarely swollen at base; *conidia* bacilliform, 2·5–3·0 × 0·5 µm.

Chemistry. No acetone-soluble compounds detected by TLC or HPLC.

Etymology. The epithet 'bifrons' means 'two-faced' and refers to the well-developed and large cephalodia occurring with the chlorobiont.

Distribution and ecology. Found scattered in montane tropical forests in the Philippines, Solomon Islands, Malaysia and New Caledonia. There are 18 collections from four of the islands of the Solomon Islands archipelago at BM, mostly collected by D. J. Hill in 1965. This represents a very thorough field study, showing that the species ranges from lowland tropical forest ('trees overhanging beach'; 'on fallen log in river bed'), to intermediate elevations (300–600 m), to 1600 m ('on many tree trunks in montane rain forest'). The broad-lobed cephalodia are characteristic of all these collections; in a couple of cases, cephalodia were found on the bark outside of its probable mother thallus, although possibly within the prothallus zone.

Major characteristics. A robust species with glossy to moderately glossy lobes, which are rather thin, commonly with small marginal pycnidia. Perispores are thick with large irregular and obtuse gibbae. Cephalodia vary in size but have broad, rhizinate lobes. Several morphologically different cyanobionts occur, mostly, but not always, with cells in chain structures. In some cases cephalodia are strongly gelatinous, appearing apparently independent from the mother thallus.

Additional specimens examined (paratypes). **Malaysia:** *Sarawak*: Gunong Mulu National Park, 4th Division, Baram District, Long Pala, Limestone Hill, *c*. 2 km E of Base Camp, S side of Sungei Melinau Paku, 70–300 m alt., 20 iv 1978, *G. Argent, B. Coppins* (5439 & 5440), *C. Jermy & P. Chai* (E00153722; BG); Valley of Ulu Jerneh, on fallen tree, amongst upper canopy and lianas, 1978, *C. Argent, B. Coppins* 5310, *C. Jermy & P. Chai* (E).— **The Philippines:** *Biliran*: vi 1914, *R. C. McGregor* as *Vainio* 11988 (TUR 012365); *Luzon*: xi 1915, *A. D. E. Elmer* (S L31698); Province of Sorsogon, Irosin, Mt. Bulusan, 1915, *A. D. E. Elmer* 14959 (S L31697; BM); *A. D. E. Elmer* as *Vainio* 11986 (TUR 12411).— **Solomon Islands:** *Guadalcanal Island*: Mt. Popomansiu, on ridge on SE side of Sutakiki River (Vunuvalukama), 4400 ft, montane rainforest, 1965, *D. J. Hill* 9744 (TROM; BM 000732072), 9745 (BM); 5700 ft, on many tree trunks in montane rainforest, 1965, *D. J. Hill* 9361 (BM), 9653 (BM); 5800 ft, little knoll supporting an isolated area of 'moss' forest, 1965, *D. J. Hill* 9433 (BM); 4800–5400 ft, montane rainforest, 1965, *D. J. Hill* 9689 (BM); central part, Sutakiki River, on ridge on S side, *c*. 2 miles from its confluence with Balasuna River, 1200–1700 ft., 1965, *D. J. Hill* 9242 (BM); central part, Balasuna River, on ridge on N side of river, path from Nuhu Village to Parina Village, *c*. 2300 ft., 1965, *D. J. Hill* 9897 (BM); ultrabasic area *c*. 0·5 mile S of Nuhu Village, 1300 ft, 1965, *D. J. Hill* 9088 (BM); NW end, Mount Gallego, small peak to right of upper end of path down ridge on right of Hidden Valley, 1500–2500 ft, 1965, *D. J. Hill* 8370 (TROM; BM000732071), 8351 (BM). *Santa Isabel Island*: Thousand Ships Bay, Kockatoo Anchorage, trees overhanging beach on mainland, 1965, *D. J. Hill* 10999 (BM). *San Cristobal Island*: Wainoni Region, Warinito River, *c*. 8 miles inland, *T. C. Whitmore* 8820 (BM). *Kolombangara Island*: 2 miles up River Kolumbangara, lowland rainforest, 1965, *D. J. Hill* 10251 (BM); on fallen log in river bed, 1965, *D. J. Hill* 10437 (BM); trees along river bed, 1965, *D. J. Hill* 10345 (BM); ridge to W of River Kolumbangara, 1000–2000 ft., 1965, *D. J. Hill* 10743 (BM); 3000 ft., 1965, *D. J. Hill* 10574, 10579 (BM).

Gibbospora boninensis (Kurok.) Elvebakk & P. M. Jørg. comb. nov.

MycoBank No.: MB 812264

Basionym: *Psoroma boninense* Kurok. *Bull. Nat. Sci. Mus. Tokyo* **12:** 688 (1969); typus: Bonin Islands, around mountain top (rugged area with many large outcrops of andesite), Mt. Tsutsuji, Chichijima Island, 25 Nov. 1968 *Hiroshi Inoue* 19066 (TNS—holotypus!).

Pannaria sphinctrina (Mont.) Tuck. ex Hue var. *microphylla* Hue. *Nouv. Arch. Mus.* Ser. 4, **vol. VIII:** p. 268 (1906); type: Japan, Bonin Island, US North Pacific

exp. under command of Ringgold and Rodgers 1893–96, coll. *C. Wright* s. n., PC (PC0012754)! (lectotypus selected here), W (isolectotypus!), BM (isolectotypus!). ≡ *Psoroma sphinctrinum* (Mont.) Nyl. var. *microphyllum* (Hue) Zahlbr., *Cat. Lich. Univ.* **3:** 276 (1925).

? *Pannaria sphinctrina* (Mont.) Tuck. ex Hue var. *confusa* Hue, *nom. nud.*, *Bull. Soc. Bot. France* **48:** 56 (1902).

(Figs 1F, 4F, 7D; other illustrations: Kurokawa 1969: Pl. I–II)

Thallus of chloromorph 5–15 cm diam., foliose, corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 180–200 µm thick, 0·8–1·5 mm broad, discrete and flat to weakly concave in peripheral parts, gradually becoming coalescent and convex in central parts of the thallus. *Upper surface* glabrous, glossy or weakly glossy, fresh specimens not seen (probably bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry), old herbarium specimens dark brown. *Upper cortex* 30–40 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 40–60 µm thick; *photobiont* myrmecioid, cells 3–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 60–100 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, dark greyish brown on herbarium material, formed on chlorobiont lobes, placodioid when young, small-foliose when mature, densely branched and ascending, 1–3 mm diam.; *lobes* convex, weakly uneven above, very narrow (0·10–0·25 mm wide), erhizinate. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–6 × 3–7 µm large, globose to short-ellipsoid, dark greyish violet cells, organized within 20–50 µm large glomeruli filling up *c.* ¾ of the medulla, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–4·0 mm diam.; *disc* orange-brown when moist, dark brown when dry; *thalline excipulum* 0·15–0·30 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 10–15 × 7·0–8·5 µm; *perispores* 14–20 × 9–13 µm, walls 0·5–1·5 µm thick in addition to irregular gibbae, some obtuse, others pointed, up to 5 µm tall.

Pycnidia rare and inconspicuous, bud-shaped; *conidia* bacilliform, 3–4 × 1 µm.

Chemistry. No TLC-detectable compounds found.

Note. The description above is in agreement with the original protologue presented by Kurokawa (1969), although the latter did not include any reference to cephalodia. These had been described by Hue (1906, below *Pannaria sphinctrina* var. *microphylla*), who considered the photobiont to be *Scytonema*. Hue (1906) and Kurokawa (1969) cited the perispore (called "exospore" and "gelatinous membrane", respectively) as being 2–3 or 3 µm thick, and the perispores are described in more detail here. Conidiomata are described here for the first time.

Nomenclatural note. Hue (1902) listed the new name *Pannaria sphinctrina* var. *confusa* Hue without any accompanying description, but referred to his species number "Hue Lich. Exot. n. 1133". This is not a specimen citation, but Hue's own number of his accepted species, and collections of several of Hue's varieties of his *Pannaria sphinctrina* carry this number. When Hue (1906) described var. *microphyllum*, he did not make any reference to his *confusa* name, but preferred the former cited with Tuckerman as author. However, this is an illegitimate author citation as he stated that Tucker's *microphylla* is an invalid herbarium name, which apparently has not been published previously with Tuckerman's authorship. There are three Wright collections from the same expedition to the Bonin Islands representing the same species in PC, all determined as var. *microphylla*, and one of them (PC0012753) additionally with the

name var. *confusa* on a separate label. Thus, *Pannaria sphinctrina* var. *confusa* is considered a *nomen nudum* here, and PC0012754 is chosen as a lectotype of *Pannaria sphinctrina* var. *microphylla*.

Distribution and ecology. Known from the isolated subtropical Japanese Ogasawara Gunto Islands (a World Heritage Site *c*. 1000 km S of Tokyo).

Major characteristics. A species with thick and glossy lobes, indistinct pycnidia, rather thin-walled perispores with dramatic gibbae, and very narrow-lobed, often fan-shaped, erhizinate cephalodia.

Additional specimens examined. **Japan:** *Bonin Island*: US North Pacific exp. under command of Ringgold and Rodgers 1893–96, *C. Wright* s. n. (PC0012753), *C. Wright* s. n. (PC).

Gibbosporina didyma Elvebakk, Hong & P. M. Jørg. sp. nov.

MycoBank No.: MB 811983

Gibbosporinae amphorellae similis sed sine pycnidiis urniformibus conspicuisque; sporis brevioribus, cephalodiis maioribus latiusque lobatis et chlorobiontibus interdum praeditis.

Typus: Réunion, *c*. 0·5 km E of the E end of Grand Étang, 4–500 m W of the parking site, 21°05'45"S, 55° 38'57"E, 525 m, on tree trunk near the path, 17 October 2011, *A. Elvebakk* 11:042 (PC—holotypus, sequenced as KM887875 and KM887876; BM, TROM, REU—isotypi).

(Figs 2A, 5A, 7E, 8E; additional illustration: Jørgensen & Tønsberg 2012: 87)

Thallus of chloromorph 3–10 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous often with a distinct black hypothallus, prothallus only developed occasionally; *lobes* subdichotomously divided, 120–180 µm thick, 0·5–1·3 mm broad, discrete and concave in distal parts, gradually becoming flat, before being coalescent and convex in central parts of the thallus. *Upper surface* glabrous and matt to weakly glossy, fresh specimens bright green with contrasting blue-green cephalodia when moist, light greenish grey when dry. *Upper cortex* 25–40 µm thick, plectenchymatous, lumina up to 12 × 18 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 15–30 µm thick; *photobiont* myrmecioid, cells 3–7 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 70–100 µm thick, lowermost part brownish; *rhizines* marginally white, otherwise black, 0·5–2·0 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes on the hypothallus between them, or apparently as independent cyanobiont thalli on bryophytes or cortex close to the main thallus, placodioid when young, then becoming foliose or subfruticose, 2–15 mm diam., with subdichotomously branched lobes, mostly erhizinate, occasionally with scattered rhizines. *Cephalodia* either foliose, with lobes 0·3–0·7 mm wide, or subfruticose with 0·2–0·3 mm wide, convex lobes, densely branched into fan-shaped, lobe systems. *Cyanobiont Nostoc*, as 3–6 × 5–8 µm large ellipsoid, dark greenish brown to brownish violet cells, blue-green on older samples, organized within 20–80 µm large glomeruli, mostly without an obvious chain structure, short chains observed in single broad-lobed cephalodia. Small chloromorph apothecia and chloromorph thallus fragments have in several cases been developed on the cephalodia.

Apothecia subsessile, laminal, 0·5–3·0 mm diam.; *disc* orange-brown; *thalline excipulum* 0·15–0·30 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 11–15 × 7·5–10·0 µm; *perispores* 15–20 × 12–16 µm, walls 2–5 µm thick, weakly gibbose when mounted in water.

Some possible pycnidia seen as poorly differentiated brown structures along margins; *conidia* not seen.

Chemistry. No acetone-soluble compounds detected by TLC analysis.

Etymology. The epithet 'didyma' means 'in pairs' and refers to the thallus being divided into a prominent cyanobiont in addition to the dominant chlorobiont. The name also refers to cephalodia occasionally being divided, by developing chlorobiont apothecia.

Distribution and ecology. A rare species known only from two localities, on Réunion and Mauritius, both in tropical forests at moderate altitudes of 5–600 m.

Major characteristics. A narrow-lobed species with matt lobes, without distinct pycnidia. Proper spores are narrow and short-ellipsoid, perispores very thick and even, with few, diffuse gibbae. Cephalodia are particularly well developed, large and foliose and broad-lobed, sometimes becoming fan-shaped and ascending. The species appears to be phytosymbiodemic, although cephalodia have so far been found only in the prothallus zone of the mother thallus.

Additional specimens examined (paratypes). **Mauritius:** Black River, along path from Plaine Champagne towards Piton de la Petite Rivière Noire, 20°25'S, 57°25'E, 600 m, corticolous, 1991, *Krog, H. & Timdal, E.* MAU09/62b (O – L 21227).—**Réunion:** Le Grand Étang along the trail from the road to the lake, 21°05'S, 55°39'E, on tree trunk, 520–540 m, 1996, *Krog, H. & Timdal, E.* RE48/12b (O).

Gibbosporina elixii Elvebakk, Hong & P. M. Jørg. sp. nov.

MycoBank No.: MB 811987

Gibbosporinae mascarenae similis sed cephalodiis maturis minus ramulosis distincteque foliosis et lobis latioribus instructis; apotheciorum thallorum marginibus distincte angustiis et subtiliter regulariterque crenulato-striatis; sporis sensu stricto angustioribus; parietibus perisporarum regulariter crassis vel leviter gibbosis.

Typus: Australia, Queensland, Mossman Gorge National Park, 6 km W of Mossman, 16°28'21"S, 145° 19'54"E, 60 m, tropical rainforest along Mossman River, on base of tree, 1 August 2006, *J. A. Elix* 39884 (CANB 00783318—holotypus, sequenced as KM887879; BRI—isotypus).

(Figs 2B, 5B, 7F)

Thallus of chloromorph 3–7 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 100–150 µm thick, 0·6–1·2 mm broad, discrete and flat in peripheral parts, gradually becoming coalescent and convex in central parts of the thallus. *Upper surface* glabrous and glossy, fresh specimens bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry. *Upper cortex* 20–30 µm thick, plectenchymatous, lumina up to 15 × 10 µm, globose or irregularly subellipsoid, and then arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 30–45 µm thick; *photobiont* myrmecioid, cells 3–7 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 50–80 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes, occasionally on the hypothallus, placodioid when young, then becoming foliose, surface slightly faveolate, 1–5 mm diam., with sparsely branched lobes, erhizinate or rarely with scattered rhizines, convex, lobes 0·2–0·3 mm wide, slightly detached from the substratum. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–6 × 4–8 µm large, ellipsoid, dark greenish brown to brownish violet cells, organized within 15–60 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–1·5 mm diam.; *disc* orange-brown; *thalline excipulum* 0·1–0·2 mm thick, regularly and finely crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI −; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 20–30 µm

thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 12–16 × 6·5–8·0 µm; *perispores* 15–19 × 10·0–12·5 µm, walls 1·5–2·5 µm thick and predominantly even or weakly gibbose when mounted in water.

Pycnidia not seen.

Chemistry. No TLC-detectable compounds found.

Etymology. The species is named in honour of the Australian lichenologist Jack Elix, who collected the type as well as many samples of other *Gibbosporina* species described here.

Distribution and ecology. Known only from two localities in lowland tropical forests of NE Australia.

Major characteristics. Lobes thin and glossy without visible pycnidia. The apothecia have narrow and regular margins, the proper spores are narrow and almost long-ellipsoid, whereas perispores are intermediately thick, rather even, with few and low gibbae. Cephalodia are mini-foliose with narrow, erhizinate lobes.

Additional samples examined (paratypes). **Australia:** *Queensland*: Wooroonooran National Park, Josephine Falls, 20 km NW of Innisfail, 17°26'16"S, 145°51'33"E, 80 m, lowland tropical rainforest, on tree trunk, 2006, *J. A. Elix* 38759 (CANB 00783310).

Gibbosporina leptospora Elvebakk sp. nov.

MycoBank No.: MB 811988

Gibbosporinae nitidae similis, sed sporis ellipsoidibus, parietibus perisporarum tenuibus et gibbis humilibus subconvexisque praeditis.

Typus: Australia, Queensland, Moses Creek, Rossville-Bloomfield River road, 35 km SSE of Cooktown, 15°47'S, 145°17'E, 240 m, lowland rainforest on flats beside creek, on shaded upper tree trunk, 21 October 1995, *H. Streimann* 57369 (H—holotypus; CANB—isotypus, not seen; B—isotypus, not seen).

(Figs 2C, 5C, 7G)

Thallus of chloromorph 3–10 cm diam., foliose, corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously branched, 100–170 µm thick, 0·8–2·5 mm broad, discrete and flat to weakly concave in distal parts, gradually becoming coalescent in central parts of the thallus. *Upper surface* glabrous, except often with minute, erect, 10–15 µm long hairs on young lobe tips, strongly glossy and mostly even, fresh specimens not seen (probably bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry), old herbarium specimens ochraceous brown. *Upper cortex* 20–35 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 25–40 µm thick; *photobiont* myrmecioid, cells 5–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 50–100 µm thick, lowermost part brownly pigmented; *rhizines* in marginal positions white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes, occasionally on the hypothallus, mostly placodioid, occasionally becoming mini-foliose and loosely attached to the substratum, surface smooth with radiating furrows, 1–3 mm diam., commonly with a corona of whitish short rhizines as seen from above, lobes convex, 0·15–0·30 mm wide, moderately branched. *Cortex* like in the chlorobiont. *Cyanobiont Nostoc*, as 3–6 × 4–6 µm large globose, subglobose or short-ellipsoid, brownish green to brownish violet cells, organized within 20–80 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–2·0 mm diam.; *disc* orange-brown, circular, often becoming strongly irregular in outline; *thalline excipulum* 0·2–0·3 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 20–30 µm thick; *algal layer* extending below the hypothecium;

paraphyses simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 12–17 × 6·5–9·5 µm, many almost twice as long as broad; *perispores* 14–19 × 8–12 µm, with thin walls, 0·5–1·0 µm thick, with low and wide gibbae, rarely protruding more than 1 µm above the general surface of the perispore.

Pycnidia present, formed like low dark brown verrucae, 0·10 × 0·05 mm. A few conidia observed, rod-shaped, 2·0 × 0·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. From 'lepto-' in Greek composite words, meaning 'thin-', referring to the thin perispores.

Distribution and ecology. Known only from two tropical lowland forest localities, one in NE Australia, one in Papua New Guinea.

Major characteristics. Strongly glossy and moderately thick lobes, with small marginal pycnidia. Proper spores are very narrow, and short- to long-ellipsoid. Perispores are very thin, with scattered low gibbae. Cephalodia are placodioid to mini-foliose, often with a conspicuous corona of white rhizines when seen from above.

Additional specimens examined (paratypes). **Papua New Guinea:** *Milne Bay Province*: Woodlark Island, Mt. Kabati-Kulumadau Road, 5 km E of Kulumadau, 9°04'S, 152°47'E, 100 m, lowland forest disturbed by roading, on *Endospermum* stem, 11 × 1984, *R. Kumei* (H; CANB, US, LAE, B – not seen).

Gibbosporina mascarena Elvebakk, Hong & P. M. Jørg. sp. nov.

MycoBank No.: MB 811989

Gibbosporinae boninensi similis, sed sporis latioribus, perisporis gibbis obtusioribus praeditis, cephalodiis latius lobatis.

Typus: Réunion, *c.* 0·5 km NE of E end of Grand Étang, at La Vue, 21°05'39"S, 55°38'43"E, 560 m, on a trunk of cf. *Dracaena* on the slope below the viewpoint, 17 October 2011, *A. Elvebakk* 11:056 (PC—holotypus, sequenced as KM887880; TROM, REU—isotypi).

(Figs 2D, 5D, 7H, 8F)

Thallus of chloromorph 3–10 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 120–180 µm thick, 0·8–2·0 mm broad, discrete and flat in peripheral parts, gradually becoming coalescent and convex in central parts of the thallus. *Upper surface* glabrous and glossy, fresh specimens bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry. *Upper cortex* 25–40 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 20–35 µm thick; *photobiont* myrmecioid, cells 3–7 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 70–100 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes, occasionally on the hypothallus, placodioid when young, then becoming mini-foliose, occasionally subfruticose, surface smooth, 1–4 mm diam., with subdichotomously branched lobes, erhizinate or rarely with scattered rhizines, convex, lobes 0·2–0·3 mm wide, moderately to densely branched into fan-shaped lobe systems. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–6 × 5–8 µm large ellipsoid, dark greenish brown to brownish violet cells, blue-green on older samples, organized within 20–50 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–3·0 mm diam.; *disc* orange-brown; *thalline excipulum* 0·2–0·3 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 20–30 µm thick; *algal layer* extending

below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 10–16 × 7·5–10·0 µm; *perispores* 15–20 × 10–16 µm, walls 0·5–3·0 µm thick and strongly and irregularly gibbose when mounted in water.

Pycnidia marginal, small, brown, bud-shaped, rarely common or well developed; *conidia* bacilliform 3·0 × 0·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. The epithet means 'from the Mascarenes', a name referring to Réunion and Mauritius.

Distribution and ecology. Known from tree trunks in tropical forests at altitudes of 5–700 m in Réunion, Mauritius and Sri Lanka, where the species is probably common.

Major characteristics. A broad-lobed, robust and strongly glossy species with indistinct marginal pycnidia and apothecia with coarse and irregular margins. Proper spores are short-ellipsoid and perispores intermediately thick with abundant high and obtuse gibbae. Cephalodia have intermediately broad lobes, become mini-foliose, rarely rhizinate, occasionally also mini-fruticose.

Additional specimens examined (paratypes). **Mauritius:** Black River, along path from Plaine Champagne towards Piton de la Petite Rivière Noire, 20°25'S, 57°25'E, 620–825 m, 1991, *Krog, H. & Timdal, E.* MAU51/95 (O–L21928), MAU51/92 (O–L21295), MAU51/93 (O–L 21926), MAU51/94 (O–L21927); 600 m, corticolous, 1991, *Krog, H. & Timdal, E.* MAU09/62 (O–L21227); without further geographical information, *Robillard* (PC); Plaines Wilhelms, Macchabee Forest, at the divide of the roads leading to Macchabee Kiosk and Mt. Bris Fer, 20°24'S, 57°27'E, 630 m, 1991, *Krog, H. & Timdal, E.* MAU14/16 (O–L21364); 0·5–1 km ESE of Macchabee Kiosk, 20°24'S, 57°26'E, 1991, *Krog, H. & Timdal, E.* MAU13/11 (O–L21343); Savanne, Mt. Cocotte, SE of the peak, along the road towards Bassin Blanc, 20°26'S, 57°28'E, 640 m, 1991, *Krog, H. & Timdal, E.* MAU21/33 (O–L21443); Mt. Cocotte, along the path towards the peak, *Krog, H. & Timdal, E.* MAU32/75 (O–L21629).—**Réunion:** Grand Étang, along the trail from the road to the lake, 21°05'S, 55°39'E, 520–540 m, on tree trunk, 1996, *Krog, H. & Timdal, E.* RE48/12, RE48/12c (O–L107313); 0·5 km E of the E end of le Grand Étang, 4–500 m W of the parking site, 21°05'45"S, 55°38'57"E, 525 m, on tree trunk near the path, 2011, *A. Elvebakk* 11:041 (TROM); 'Bourbon', 1840, *Lepervanche-Mézières* (PC).—**Sri Lanka:** *Twaites* 52 (S–L31706); '*Leighton* 52' (= '*Twaites* 52') (S–L31705).

Gibbosporina nitida Elvebakk, Hong & P. M. Jørg. sp. nov.

MycoBank No.: MB 811990

Gibbosporinae mascarenae similis, sed superficie loborum aspera et valde nitida, pycnidiis marginalibus saepe conspicuis, cephalodiis rosettiformis, perisporis crassioribus gibbisque maioribus praeditis.

Typus: Australia, Queensland, Mossman Gorge National Park, 6 km W of Mossman, 16°28'21"S, 145°19'54"E, 60 m, tropical rainforest along Mossman River, on base of tree, 1 August 2006, *J. A. Elix* 39883 (CANB 00783317—holotypus, sequenced as KM887889; BRI—isotypus).

(Figs 2E, 2F, 5E, 7I)

Thallus of chloromorph 3–10 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* densely and irregularly divided, 120–180 µm thick, 0·8–2·5 mm broad, discrete and flat in distal parts, gradually becoming coalescent and convex in central parts of the thallus, where they form scalariform side lobules, apparently in vertically-oriented individuals. *Upper surface* glabrous, strongly glossy and uneven, fresh specimens bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry, becoming pale brown in old herbarium samples. *Upper cortex* 20–35 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 25–40 µm thick; *photobiont* myrmecioid, cells 5–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 50–100 µm thick, lowermost part brownly pigmented; *rhizines* in marginal positions white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes,

occasionally on the hypothallus, placodioid when young, then becoming mini-foliose and loosely attached to the substratum, surface smooth, 1–4 mm diam., with densely branched lobes, erhizinate or rarely with scattered rhizines, convex, 0·15–0·30 mm wide, densely branched into rosette-shaped lobe systems. *Cortex* like in the chlorobiont. *Cyanobiont Nostoc*, as 3–6 × 3–7 µm large globose, subglobose or short-ellipsoid, dirty green cells, brownish violet on older samples, organized within 20–50 µm large glomeruli, without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–4·0 mm diam.; *disc* orange-brown, circular, often becoming strongly irregular in outline; *thalline excipulum* 0·15–0·30 mm thick, crenate-striate; *epithecium* pale brown,10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 10–15 × 7·5–10·0 µm; *perispores* 15–20 × 10–16 µm, walls 0·5–3·0 µm thick and strongly and irregularly gibbose when mounted in water.

Conidiomata pycnidia, scattered to common, marginal on ascending lobes, verruciform 0·1 × 0·1; *conidia* bacilliform to cigar-shaped, 2·0 × 0·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. From Latin 'nitidus' (= glossy), referring to the structure of the upper lobe surfaces.

Distribution and ecology. Found in several places in NE Australia, Papua New Guinea and the Philippines, and probably widespread in tropical rainforest from lowlands to *c.* 1000 m.

Major characteristics. Lobes moderately thick, but upper surfaces strongly glossy and with regular depressions in well-developed parts of thalli, and with abundant and conspicuous marginal pycnidia. Apothecia have regular margins, short-ellipsoid proper spores, and particularly large and obtuse gibbae. The cephalodia are conspicuous, but erhizinate, narrow-lobed and form appressed rosettes.

Additional specimens examined (paratypes). **Australia:** *Queensland*: Mossman Gorge National Park, 6 km W of Mossman, 16°28'21"S, 145°19'54"E, 60 m, tropical rainforest along Mossman River, on base of tree, 2006, *J. A. Elix* 39880 (CANB 00783314; BRI), 39881 (CANB 00783315), 39882 (CANB 00783316; BRI), 39885 (CANB 00783319; BRI), 39886 (CANB 00783320; BRI); Josephine Falls, Wooroonooran National Park, 20 km NW of Innisfail, 17°26'16"S, 145°51'33"E, 80 m, lowland tropical rainforest, on base of tree, 2006, *J. E. Elix* 38756 (CANB 00783308), 38757 (CANB 00783309; BRI).—**Papua New Guinea:** *Central Province*: near Dabamura on Ower's Corner Road, 40 km NE of Port Moresby, 9°23'S, 147°27'E, 580 m, *Castanopsis* dominated forest on gentle slopes, on tree trunk, 1981, *H. Streimann & E. K. Naoni* 14893 (H; CANB - not seen; B - not seen). *Eastern Highlands*: Kassem Pass, east end of Bismarck Ranges between Kaiapit and Kainantu, *c.* 3000 ft, clay banks on summit of pass, and on scattered rainforest trees on steep slope of ravine, on buttress, 21 vi 1968, *W. A. Weber & D. McVean* (UPS L-50422).—**The Philippines:** *Luzon*: Province of Sorsogon, Irosin, Mt. Bulusan, 1915, *A. D. E. Elmer* 14904 (S L31961); Province of Tayabas, Quinatacutan, 1911, *F. W. Foxworthy & M. Ramos* as *Vainio* 11983 (TUR 12415); Province of Pampanga, Mt. Arayat, iii 1910, *H. M. Curran* as *Vainio* 11981 (TUR 012406); Province of Rizal, on tree, *M. Ramos* as *Vainio* 11974 (TUR 012320). *Mindanao*: Lake Lanao, Camp Keithly, 1907, *M. S. Clemens* 1325 as *Vainio* 11977 (TUR 011308).

Gibbosporina papillospora Elvebakk sp. nov.

MycoBank No.: MB 811991

Gibbosporinae elixii similis, sed lobis latioribus, crassioribus minusque nitidis, pycnidiis conspicuis et abundantibus, perisporis papillis numerosis bulliformibusque praeditis.

Typus: The Philippines, Luzon, Prov. Bataan, Mount Mariveles, December 1908, *E. D. Merrill* 6260 (as *Vainio* 11987) (TUR 012322—holotypus).

(Figs 3A, 5F, 7J)

Thallus of chloromorph 3–7 cm diam., foliose, corticolous with a distinct black hypothallus/prothallus; *lobes* subdichotomously divided, 130–200 µm thick, 0·8–1·5 mm broad, discrete and flat in peripheral parts, gradually becoming coalescent and convex in central parts of the thallus. *Upper surface* glabrous

and matt to weakly glossy, fresh specimens not seen (probably bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry), old herbarium specimens pale brown. *Upper cortex* 30–40 µm thick, plectenchymatous, lumina up to 15 ×10 µm, globose or irregularly subellipsoid, and then arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 40–50 µm thick; *photobiont* myrmecioid, cells 4–9 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 70–120 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, formed on chlorobiont lobes, placodioid when young, then becoming mini-foliose, surface even, 1·0–2·5 mm diam., with sparsely branched lobes, erhizinate or rarely with scattered rhizines, flat to weakly convex, lobes 0·2–0·3 mm wide, becoming loosely attached to the substratum. *Cortex* like in the chloromorph, 30–40 µm thick. *Cyanobiont Nostoc*, as 3–6 × 4–7 µm large ellipsoid, bluish to brownish violet cells, organized within 15–60 µm large glomeruli, filling ¾ of the medulla; without a discernible chain structure.

Apothecia subsessile, laminal, 0·5–2·0 mm diam.; *disc* orange-brown; *thalline excipulum c.* 0·2 mm thick, regularly and densely crenate-striate; *epithecium* pale brown,10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 30–40 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 11·5–17·0 × 7–10 µm; *perispores* 14–20 × 11–15 µm, walls *c.* 1·5 µm thick, almost even except for bubble-like small gibbae and/or papillae-like outgrowths on most spores.

Pycnidia common, dark brown, 0·05–0·10 mm diam., bud-like, marginal or laminal on strongly convex coaslescent lobes in central parts of thalli; *conidia* bacilliform, 2·5 × 0·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. From Latin 'papilla' (= small wart, nipple), referring to the irregular surface of the perispores.

Distribution and ecology. Known only as two collections from the Philippines.

Major characteristics. A species with rather broad and thick lobes, matt to weakly glossy, and commonly with marginal conspicuous pycnidia. The apothecia have regular, thin margins, proper spores are short-ellipsoid, perispores are intermediately thick and almost even, except small bubble-like gibbae and/or small papillae-like outgrowths on most spores. Cephalodia are small, narrow-lobed, placodioid to mini-foliose, forming loosely appressed rosettes, rarely with rhizines visible from above.

Additional specimen examined (paratype). **The Philippines:** *Luzon*: Province of Rizal, on tree, vii 1911, *M. Ramos* as *Vainio* 11985 (TUR 012321).

Gibbosporina phyllidiata Elvebakk sp. nov.

MycoBank No.: MB 811992

Gibbosporinae boninensi similis, sed lobis angustioribus, phyllidiis lateralibus praesentibus et apotheciis deficientibus, cyanobionte in cephalodiis minutissimis indistinctisque incolente.

Typus: Solomon Islands, Guadalcanal Island, Mt. Popomansiu, on ridge SE of Sutakiki River (Vunuvalukama), *c.* 4400 ft, montane rainforest, 9 November 1965, *D. Jackson Hill* 9729 (BM 000731914 —holotypus).

(Figs 3B, 6A & B)

Thallus foliose, dominated by the chlorobiont, corticolous, forming rosettes 5–10 cm diam.; *lobes* dichotomously to subdichotomously divided, 120–170 µm thick, *c.* 0·5 mm broad, flat, adpressed, discrete in peripheral parts, imbricate centrally, resting on a distinct black hypothallus forming a peripheral 2–4 mm wide prothallus of thin byssoid hyphae as a film over the cortex and bryophytes growing on the cortex, with small, secondary chlorobiont thalli commonly developing on the prothallus; *upper surface* glabrous and glossy, fresh specimens

supposedly light greenish grey when dry, old herbarium specimens pale brown; *phyllidia* common, 0·1–0·4 × 0·1mm, mostly developed along lobe margins, ascending to subascending, upper side corticate, ecorticate on the lower side. *Upper cortex* 30–50 µm thick, upper 10 µm sclerenchymatous with ochraceous pigmentation on old herbarium specimens, plectenchymatous below, with cell lumina 10–15 × 5–7 µm in size, arranged perpendicularly to the surface with walls *c.* 5 µm thick. *Photobiont layer* 15–25 µm thick, with globose to semiglobose cf. *Myrmecia* cells, 4–7 µm diam. *Medulla* pale, 60–80 µm thick, lowermost 15–10 µm with brown pigmentation, with scattered simple to sparingly branched rhizines; no lower cortex present.

Cephalodia scattered and inconspicuous, laminal on the upper surface, 0·3–1·0 mm diam., placodioid, with short, nodulose lobes, *c.* 0·2 mm broad, upper surface smooth, upper cortex as in the chlorobiont. *Cyanobiont Nostoc*, cells blue-green, ellipsoid to irregularly shaped, 2·5–3·0 × 4–6 µm, in clusters without any obvious visible chain or glomerulae structures.

Apothecia and *conidiomata* not seen.

Chemistry. No TLC-detectable secondary substances were found.

Etymology. Named after its phyllidia, as it is the only *Gibbosporina* species known at present where the chlorobiont has distinctly differentiated vegetative propagules.

Distribution and ecology. Known only as the holotype specimen from montane rainforest in the Solomon Islands.

Major characteristics. A narrow-lobed species, primarily characterized by the presence of phyllidia, and the only known species in the genus which is not primarily fertile. It has not been found with apothecia, and the cephalodia are minute and inconspicuous with distinct and blue-green *Nostoc* cells.

Gibbosporina sphaerospora Elvebakk & Hong sp. nov.

MycoBank No.: MB 811993

Gibbosporinae bifronti similis, sed cephalodiis minoribus, pycnidiis maioribus, sporis humilibus et plerumque gibbosis, parietibus perisporarum tenuioribus et plerumque aequatis gibbisque tantum dispersis praeditis.

Typus: Australia, Queensland, Millaa Millaa Falls, 4 km S of Millaa Millaa, 17°29'44"S, 145°36'41"E, 750 m, remnant rainforest near falls, on fallen branches, 29 July 2006, *J. A. Elix* 39319 (CANB 00783311—holotypus, sequenced as KM887877).

Psoroma sphinctrinum var. *endoxanthellum* Zahlbr. in Rechinger, *Denkschr. Mat. Nat. Kl. K. K. Akad. Wiss. Wien* **81:** 258 (1907); typus: Samoa, Upolu, Launtoo, 700 m, 1–4 August 1905, *K & L. Rechinger* (W—holotypus!).

(Figs 3C, 6C, 7K)

Thallus of chloromorph 3–15 cm diam., foliose, corticolous or muscicolous on corticolous bryophytes, when corticolous with a distinct black hypothallus, often also prothallus; *lobes* subdichotomously divided, 150–200 µm thick, 1·0–2·5 mm broad, discrete and flat in peripheral parts, gradually becoming coalescent and convex in central parts of the thallus. *Upper surface* matt, moderately glossy on peripheral lobes, glabrous, except weakly tomentose on young lobe tips, light greenish grey when young and dry, old herbarium specimens dark brown. *Upper cortex* 25–40 µm thick, plectenchymatous, lumina up to 10 × 15 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 15–25 µm thick; *photobiont* myrmecioid, cells 4–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 70–120 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, pale grey when dry, brown on old herbarium specimens, 0·5–3·0 mm diam., formed on chlorobiont lobes, occasionally on the hypothallus, placodioid when young, then becoming foliose, with moderately branched, short, 0·3–0·4 mm wide, moderately faveolate and weakly ascending lobes, rhizines common on the lower side, even on very small cephalodia. *Cortex* as in the chloromorph. *Cyanobiont Nostoc*, as 3–7 × 4–8 µm large globose to short-ellipsoid, dark greenish brown to brownish violet cells, bluish on older samples, organized within 20–50 µm large glomeruli, without obvious chain structures.

Apothecia subsessile, laminal, 0·5–3·0 mm diam.; *disc* orange-brown on young specimens, dark brown on old herbarium specimens; *thalline excipulum* 0·15–0·20 mm thick, crenate-striate, sometimes with 0·1–0·2 mm long bundles of hyphae, resembling white rhizinomorphs, but mostly radiating from central parts of the excipulum; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI −, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, globose to short-ellipsoid, 9–14 × 9·0–12·5 µm; *perispores* of similar shape, 13–18 × 12·5–15·0 µm, walls 0·5–2·5 µm thick, even and with scattered low gibbae.

Conidiomata pycnidia, common, blackish, 0·1–0·2 mm wide, button-like, formed apically on swollen, short erect lobules developed from laminal or marginal parts of main lobes; *conidia* bacilliform with obtuse ends, 0·5 × 2·0–2·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. Named from 'sphaero-' in Greek composites (= globose), referring to the shape of the spores.

Notes. The type of *P. sphinctrinum* var. *endoxanthellum* has spores which match exactly the distinct ones of the present taxon, in addition to the presence of pycnidia, and relatively broad cephalodium lobes, although the thallus lobes are more glossy than in normal *G. sphaerospora*. The yellow pigment referred to by Zahlbruckner (1907) is invisible and no compound could be detected by TLC. Still, dried herbarium specimens of tripartite *Pannariaceae* species remain greyish green for *c.* 10 years and gradually take on a brownish colour. However, as soon as the chlorobiont cells have died, which normally takes place after a little more than one month during dry storage, the thallus turns rapidly brownish when exposed to water. This process, which is not well understood but is probably due to degradation of the chlorobiont [see discussion in Elvebakk (2007)], may explain Zahlbruckner's choice of epithet. For this reason, the name *endoxanthellum* was avoided as an alternative epithet for this taxon when raised to species level. *Psoroma sphinctrinum* var. *endoxanthellum* has previously been placed into synonomy with *Psoroma boninense* by Jørgensen (2003).

Distribution and ecology. Widely distributed in SE Asia and NE Australia in lowland and montane tropical rainforests.

Major characteristics. A matt to weakly glossy species, having cephalodia with short and broad lobes with well-developed rhizines. Pycnidia are common and relatively large. The spores are very distinct, as this is the only known *Gibbosporina* species where both the proper spores and the perispores are predominantly globose. Some proper spores are subglobose to short-ellipsoid, but are broader than those of other species. The perispore walls are mostly even, although scattered gibbae occur. Most perispore walls are thin, 0·5–1·0 µm thick, but some are occasionally thicker.

Additional specimens examined (paratypes). **Australia:** *Queensland*: 39 km WSW of Ingham, Lannercost State Forest, along Blue Water Creek close to Old Mill Road, 18°42'S, 145°50'E, *c.* 600 m, dense montane rainforest, 1985, *G. Thor* 6709 (S L31986); Boonjie State Forest, 22 km SE of Yungaburra, 17°24'S, 145°45'E, 600 m, logged rainforest on flats, crown of medium-sized *Endiandra* sp. nov., 1983, *H. Streimann* 27603B (H); Eungella National Park, 66 km W of Mackay, 21°11'S, 148°20'E, close to the campsite along Broken River, fringe of rainforest, on bark, 1983, *L. Tibell* 14691 (UPS 170715).—**Indonesia:** *Java*: *Jungh* (PC); Supra Tjibodas, *V. Schiffner* (O–L106899).—**Malaysia:** *Sarawak*: Gunong Mulu National Park, 4th Division, Baram District, Bukit Long Pala, 70–100 m, on trunk of old tree on small limestone hill, 1978, *G. Argent*, *B. Coppins* 5021, *C. Jermy & P. Chai* (E 00153721).—**The Philippines:** *Luzon*: Benguet Subprovince, v 1911, *M. Ramos* as *Vainio* 11984 (TUR 012407); Bataan Prov., Mt. Mariveles, iii 1905, *E. D. Merrill* as *Vainio* 11996 (TUR 011320); Bataan Province, Mt. Mariveles, 1905, *E. D. Merrill* 3977(B) as *Vainio* 11978 (TUR 011310); Sorsogon, Irosin, on *Radermachera*, *E. D. Merrill* as *Vainio* 11973 (TUR 012314); *Elmer* as *Vainio* 11980 (TUR 12414); Prov. of Pampanga, Mt. Arayat, iii 1910, *H. M. Curran* as *Vainio* 11979 (TUR 012404); District

of Lepanto, Mt. Data, on trees at 1000 ft., 1905, *E. D. Merrill* 4886 as *Vainio* 11982 (TUR 12413). *Mindanao*: District of Zamboanga, 3900 ft., on *Agathis philippinensis*, iv 1905, *E. B. Copeland* as *Vainio* 11975 (TUR 011340); on *Agathis*, 3900 ft., iv 1905, *E. B. Copeland* as *Vainio* 11995 (TUR 012417); Bukidnon Subprovince, Mt. Dumalucpihan, vi–vii 1920, *M. Ramos & G. Edaño*, Bureau of Science Hb. No. 38392 (H); Butuan Subprovince, alt. 129·5 m, on bark of trees, 1911, *C. M. Weber* 1372 as *Vainio* 11994 (TUR 012377).

Gibbosporina thamnophora Elvebakk & P. M. Jørg. sp. nov.

MycoBank No.: MB 811994

Gibbosporinae acuminatae similis, sed apotheciis rarioribus, cephalodiis structuras dense ramulatas coralloideasque ut organa vegetativo-dispersalia formantibus.

Typus: Australia, Queensland, Eungella National Park *c.* 70 km W of Mackay, close to Broken River 1–2 km ESE of Broken River camping area, tropical rainforest, 21°02'S, 148°20'E, 11 November 1985, *G. Thor* 4983 (S L31957—holotypus; UPS 36646— isotypus).

(Figs 3D, 6D, 7L)

Thallus of chloromorph 5–10 cm diam., foliose, corticolous with a distinct black hypothallus/prothallus; *lobes* subdichotomously divided, 120–180 µm thick, 0·5–1·5 mm broad, discrete and flat to weakly concave in peripheral parts, gradually becoming coalescent and convex, and often with small geotropically oriented lobules in central parts of the thallus. *Upper surface* glabrous, matt to glossy, fresh specimens not seen (probably bright green with contrasting blue-grey cephalodia when moist, light greenish grey when dry), old herbarium specimens pale to dark brown. *Upper cortex* 30–40 µm thick, plectenchymatous, lumina up to 15 × 10 µm, irregularly subellipsoid, arranged perpendicularly to the surface, surface weakly sclerenchymatous, lower cortex absent. *Algal layer* 30–35 µm thick; *photobiont* myrmecioid, cells 3–8 µm, globose to ellipsoid or slightly irregular. *Medulla* of loosely interwoven hyphae, 60–100 µm thick, lowermost part brownly pigmented; *rhizines* marginally white, otherwise black, 0·5–1·5 mm long, simple or in bundles, fibrillose.

Cyanomorph as cephalodia, very abundant and conspicuous, bluish grey to dark brown, 2–6 mm diam., on the chlorobiont lobes, occasionally in the prothallus zone, pulvinate when very young, then becoming umbilicate before starting to branch densely into coralloid mini-fruticose mature cephalodia, branchlets 0·05–0·10 mm wide, breaking off and acting as vegetative propagules. *Cortex* like in the chloromorph. *Cyanobiont Nostoc*, as 3–5 × 4–6 µm large, globose to short-ellipsoid, dark brownish green to greyish violet cells, blue-green on some older samples, organized within 20–50 µm large glomeruli, without obvious chain structure.

Apothecia subsessile, laminal, 0·5–2·0 mm diam.; *disc* orange-brown when wet; *thalline excipulum* 0·2–0·3 mm thick, crenate-striate; *epithecium* pale brown, 10–20 µm thick, IKI−; *hymenium* colourless, but strongly IKI+ blue, 80–100 µm thick; *hypothecium* pale brown, IKI−, 20–30 µm thick; *algal layer* extending below the hypothecium; *paraphyses* simple to sparingly branched, with slightly swollen apices, septate; *asci* clavate, 8-spored, with pronounced, internal, apical, IKI+ blue amyloid tube structures, 50–70 × 10–15 µm. *Proper ascospores* colourless, simple, ellipsoid, 10–14 × 7·0–9·5 µm; *perispores* 14–20 × 9–13 µm, walls 0·5–1·5 µm thick in addition to irregular gibbae, some bullate, others up to 4 µm tall, acuminate and sometimes asymmetrically oriented.

Pycnidia marginal, dark brown, bud-shaped; *conidia* bacilliform, 2·5 × 0·5 µm.

Chemistry. No TLC-detectable compounds found.

Etymology. The specific epithet is derived from 'thamnos' (= 'shrub' in Greek) and '-phora' ('carrier' in Greek composite words) and refers to the finely branched, mini-fruticose cephalodia 'carried' by the chlorobiont.

Distribution and ecology. Known from lowland and montane tropical forests in Australia and Papua New Guinea, but all known Australian collections are from Eungella National Park.

Major characteristics. The species has ellipsoid proper spores and thin-walled perispores with irregular and acuminate gibbae, and are of the same type as those of

G. acuminata, whereas the lobes and thallus surfaces are quite variable. However, the cephalodia are unique in being umbilicate when juvenile, but then becoming densely fine-branched and mini-fruticose, obviously serving as vegetative dispersal units through fragmentation. This is consistent with the fact that apothecia are less common here than in other *Gibbosporina* species and have only been observed on the type material.

Additional specimens examined (paratypes). **Australia:** *Queensland*: Eungella National Park, 66 km W of Mackay, 21°11'S, 148°20'E, close to the campsite along Broken River, fringe of rainforest, on bark, 1983, *L. Tibell* 14691 (UPS 170715), 14683 (UPS); *c.* 70 km W of Mackay, along the Discovery Walk W of Broken River camping area, 21°10'S, 148°20'E, tropical rainforest, 1985, *G. Thor* 4919 (S: L31988); Sky Window Lookout, *c.* 2·5 km NW of Broken River camping area, 21°09'S, 148°20'E, tropical rainforest, 1985, *G. Thor* 5098 (S: L31992).—**Papua New Guinea:** *Morobe Province*: Herzog Mountains, 15 km WSW of Lae, 6°45'S, 146°51'E, 760 m, on *Castanopsis* and *Dipterocarpaceae* dominated ridge, large tree trunk, 1981, *H. Streimann* 10990 *&* *T. Umba* (H; CANB – not seen, B – not seen).

Phylogenetic analyses

The genus *Gibbosporina* was found to be monophyletic in all phylogenetic analyses performed, and it is statistically supported in the Bayesian analyses (Figs 9 & 10). The genus was closely related to *Lepidocollema* and *Physma*, and the monophyletic grouping of these genera was strongly supported in the Bayesian analysis and maintained by all phylogenetic analyses, including NJ, MP, ML, and Bayesian analyses. However, relationships among these genera were not clearly resolved, and the genus *Physma* formed polyphyletic or paraphyletic relationships with *Lepidocollema* within the clade, depending on the phylogenetic algorithms used. In all cases, the genus *Gibbosporina* was clearly separated from the *Lepidocollema* and *Physma* clades. The major phylogenetic *Pannariaceae* clades defined by Magain & Sérusiaux (2014) and Ekman *et al.* (2014) were generally well maintained in the present study. The position of the genus *Xanthopsoroma* in Fig. 9 was more similar to the phylogeny based on 5.8S, mtSSU, LSU, and *RPB1* (Magain & Sérusiaux 2014) than the phylogeny based on ITS, mtSSU, and *RPB1* (Ekman *et al.* 2014). Relationships among *Gibbosporina* species were calculated based on 1593 aligned nucleotide positions spanning ITS1, 5.8S, ITS2 and LSU sequences (Fig. 10), and the relationships among species and specimens were maintained as in the LSU only phylogeny (Fig. 9). Support for monophyly of each species was, however, stronger. The clear distinction among species was also supported by the multiple insertion/deletion fragments in the ITS1 and ITS2 domains, which were not included in the phylogenetic analyses (data not shown).

Key to the known species of *Gibbosporina*

1 Phyllidia present, apothecia not observed . . . . . **G. phyllidiata**
Phyllidia absent, apothecia common 2

2(1) Cephalodia forming vegetative dispersal units of strongly and densely divided, thin, coralloid branches developing from an almost umbilicate basis; only in Australia and Papua New Guinea . . . . . **G. thamnophora**
Cephalodia placodioid to mini-foliose or mini-fruticose as ascending and fan-shaped, but not forming corallioid vegetative dispersal units; distributions within large parts of the Palaeotropics 3

3(2) Most perispores with numerous papillae and/or bubble-like gibbae . . . . . **G. papillospora**
Perispores without papillae and/or bubble-like gibbae 4

4(3) Lobes strongly glossy, at least in well-developed peripheral parts; pycnidia dark, distinct, and verruciform (0·1 mm wide, 0·05–0·10 mm tall) 5
Lobes glossy to moderately glossy or matt in peripheral parts; pycnidia mostly absent or small and bud-shaped (0·05 mm wide, *c.* 0·1 mm tall), if large (0·1–0·2 mm across) then distinctly urn- or button-shaped 6

5(4) Perispore walls very thin with low, weakly convex gibbae (Fig. 7G); lobes mostly smooth . . . . . **G. leptospora**
Perispore walls thicker (1–3 μm) with tall, obtuse, irregular gibbae (often >3 μm tall); lobes mostly with depressions . . . . . **G. nitida**

6(4) Lobes distinctly matt; perispores either globose, very thick-walled or with strongly acuminate gibbae; or intermediately thick and even, but then with large urn-shaped pycnidia 7
Lobes moderately glossy to glossy; perispores ellipsoid, moderately thick, gibbae moderate or high but then obtuse; pycnidia absent or small and bud-shaped 10

7(6) Proper spores ellipsoid, perispores thin, but some with tall, acuminate gibbae (like ray-fish fins in outline) (Fig. 7A). . . . . **G. acuminata**
Proper spores globose, of if ellipsoid then with even perispores without high gibbae 8

8(7) Proper spores globose to weakly subglobose, perispores thin (Fig. 7K) . . . . . **G. sphaerospora**
Proper spores ellipsoid, perispores thick 9

9(8) Cephalodia up to 2 cm large, sometimes apparently independent, foliose, broad-lobed and ascending; pycnidia inconspicuous, only in Réunion and Mauritius . . . . . **G. didyma**
Cephalodia narrow-lobed, on the chlorobiont lobes; pycnidia urn-shaped, conspicuous; only New Caledonia . . . . . **G. amphorella**

10(6) Cephalodia robust, broad-lobed (>0·3 mm), 2–10 mm large, rhizines common and visible from above; perispores thick (2–5 μm) and rather even, except for obtuse gibbae; *Nostoc* cells mostly in chains; from different strains, some small-celled (2–4 μm). . . . . **G. bifrons**
Cephalodia less robust, lobes rarely > 0·3 mm, rhizines only occasionally visible from above, perispores moderately thick (1–3 μm); *Nostoc* cells relatively large (3–6 μm), in glomeruli without obvious chain structures. 11

11(10) Cephalodia much branched, with very narrow lobes (0·1–0·2 mm); known only from tropical Japanese islands . . . . . **G. boninensis**
Cephalodium lobes intermediately broad (0·2–0·3 mm), poorly or moderately branched, distributed elsewhere 12

12(11) Thin, crenulate, regular apothecium margins, proper spores narrow (6·5–8·0 μm), perispores even or with moderate gibbae; Australia. . . . . **G. elixii**
Coarse and irregular striate-crenate apothecium margins, proper spores broader (7·5–10·0 μm), perispores with high, obtuse gibbae; Indian Ocean area. . . . . **G. mascarena**

Discussion

According to our current knowledge, the genus *Gibbosporina* comprises 13 species which have a total distribution ranging from Samoa and Ogasawara (Bonin) Islands in the Pacific Ocean, through South-East Asia and northern Queensland in Australia to the islands Réunion, Mauritius and Sri Lanka in the Indian Ocean. Material obviously belonging to this genus has also been published from Taiwan (Zahlbruckner 1933; Kurokawa 1969), and we have also seen material from Fiji and Madagascar, which will be restudied for a future publication. Material representing reports of '*Psoroma sphinctrinum*' from South Africa (Doidge 1950) has been searched for in vain in South African herbaria. Three immediate questions arise: is there good support for such an unexpectedly large number of species in a previously unrecognized genus, what patterns can be found in its species diversity, and what can we hypothesize about its evolutionary history?

Evaluation of characters

Spores

To evaluate whether the many new species are well supported, characters are discussed and compared with phylogenetic data when available. Spore attributes, including proper spore and perispore shape and size, perispore wall thickness and surface structure, represent the most important set of characters found here for separating the species. A thorough examination of *c.* 10 spores in one sample alone will normally show the specific traits and their variation, and make it possible to determine the sample to species level by comparing it with the illustrations in Fig. 7. The exceptions are *G. acuminata* and *G. thamnophora* which have similar spores (both with characteristic acuminate gibbae), *G. bifrons* and *G. nitida* which also have similar spores, and *G. phyllidiata* which has not been found fertile.

The most striking spores are those with very thick perispore walls and those with high gibbae. The former type appears like fried eggs in outline. It should be noticed that the sequences of the two species with the thickest perispore walls, *G. didyma* from Réunion and *G. bifrons* from New Caledonia, have basal and neighbouring positions in the phylograms. The sister species in the phylograms, *G. amphorella* and *G. nitida*, have perispores with intermediate thickness, whereas the three remaining and associated sequenced species and the two remaining non-sequenced species have thin to moderately thin perispores. Only two collections have been determined as *G. papillospora*; however, a thorough examination of many spores indicated that the presence of papillae and small bubble-like gibbae is a general characteristic and not a casual variation.

Cephalodia

The morphology of the cephalodia also helps in definition and identification of the species. Those of *G. thamnophora* are very distinct and develop into conspicuous mini-fruticose vegetative reproductive structures (Fig. 6D). This species is comparable, both in general appearance and function to *Pannaria durietzii* (Henssen & James) Elvebakk & D. J. Galloway, a very conspicuous pan-austral species (James & Henssen 1975). The cephalodia of *G. phyllidiata* are so small (Fig. 6B) that they were first overlooked, whereas *G. bifrons* and *G. didyma* can have very large cephalodia (Fig. 4C, 4D & 5A), apparently capable of existing independently, although they have not yet been observed with certainty outside of the prothallus zone. In a species like *G. sphaerospora*, the cephalodia are less than 3 mm large but relatively broad-lobed and with rhizomorphs clearly visible from above, even in several small cephalodia (Fig. 6C). The remaining species have relatively narrow-lobed cephalodia. In two species, *G. mascarena* and *G. nitida*, the cephalodia become rather prominent and mini-foliose or even subfruticose, up to 4 mm across, with lobes loosening from the substratum and becoming suberect, but still erhizinate. These two species also have spores which are somewhat similar, and were morphologically the most closely related species, even though they have very different

distributions. Their close relationship was confirmed by the phylogenetic analyses, where they are in a sister species position (Fig. 10). Genetic distances, morphological differences and distribution patterns support their status as different species.

Photobiont diversity

Although photobionts have not been sequenced here, all samples have been studied microscopically, and it is possible to discuss general patterns from these studies, and form hypotheses for future phylogenetic studies. The chlorobiont appears in all cases to be myrmecioid, but varies greatly in cell size. Even two specimens of *Gibbosporina amphorella* which grew quite close to each other in New Caledonia had large (6·0–12·5 µm) versus very small (3–7 µm) chlorobiont cells, obviously representing different strains.

There is a high morphological diversity of cyanobionts. One extreme case is the *Coppins et al.* 5440 sample of *G. bifrons* from Malaysia. The *Nostoc* cells are intensely mauve-violet, strictly arranged in chains within medullary compartments, with a photobiont layer 150 µm thick, filling out almost the whole thallus, except a reduced 20 µm thick upper cortex and a similarly sized lower medulla. This pattern comes close to a homoiomerous thallus, and is strongly gelatinous. The dominance of the gelatinous *Nostoc* layer in this specimen is easily observed macroscopically when cephalodia are dry, due to their strongly wrinkled upper surface.

When transferring four gelatinous ex-*Collemataceae* genera to *Pannariaceae*, Wedin *et al.* (2009) provided a review of gelatinous representatives already included in *Pannariaceae*, both as bipartite lichens and cyanobionts in tripartite ones. Later, Magain & Sérusiaux (2014) studied the phylogeny of cyanobionts in lichens, with a focus on *Pannariaceae*. They introduced the terms 'collematoid' and 'pannarioid', to separate two types of cyanobacterial bipartite thalli. The former has a homoiomerous anatomy and the latter is heteromerous. Magain & Sérusiaux (2014) described a tripartite species from Réunion named as '*Pannaria* tripartite R969'. We have not examined the sample itself, however its sequence is identical to *G. mascarena* except for a single base pair in the ITS domain, and can therefore be determined as this species. Its cyanobiont was analyzed phylogenetically by Magain & Sérusiaux (2014), and was classified as a distinct 'Phylotype E', shared by four samples from *Physma byrsaeum*. They concluded that the cephalodia of R969 (= *Gibbosporina mascarena*) is comparable to the collematoid thallus of *Physma byrsaeum*. In their mycobiont tree, R969 is in a basal position in their *Physma* clade, and their hypothesis is that the cyanolichen genera dominating this clade arose through emancipation of cephalodia in ancestral tripartite lichens. With this hypothesis in mind, a better knowledge of the cyanobionts of *Gibbosporina* would be highly desirable. This is illustrated by the cyanobiont phylogram of Magain & Sérusiaux (2014), where three phylotypes exclusively consisted of *Nostoc* strains of the three collematoid *Pannariaceae* genera *Physma*, *Kroswia*, and *Gibbosporina* (R969), partly associated with cyanobionts of *Leptogium*.

Our material of *G. mascarena* and *G. didyma* have *Nostoc* cells arranged in glomeruli, and only occasionally with short chain structures clearly discernible. The pattern agrees very well with *Nostoc* of our own *Physma radians* material from the same island, where there is a transition from cells in glomeruli with indistinct chain structures above, through short chains and then longer ones in the lower part of a rather thin cyanobiont layer. *Physma byrsaeum* from Réunion, on the other hand, has a typical homoiomerous anatomy, dominated by the cyanobiont layer with the filamentous morphology of *Nostoc* clearly discernible. It should be added that several *Physma* determinations are unreliable, as illustrated by strongly different phylogenetic positions of the same mycobiont species in the phylograms where several samples of the genus are represented (Magain & Sérusiaux 2014; the present study).

However, the anatomy of the *G. bifrons* cyanobiont of *Coppins et al.* 5440, which is similar to the homoiomerous one of *Physma*

byrsaeum, is neither representative of *Gibbosporina*, nor of *G. bifrons*. Even a sample from the same area (*Coppins et al.* 5310) has a very different *Nostoc* strain, with small greyish blue cells, a distinct morphotype which is also present in a sample from the Philippines. Apart from these two extreme cases, most samples of *G. bifrons* have rather large, dark brownish violet *Nostoc* cells. In most cases these have discernible chain structures, although these are weak, and apparently represent a transition state to strains where chain structures are lacking. Sometimes the cyanobiont layer occupies only *c.* ¼ of the medulla, and in such cases the cephalodium is only moderately gelatinous. These cephalodia are heteromerous and represent a parallel to pannarioid thalli of bipartite cyanolichens. Their upper surface is smooth when dry, indicating moderate swelling in the moist state.

Two of the cyanobionts of *G. bifrons* were not found to have any discernible chain structures, and *Nostoc* cells were arranged in glomeruli. This is also the dominant state in *Gibbosporina*, involving greenish-brownish violet *Nostoc* cells, organized in glomeruli and with no discernible chain structures. Even within this morphological type, there is obviously a strong diversity, revealed as differences in both *Nostoc* cell shapes, colours and sizes. The cells of the tiny cephalodia of *G. phyllidiata* have a distinct blue-green colour not seen in any other *Gibbosporina* sample.

The conclusion, even without a phylogenetic analysis, is that there is a surprisingly high cyanobiont diversity in *Gibbosporina*. Our hypothesis for a future extended phylogenetic study of *Gibbosporina* cyanobionts, based on the morphological pattern presented here, is that they would be expected to show a pattern similar to the one presented by Magain & Sérusiaux (2014) for the major collematoid family *Collemataceae*. This family has *Leptogium* and *Collema* cyanobionts distributed widely within the species represented in their phylogram.

Surface structure, lobe thickness and pycnidia

The chlorobiont thalli are quite similar in most species, with coalescent short convex lobes centrally, often with short lobules, and with more discrete lobes peripherally, the latter more appressed on smooth bark than when growing over a mat of epiphytic bryophytes. The lobes of *G. didyma* are clearly broader than those of the sympatric *G. mascarena*. Some species are more robust than others, an impression explained by thicker lobes. The most useful thallus character, however, is the upper surface structure. The species *G. leptospora* and *G. nitida* have strongly glossy lobes, whereas they are matt in *G. acuminata, G. amphorella, G. didyma*, and *G. sphaerospora.* The remaining species are intermediate, and upper surface structure is therefore used in combination with other characters in the key.

The apothecia are substipitate and similar in most species, with thalline excipuli more finely crenate in some species than in others. Pycnidia, on the other hand, which are known in 70% of the species, differ both in external morphology and in their pycnoconidia. The most distinct ones are the urn-shaped pycnidia of *G. amphiphorella*, even visible in Fig. 4B. In *G. sphaerospora*, the pycnidia are wide and conspicuous, whereas they are verruciform or bud-shaped in the remaining pycnidiate species. When abundant, they are conspicuous, even when they only measure 0·05 mm across. In two of the species (*G. amphorella* and *G. boninensis*), the pycnoconidia are significantly larger (1 ×2·5–4·0 μm) than in the other species (0·5 × 2–3 μm).

The main conclusion is that there is variation in quite a number of characters which makes it possible to define the species based on morphology and anatomy. In several cases the species which are most similar according to some given characters are also most closely positioned in the phylograms. The phylograms provide good support for the seven species which have been sequenced. The genus is common in some areas where fieldwork has focused on it, and there are already quite a number of herbarium specimens which could not be included in the present study. We have also treated some species in a wide sense, for example included the Sri Lankan material in *G. mascarena*, and the single *Kumei* s. n. specimen at H from

Papua New Guinea in *G. leptospora*. When *G. leptospora* is compared with the holotype from Australia, it has some lobe depressions, larger pycnidia, and has slightly broader proper spores, which are not only long-ellipsoid, but also can be short-ellipsoid and in some cases even subglobose. The tiny erect hairs on young lobes of the holotype are replaced by more diffuse tomentum in the *Kumei* s. n. specimen, but the distinctly thin perispore is shared with the holotype. Future studies of additional material will decide whether these species will be split up or not. Nevertheless, these are many reasons to believe that the genus contains more than 13 species and that it has a long evolutionary history.

Species and diversity pattern in the Indian Ocean area

Gibbosporina mascarena appears to be the most common species in Réunion and Mauritius. A total of 16 specimens have been examined from these islands, while the endemic *G. didyma* is known only from three collections. The holotypes of both these species were collected SE of the lake Grand Étang in east Réunion, in a closed valley opening towards the cyclones from the east. The amount of rainfall in this area is extremely high, and van den Boom *et al.* (2011) reported no less than 10–12 000 mm annually at Hauts-de-Sainte-Rose, slightly further to the east.

The holotype of *G. mascarena* was collected among 15–20 specimens growing on a single trunk, with a population of *G. didyma* present only 10 m away. The obvious difference noted immediately in the field was that most cepholodia in *G. didyma* were much more prominent than those of *G. mascarena*. In addition, those of *G. didyma* were partly foliose with relatively broad, matt lobes, and several cephalodia were growing apparently independently on bryophytes close to the major thalli. There may also be a third species in the Mascarenes, which is not yet sufficiently understood.

Two old collections from Sri Lanka have been studied and found to match *G. mascarena*. The *Leighton* 52 collection is heterogeneous, with one deviating individual where the perispores are much more even than those of *G. mascarena*. The cephalodia are strongly branched with thin and delicate, appressed lobes and the cephalodia are frequently positioned directly on a strongly developed prothallus. Its *Nostoc* cells appear visually identical to those of *G. mascarena* from Réunion/Mauritius. The neighbouring individual in this collection has spores which are identical to Mascarene material, but the cephalodia are more broad-lobed, semi-erect and partly rhizinate, and the *Nostoc* symbiont has smaller cells with short chain structures. Both Sri Lankan collections are placed within *G. mascarena* here, although future studies might well discover more than one taxon from this island.

The reports from Mauritius and Réunion by Nylander (1859) of '*Psoroma sphinctrinum*' and from the 'Central province' of Sri Lanka by Leighton (1869) of '*Pannaria pholidota*' are based on the old collections of *G. mascarena* at PC and S studied here, although Leighton (1869) may have studied a duplicate of the latter.

Species and diversity patterns in Australia, SE Asia and Pacific Islands

Four of the species (*G. acuminata, G. bifrons, G. nitida*, and *G. sphaerospora*) are now known from 13–26 collections originating from two to five countries, and *G. sphaerospora* (19 collections from Australia, Indonesia, Malaysia, the Philippines, and Samoa) and *G. bifrons* (26 collections from the Philippines, Malaysia, Solomon Islands and New Caledonia) in particular appear to be common and widespread. The remaining species are rare, and with the exception of *G. leptospora* (known from Australia and Papua New Guinea), endemic: *G. amphorella* from New Caledonia, *G. boninensis* from the Japanese Ogasawara Islands, *G. elixii* and *G. thamnophora* from Australia, *G. papillospora* from the Philippines and *G. phyllidiata* from the Solomon Islands. This pattern can of course change with future studies.

A centre of diversity is Queensland in Australia, where six species are known, and

many additional samples are awaiting determination. None of the *c.* 11 austral tripartite *Pannaria* species in Australia are known with certainty as far north as Queensland, except *P. phyllidiata* close to its southern boundary (Lumbsch *et al.* 2011). However, they resemble *Gibbosporina* species, and a specimen at BM from the Atherton Tableland in northern Queensland, published as *Psoroma sphinctrinum* (Jørgensen & Galloway 1992: 288), *Psoroma contortum* (Passo *et al.* 2004: 364) and *Pannaria contorta* (Passo & Calvelo 2006: 554), represents a *Gibbosporina*, but has not been studied sufficiently yet.

In Australia, most of the collections are from the forests of the mountain range between the latitudes of Cairns and Ingham (*c.* 16°30' – 18°40'S). The single Australian collection of *G. leptospora* was found somewhat further north (15°47'S), while all six Australian collections of *G. thamnophora* are from Eungella National Park, quite a bit further south (*c.* 21°S). However, these two species have also been found in Papua New Guinea, and it is not reasonable to compare the distribution patterns of the Australian species from the present data. Nevertheless, it should be emphasized that two different species have been found to co-occur in six of the areas (mostly national parks and state forests) where *Gibbosporina* species have been collected and studied.

A rather large number of specimens were collected in the Philippines in the early 20th century by persons associated with the US Bureau of Science established in Manila. Among the samples studied here, some have been deposited at S and H, but most of the material had been sent to Vainio, who published *c.* 25 specimens as *Psoroma sphinctrinum* (Vainio 1920). However, the material is diverse and represents five species of *Gibbosporina*. Four of these appear to be widespread, *G. acuminata*, *G. nitida* and *G. sphaerospora* also well represented in Australia, with *G. bifrons* appearing to have a more northern distribution. The most abundant species are *G. sphaerospora*, represented by 11 specimens, and *G. acuminata* with 9. Two collections from two different regions in southern Luzon near 14°N have strange papillose to small-bullate persipores and have been described as the endemic species *G. papillospora*.

Only eight samples among the widely distributed species have been seen from the large territory represented by the countries Indonesia, Malaysia and Papua New Guinea. However, the genus is probably widespread there, as illustrated by the 17 collections from Papua New Guinea present at CANB, but not yet studied. The Pacific area houses both widespread species and species at present known as endemics. The former category includes the isolated occurrence of *G. sphaerospora* in Samoa and a very large collection of *G. bifrons* from the Solomon Islands, in addition to a collection from its easternmost locality in New Caledonia. The endemics are *G. amphorella* from New Caledonia, *G. boninensis* from Ogasawara (Bonin) Islands and *G. phyllidiata* from the Solomon Islands. *Gibbosporina boninensis* resembles *G. acuminata*, as indicated in the diagnosis of the latter, whereas the two others are very distinctive species.

Evolution

Transoceanic dispersal has certainly played an important role in the distribution of *Gibbosporina* species. The distribution coincides well with the cyclone belt, at least as it is now, and there are no alternative explanations other than long-distance dispersal for the occurrences on isolated islands such as Samoa and Fiji. Also the phylogram shown in Fig. 10 does not show any geographical trend, and indicates that several migrations of groups within *Gibbosporina* have taken place. However, the specimens from the islands in the Indian Ocean are all from different species to those from further east, indicating that transoceanic dispersal across the Indian Ocean is a very rare event, even with the aid of easterly winds in the cyclone belt. The evolution of the sister species *G. elixii* and *G. mascarena*, as they are known today, requires a postulated, rather young, but rare transoceanic long-distance dispersal event between Réunion and Australia to have taken place.

Co-occurrences of different and distantly related species in Réunion, New Caledonia and Australia, and two mixed samples from the Philippines and Mauritius, as well as an undetermined admixture to *G. boninense*, testify to an evolution involving both migration and vicariance.

The well-known Réunion endemic *Acacia heterophylla* is closely related to Australian *Acacia* s. str. species, a group with a newly proposed position in *Austroacacia* (Miller *et al.* 2014), and poses a similar biogeographical challenge to *Gibbosporina*. A most extraordinary migration event was recently presented by Le Roux *et al.* (2014), who showed that *Acacia heterophylla* is derived from long-distance dispersal, potentially by means of petrels, to Réunion 1·4 million years ago, not directly from its ancestral stock in Australia, but from its more closely related species, *A. koa* from the Hawaiian Islands. Dispersal over very long distances can obviously occur as very rare events. However, there is no evidence that *Gibbosporina* ever made it to tropical America, nor mainland Africa, except for unconfirmed reports from South Africa. Its centre is in South-East Asia and NE Australia, as is the case for species in several other genera (see e.g. Jørgensen 1983).

As compared with other lichen genera, a strikingly high proportion of *Gibbosporina* species are primarily fertile. The phyllidiate and sterile *G. phyllidiata* sample from the Solomon Islands is an exception. Its tiny cephalodia and morphological dissimilarity to typical *Gibbosporina* samples may explain why this and possibly similar species with vegetative propagules have probably been overlooked. On the other hand, the very finely branched cephalodia of *G. thamnophora* obviously disperse the cyanobiont, in an adaptation shared as a convergence with *Pannaria durietzii*. These two examples indicate that future studies on *Gibbosporina* should involve a search for both bipartite chlorolichens and cyanolichens, the latter from truly emancipated cephalodia, which are not yet known. *Gibbosporina bifrons* and *G. didyma* have some large rhizinate cephalodia which appear to have developed physiological independence. However, they cannot be confirmed at present to be fully photosymbiodemic, as cephalodia have not been found with certainty outside of the prothallus zone. In addition, cephalodiate cyanomorphs appear to be sexually independent, because when cephalodia were collected as fertile for the first time, the apothecia were unexpectedly found to belong to the chloromorph (Fig. 8E).

Magain & Sérusiaux (2014) indicated, in their hypothesis on the evolution of the whole *Physma* group, that a tripartite thallus is the most likely ancestral form, based on the positions of *Xanthopsoroma* and *Gibbosporina* in their phylogram. Interestingly, the two most ancestral species of *Gibbosporina* in our phylograms are *G. didyma* and *G. bifrons*, with entirely different distributions, but sharing a particularly thick-walled perispore and large cephalodia, the latter being almost independent. Thus the evolution within *Gibbosporina* seems to be the opposite, from an almost photosymbiodemic state to a more specialized tripartite thallus type, with smaller and independent cyanomorphs as distinctly epiphytic cephalodia in the latter.

Gibbosporina species are superficially similar to austral tripartite *Pannaria* species. Old herbarium samples of both groups take on a similar dark brown colour, which is probably an effect of decomposition of the chlorobiont (see Elvebakk 2007). Small cephalodia tend to acquire the same colours, while large ones maintain a greyish colour. However, *Pannaria* is very remotely related to *Gibbosporina*, as shown in Fig. 9, and differs by lacking internal ascus amyloid structures, by the different perispores and by the presence of diverse and characteristic sets of TLC-detectable secondary compounds.

A discussion of the potential evolutionary history of *Gibbosporina* should therefore focus instead on the '*Physma* group', where *Gibbosporina* forms a well-supported clade associated with *Physma* and *Lepidocollema* (Fig. 9). There are no modern taxonomic studies on *Physma*, except for a study from Australia (Verdon & Elix 1994). However, it should be noted that *Physma* was shown to be paraphyletic by Magain & Sérusiaux (2014), and appears even polyphyletic in Fig. 9. Also,

Lepidocollema was paraphyletic according to Magain & Sérusiaux (2014, as *Parmeliella* pro parte). Recent phylogenetic studies of *Pannariaceae* (Ekman *et al.* 2014; Magain & Sérusiaux 2014; the present study) all have constraints, in terms of numbers of loci analyzed, selections of loci, numbers of samples in each clade, and incompatability of loci analyzed for different sequences compared. Thus, many remaining challenges represented by *Physma* and related genera should be left for future studies.

The inclusion of *Gibbosporina* in the '*Physma* group' adds to its general gross morphological heterogeneity, a feature strongly enhanced if *Xanthopsoroma* is also added. Nonetheless, *Physma*, *Lepidocollema* and *Gibbosporina* share tropical distribution patterns, a lack of TLC-detectable compounds, and the presence of distinct ring-like thalline excipuli and amyloid internal ascus structures, as pointed out in previous studies. However, we propose here that perispore structure (gibbose surfaces and/or presence of apical extensions) could be an additional synapomorphy of the '*Physma* group', even including *Xanthopsoroma*. All specimens in these four genera studied by us have perispores corresponding to this pattern. It can even be presented here that the *Jones* s. n. sample of '*Physma byrsaeum*' from Tahiti (an unreliable species identification like several other sequenced *Physma* samples), included in the phylograms by Wedin *et al.* (2009), Muggia *et al.* (2011), Magain & Sérusiaux (2014), Ekman *et al.* (2014) and by the present study, has perispores which are neatly intermediate between those of *Gibbosporina* and *Xanthopsoroma*; gibbose, but with wide nodulose apical extensions.

The old evolutionary history of both Lecanoromycetes and *Peltigerales* (Prieto & Wedin 2013; Beimforde *et al.* 2014), and early diversification of *Pannariaceae* versus *Collemataceae* (Wedin *et al.* 2009; Spribille & Muggia 2013), would indicate that the '*Physma* group' as a basal diversification within *Pannariaceae* is also of considerable age. We have made a tentative secondary calibration (only conclusion referred to here) following the procedures of a previous molecular dating study involving nucleotide differences of ITS in *Erysiphales* (Takamatsu & Matsuda 2004), where nucleotide substitution rates of the ITS region were found to be $2{\cdot}52 \times 10^{-9}$ per site per year. The divergence between *Physma radians* (NK-180) and *Gibbosporina elixii* corresponds to 75 Ma. Although not incompatible with the datings by Beimforde *et al.* (2014), we should treat this estimate with care.

In the northern part of the Great Dividing Range in east Australia, the *Pannariaceae* flora is dominated by '*Physma* group' genera and members of the *Pannaria lurida* group (Jørgensen 2015), whereas a very different flora of austral *Pannariaceae* genera and groups instead dominate in temperate areas further south along the same mountain range. It could be tempting to postulate an evolutionary connection between the '*Physma* group' and representatives among the numerous austral *Pannariaceae* genera in this area, coupled with migrations into South-East Asia. The high-latitude cooling during the Eocene associated with the opening of the Drake Passage at 33·7 Ma (e.g. Pagani *et al.* 2005), as well as New Guinean orogeny, initiated important northern migrations. The classic example is the genus *Nothofagus*, with its subgenus *Brassospora*; now the genus *Trisyngyne* according to Heenan & Smissen (2013). A recent study on the liverwort family *Schistochilaceae* is another example. Yu *et al.* (2014) showed that the group migrated into New Guinea at *c.* 19 Ma, shortly after the orogeny had been initiated there.

However, all phylogenies presented so far indicate that the separation of the '*Physma* group' from remaining clades in *Pannariaceae* is far older than the austral biogeographical events taking place after the Eocene cooling. Most austral *Pannariaceae* genera have now been represented in *Pannariaceae* phylogenies, but they are all well nested within the four clades presented by Magain & Sérusiaux (2014), Ekman *et al.* (2014) and the present study. The only exception is *Xanthopsoroma*, the only *Pannariaceae* genus with usnic acid (Elvebakk *et al.* 2010), which had deviating and surprising positions in all these studies. Its basal position in the *Physma* group of Magain

& Sérusiaux (2014) was not well supported, and was not confirmed by Ekman *et al.* (2014), where instead a clade of two samples was a sister group to their whole 'Clade 2', comprising no less than 16 *Pannariaceae* genera. In our LSU-based phylogram (Fig. 9), *Xanthopsoroma* forms, together with *Psorophorus*, two unresolved sister groups to the *Physma* clade. The topic obviously needs to be restudied with better multi-locus sequence data.

The conclusion is that the evolutionary history of the '*Physma* clade' remains unresolved and with open gaps, although *Gibbosporina* obviously belongs there. At present, the studied members of the clade should be considered to represent a small, remaining part of a diverse and probably large group with an old evolutionary history.

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