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## Taxonomic studies in foliicolous species of the genus *Porina* (lichenized *Ascomycotina: Trichotheliaceae*) – II. The *Porina epiphylla* group

### Abstract

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The taxonomy of foliicolous representatives of the *Porina epiphylla* group is revised. As a result of our studies of world-wide material, a more subtle species concept within the *Porina epiphylla* aggregate, i.e. species with 7-septate ascospores, is given. Thallus structure, perithecial morphology and development, and ascospore shape and size proved to be most valuable for species delimitation. A key to all known foliicolous species of the *Porina epiphylla* group, including facultatively foliicolous taxa, is presented. Eight species and one variety are described as new to science: *Porina andreana*, *P. atropunctata*, *P. guianensis*, *P. mazosioides*, *P. minutissima*, *P. mirabilis*, *P. subepiphylla*, *P. subnucula*, and *P. lucida* var. *australiensis*. The combination *Porina foliicola* (Bas.: *Clathroporina foliicola*) is formally proposed. *P. radiata* is introduced as a new name for the illegitimate younger homonym *P. rugosa*. *Porina atriceps* is reinstated as an autonomous species, and *P. multiseptata* is reduced to synonymy with *P. virescens*. *P. distans* is a sterile taxon, which most probably belongs to one of the several species in the genus producing cylindrical isidia, but cannot be identified at present. Notes on the distribution and ecology of the species are given, and the systematics and evolution of the group is outlined.

The *Porina epiphylla* group (Santesson 1952, Hafellner & Kalb 1995, Harris 1995), or *Porina* s.str. according to Harris (1995), comprises a large number of foliicolous, corticolous and saxicolous lichens, characterized by their perithecial and thallus anatomy. A more or less thin layer of colourless crystals (“crystallostratum”, Hafellner & Kalb 1995) is found between the yellowish to reddish brown outer perithecial wall and the covering algiferous thallus tissue. The perithecial walls are encrusted with a yellowish to brownish red, KOH+ orange red pigment (“*Porina* yellow”, Hafellner & Kalb 1995).

Like in the *Porina rufula* group (Santesson 1952, Lücking 1996), little variation is found with regard to ascospore septation; most species have 7-septate ascospores. However, considerable diversification is obvious as to thallus and perithecial morphology, making the delimitation and identification of species difficult and sometimes arbitrary.

The aim of the present study, which continues the first part of the series (Lücking 1996), is to evaluate the taxonomic value of morphological and anatomical features for the delimitation of species in foliicolous representatives of the *Porina epiphylla* group. Attention was paid to ontogene-

tic variation and correlations between characters. The work concentrates on species with 7-septate ascospores. A key is presented to all known foliicolous taxa of the *P. epiphylla* group.

Since the present paper focuses on taxonomic problems, we do not discuss the recent systematic considerations concerning generic divisions in the *Trichotheliaceae* (Hafellner & Kalb 1995, Harris 1995, McCarthy & Malcolm 1997, Lücking 1998). We follow the conservative concept outlined by Santesson (1952) and McCarthy & Malcolm (1997), maintaining *Porina* in its original sense and including the species with muriform ascospores usually assigned to *Clathroporina*. Though we are convinced that the groups proposed by Santesson (1952), Hafellner & Kalb (1995) and Harris (1995) are largely natural entities, they seem to be too narrowly defined to be worth generic status. The circumscription of *Clathroporina* as given by Harris (1995) needs further studies, but it is obvious that the foliicolous species involved form a distinctive unit, closely related to corticolous taxa centered around *P. mastoidea* and *Clathroporina eminentior*.

### Material and methods

Recent collections and herbarium material from the following regions were studied: Guatemala (herb. Lücking), Costa Rica (CR, USJ, herb. Lücking), Panamá (herb. Etayo), Cocos Island (CR, USJ, herb. Lücking), Colombia (B, herb. Henssen), Ecuador (OCA, QCNE, herb. Lücking), Peru (UPS), The Guianas (B, BRG, US, herb. Lücking), Brasil (UPS, URM, herb. Kalb, herb. Lücking), Guinea (UPS, herb. Vězda), Ivory Coast (UPS, herb. Becker), Congo (LG, herb. Vězda), Tanzania (VBI, herb. Vězda), South Africa (herb. Henssen), Vietnam (herb. Vězda), Sri Lanka (W), Papua New Guinea (B), Australia (B, CBG, herb. Henssen, herb. Kalb, herb. Vězda), Japan (HIRO, TNS, herb. Thor). Corticolous and saxicolous material from all tropical regions deposited in B, BM, G, S, UPS and in our own collections was also surveyed.

The following morphological and anatomical characters were considered: (A) thallus [1: *shape*; 2: *size*; 3: *structure*; 4: *colour*; 5: *brightness*; 6: *prothallus*]; (B) phycobiont [7: *cell shape*; 8: *cell arrangement*]; (C) perithecia [9: *shape* (young and mature); 10: *size*; 11: *colour*]; (D) ascospores [12: *septation*; 13: *shape*; 14: *size* (including length/width relation)].

For the study of morphological features, ZEISS stereomicroscopes (8-50) were used. Anatomical details were investigated using a ZEISS microscope (32-1000) and a MEOPTA microscope (40-1000). Squash mounts and thin hand sections were first studied in water and eventually also in Lugol's solution. For test on KOH-reaction a 10% KOH solution was used.

### Morphological and anatomical variation in the *Porina epiphylla* group

**Thallus.** – Thallus *shape* [1] can help to characterize species, though it is not strictly species specific. Usually, e.g. in *Porina atropunctata*, the thallus is continuous in central parts but marginally dispersed into single patches. In some instances, it might cover large areas of the leaf. A completely dispersed thallus is often found in *P. atriceps*, whereas *P. subepiphylla* or *P. imitatrix* have entire margins. In specimens with a marginally dispersed thallus, the margin may be entire when bordered by other lichens. In most species, thallus *size* [2] is between 10-20 mm in diam. (medium-sized); it may, however reach more than 20 mm (large), e.g. in *P. imitatrix*, whereas in a few taxa, e.g. *P. epiphylloides*, *P. guianensis* or *P. subepiphylla*, it is usually less than 10 mm (small).

Thallus *structure* [3] depends on the encrustation with calcium oxalate crystals. The crystals are either evenly distributed over the thallus surface, then forming small agglomerations, which might give the thallus a minutely and irregularly verrucose or rugose surface, or they are restricted to distinct verrucae or radiate ridges (*Porina epiphylloides*, *P. guianensis*, *P. mazosoides*, *P. follmanniana*, *P. radiata*). This character correlates with the cell arrangement of the phycobiont and is highly specific.

Thallus colour [4] varies from yellowish to greenish grey, and most species show a tendency to form either more yellowish (*Porina mirabilis*, *P. subepiphylla*) or more greenish grey thalli (*P. epiphylla*, *P. lucida*). Specific differences, e.g. between *P. epiphylla* and *P. subepiphylla*, are best seen in fresh material or in the field. Unfortunately, the practical use of thallus colour for taxonomic purposes is limited, as it also depends on the pigmentation of the phycobiont, which is correlated with the microclimatic conditions where the specimen was collected. Further, the preservation of a specimen has great influence on the thallus colour in the dried material (decomposition of green chlorophyll into brown phaeophytine). The brightness [5] of the thallus is an additional taxonomic character. In most species the thallus is matt (e.g. *P. subepiphylla*) to slightly nitidous, whereas some taxa (e.g. *P. atropunctata* and *P. imitatrix*), have a strongly nitidous appearance. The brightness is usually correlated with the formation of a prothallus and the surface structure.

A distinct prothallus [6] is present in several species. In *P. imitatrix* and related species, it forms a characteristic dark purplish black, nitidous margin. In *P. atropunctata*, the prothallus is translucent to whitish and forms a broad marginal zone. For the study of thallus shape and size and the formation of a prothallus, it is necessary to have specimens with free margins, as many species form an entire margin and a thin brownish prothallus when bordered by other lichens.

Two types of isidia might be found on the thalli of *Porina* species (Aptroot & Sipman 1993): the first type are cylindrical to coralloid outgrowths, whose function as isidia is not quite certain (Harris 1995); they are mostly found in species with a dark prothallus related to *P. mastoidea* and the foliicolous *P. imitatrix*, e.g. *P. conspersa* and *P. exasperatula*, but also known from taxa close to *P. nucula* (Harris 1995). The second type are the disciform isidia described as *Phyllophiale alba* (Santesson 1952), whose relationship to the *Porina* species is discussed (see below *P. mirabilis*).

**Phycobiont.** – All species of the *Porina epiphylla* group possess either *Phycopeltis* or *Trentepohlia* as phycobiont. In most taxa the phycobiont seems to be *Phycopeltis*, but can be mistaken for *Trentepohlia* due to its irregular cell shape. Genuine *Trentepohlia* is found in *P. conspersa*, *P. imitatrix*, or *P. nucula*. The shape [7] of the algal cells, which is either rectangular or angular-rounded (Fig. 1A), seems to be specifically influenced by the mycobiont, as it is also assumed for other taxa (Lücking 1996). Their size is similar in almost all species and thus useless for taxonomic purposes.

The arrangement [8] of the algal cells is highly correlated with the thallus structure. In species with a rather equal distribution of crystals, the algal cells are more or less angular rounded to irregular in outline, whereas in species with the crystals concentrated in distinct verrucae or ridges, the algal cells are rectangular and arranged in radiate rows (Fig. 1A).

**Perithecia.** – Besides ascospore size and shape, perithecial morphology provides the most important characters within the *Porina epiphylla* group. Four types of perithecial shape [9] can be distinguished: (a) lens-shaped, with a broad, often expanding base; (b) hemispherical, with the base not or slightly expanded; (c) wart-shaped, with the base slightly to distinctly expanded and straight sides from about half of the perithecial height to the base; and (d) conical, with the base not or slightly expanded and straight sides up to the pointed top (Fig. 1B).

Not only the shape of mature perithecia but also the variation during their development is specific. In *Porina atropunctata*, young perithecia are almost conical with a small dark spot around the ostiole, whereas mature perithecia become wart-shaped, probably due to the expansion of the perithecial contents, and the ostiolar spot gets paler. In *P. mirabilis*, young and mature perithecia are usually lens-shaped, but very old perithecia may become wart-shaped due to the elevation of their central part. In *P. epiphylla* and *P. lucida*, the young perithecia are lens-shaped, whereas mature perithecia become hemispherical.

Perithecial size [10] varies within a species and is thus only of secondary importance. In *Porina atropunctata*, very large perithecia twice the size of the smallest ones (with mature

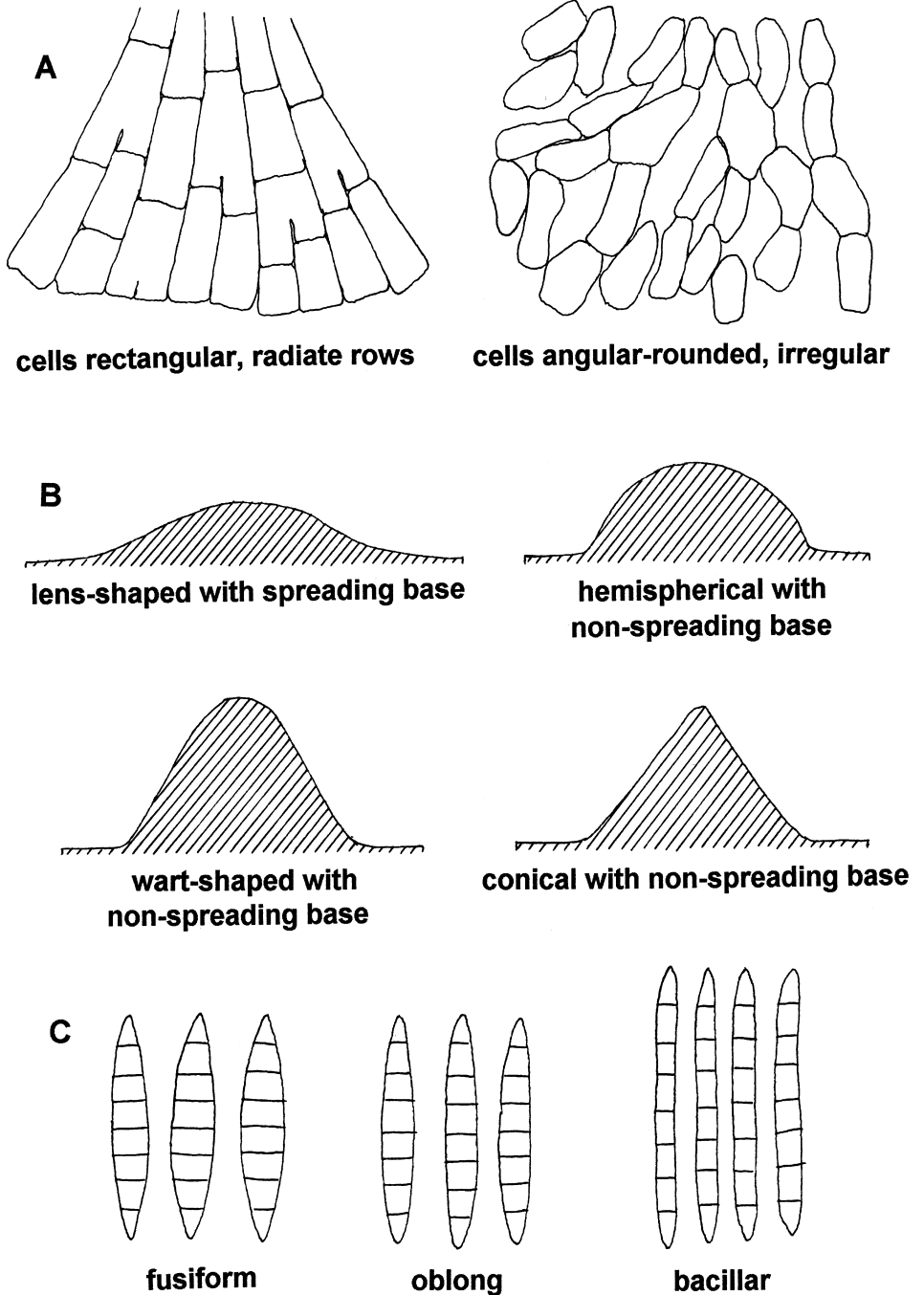


Fig. 1. Taxonomically useful characters in the *Porina epiphylla* group. – A. phycobiont cells and their arrangement; B. perithecial shape; C. ascospore shape.

ascospores!) on the same thallus are not rare. In a few cases, however, differences in perithecial size appeared to be constant within certain limits, so that they were used for taxonomic purposes in combination with ascospore size. This is the case in *P. minutissima*, *P. epiphylla* and *P. lucida*.

Perithecial colour [11] is similar to thallus colour and can be used in the same restricted way for species delimitation. In many species, the upper part of the perithecia around the ostiole becomes reddish or blackish brown when mature, due to a reduction of the outer, crystalline perithecial cover and the simultaneous production of dark pigments. This character is used for taxonomic purposes in some cases since it correlates with other features. A small, sharply delimited dark point around the ostiole is characteristic for the perithecia of *Porina atropunctata*. *P. lucida* often develops a light to dark brown, broad spot around the ostiole in old perithecia. In *P. atriceps*, a larger blackish area around the ostiole is found in both young and mature perithecia. Without any dark pigmentation are, for example, *P. albicera*, *P. conica* or *P. subepiphylla*.

The perithecial anatomy is very similar in all species of the *Porina epiphylla* group and provides no further character for their delimitation. The perithecial wall consists of two parts: an inner, prosoplectenchymatous wall and an outer wall which is covered by a more or less developed, compact layer of colourless crystals and an algal layer. Particularly the outer perithecial wall contains “*Porina* yellow” and reacts K+ orange red (Santesson 1952; Hafellner & Kalb 1995). Ascus shape and size vary slightly along with ascospore shape and size, but give no reliable feature for taxonomic purposes.

**Ascospores.** – Besides perithecial morphology, ascospores are the most important feature for species delimitation. As regards septation [12], most species have 7-septate ascospores, so that only a few species with a lower or higher number of septa can be set apart. In some cases, specimens supposedly belonging to the same species exhibit variable ascospore septation. Since they are otherwise identical, and their separation is not supported by ecogeographical differentiations, we consider them to be genetically aberrant specimens not worth of any taxonomic rank. Such cases are *Porina guianensis*, with 3- or 5-septate ascospores, and *P. virescens*, with 7- or 7-11(-15)-septate ascospores, in which the multiseptate form has been described as *P. multiseptata*. Similar phenomena have been described from other taxa, e.g. *Trichothelium sipmanii* (Lücking 1998), and probably represent early stages of speciation.

In the species with 7-septate ascospores, shape and size provide additional characters for species delimitation. The ascospore shape [13] varies from fusiform (broadest at the middle and usually with acute apices), to oblong (only slightly broader at the middle and usually with rounded apices) or bacillar, with ± parallel sides (Fig. 1C), and is rather constant within a species. In some taxa, the ascospores are very long and filiform and often tapering towards the proximal end. Ascospore size [14], and particularly length/width relation, seem also to be specific within certain limits.

**Key to the foliicolous species of the *Porina epiphylla* group** (including non-foliicolous taxa of which facultatively foliicolous collections are known)

For a confident determination of species of the *Porina epiphylla* group, it is necessary to have specimens which are well developed and, if possible, not entirely bordered by other lichens. Before using the key, the characters [1-14] outlined above should be evaluated. We have tried to adopt a natural key, so that related species stand close together. Characters or statements on distribution that do not have a counterpart in the key couple are separated by a dash.

- 1 Thallus with a purplish black prothallus, usually very nitidous (*P. mastoidea* subgroup) . 2
- Thallus without purplish black prothallus; prothallus, if present, translucent or whitish . . 7
- 2 Thallus surface with cylindrical to coralloid isidia . . . . . 3
- Thallus without isidia . . . . . 5

- 3 Perithecia absent. – Pantropical . . . . . see *Porina distans*  
 – Perithecia present . . . . . 4
- 4 Ascospores 25-35-septate, tapering, 90-150 × 3-5 μm, in a regular bundle; tropical America  
 . . . . . *Porina exasperatula*  
 – Ascospores 7(-9)-septate, broadly fusiform, 50-70 × 7-12 μm, irregularly arranged; tropical  
 America and Africa . . . . . *Porina conspersa*
- 5 Ascospores broadly fusiform, 38-64 × 6.5-10 μm, with gelatinous sheath. – Pantropical .  
 . . . . . *Porina imitatrix*  
 – Ascospores narrowly fusiform, 27-45 × 3.5-6 μm, without gelatinous sheath . . . . . 6
- 6 Ascospores 30-45 × 4-6 μm; perithecia 0.4-0.7 mm diam., hemispherical to wart-shaped;  
 thallus greenish grey, with an uneven surface; pantropical . . . . . *Porina tetracerae*  
 – Ascospores 27-35 × 4-5.5 μm; perithecia 0.35-0.55 mm diam., wart-shaped to almost conical;  
 thallus yellowish grey, with a minutely verrucose surface; tropical America . . . . .  
 . . . . . *Porina curtula*
- 7 Thallus with disc-like isidia of the *Phyllophiale* type. – Perithecia, if present, appanately  
 lens-shaped with broadly spreading base; ascospores 7-septate, bacillar, 35-45 × 3-4.5 μm  
 . . . . . *Porina mirabilis*  
 – Thallus without such isidia . . . . . 8
- 8 Ascospores muriform. – Asia . . . . . *Porina foliicola*  
 – Ascospores transversely septate . . . . . 9
- 9 Thallus with distinct verrucae or radiate ridges; phycobiont cells rectangular or angular-ro-  
 unded, in radiate rows or irregularly arranged; ascospores in some species rather broad  
 (10-20 μm, about 4-6 times as long as broad) and with gelatinous sheath (*P. nucula* and *P.*  
*epiphyloides* subgroup) . . . . . 10  
 – Thallus without distinct verrucae or ridges, although often with an irregular surface (except  
 for *P. similis* with large, scattered verrucae); phycobiont cells angular-rounded, irregularly  
 arranged; ascospores always narrow (3-6 μm, about 7-14 times as long as broad) and  
 without gelatinous sheath (*P. epiphylla* subgroup) . . . . . 20
- 10 Ascospores rather broad (10-20 μm), about 4-6 times as long as broad, with gelatinous  
 sheath . . . . . 11  
 – Ascospores narrow (3-9 μm), about 6-14 times as long as broad, without gelatinous sheath  
 . . . . . 13
- 11 Ascospores 9-13-septate, 65-80 × 15-20 μm. – Pantropical . . . . . *Porina rudiuscula*  
 – Ascospores 7(-9)-septate, 40-70 × 10-12 μm . . . . . 12
- 12 Phycobiont cells rectangular, in radiate rows; Cuba . . . . . *Porina pocsii*  
 – Phycobiont cells angular-rounded, irregularly arranged; pantropical . . . . . *Porina nucula*
- 13 Thallus with radiate ridges . . . . . 14  
 – Thallus with small but distinct verrucae . . . . . 15
- 14 Perithecia appanately lens-shaped, their top sometimes with a broad darker spot; ascospo-  
 res 7-septate, 28-35(-43) × 3.5-4.5 μm; tropical America and Africa . . . . . *Porina radiata*  
 – Perithecia appanately conical, their top with a small blackish brown spot; ascospores  
 7-septate, 23-30 × 3-4 μm; tropical Africa . . . . . *Porina follmanniana*
- 15 Phycobiont cells rectangular, in radiate rows . . . . . 16  
 – Phycobiont cells angular-rounded, irregularly arranged . . . . . 19
- 16 Ascospores 15-septate, 80-100 × 6-9 μm. – Tropical Africa . . . . . *Porina longispora*  
 – Ascospores 3-7-septate, 19-50 × 3-6 μm . . . . . 17
- 17 Ascospores very large, 40-50 × 5-6 μm, 7-septate. – Tropical Africa . . . . . *Porina mazosioides*  
 – Ascospores small, 19-27 × 3-3.5 μm, 3-7-septate . . . . . 18

- 18 Ascospores 3(-5)-septate, 19-22 µm long; tropical America . . . . . *Porina guianensis*  
 – Ascospores 7-septate, 21-27 µm long; tropical Africa . . . . . *Porina epiphyllodes*
- 19 Ascospores 5-septate, 15-21 × 3-5 µm; tropical America . . . . . *Porina verruculosa*  
 – Ascospores 7-septate, 30-40 × 5-6 µm; palaeotropical . . . . . *Porina subnucula*
- 20 Ascospores (1-)3-septate, 10-25 µm long . . . . . 21  
 – Ascospores 7(-15)-septate, 20-80 µm long . . . . . 22
- 21 Perithecia applanately lens-shaped with broadly spreading base, hardly delimited from the surrounding thallus; ascospores 1-3-septate, 10-15 µm long; tropical America . . . . .  
 . . . . . *Porina andreana*  
 – Perithecia hemispherical, sharply delimited from the surrounding thallus; ascospores 3-septate, 13-25 µm long; tropical Africa and Australasia . . . . . *Porina albicera*
- 22 Perithecia (and thallus) furnished with dense cushions of soft hairs; ascospores 7-septate (“*virescens*” form) or irregularly (7-)8-10(-15)-septate (“*multiseptata*” form), 45-75 µm long. – Tropical Australasia . . . . . *Porina virescens*  
 – Perithecia and thallus glabrous; ascospores with some very few exceptions 7-septate, 20-48 µm long (*P. epiphylla* aggregate) . . . . . 23
- 23 Perithecia distinctly conical, their top not darkened but with a short cylindrical, upwards expansion. – Tropical Africa and Australasia . . . . . *Porina conica*  
 – Perithecia lens-shaped, hemispherical, or wart-shaped, if conical, then their top with a small blackish brown spot and not upwards expanded . . . . . 24
- 24 Perithecia applanately lens-shaped with broadly spreading base, hardly delimited from the surrounding thallus; ascospores narrowly bacillar, 10-13 times as long as broad; thallus often provided with disk-like isidia of the *Phyllophiale* type. – Pantropical *Porina mirabilis*  
 – Perithecia lens-shaped, hemispherical, or wart-shaped, their base usually well delimited from the surrounding thallus; ascospores oblong to fusiform, 6-9 times as long as broad; thallus never with disc-like isidia of the *Phyllophiale* type . . . . . 25
- 25 Perithecia at their top, around the ostiole, with a dark brown to blackish brown spot . . . . . 26  
 – Perithecia at their top of the same colour as the rest of the perithecium or with a slightly reddish tinge (*P. epiphylla* s.lat.) . . . . . 29
- 26 Perithecia with a distinct, rather small blackish brown spot, especially when young; ascospores 25-35 µm long. – Tropical America and Australasia . . . . . 27  
 – Perithecia with an often indistinct, rather broad brownish spot, which is best seen in old but usually absent in young perithecia; ascospores (30-)35-48 µm long . . . . . 28
- 27 Young perithecia distinctly conical, with a very small dark spot; mature perithecia wart-shaped, the ostiolar spot often paler; thallus usually with a distinct whitish prothallus . . . . .  
 . . . . . *Porina atropunctata*  
 – Young and mature perithecia lens-shaped, always with a broader dark spot; thallus without a whitish prothallus . . . . . *Porina atriceps*
- 28 Perithecia lens-shaped to hemispherical, their top often applanate; thallus ± smooth, usually greenish grey; pantropical . . . . . *Porina lucida* var. *lucida*  
 – Perithecia (hemispherical to) wart-shaped, their top not applanate; thallus often with rather large, irregular verrucae, yellowish grey; tropical Australia . . . . . *Porina similis*
- 29 Mature perithecia wart-shaped; thallus usually yellowish grey . . . . . 30  
 – Mature perithecia lens-shaped to hemispherical; thallus usually greenish grey . . . . . 31
- 30 Ascospores fusiform, 6-7 times as long as broad; thallus smooth, matt; tropical America . . . . .  
 . . . . . *Porina subepiphylla*  
 – Ascospores oblong, 8-9 times as long as broad; thallus often with rather large, irregular verrucae; tropical Australasia . . . . . *Porina similis*



- 31 *Perithecium* 0.4-0.7 mm diam., usually lens-shaped; ascospores larger, (30-)35-48  $\mu$ m long (*P. lucida*) . . . . . 32  
 – *Perithecium* 0.2-0.35(-0.45) mm diam., usually hemispherical; ascospores smaller, 20-32  $\mu$ m long . . . . . 33
- 32 Ascospores narrowly oblong, (30-)35-48  $\times$  4-5.5  $\mu$ m, 8-10 times as long as broad; pantropical . . . . . *Porina lucida* var. *lucida*  
 – Ascospores broadly oblong, 30-38  $\times$  5-6  $\mu$ m, 6-7 times as long as broad; tropical Australasia . . . . . *Porina lucida* var. *australiensis*
- 33 *Perithecium* 0.2-0.25(-0.3) mm diam.; ascospores 20-25  $\times$  2.5-3  $\mu$ m; tropical Australasia . . . . . *Porina minutissima*  
 – *Perithecium* 0.25-0.35(-0.45) mm diam.; ascospores 26-32  $\times$  3-4  $\mu$ m; pantropical . . . . . *Porina epiphylla* s.str.

### Taxonomic account

The species are listed in alphabetical order. For each species, the diagnostic features are given and its taxonomic relationships are discussed, complemented by notes on its distribution and ecology. The list of examined specimens always and only includes follicolous specimens; in facultatively follicolous taxa, non-follicolous specimens are not cited. The cited collections refer to representative, recently examined material which reflects the distribution of a species, or to specimens incorrectly identified in other papers as far as we have seen them. We do not intend to give a complete list of specimens for such common taxa as *Porina epiphylla* or others.

#### *Porina albicera*

*Porina albicera* (Kremp.) Overeem in Bull. Jard. Bot. Buitenzorg, ser. 3, 4: 112. 1922 = *Verrucaria albicera* Kremp., Lich. Foliicol.: 16. 1874 [& in Nuovo Giorn. Bot. Ital. 7: 53. 1875]. – Typus: Australasia, Malaysia, Borneo, Sarawak, *Beccari 225b* (M, holotype!). = *Phylloporina myriocarpa* Müll. Arg. in Hedwigia 30: 188. 1891. – Typus: Australasia, Vietnam, Tonkin, Mt. Bavi, *Balansa s.n.* (G, holotype!).

Diagnostic features: *Thallus* continuous, small, smooth (rarely with irregular, small verrucae), yellowish grey, matt (to slightly nitidous), no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded (to rectangular), irregularly arranged. *Perithecium* young lens-shaped, mature ones hemispherical, basally well delimited from the thallus (Fig. 2A), 0.15-0.2 mm diam., often with a reddish tinge, numerous. *Ascospores* 3-septate, oblong-fusiform, 13-25  $\times$  2-4  $\mu$ m, 6-7 times as long as broad.

Notes: *Porina albicera* is a rather characteristic species due to its small, hemispherical perithecia and 3-septate ascospores. The thallus is usually smooth, but a specimen was found with scattered, small verrucae (Papua New Guinea, *Aptroot 17381b* (B)). Contrary to *P. guianensis*, the phycobiont cells are always non-radiate. *P. andreana* differs by lens-shaped, basally hardly delimited perithecia and smaller, often 1-septate ascospores. Externally, *P. albicera* is somewhat reminiscent of *P. fulvella* Müll. Arg. (Santesson 1952), in which crystals are always absent.

Due to their very small ascospores (13-16  $\times$  2-3  $\mu$ m), the collections from tropical Africa were first considered to represent a different taxon to be recognized at subspecific rank, but a survey on ascospore size variation in the Asian collections revealed specimens with equally small ascospores, e.g. 14-16  $\times$  2-2.5  $\mu$ m [Philippines, *Robinson s.n.* (UPS)] or 16-18  $\times$  2-3  $\mu$ m [Australia, *Tibell 14328* (UPS)].

#### Distribution and ecology

Known from tropical Africa and Australasia. The record from the Neotropics (Aptroot & Sipman 1993) could not be checked; it might represent *Porina andreana* or *P. guianensis*. *P.*

*albicera* is usually found in lowland rain forest areas but occasionally extends into dryer ever-green forests.

#### Additional specimens examined

AFRICA: IVORY COAST: Forêt de Yapo, 11.1976, *Aké Assi 13620* (herb. Vězda); Abidjan, Forêt du Banco Nature Reserve, 8. 1974, *Aké Assi s.n.* (herb. Vězda). — CONGO: Haut-Zaïre, Ituri, Mont Tatotudu, forêt primaire, 4.1976, *Lisowski 42590* (herb. Vězda).

AUSTRALASIA: VIETNAM: Tonkin, Mt. Bavi, *Balansa s.n.* (G). — INDONESIA: Sumatra, Enggano Isl., forest behind Ekinoia, 6.1936, *Lütjeharms 49491* (UPS). — PHILIPPINES: Polillo, 1909, *Robinson s.n.* (UPS, *Vainio 31627*). — PAPUA NEW GUINEA: Madang, Wasabamal logging area, 04°50'S, 145°40'E, 25 m, 2.1987, *Aptroot 17381b* (B). — AUSTRALIA: Queensland, Mt. Alexandra, 16°16'S, 145°32'E, 10.1983, *Tibell 14328* (UPS).

### *Porina andreana*

*Porina andreana* Lücking & Vězda, **sp. nova**

Typus: America, Costa Rica, Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-1793* (M, holotype!).

A *Porina mirabilis* peritheciis minoribus ascosporis (1-)3-septatis minoribusque differt.

Diagnostic features: *Thallus* continuous, small, slightly uneven-rugose, yellowish grey, (slightly) nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* applanately lens-shaped, basally hardly delimited from the thallus (Fig. 2B), 0.2-0.25 mm diam., sometimes with a slight reddish tinge. *Ascospores* (1-)3-septate, oblong, 10-15 × 2.5-3 µm, 4-5 times as long as broad.

Notes: *Porina andreana* is one of the few species of this group with 3-septate ascospores. From the other species with similar ascospores, i. e. *P. albicera* and *P. guianensis*, it differs by its applanately lens-shaped perithecia which are not sharply delimited from the surrounding thallus, and by its very small ascospores. The ascospores are often badly developed or remain 1-septate for a long time prior to maturity [e.g. Guyana, *Sipman & Aptroot 18942* (B)]. Externally, *P. andreana* is reminiscent of *P. mirabilis*, which has larger perithecia and larger, 7-septate ascospores.

#### Distribution and ecology

The species is thus far known from a few collections in Central and South America in lowland rain forests.

#### Additional specimens examined

AMERICA: COSTA RICA: Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-5554* (herb. Lücking); Cartago, Centro Agronómico Tropical de Investigación y Enseñanza, near Turrialba, 09°53'N, 83°39'W, 600 m, lower montane rain forest, 3.1991, *Lücking 91-3473* (herb. Lücking). — GUYANA: Upper Mazaruni, Kamarang, 05°52'N, 60°37'W, 500 m, 25 m tall, mixed forest, 2.1985, *Sipman & Aptroot 18942b* (b). — BRAZIL: Pernambuco, Recife, remnants of Mata Atlântica, *Cáceres & Lücking s.n.* (URM, herb. Cáceres).

### *Porina atriceps*

*Porina atriceps* (Vain.) Vain. in Ann. Acad. Sci. Fenn., ser. A, 15: 364. 1921 ≡ *Porina epiphylla* var. *atriceps* Vain. in J. Bot. 34: 295. 1896. — Typus: America, Dominica, s. loc., 1892, *Elliott 517* (TUR, holotype!).

?= *Phylloporina cupreofusca* Zahlbr. in Ann. Crypt. Exot. 1: 114. 1928. — Typus: Australasia, Indonesia, Java, Batavia, Mt. Panerango, Artja, 1100 m, 4.1894, *Schiffner 3450* (UPS, isotypus!).

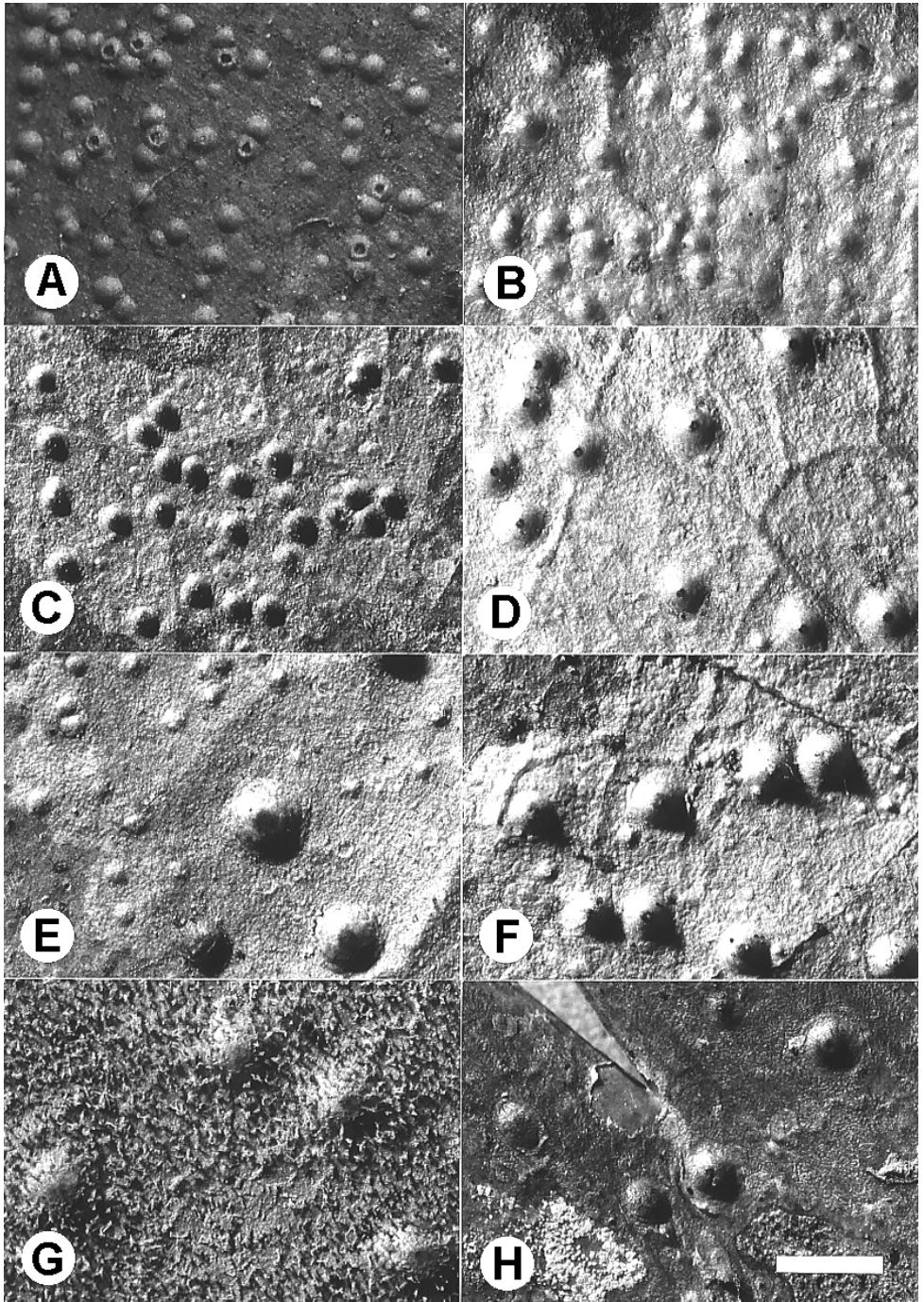


Fig. 2. General appearance of *Porina* species – A: *P. albicera* [Philippines]; B: *P. andreana* [Costa Rica]; C: *P. atriceps* [Philippines]; D: *P. atropunctata* [Costa Rica]; E: *P. similis* [Australia]; F: *P. conica* [Indonesia, isotype]; G: *P. virescens* [Papua New Guinea]; H: *P. foliicola* [Vietnam, isotype]. – Scale = 1 mm.

Diagnostic features: *Thallus* dispersed but centrally confluent, small, uneven, yellowish grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones lens-shaped (to wart-shaped), 0.2-0.4 mm diam., with a blackish brown, 0.1-0.2 mm broad spot around the ostiole (Fig. 2C). *Ascospores* 7-septate, (narrowly fusiform to) oblong, 27-35 × 3-4.5 µm, 7-10 times as long as broad.

Notes: *Porina atriceps* was regarded as a variety of *P. epiphylla* (Vainio 1896, Santesson 1952), differing by the dark brown to black perithecial top. The statements of Santesson (1952: 239) that var. *atriceps* is "... varying in the same way as typica" and found "... side by side on the same leaf ..." already indicates this status to be inappropriate, since a variety would be expected to have less variation and a different, more restricted geographical distribution. The reason for the correct view of Santesson (1952: 239) that in some cases both taxa are "... well distinguished, but in other cases the limit between them seems very indistinct." is due to the fact there are three to four different taxa involved when using the dark perithecial top as a single character: *P. atriceps*, *P. atropunctata*, *P. lucida* and sometimes *P. similis*, and these are separated in a more or less different way from *P. epiphylla*.

*Porina atriceps* s.str. is characterized by rather small, lens-shaped perithecia with a comparatively broad blackish brown spot around the ostiole. The species is closely related to *P. atropunctata*, in which the perithecia are conical to wart-shaped and larger, and there is only a small dark spot around the ostiole which disappears in old perithecia. A pale to dark, rather broad, reddish brown spot may be developed in old perithecia of *P. lucida*, but here the perithecia and ascospores are larger than in *P. atriceps*. In some few cases, specimens attributed to *P. similis* also exhibit a blackish brown spot around the ostiole; here as well the perithecia are larger than in *P. atriceps* and usually wart-shaped. Typical perithecia in *Porina atriceps* are lens-shaped, e.g. in collections from Papua New Guinea, while a few specimens with hemispherical to almost wart-shaped perithecia (e.g. from Guadeloupe or the Philippines, and the type!) are akin towards *P. atropunctata*.

The type of *Phylloporina cupreofusca* was considered a synonym of *Porina epiphylla* by Santesson (1952), but the dark top of the strongly discoloured perithecia and the general habit indicate conspecificity with *P. atriceps*.

#### Distribution and ecology

*Porina atriceps* is perhaps a pantropical taxon, which is, however, only known from the Neotropics and Australasia. The records from tropical Africa (Santesson 1952) are incorrect and represent other species. The species is most common and most typically developed in the Caribbean and SE Asian Islands, such as Guadeloupe or Papua New Guinea, i.e. in lowland areas with highly oceanic character.

#### Additional specimens examined

AMERICA: HONDURAS: Atlántida, Lancetilla Valley, 20-600 m, 12.1927 to 3.1928, *Standley 54893d* (UPS, filed under *Trichothelium minus*). — COSTA RICA: Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-5277* (herb. Lücking). — DOMINICA: 1892, *Elliott 517* (TUR); Emerald Pool Waterfall, 300-340 m, 7.1996, *Vězda* (herb. Lücking). — GUADELOUPE: Basse-Terre Isl., Baillif-Banin, 700-800 m, 3.1990, *Vivant s.n.* (herb. Vězda). — COLOMBIA: Caquetá, Araracuara, 00°36'S, 72°26'W, 350 m, low forest on podsolized soil, 10.1988, *Sipman & Duivenvoorden 27785* (B). — GUYANA: East Demarara, Timehri, 06°29'N, 58°15'W, 10 m, 2.1985, *Aptroot 18097a* (B). AUSTRALASIA: MALAYSIA: Borneo, Sabah, Kinabalu National Park, 06°05'N, 116°35'E, 1650 m, 5.1989, *Sipman & Tan 29465* (B). — INDONESIA: Sumatra, Oostkust, Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25 b, c, d* (UPS, filed under *P. conica* and *P. epiphylla*); Java, Salak, 4.1897, *Nyman 45a* (UPS); Mt Gedeh, Tjibodas, 1380 m, 5.1950, *Schröter 5525* (UPS; ex Bogor 6516b). — PHILIPPINES: Luzon, Laguna, Los Baños, Mt. Makiling, 250 m, I. 1977, *Gruezo 2479* (herb.

Vězda). — PAPUA NEW GUINEA: Morobe, Mt. Manke, *Castanopsis-Lithocarpus* forest, 3.1974, *Van Zanten s.n.* (herb. Vězda); Morobe, Busom Valley, 06°34'S, 146°58'E, 600 m, 3.1987, *Sipman 24542* (B); Madang, Karkar Isl., 04°37'S, 145°55'E, 50 m, 3.1987, *Sipman 24269* (B); Balek Wildlife Reserve, 05°18'S, 145°43'E, 20 m, 3.1987, *Sipman 24287a* (B); Varirata National Park, 09°27'S, 147°22'W, 800 m, 3.1987, *Sipman 22429* (B). — AUSTRALIA: Queensland, Atherton Tableland, 9.1983, *Henssen 29351* (herb. Lücking, filed under *P. lucida*); Eacham Shire, Souita Falls, tropical rain forest, 8.1987, *Henssen 31245* (herb. Henssen, herb. Lücking); Cairns, Bellenden Ker Range, 8. 1987, *Lumbsch 5399/8-V* (herb. Vězda); Kuranda, The Maze, mixed rain forest, 7.1927, *Du Rietz 4266a* (UPS). — FIJI: Viti Levu, Novai, 12.1986, *Degener & Degener 31815aa* (B). — NEW CALEDONIA: Grande-Terre, Province Sud, Monts Koghis-Dumbéa, rain forest, 22°14'S, 166°30'E, 550 m, 8.1994, *Kalb & Kalb s.n.* (herb. Lücking).  
 Incorrect records: Africa, Cameroon, Bipinde, rain forest, 10.1913, *Zenker 4819* (UPS) is indeterminate (possibly *Porina lucida*). Bibundi, 1891, *Jungner 51b* (UPS) is a badly developed *P. radiata*.

### *Porina atropunctata*

*Porina atropunctata* Lücking & Vězda, **sp. nova**

Typus: America, Costa Rica, Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-2742* (M, holotypus!).

A *Porina atriceps* prothallo albo et peritheciis majoribus conicis ad verruciformibusque differt.

Diagnostic features: *Thallus* marginally dispersed, medium-sized, rough, yellowish grey, (slightly) nitidous, usually with a whitish prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young conical, mature ones wart-shaped, 0.3-0.5 mm diam., with a small, 0.05-0.10 mm broad, blackish spot around the ostiole (Fig. 2D), sometimes light brown in mature perithecia. *Ascospores* 7-septate, narrowly fusiform (to oblong), (20-)25-32(-35) × 3-5 μm, 6-9 times as long as broad.

Notes: This new species agrees with *Porina atriceps* in having a dark spot around the ostiole, but differs in that the perithecia are larger and, at least the younger ones, almost conical. Furthermore, the dark spot is very small and gets paler in old perithecia, and a whitish prothallus is usually present. Both species seem to be closely related, however, and intermediate forms have been found. A particular feature of *P. atropunctata* is the conical shape of young perithecia, with a distinct blackish spot around the ostiole, whereas mature perithecia are wart-shaped and the ostiolar spot becomes brownish or even disappears in old perithecia. Such forms, particularly when growing on densely colonized leaves, may resemble *P. subepiphylla* but can be distinguished by their smaller ascospores. The species is also similar to the Australian *P. similis*, which has somewhat larger perithecia which are never conical in shape and a thallus provided with irregularly appanate verrucae. Specimens with predominantly conical perithecia can be distinguished from *P. conica* by the dark spot and lack of a cylindrically expanded top, by the smaller ascospores, and by the marginally dispersed thallus with a whitish prothallus.

Local populations of *Porina atropunctata* may vary in the size of the perithecia and in the formation of the dark spot. In a few otherwise typical specimens, the dark spot was found to be completely absent in mature perithecia [Brazil, *Kalb 53* (herb. Vězda)]. Collections from Cocos Island (Lücking & Lücking 1995) and Colombia [*Aguirre & Sipman 5691e* (B)] have extremely large, well-developed perithecia. The Australian specimens do not differ from neotropical ones.

### Distribution and ecology

The species has a very similar distribution and ecology as *Porina atriceps*, being known from the Neotropics and Australasia, and apparently absent in tropical Africa. *P. atropunctata* is, however, more common in Central and South America than on the Caribbean islands, and typical specimens are only rarely found in Australasia.

## Additional specimens examined

AMERICA: HONDURAS: Atlántida, Lancetilla Valley, 20-600 m, 12.1927 to 3.1928, *Standley 54893d* (UPS, filed under *Trichothelium minus*). — COSTA RICA: Puntarenas, Monteverde Reserve, montane rain forest, *Henssen 26263* (herb. Lücking); Corcovado National Park, 8°28'N, 83°35'W, 50-150 m, lowland rain forest, 7. 1992, *Lücking 92-3559* (herb. Lücking); Heredia, La Selva Protection Zone, 10°26'N, 84°03' W, 50 m, lowland rain forest, 9.1991, *Lücking 91-5718* (herb. Lücking); San José, Braulio Carrillo National Park, 10°09'N, 83°58'W, 700-800 m, lower montane rain forest, 9.1991, *Lücking 91-3115* (herb. Lücking). — DOMINICA: Emerald Pool Waterfall, 300-340 m, 7.1996, *Vězda* (herb. Lücking). — GUADELOUPE: Marie-Galante Isl., St. Louis valley, 20-30 m, 3.1992, *Vivant s.n.* (herb. Vězda); Marie-Galante Isl., Rivière de Saint Louis, 50 m, mesophilous forest, 1.1993, *Vivant s.n.* (herb. Lücking, filed under *P. lucida*); St. Louis Isl., St. Louis river, 50 m, 7. 1990, *Vivant s.n.* (herb. Vězda); Basse-Terre Isl., Baillif-Banin, St. Louis, 700-800 m, 3.1990, *Vivant s.n.* (herb. Vězda, filed under *P. atriceps*). — COLOMBIA: Meta, Villavicencio, Guaitiquia River, 600 m, 9.1984, *Aguirre & Sipman 5691e* (B). — FRENCH GUIANA: Saül, 1-2 km SSW of Saül, 03°37'N, 53°13'W, 300 m, 1.1988, *Sipman 32228* (B, filed under *P. lucida*). — BRAZIL: São Paulo, Serra do Mar, Serra do Garrãozinho, 850 m, humid primary forest, 3.1980, *Kalb 227* (B); *ibid.*, 10.1978, *Kalb 53* (herb. Vězda, filed under *P. epiphylla*); Manuel Ferreira, along road SP-39, 850 m, 15 m tall forest on slope, 7. 1979, *Sipman 12707, 12707c* (B–H. Sipman: *Lichenotheca Latinoamericana*); Ilha de São Sebastião, Morro das Tacas, 600 m, very humid lower montane rain forest, 4.1978, *Kalb & Plöbst s.n.* (B, filed under *P. epiphylla* – K. Kalb: *Lichenes Neotropici* 27); Fazenda São João, 600 m, 8.1980, *Kalb 302* (herb. Vězda); Santos, 10.1894, *Malme 4011a* (UPS); Rio Grande do Sul, Hamburgerberg, 10.1892, *Malme 627a* (UPS). AUSTRALASIA: INDIA: Khasia montes, Cherrapunji, 1300-1500 m, 9.1967, *Topál s.n.* (herb. Vězda). — PAPUA NEW GUINEA: Kaiser Wilhelms Land, Friedrich-Wilhelms Hafen, 10.1899, *Nyman 62c* (UPS). — AUSTRALIA: Queensland, Atherton Tablelands, Lake Barrine, 17°15'S, 145°38'E, 750 m, forest remnant, 3.1988, *Aproot & Aproot 22652* (B, filed under *P. conica*); *ibid.*, 9.1983, *Henssen 29351* (herb. Henssen, herb. Lücking); Eacham Shire, Souita Falls, 17°35'S, 145°40'E, 8.1987, *Henssen 31242* (herb. Lücking).

***Porina conica***

*Porina conica* R. Sant. in Symb. Bot. Upsal. 12: 232. 1952. – Typus: Australasia, Indonesia, Sumatra, Oostkust: Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25c* (UPS, holotypus!).

Diagnostic features: *Thallus* continuous, medium-sized (to large), smooth (to slightly rough), (yellowish) grey, matt; no prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* conical with an upwards expanded, cylindrical top (Fig. 2F), (0.25-)0.35-0.6 mm diam., sometimes with a yellowish red tinge, ostiolar region rarely reddish brown. *Ascospores* 7-septate, narrowly fusiform (to oblong), (27-)34-48 × (2.5-)4-6 µm, 8-10 times as long as broad.

Notes: *Porina conica* differs from all other species of the group by its conspicuously conical perithecia with a cylindrically expanded top. The species is probably related to *P. subepiphylla*, which has similar ascospores and thallus morphology but wart-shaped perithecia, and is only known from tropical America. The hitherto known collections of *P. conica* are rather homogeneous, except that the African and some Australian specimens have smaller perithecia (0.25-0.4 vs. 0.35-0.6 mm) and ascospores (27-38 vs. 34-48 µm). The type material consists of several leaves with abundant, well-developed and typical specimens.

## Distribution and ecology

*Porina conica* is known from lowland to lower montane rain forests in Africa and Australasia; especially in tropical Asia it is locally abundant.

## Additional specimens examined

AFRICA: IVORY COAST: Forêt du Banco, 8.1974, *Ake Assi 12597, 12602* (herb. Vězda). Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101033* (herb. Lücking).

AUSTRALASIA: VIETNAM: Tonkin, Vinh-Phuc Prov., Tuyen Quang, 4.1974, *Zsolt s.n.* (herb. Vězda, filed under *P. mirabilis*). — MALAYSIA: Sabah, Kinabalu National Park, 06°05'N, 116°35'E, 750 m, tall forest, 5.1989, *Sipman & Tan 29566* (B); *ibid.*, 700 m, tall forest, 5.1989, *Sipman & Tan 29530* (B). — INDONESIA: Sumatra, Oostkust, Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25b* (UPS, filed under *P. epiphylla*); Java, Tjibodas, 6.1898, *Fleischer s.n.* (UPS); Salak, 4.1897, *Nyman 45a* (UPS, filed under *P. atriceps*). — PAPUA NEW GUINEA: Morobe, Mt. Manke, *Castanopsis-Lithocarpus* forest, 15.3.1974, *van Zanten s.n.* (herb. Vězda); Mt. Kaise-nik, rain forest, 1500 m, 13.4.1974, *van Zanten s.n.* (herb. Vězda); Busom valley, 06°34'S, 146°58'E, 600 m, lowland rain forest, 3.1987, *Sipman 24540* (B); Madang, Balek Wildlife Reserve, 05°18'S, 145°43'E, 20 m, lowland rain forest, 3.1987, *Sipman 24289* (B). — AUSTRALIA: Queensland, Atherton Tablelands, Lake Barrine, 17°15'S, 145°38'E, 750 m, forest remnant, 3.1988, *Aptroot & Aptroot 22652* (B); *ibid.*, 9.1983, *Henssen 29351* (herb. Lücking, filed under *P. lucida*); Eacham Shire, Souita Falls, 17°35'S, 145°40'E, 8.1987, *Henssen 31243* (herb. Henssen, herb. Lücking).

***Porina conspersa***

*Porina conspersa* Malme in Ark. Bot. 23A: 16. 1929. – Typus: America, Brazil, Mato Grosso, between S. Antonio and Cuiabá, corticolous, *Malme 2630* (S, holotypus!; UPS, isotypus!).

Diagnostic features: *Thallus* continuous, large, smooth, greenish grey, nitidous, with scattered to numerous cylindrical to coralloid isidia and a purplish black prothallus. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* wart-shaped, 0.5-0.7 mm diam. *Ascospores* 7(-9)-septate, fusiform, 50-70 × 7-12 µm, 6-8 times as long as broad.

Notes: *Porina conspersa* is one of several species in the *Porina mastoidea* subgroup which form cylindrical to coralloid thallus outgrowths interpreted as isidia. The follicolous material from Africa (Lücking & al. 1998) has abundant perithecia and isidia and is certainly conspecific with *P. conspersa*, which was described by Malme (1929) from Brazil. On the other hand, taking into account that the formation of isidia might be a facultative character (see below *P. exasperatula*), it cannot be excluded that *P. conspersa* is the same as *P. imitatrix*. Except for the formation of isidia, both species are remarkably similar, although the perithecia of *P. imitatrix* are more lens-shaped. Similar cases are known in foliose genera like *Coccocarpia* (Arvidsson 1982), where forms which only produce apothecia (e.g. *Coccocarpia stellata* Tuck.) are separated on specific level from those which produce isidia and apothecia (e.g. *C. domingensis* Vain.).

## Distribution and ecology

Known from tropical America and Africa, probably restricted to lowland rain forest areas.

## Additional, follicolous specimen examined

AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker s.n.* (herb. Lücking).

***Porina curtula***

*Porina curtula* Malme in Ark. Bot. 23A: 20. 1929. – Typus: America, Brazil, São Paulo, Santos, corticolous, 10.1894, *Malme s.n.* (S, lectotypus, designated by McCarthy 1993).

Diagnostic features: *Thallus* continuous, medium-sized (to large), rough to finely verrucose, yellowish grey, nitidous, with a thin, purplish black prothallus (Fig. 3G). *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* young wart-shaped (to almost conical), mature ones wart-shaped (Fig. 3G), 0.35-0.55 mm diam., often with a small

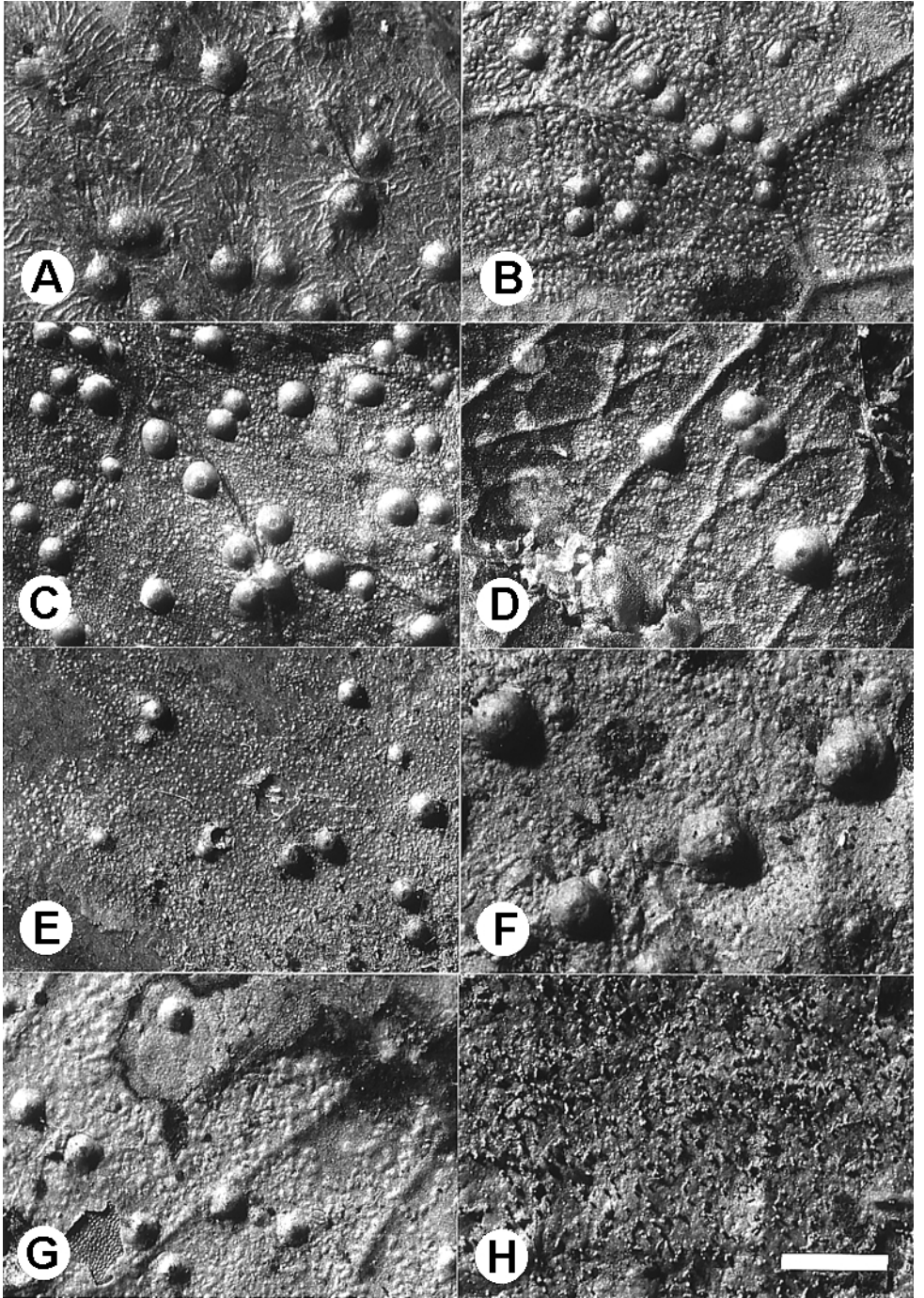


Fig. 3. General appearance of *Porina* species – A: *P. radiata* [Costa Rica]; B: *P. guianensis* [Guyana]; C: *P. epiphylloides* [Tanzania, holotype]; D: *P. mazosioides* [Tanzania, holotype]; E: *P. longispora* [Tanzania, isotype]; F: *P. nucula* [French Guiana]; G: *P. curtula* [Costa Rica]; H: *P. “distans”* coll. [Costa Rica]. – Scale = 1 mm, in E = 2 mm.



dark spot around the ostiole. *Ascospores* 7-septate, narrowly fusiform to oblong, 27-35 × 4-5.5 μm, 6-7 times as long as broad (Fig. 4A).

Notes: The present specimens were formerly identified as *Porina tetracerae*. The circumscription of the latter differs according to the author. While Aptroot & Sipman (1993) include specimens with small perithecia and predominantly 3-septate ascospores as well as with larger perithecia and broad ascospores with up to 11 septa, McCarthy (1993) adopts a comparatively narrow species concept. We have seen a lot of corticolous and foliicolous material and believe that several taxa are involved in this difficult group. Most of the corticolous specimens with 7-septate ascospores can be assigned to *P. tetracerae* in the sense of McCarthy (1993), while those with 3-septate or up to 11-septate ascospores probably represent other species. The foliicolous material is very constant and differs from *P. tetracerae* s.str. by the smaller, often almost conical perithecia without constricted base and with a dark spot at the top, the smaller ascospores, and the yellowish thallus with numerous minute verrucae.

*Porina curtula* was only known from the corticolous type collection and a saxicolous specimen from Paraguay (Malme 1929, McCarthy 1993). Both specimens agree very well with the foliicolous collections, and we therefore have decided to adopt this name, although further studies might reveal an earlier name for that taxon. The differences between *P. curtula* and *P. tetracerae* observed by us are essentially those indicated by McCarthy (1993). *P. curtula* also resembles *P. atropunctata* in the *P. epiphylla* subgroup. Both have similar perithecia and ascospores, but *P. atropunctata* has a non-verrucose, marginally dispersed thallus and a translucent to whitish prothallus.

#### Distribution and ecology

*Porina curtula* is thus far only known from tropical America. Foliicolous specimens are occasionally found in humid lowland rain forests and may be locally abundant in evergreen moist forests with a pronounced dry season. As far as it is known at present, the species is more common on leaves than on other substrates.

#### Additional, foliicolous specimens examined

AMERICA: COSTA RICA: Guanacaste, Rincón de la Vieja National Park, 10°45'N, 85°18'W, 900-1000 m, evergreen moist forest, 2.1992, *Lücking 92-186* (herb. Lücking); Puntarenas, Manuel Antonio National Park, 09°22'N, 84°09'W, sea level, coastal evergreen moist forest, 3.1991, *Lücking 91-1349* (herb. Lücking); Limón, Barra del Colorado Wildlife Refuge, 10°46'N, 83°36'W, sea level, lowland rain forest, 5.1992, *Lücking 92-2381* (herb. Lücking). — COLOMBIA: Santa Marta, 1898, *Baker s.n.* (UPS; ex G). — FRENCH GUIANA: Sinnamary, Piste de St. Elie, 05°19'N, 53°02'W, 50 m, disturbed remnants of forest along road, 1.1988, *Sipman 32688* (B); Maripasoula, Saül, trail to Monts La Fumée, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32046* (B); Roura, Montagne de Kaw, 04°41'N, 52°19'W, 200 m, moist primary forest, 1.1988, *Sipman 32517* (B); Cayenne, 1835-49, Leprieur (UPS). — BRAZIL: Pernambuco, Dois Irmãos, 3.1998, *Cáceres & Lücking s.n.* (URM).

#### *Porina distans*

*Porina distans* Vězda & Vivant in Nova Hedwigia 58: 136. 1994. — Typus: America, Guadeloupe, Basse-Terre Isl., St. Claude, Quartier de Parnasse, 700 m, 11.1990, *Vivant s.n.* (herb. Vězda, holotypus!).

Diagnostic features: *Thallus* continuous, (medium sized to) large, smooth (to slightly uneven), greenish, nitidous, with a purplish black prothallus. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* absent but thallus with abundant, cylindrical to coralloid isidia (Fig. 3H).

Notes: This taxon was described as the isidiate counterpart of *Porina imitatrix* (Vězda 1994), a frequent foliicolous representative of a group of mainly corticolous species with a blackish

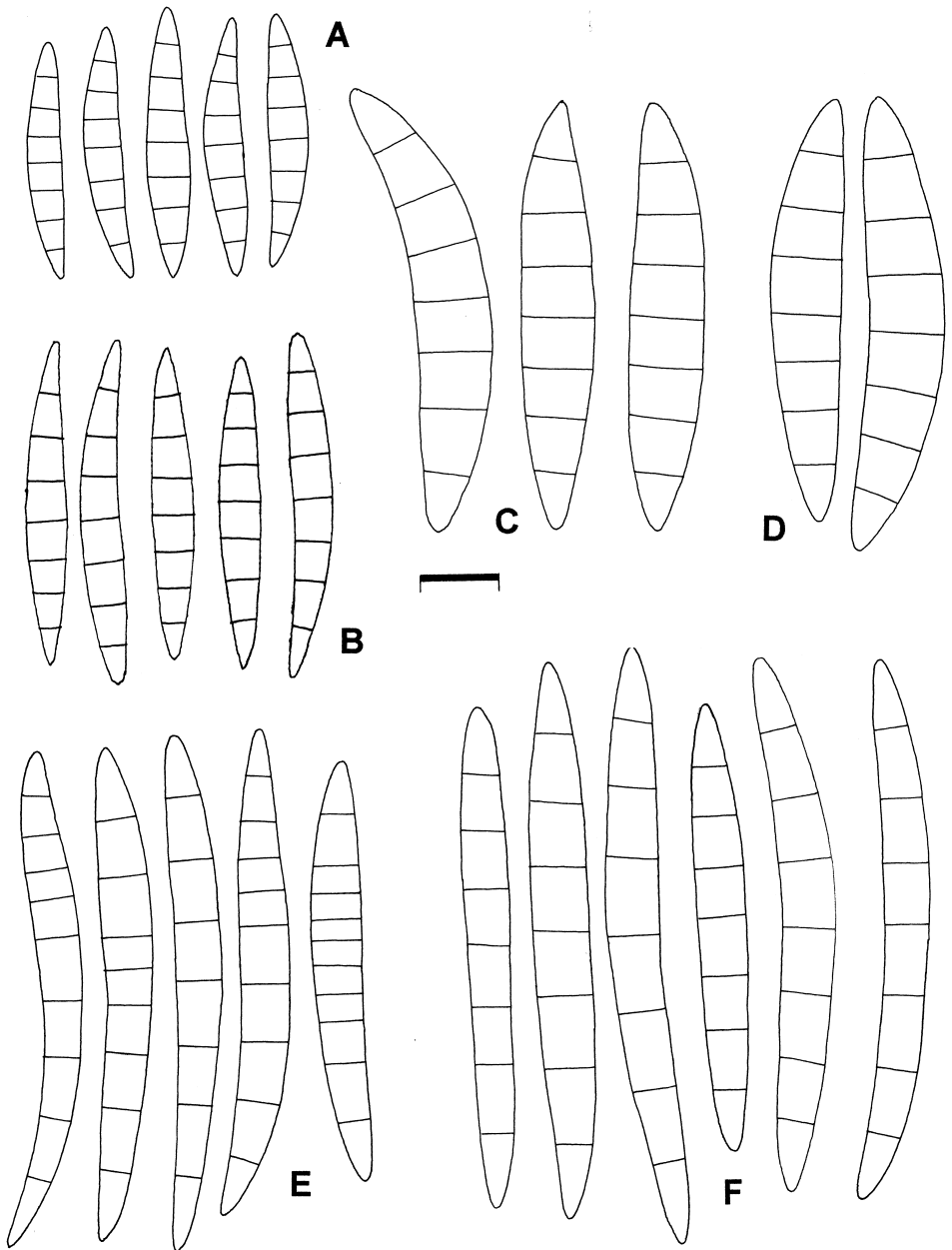


Fig. 4. Ascospores of *Porina* species – A: *P. curtula* [Brazil]; B: *P. tetracerae* [Papua New Guinea]; C-D: *P. imitatrix* [C: Philippines, holotype of *P. hypothetica*; D: Costa Rica]; E-F: *P. virescens* [Australia; E: “multi-septata” form; F: “virescens” form]. – Scale = 10  $\mu$ m.

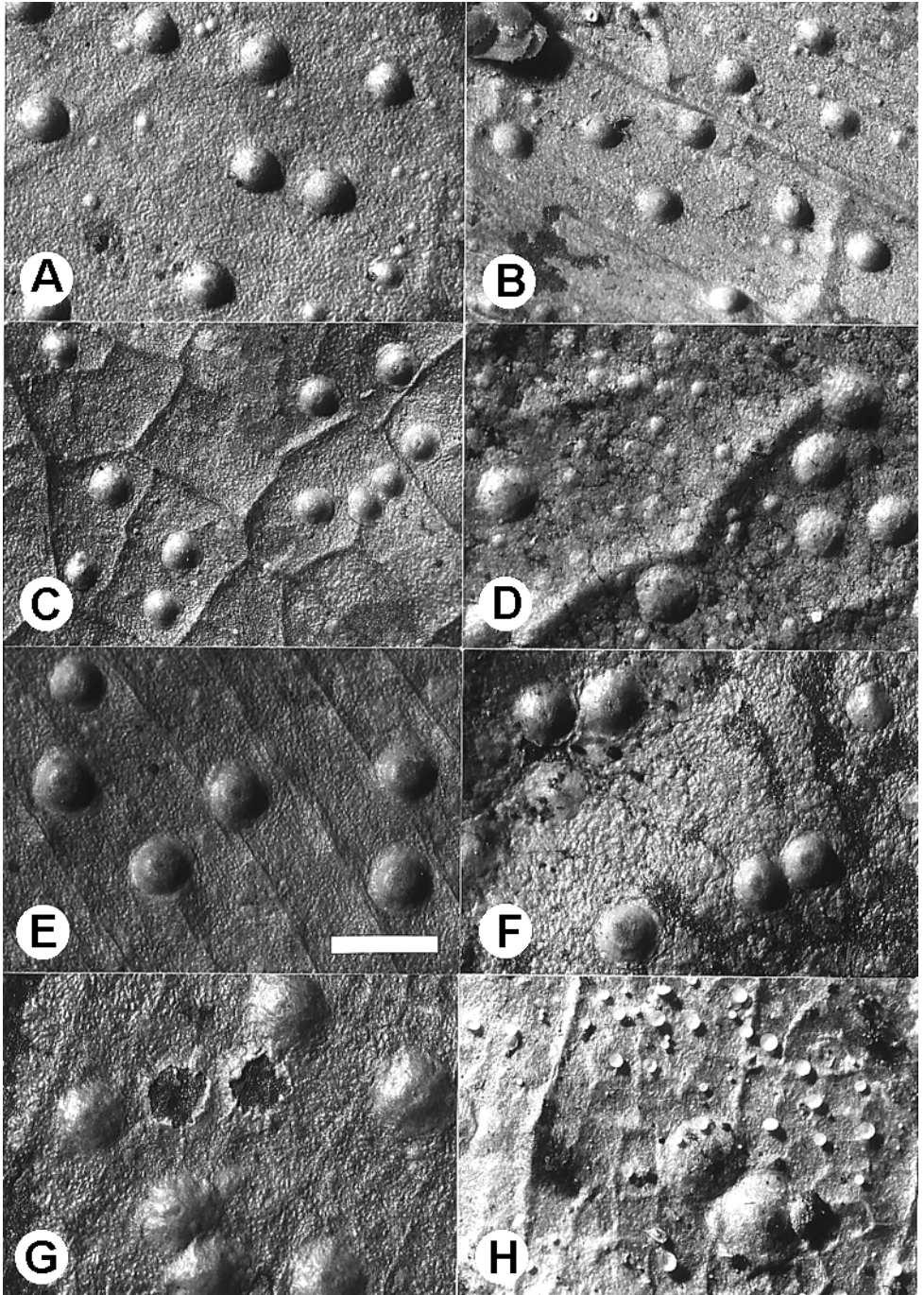


Fig. 5. General appearance of *Porina* species – A-B: *P. subepiphylla* [Costa Rica]; C: *P. epiphylla* [South Africa]; D: *P. lucida* var. *australiensis* [Australia]; E-F: *P. lucida* var. *lucida* [E: Cocos Island; F: Indonesia, holotype]; G-H: *P. mirabilis* [G: Costa Rica; H: French Guiana, with *Phyllophiale* type isidia]. – Scale = 1 mm.

prothallus referred to as *Clathroporina* by Harris (1995). Recent molecular studies seem to indicate that the traditional species pair concept (Poelt 1970, 1972, Tehler 1982) is flawed (see Mattson & Lumbsch 1989), since in almost every case the sorediate or isidiate counterparts come out as several lines nested within the sexual form (Kroken & Taylor, pers. comm. 1998, Lohtander & al., pers. comm. 1998). It is suggested that these lines represent cryptic species but they could also be part of a complex life cycle of a single species. In the case of *Porina distans*, the isidiate thalli might not only represent various independent lines originating from a single sexual counterpart but probably do belong to different species, since several taxa in this group are known to produce isidia, e.g. *Porina conspersa*, *P. exasperatula*, forms of *P. tetracerae* formerly known as *P. variegata* Fée (e.g. Puerto Rico, Rio Pudras, corticolous, 1.1916, *Fink 2/64* (S!); see McCarthy 1993), and *Clathroporina isidiifera* Harris (1995), all of them known by populations with both perithecia and isidia. Hence, *Porina distans* can no longer be treated as part of a species pair together with *P. imitatrix*. However, since the name *P. distans* is nomenclaturally connected to its type, it cannot be simply rejected but its correct application requires molecular studies to clarify the identity of the type material.

For the time being and until there is no generally accepted solution towards a new concept covering isidiate or sorediate counterparts of sexual forms, we suggest using the name *Porina distans* in a practical sense as *P. distans* (coll.). This would at least provide a common label for sterile specimens with isidia belonging to the *P. imitatrix* group and allow to gain more information about their distribution and co-occurrence with fertile material. We are aware that such a use has no biological background, but for the moment we hardly see any other possibility. Such an application would even be consistent with the proposal of Weber (1998), to conserve certain aggregate names for apomictic species aggregates while rejecting them on the segregate species level. Moreover, it is uncertain whether *P. distans* s.str. can really be characterized by molecular methods. A more conservative alternative would be to use the name as *P. cf. distans* (isidia), following a similar case known in the genus *Asterothyrium*, where several species produce characteristic pycnidia, and sterile material is usually identified as *A. cf. microsporium* (pycnidia).

#### Distribution and ecology

Sterile, foliicolous thalli with this type of isidia are known from lowland rain forests in all tropical regions.

#### Additional specimens examined

AMERICA: COSTA RICA: Limón, Río Siquirres, 10°06'N, 83°31'W, 100 m, lowland rain forest, 3.1991, *Lücking 91-2868* (herb. Lücking). — GUYANA: Upper Mazaruni District; Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall riverain forest, 2.-3.1985, *Sipman & Aptroot 19223f* (B).

AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101014* (herb. Lücking, with *P. imitatrix*), *101018* (herb. Lücking).

AUSTRALASIA: MALAYSIA: Kuala Lumpur, Templer Park, 300 m, 5.1997, *Vězda & Ceni s.n.* (herb. Vězda). — AUSTRALIA: Queensland, Cairns, Mount Whitfield, S-slope near Botanical Garden, 16°45'S, 145°44'E, 50 m, rainforest relict, 3.1988, *Aptroot & Aptroot 22266* (B).

#### *Porina epiphylla*

*Porina epiphylla* (Fée) Fée, Essai Crypt. Écorc.: 76. 1837 ≡ *Porina americana* var. *epiphylla* Fée in Bory de Saint-Vicent & al., Dict. Class. Hist. Nat. 17: 26. 1831. — Typus: America, French Guiana, unknown loc., s.d., *s. coll.*, *s.n.* (PC, lectotypus, not seen).

= *Verrucaria praestans* Nyl. in Bull. Soc. Linn. Normandie, ser. 2, 2: 520. 1868. — Typus: Africa, Angola, Luanda, s.d., *Welwitsch 238* (LISU, holotypus; UPS, isotypus!).

= *Porina insperata* Müll. Arg. in Flora 66: 333. 1883. — Typus: Australasia, Malaysia, Malacca, s.d., *Yvan s.n.* (G, holotypus!).

= *Micropeltis schmidtiana* Rostr. in Bot. Tidskr. 24: 211. 1902. — Typus: Australasia, Siam,

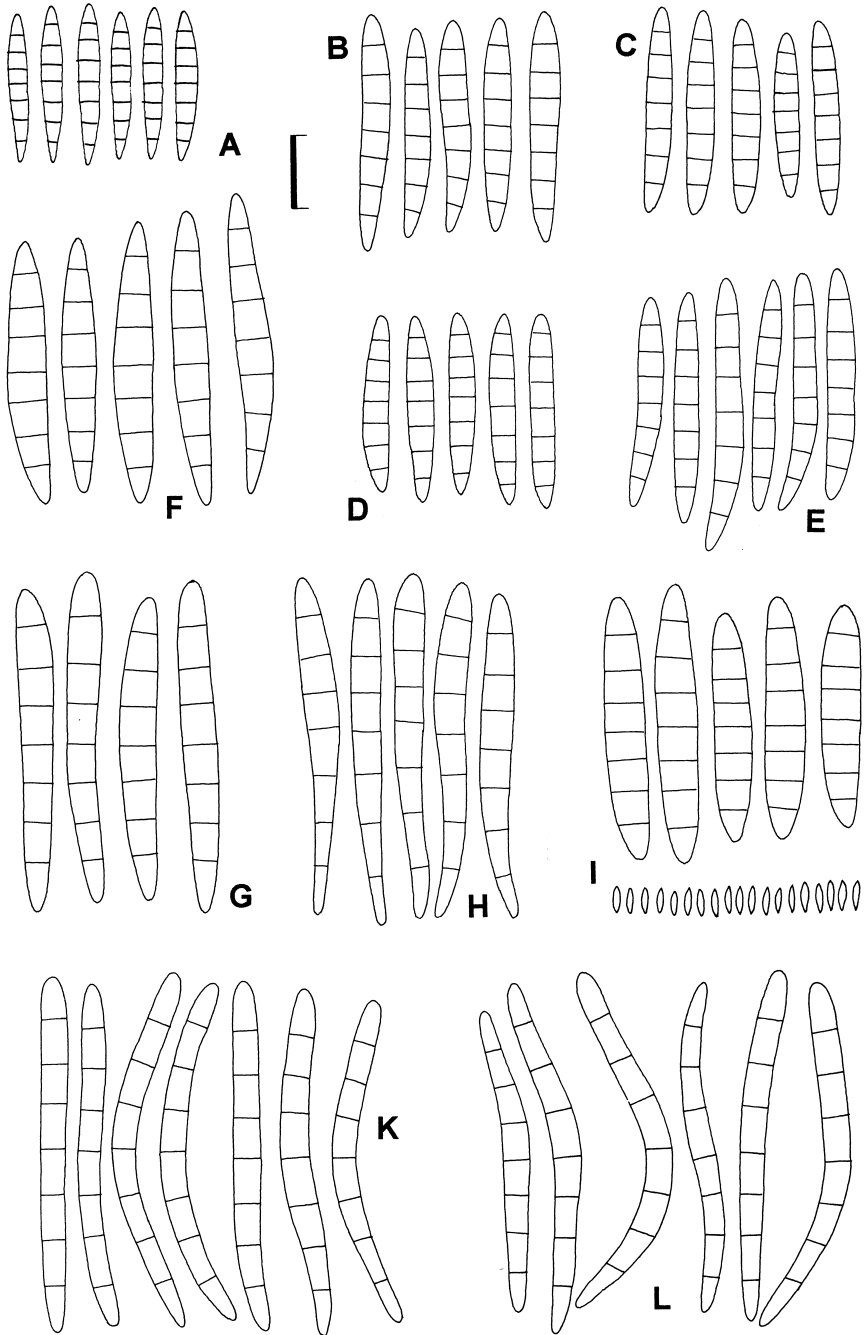


Fig. 6. Ascospores of *Porina* species – A: *P. minutissima* [Australia, holotype]; B-E: *P. epiphylla* [B: Angola, isotype of *Verrucaria praestans*; C: Cocos Island; D: Costa Rica; E: Tanzania]; F: *P. subepiphylla* [Costa Rica]; G-H: *P. lucida* var. *lucida* [G: Cocos Island; H: Australia]; I: *P. lucida* var. *australiensis* [Australia, with microconidia]; K-L: *P. mirabilis* [K: Congo; L: Tanzania]. – Scale = 10  $\mu$ m.

Koh Chang Isl., s.d., *Schmidt 675* (S, isotypus!).

= *Porina epiphylla* var. *major* Vain. in Ann. Acad. Sci. Fenn., ser. A, 15: 365. 1921. – Typus: Australasia, Philippines, Luzon, Albay, Batan, s.d., *Robinson 6424* (TUR, lectotypus!).

Diagnostic features: *Thallus* continuous but marginally often dispersed, medium-sized, rough, greenish grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones lens-shaped to hemispherical (Fig. 5C), 0.25-0.45 mm diam., sometimes with a slight reddish tinge. *Ascospores* 7-septate, oblong, 26-32 × 3-4 µm, 8-9 times as long as broad (Fig. 6B-E).

Notes: *Porina epiphylla* is the most abundant taxon of the group studied here. Typical specimens are found throughout all tropical regions and characterized by a greenish grey thallus, lens-shaped to hemispherical perithecia and rather small ascospores. Most similar and most closely related are *P. lucida* var. *lucida*, *P. minutissima*, and *P. subepiphylla*, differing by perithecia and ascospore size and shape. These species form a rather difficult aggregate which might be the evolutionary centre within the *P. epiphylla* subgroup.

In spite of repeated search by the very helpful staff in PC, it was not possible to locate the type material of *Porina americana* var. *epiphylla* as indicated by Santesson (1952). Additional material of the abundant original collection from Cayenne was found, however, and allowed a more detailed investigation. Three different taxa are present on the leaves: *P. epiphylla* s.str., *P. lucida*, and *P. mirabilis*. The specimens corresponding to *P. epiphylla* as defined here are abundant and typical. On the other hand, we strongly suspected that some of the synonyms listed under *P. epiphylla* by Santesson (1952) might cover another species, but all examined specimens correspond rather well to our concept of *P. epiphylla*, particularly the type material of *Verrucaria praestans* and *Micropeltis schmidtiana*.

#### Distribution and ecology

*Porina epiphylla* is the most common and most widely distributed of the species treated here. Typical specimens are found in all tropical regions, though apparently more common in tropical America and Africa. In spite of its abundance, the species is mainly found in lowland rain forest areas, but to some degree extends into evergreen dry forest.

#### Additional specimens examined

AMERICA: GUATEMALA: Quezaltenango, Chiquihuite, 1410 m, damp forest, 3.1939, *Standley s.n.* (UPS); Retalhuleu, between Retalhuleu and Nueva Linda, 120-220 m, 2.1941, *Standley s.n.* (UPS). — HONDURAS: Atlántida, Lancetilla Valley, 20-600 m, 12.1927 to 3.1928, *Standley 54893d* (UPS, filed under *Trichothelium minus*). — COSTA RICA: San José, Braulio Carrillo National Park, 10°09'N, 83°58'W, 700-800 m, lower montane rain forest, 9.1991, *Lücking 91-3146* (herb. Lücking); Limón, Río Siquirres, 10°06'N, 83°31'W, 100 m, lowland rain forest, 3.1991, *Lücking 91-2890* (herb. Lücking). — CUBA: Oriente, Bayate, 1917, *Ekman L 124, L 128a* (UPS). — DOMINICA: Emerald Pool Waterfall, 300-340 m, 7.1996, *Vězda* (herb. Lücking). — GUADELOUPE: Marie-Galante Isl., Rivière de Saint Louis, 50 m, mesophilous forest, 1.1993, *Vivant s.n.* (herb. Lücking, filed under *P. lucida*). — COLOMBIA: Amazonas, Villazul, Caquetá River, 00°42'S, 72°07'W, 240 m, 11.1988, *Sipman & Duivenvoorden 28255* (B). — VENEZUELA: Bolívar, Cerro Guaiquinima, 05°35'N, 63°32'W, 320 m, 15 m tall, light forest on poor soil, 2.1990, *Sipman 27321* (B); El Limón, Valle de Puerto, La Cruz, 1.1928, *Sydow 239b* (UPS). — GUYANA: Upper Mazaruni, Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall riverain forest, 2.-3.1985, *Sipman & Aptroot 19223f* (B, filed under *P. distans*); Demerara, Mabura Hill, 3.1985, *Cornelissen & ter Steege 94* (B). — FRENCH GUIANA: Maripasoula, Saül, Cambrouze, 03°38'N, 53°14'W, 300 m, 1.1988, *Sipman 32453* (B). Roura: Montagne de Kaw, 04°41'N, 52°19'W, 200 m, 1.1988, *Sipman 32518* (B); *ibid.*, 04°37'N, 52°18'W, 200 m, 1.1988, *Sipman 32542* (B); Sinnemary, Piste de St.-Elie, 05°19'N, 53°02'W, 50 m, 1.1988, *Sipman 32691* (B). — BRAZIL: Amazonas, Panuré, *Spruce 584* (UPS); s. loc., 1874,

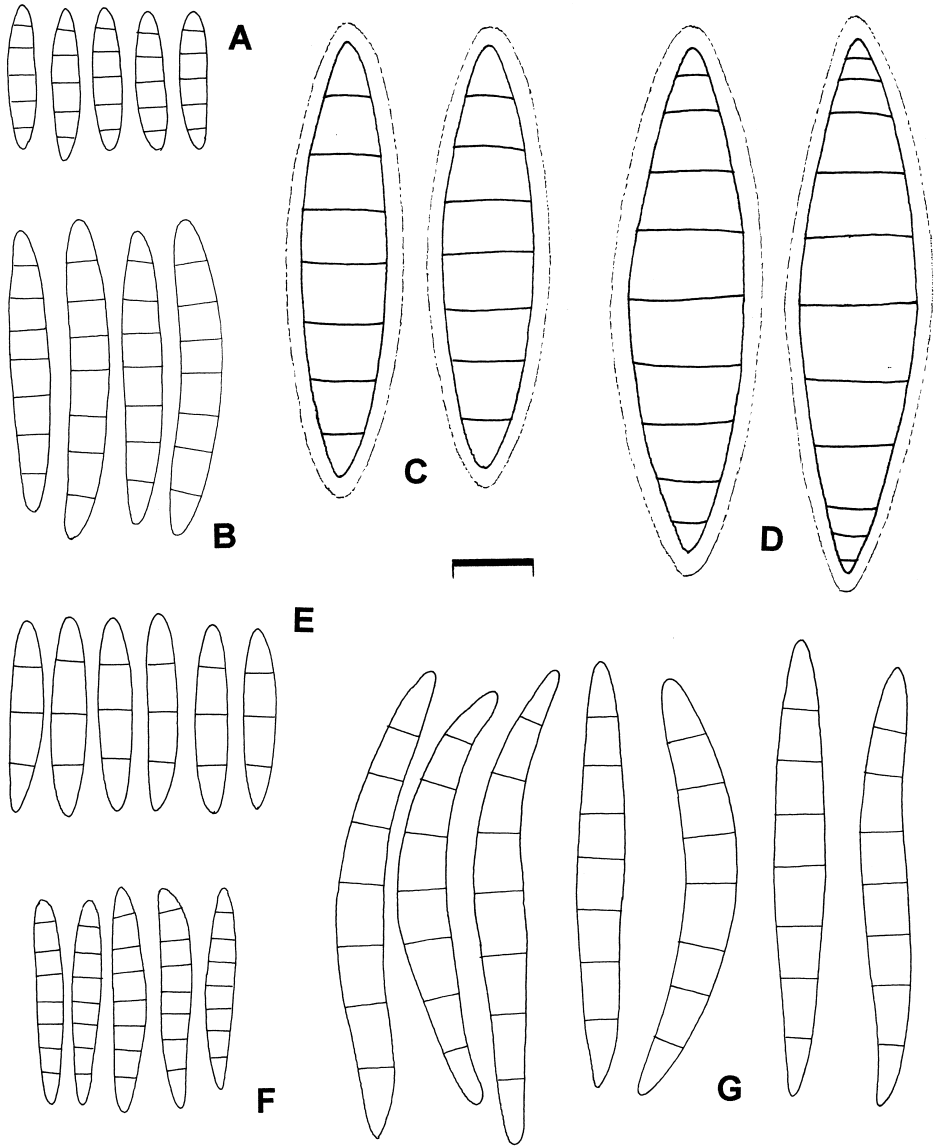


Fig. 7. Ascospores of *Porina* species – A: *P. verruculosa* [Brazil, holotype]; B: *P. subnucula* [Australia, holotype]; C: *P. nucula* [Papua New Guinea]; D: *P. rudiusscula* [French Guiana]; E: *P. guianensis* [Guyana, holotype]; F: *P. epiphylloides* [Tanzania, holotype]; G: *P. mazosioides* [Tanzania, holotype]. – Scale = 10  $\mu$ m.

*Trail s.n.* (UPS); São Paulo, Apiahy, 9.1886, *Puiggari 1031* (UPS); Serra do Mar, 850 m, humid primary forest, 3.1980, *Kalb 227* (B, filed under *P. atropunctata*). Río Aguapihú near Conceição de Itanhaen, 20 m, 7.1901, *Wettstein & Schiffner s.n.* (B); *ibid.*, 7.1911, *Schiffner s.n.* (B). Ilha de São Sebastião, Morro das Tacas, 600 m, very humid rain forest, 4.1978, *Kalb &*

*Plöbst s.n.* (B – K. Kalb: *Lichenes Neotropici* 27). Rio de Janeiro: *Glaziou 6346* (UPS).

AFRICA: IVORY COAST: Taï National Park, 5°52'N, 7°27'W, 200 m, 9.-10.1992, *Becker 101045* (herb. Lücking, filed under *P. lucida*), *101079* (herb. Lücking). — CAMEROON: Debundja, 2.1905, *Busse 3660* (UPS). — CONGO: Haut-Zaire: Kongolo Isl., dense primary forest, 6.1975, *Lisowski s.n.* (herb. Vězda). Sanda, Banga Boma, 1932, *Vanderyst 31679* (UPS). — GHANA: Kacle, swampy forest, 4.1966, *Jenik s.n.* (herb. Vězda). Esukawkaw F.R., 4.1966, *Jenik s.n.* (UPS). — TANZANIA: Uluguru Mts., 1600 m, wet montane rain forest, 5.1970, *Pócs & Harris 6181* (herb. Vězda); *ibid.*, Mzinga valley, 140-1600 m, 11.1970, *Pócs & al. 6290* (herb. Vězda); *ibid.*, Morogoro, 1400-1500 m, 3.1971, *Pócs 6418* (herb. Vězda). Kilimanjaro Mts., S slopes, 1900-2200 m, montane rain forest, 5.1970, *Pócs 6191* (herb. Vězda). West Usambara Mts., E of Mgwashi, 1700 m, 1.1985, *Pócs 8505* (B); *ibid.*, Mt. Mali, 1600-1700 m, 2.1984, *Pócs 8410* (B); *ibid.*, 1000-1100 m, submontane rain forest, 3.1984, *Borhidi 8436* (UPS). — KENYA: South Western Mau Forest Reserve, 00°36'S, 35°18'E, 1920 m, dense forest along Itare river, 8.1949, *Maas Geesteranus 5793* (UPS). Kakamega Forest, 00°11'N, 34°52'E, 1500-1700 m, 1.1970, *Santesson 21897* (UPS). — SOUTH AFRICA: s.loc., s.dat., *Henssen 28372, 28413* (herb. Henssen, herb. Lücking).

AUSTRALASIA: VIETNAM: Tonkin, Vinh-Phuc Prov., 4.1974, *Zsolt s.n.* (herb. Vězda, filed under *P. mirabilis*). — MALAYSIA: Borneo, Sarawak, s.loc., 1886, *Puiggari s.n.* (B). — INDONESIA: Sumatra, Oostkust, Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25b* (UPS); Java, Noesa Kembangan, 11.1907, *Valeton s.n.* (UPS); Tjibodas, primeval forest, 1898, *Nyman s.n.* (UPS). — PAPUA NEW GUINEA: Port Moresby, 3.1965, *Bologh* (herb. Vězda); Morobe, Busom Valley, 6°34'S, 146°58'E, 600 m, 3.1987, *Sipman 24541, 24542a* (B). — AUSTRALIA: Queensland, Atherton Tableland, 9.1983, *Henssen 29351* (herb. Henssen, herb. Lücking, filed under *P. atropunctata*); *ibid.*, 145°38'E, 17°15'S, 750 m, forest remnant, *Aptroot & Aptroot 22654* (B, filed under *P. lucida*); *ibid.*, *Aptroot & Aptroot 22694* (B); New South Wales, Dorrigo National Park, 30°23'S, 152°43'E, 650 m, subtropical rain forest, 4.1981, *Tibell 12495* (UPS). — NEW CALEDONIA: Grande-Terre, Province Sud: Monts Koghis-Dumbéa, rain forest, 22°14'S, 166°30'E, 550 m, 8.1994, *Kalb & Kalb s.n.* (herb. Lücking).

### *Porina epiphylloides*

*Porina epiphylla* Vězda in Folia Geobot. Phytotax. 10: 393 (1975). – Typus: Africa, Tanzania, SW slope of Rwunge volcano, 1800-1900 m, 8.1972, *Pócs 6762* (herb. Vězda, holotypus!).

Diagnostic features: *Thallus* dispersed, small, distinctly verrucose (Fig. 3C), yellowish green, nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, distinctly radiate. *Perithecia* young lens-shaped, mature lens-shaped to hemispherical (Fig. 3C), 0.2-0.3 mm diam., sometimes with a slight reddish tinge. *Ascospores* 7-septate, oblong, 21-27 × 3 µm, 7-9 times as long as broad (Fig. 7F).

Notes: *Porina epiphylloides* was originally distinguished from *P. epiphylla* on account of its smaller ascospores and smaller, densely arranged perithecia. This has led to some confusion and misidentification of specimens which actually represent a new species described below as *P. minutissima* (e.g. Aptroot & Sipman 1991; Sipman 1991, 1993). In fact, the distinctive traits of *P. epiphylloides* are not the ascospores or perithecia but the finely verrucose thallus with the phycobiont having rectangular cells arranged in regularly radiating rows. The only other species with such thallus characteristics and 7-septate ascospores is the newly described *P. mazosioides*, with larger perithecia and ascospores.

*Porina epiphylloides* is somewhat variable as regards the formation of thallus verrucae. In a few specimens [e.g. Tanzania, Farkas 89112 (herb. Lücking)], some verrucae are radiately elongated and akin towards *P. radiata* or *P. follmanniana*, with which some specimens have been confused. The holotype is a very typical and well-developed specimen.



### Distribution and ecology

Known from tropical East Africa and adjacent islands; mainly found in submontane to montane rain forest.

### Additional specimens examined

AFRICA: TANZANIA: Morogoro region, Mt. Kanga, 850-1250 m, 3.1989, *Farkas 89112* (herb. Vězda); *ibid.*, Nguru Mts., 900 m, submontane rain forest, 3.1989, *Farkas 89100* (herb. Lücking); Tanga region, Mazumbai University, 1500 m, submontane rain forest, 2.1982, *Pócs 6962* (herb. Vězda); N Uluguru Mts., 1000 m, submontane rain forest, 8. 1970, *Pócs & Chambuko 6224* (herb. Vězda); *ibid.*, 1400 m, 12.1972, *Pócs & al. 6855* (herb. Vězda); *ibid.*, E slope of Bondwa, 1700-1900 m, 9.1970, *Pócs & al. 6259* (herb. Vězda). — COMORES: Anjonan, Dzialandje, 800 m, 10.1903, *Voeltzkow s.n.* (B).

Incorrect records: AUSTRALASIA: MALAYSIA: Sabah, Kinabalu National Park, 700 m, *Sipman & Tan 29532* (B) is *Porina minutissima*. — AUSTRALIA: Queensland, Fitzroy Island, 16°56'S, 145°59'E, 50-100 m, 3.1988, *Aptroot & Aptroot 22298* (B) is *P. minutissima*.

### *Porina exasperatula*

*Porina exasperatula* Vain., Add. Lichenogr. Antill.: 200. 1914. – Typus: America, Lesser Antilles, Dominica, Prince Rupert, corticolous, *Elliott 1313* (TUR, holotypus, not seen).

Diagnostic features: *Thallus* continuous, medium-sized to large, uneven, greenish, nitidous, with a purplish black prothallus and with or without cylindrical to coralloid isidia. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, non-radiate. *Perithecia* young lens-shaped to hemispherical, mature hemispherical to wart-shaped, 0.6-1.2 mm diam. *Ascospores* 25-35-septate, filiform and tapering, 90-150 × 3-5 µm, 30 times as long as broad.

Notes: *Porina exasperatula* belongs to a group of species with blackish prothallus and well developed, rather thick, often nitidous thallus, recognized as *Clathroporina* by Harris (1995). The species is well distinguished by its long, filiform, multiseptate ascospores arranged in a regular bundle. It is very rarely foliicolous. According to Aptroot & Sipman (1993), both thalli with and without isidia are known, but the identical perithecial anatomy seems to prove their conspecificity.

### Distribution and ecology

Neotropical, probably restricted to lowland rain forest areas, usually corticolous.

### Additional, foliicolous specimen examined

AMERICA: FRENCH GUIANA: Maripasoula, Saül, *Sipman 32289* (B).

### *Porina foliicola*

*Porina foliicola* (Vězda) Lücking & Vězda, **comb. nova**

≡ *Clathroporina foliicola* Vězda in Čas. Sle. Mus. v Opavě, Ser. A., Hist. Nat. 26: 25. 1977 [≡ *Porina foliicola* (Vězda) Lücking & Vězda in [McCarthy in] Lichenologist 27: 323. 1995, comb. inval.]. – Typus: Australasia, Vietnam, Tonkin, Vinh-Phuc, rain forest, 4.1974, *Zsolt s.n.* (herb. Vězda, holotypus!).

Diagnostic features: *Thallus* marginally dispersed, small to medium-sized, rough, nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones hemispherical (Fig. 2H), 0.35-0.50 mm diam., with a darker, broad spot around the ostiole. *Ascospores* muriform, oblong, 85-110 × 17-22 µm, 5 times as long as broad, with gelatinous sheath.

Notes: The species was originally referred to *Clathroporina* because of its muriform ascospores. This genus has recently received considerable attention and a new circumscription, giving up

the muriform ascospores as the single character for its delimitation (Harris 1995, McCarthy 1995). Species with muriform ascospores can be assigned to at least two subgroups related to *Porina mastoidea* [e.g. *Clathroporina eminentior* (Nyl.) Müll. Arg., the type of *Clathroporina*] and *Porina nucula* [e.g. *Porina nuculastrum* (Müll. Arg.) R. C. Harris]. The *P. mastoidea* subgroup is usually characterized by a nitidous, smooth thallus with a dark prothallus, while species of the *P. nucula* subgroup have a matt, often verrucose thallus without dark prothallus. Harris (1995) therefore restricted the name *Clathroporina* to the species with dark prothallus, while McCarthy (1995) suggested synonymy with *Porina*.

On account of its thallus morphology, *Porina foliicola* does probably not belong to either of the two groups mentioned above but might be close to *P. epiphylla* and *P. lucida*. The few specimens of *P. foliicola* known so far are externally indistinguishable from *P. lucida*, and ascospores have to be checked for a definite identification. The combination *P. foliicola* was anticipated in McCarthy (1995) and is here validated, in spite of the difficult nomenclatorial situation which requires conservation of *Porina* Müll. Arg. against *Clathroporina* Müll. Arg. (McCarthy 1995).

#### Distribution and ecology

Known only from lowland rain forest in tropical Asia (see Vězda & al. 1997).

#### Additional specimen examined

AUSTRALASIA: SRI LANKA. Sinharaja Forest, 300-500 m, 2.1984, *Brunnbauer 6370* (W).

#### *Porina follmanniana*

*Porina follmanniana* Becker & Lücking in Daniels & al., Flechten Follmann: 168. 1995. – Typus: Africa, Ivory Coast, Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101125* (M, holotypus!).

Diagnostic features: *Thallus* dispersed but centrally confluent, small to medium-sized, with regular radiate ridges, yellowish green, nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate rows. *Perithecia* young applanately conical to lens-shaped, mature ones applanately wart-shaped, 0.35-0.5 mm diam., usually with a narrow blackish brown spot around the ostiole. *Ascospores* 7-septate, oblong, 23-30 × 3-4 µm, 7-8 times as long as broad.

Notes: *Porina follmanniana* is, besides *P. radiata*, the only species with radiate thallus ridges. It differs from the latter by the wart-shaped to almost conical perithecia with narrow dark spot around the ostiole and by the smaller ascospores. Its delimitation must be studied further since the African populations of *P. radiata* are poorly known. Except for the thallus structure, the perithecial morphology is reminiscent of *P. atropunctata*.

#### Distribution and ecology

Known from tropical West Africa, where it is apparently widely distributed (although rare) in lowland rain or evergreen dry forest.

#### Additional specimens examined

AFRICA: IVORY COAST: Taï National Park, 5°52'N, 7°27'W, 200 m, 9.-10.1992, *Becker 101008* (herb. Lücking). — CAMEROON: Debundja, 2.1905, *Busse 3660* (UPS, filed under *P. epiphylla*). — GHANA: Esukawkaw F.R., 4.1966, *Jeník s.n.* (UPS).

#### *Porina guianensis*

*Porina guianensis* Lücking & Vězda, **sp. nova**

Typus: America, Guyana, Paramakatoi, 04°42'N, 59°43' W, 500-800 m, submontane rain forest, 2.1996, *Lücking 96-3869* (M, holotypus!).

A *Porina epiphyloides* ascosporis 3-5-septatis minoribusque differt.

Diagnostic features: *Thallus* continuous, small, verrucose or with short radiate ridges (Fig. 3B), yellowish to orange grey, matt, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate rows. *Perithecia* young hemispherical, mature ones wart-shaped (Fig. 3B), 0.20-0.25 mm diam., often with a reddish tinge. *Ascospores* 3-septate (“*triseptata*” form), rarely 5-septate (“*pentaseptata*” form), fusiform (with rounded ends) to oblong, 19-22 × 3-3.5 µm, 6-7 times as long as broad (Fig. 7E).

Notes: This new species was treated as *Porina verruculosa* by Aptroot & Sipman (1993). The authors already noted the differences with the type material, particularly the different phycobiont. Actually, *P. verruculosa* s.str. is not related to *P. guianensis* but belongs to a group of predominantly corticolous species related to *P. nucula*. *P. guianensis* differs not only in the phycobiont, but also in the usually 3-septate ascospores. It seems to be closely related to the African *P. epiphyloides*, which has larger, 7-septate ascospores and smaller thallus verrucae.

*Porina guianensis* occurs in two different forms with 3- and 5-septate ascospores. Both are otherwise completely identical and neither differentiated in their ecogeography, though the 5-septate form is thus far only known from South America.

#### Distribution and ecology

*Porina guianensis* is known from Central and South America, being most common in the northern Amazon and the Guianas. It is a typical lowland species and restricted to primary forests, where it may be locally abundant.

Additional specimens examined (“*triseptata*” form)

AMERICA: COSTA RICA: Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-2741* (M). — GUYANA: Upper Mazaruni, Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall, riverain forest, 2.-3.1985, *Sipman & Aptroot 19225e* (B). — FRENCH GUYANA: Maripasoula, Saül, 03°37'N, 53°13'W, 300 m, primary forest, 1.1988, *Sipman 32285* (B); *ibid.*, Piste de Carbet Maïs, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32157* (B); *ibid.*, trail to Monts La Fumée, 03°38'N, 53°11'W, 300 m, primary forest, 1.1988, *Sipman 32183* (B). — BRAZIL: Pará, Belem, 10 m, lowland rain forest, 10.1980, *Kalb 311* (herb. Vězda, filed under *P. radiata*).

(“*pentaseptata*” form): GUYANA: Upper Mazaruni, Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall, riverain forest, 2.-3.1985, *Sipman & Aptroot 19225e* (B). — FRENCH GUYANA: Maripasoula, Saül, Piste de Carbet Maïs, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32157* (B).

#### *Porina imitatrix*

*Porina imitatrix* Müll. Arg. in *Flora* 73: 196. 1890. – Typus: America, Brazil, Rio de Janeiro, Rio de Janeiro, *Glaziou 18086* (G, lectotypus!).

= *Phylloporina schiffneri* Zahlbr. in *Denkschr. Math.-Nat. Kl. Akad. Wiss. Wien* 83: 96. 1909. – Typus: America, Brazil, São Paulo, S. Bernardo, 800 m, 1901, *Schiffner s.n.* (W, holotypus!).

= *Porina hypothetica* Vain. in *Ann. Acad. Sci. Fenn.*, ser. A, 15: 366. 1921. – Typus: Australasia, Philippines, Polillo, unknown loc., 1909, *Robinson s.n.* (TUR, holotypus!).

= *Porina affinis* F. Schill. in *Hedwigia* 67: 287. 1927. – Typus: Africa, Cameroon, Debundja, 1905, *Busse 3660* (GOET, holotypus!).

= *Phylloporina caerulescens* Müll. Arg. in *Flora* 73: 198. 1890. – Typus: America, Brazil, Rio de Janeiro, Rio de Janeiro, *Glaziou 18105* (G, lectotypus!).

Diagnostic features: *Thallus* continuous, medium-sized to large, uneven, greenish, nitidous, with a purplish black prothallus. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones lens-shaped (to wart-shaped), 0.6-1.0 mm diam. *Ascospores* 7(-9)-septate, fusiform, 38-64 × 6.5-10 µm, 5-6 times as long as broad, with a gelatinous sheath (Fig. 4C-D).

Notes: *Porina imitatrix* is the most common foliicolous representative of the *Porina mastoidea* subgroup. From the regularly foliicolous species of the *Porina epiphylla* group, *P. imitatrix* is easily distinguished by its dark prothallus and its large perithecia with large, broad ascospores. The species is regularly found on bark as well. From its usually corticolous relatives (e.g. *P. mastoidea*, *P. tetracerae*), *P. imitatrix* differs by its applanate perithecia without dark ostiolar spot, in combination with its broadly fusiform, 7-septate ascospores. However, the taxonomy of the mainly corticolous species of this group is not yet settled and open to future changes (see Santesson 1952; McCarthy 1993, 1994).

The lectotype of *Porina imitatrix* (G) is a rather typical specimen. The same is true for the holotype of *Porina hypothetica* (TUR) and the lectotype of *Phylloporina caerulescens* (G), both matching the species very well. In the holotype of *Phylloporina schiffneri* (W), no perithecia are left, but according to the original description and the statements given by Santesson (1952), there is little doubt that this taxon also belongs to *P. imitatrix*.

#### Distribution and ecology

Pantropical but more common in tropical America and Africa, and apparently not known from Australia. A common species in lowland rain forest areas, also found corticolous.

#### Additional specimens examined

AMERICA: COSTA RICA: Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-5056* (herb. Lücking); Cartago, Centro Agronómico Tropical de Investigación y Enseñanza, near Turrialba, 09°53'N, 83°39'W, 600 m, lower montane rain forest, 3.1991, *Lücking 91-3319* (herb. Lücking). — COLOMBIA: Cauca, Popayan, Los Robles, 02°24'N, 76°39'W, 1750 m, strongly disturbed forest relict, 6.1986, *Sipman & al. 29779* (B); Caquetá, 2.5 km NE of Araracuara, 00°37'S, 72°23'W, 250 m, 30 m tall, hardly disturbed forest, 10.1988, *Sipman & Duivenvoorden 28044* (B). — VENEZUELA: Bolivar, Cerro Guaiquinima, 05°35'N, 63°32'W, 320 m, 15 m tall, light forest, 2.1990, *Sipman 27322* (B). — GUYANA: Upper Mazaruni, Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall riverain forest, 2.-3.1985, *Sipman & Aptroot 19223f* (B, filed under *P. distans*). — FRENCH GUIANA: Maripasoula, Saül, route to Monts La Fumée, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32089* (B); Roura, Montagne de Kaw, 04°34'N, 52°14'W, 200 m, moist primary forest, 1.1988, *Sipman 32560* (B); *ibid.*, 04°41'N, 52°19'W, 200 m, moist primary forest, 1.1988, *Sipman 32517* (B, filed under *P. curtula*). AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101041, 101163* (herb. Lücking). — CAMEROON: Debundja, 2.1905, *Busse 3660* (UPS; ex GOET).

AUSTRALASIA: MALAYSIA: Kuala Lumpur, Templer Park, 300 m, 5.1997, *Vězda & Ceni s.n.* (herb. Vězda). — PHILIPPINES: Luzon, Prov. Laguna, 6.-7.1915, *McGregor s.n.* (UPS; ex *Vainio 31715*). — PAPUA NEW GUINEA: Madang, Balek Wildlife Reserve, 05°18'S, 145°43'E, 20 m, lowland rain forest, 3.1987, *Sipman 24288a* (B).

#### *Porina longispora*

*Porina longispora* Vězda in Folia Geobot. Phytotax. 10: 394. 1975. – Typus: Africa, Tanzania, Tanga, East Usambara Mts., 1000 m, submontane rain forest, 12.1969, *Pócs 6097* (herb. Vězda, holotypus!).

Diagnostic features: *Thallus* continuous to marginally dispersed, medium-sized, finely verrucose (Fig. 3E), greenish grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate rows. *Perithecia* young hemispherical, mature ones hemispherical to wart-shaped (Fig. 3E), 0.5-0.6 mm diam. *Ascospores* 15-septate, oblong or tapering, 80-100 × 6-9 µm, 11-14 times as long as broad.

Notes: *Porina longispora* belongs to the group of species with finely verrucose thallus and

radiate phycobiont. It is most closely related to *P. mazosioides*, a new species described below, but differs in the much longer, 15-septate ascospores.

Distribution and ecology: Known only from the type locality.

### ***Porina lucida* var. *lucida***

*Porina lucida* R. Sant. var. *lucida* in Symb. Bot. Upsal. 12: 240. 1952. – Typus: Australasia, Indonesia, Java, Preanger, Tjibodas, 6.1898, *Nyman 6b* (UPS, holotypus!);

[= *Porina lenticulata* Lücking, Foliikole Flechten Costa Rica: 70. 1994, nom. nud.; Lücking & A. Lücking in Herzogia 11: 156. 1995, nom. nud.].

Diagnostic features: *Thallus* continuous to marginally dispersed, medium-sized to large, smooth to rough, greenish (to yellowish) grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones lens-shaped to hemispherical and often with appanate top (Fig. 5E-F), 0.4-0.6 mm diam., often with a 0.2 mm broad brown spot around the ostiole. *Ascospores* 7-septate, oblong, (30-)35-48 × 4-5.5 µm, 8-10 times as long as broad (Fig. 6G-H).

Notes: The distribution of *Porina lucida* was given as Australasian by Santesson (1952). For that reason, when beginning our study on the *P. epiphylla* aggregate, we assigned that name to a taxon that we knew from Australian collections. Another species with very similar perithecial shape and dimensions, which by then was only found in material from the Neotropics, and which differed by its longer and narrower ascospores, was intended to be described as *P. lenticulata*, a name which has been spread in a few publications (Lücking 1994, Lücking & Lücking 1995). However, we realized that the supposedly neotropical taxon with long and narrow ascospores also occurs in other parts of the tropics, even in Australia, where it was readily separated from the taxon with shorter, broader ascospores, which is here distinguished as a variety. When we studied the holotype of *P. lucida*, we found it fitting the pantropical taxon with long and narrow ascospores, which means that the name *P. lenticulata* for that species is superfluous.

*Porina lucida* is very close to *P. epiphylla* and differs mainly by its larger perithecia, often with a darker spot around the ostiole, and by its larger ascospores. The species makes the impression of being a (post)mature form of *P. epiphylla*, but typical specimens of the latter with small perithecia do have mature ascospores, and both species might be found growing on the same leaves. Very well-developed specimens of *P. lucida* might have perithecia twice as large as in typical *P. epiphylla*. The species shows a slight regional variation: American populations have usually smaller perithecia, probably the reason why the species was not recognized by Santesson (1952) for the Neotropics, but larger ascospores (mostly 35-45 m), whereas African specimens have larger perithecia but smaller ascospores (mostly 30-35 m). Australasian specimens have large perithecia and ascospores, and here the distinction towards *P. epiphylla* provides less difficulties.

*Porina lucida* was confused with *P. mirabilis* (Lücking 1992, Aptroot & Sipman 1993) but differs by the larger thallus with smaller, more hemispherical, basally delimited perithecia, different ascospore shape, and the absence of *Phyllophiale* type isidia.

### Distribution and ecology

Pantropical, found in primary or oldgrowth secondary forests from the lowland to the lower montane rain forest zone.

### Additional specimens examined

AMERICA: COSTA RICA: Puntarenas, Corcovado National Park, 08°28'N, 83°35'W, 50-150 m, lowland rain forest, 7.1992, *Lücking 92-3592* (herb. Lücking); Cartago, Guayabo National Monument, 09°59'N, 83°43'W, 1400 m, montane rain forest, 5.1992, *Lücking 92-1746* (herb. Lücking); Limón, Río Siquirres, 10°06'N, 83°31'W, 100 m, lowland rain forest, 3.1991, *Lücking*

91-2891 (herb. Lücking). — DOMINICA: Emerald Pool Waterfall, 300-340 m, 7.1996, *Vězda* (herb. Lücking). — GUADELOUPE: Basse Terre Isl., Community of Baillif-Banin, 700-800 m, 3.1990, *Vivant s.n.* (herb. Vězda, filed under *P. atriceps*); Marie-Galante Isl., Rivière de Saint Louis, 50 m, mesophilous forest, 1.1993, *Vivant* (herb. Lücking). — COLOMBIA: Meta, Villavicencio, 600 m, 9.1984, *Aguirre & Sipman 5691b* (B, filed under *P. mirabilis*). — GUYANA: Upper Mazaruni, Pwipwi Mt., 05°48'N, 60°47'W, 600 m, 2.-3.1985, *Sipman & Aptroot 19223c* (B); Demerara, Mabura Hills, 3.1985, Cornelissen & Ter Steege 96 (B). — FRENCH GUIANA: Roura, Montagne de Kaw, 04°41'N, 52° 19'W, 200 m, 1.1988, *Sipman 32518* (B, filed under *P. epiphylla*); Maripasoula, Saül, Route de Belizon, 03°38'N, 53°12'W, 300 m, 1.1988, *Sipman 32044* (B, filed under *P. epiphylla*). — BRAZIL: Amazonas, Rio Negro, 40 m, 10.1980, *Kalb 310* (herb. Vězda, filed under *P. mirabilis*); São Paulo, Serra do Garrãozinho, S of Manuel Ferreira along road SP-39, 850 m, 15 m tall forest on slope, 7.1979, *Sipman 12707c* (B, filed under *P. atropunctata*).

AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101016, 101045* (herb. Lücking). — TANZANIA: Unknown locality, Pócs 6922 (herb. Vězda). Tanga region, SE corner of Mazumbai University forest Reserve, 1500 m, submontane rain forest, 2.1982, *Pócs 6962* (herb. Vězda, filed under *P. epiphylloides*); Morogoro region, SE slope of Mt. Kanga, 1200-1300 m, rocky forest, 3.1989, *Farkas 89112* (herb. Lücking). — KENYA: Taita District, Taita Hills, intermediate wet evergreen forest, 03°21'S, 38°27'E, 1525-1850 m, 10.1970, *Faden & Githui 70* (herb. Vězda, filed under *P. mazosioides*). — MADAGASCAR: Antsiranana, Reserve Integrale Nationale de Marojezy, 200-500 m, 3.1990, *Pócs & al. 90111* (VBI, herb. Lücking).

AUSTRALASIA: SRI LANKA: Sinhajara Forest, 300-500 m, 2.1984, *Brunnbauer 6365* (W); MALAYSIA: Sabah, Kinabalu National Park, 06°05'N, 116°35'E, 1650 m, mossy oak forest, 5.1989, *Sipman & Tan 29469* (B, filed under *P. virescens*). *ibid.*, 29464 (B). — INDONESIA: Java, Preanger, Tjibodas, 1500 m, 6.1898, *Nyman 6b* (UPS); Batavia, Mt. Megamendong, Telaga Warna, 1400 m, 1.1894, *Schiffner 3349* (UPS); Sumatra, Oostkust, Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25c* (UPS, filed under *P. conica*). — PAPUA NEW GUINEA: Mt. Kaisenik, vicinity of Wan, 1500 m, rain forest, 13. 4.1974, *van Zanten s.n.* (herb. Vězda, filed under *P. conica*); Stephansort, 1.1899, *Nyman 100b* (UPS). — AUSTRALIA: Queensland, Eacham Shire, Souita Falls, tropical rainforest, 17°35'S, 145°40'E, 8.1987, *Henssen 31243* (herb. Lücking); Atherton Tablelands, Lake Barrine, 17°15'S, 145°38'E, 750 m, forest remnant, 3.1988, *Aptroot & Aptroot 22652, 22654* (B).

### *Porina lucida* var. *australiensis*

*Porina lucida* var. *australiensis* Lücking & Vězda, **var. nova**

Typus: Australia, Queensland, Crediton State Forest, 840 m, rain forest, 6.1986, *Streimann 37663a* (UPS, holotypus!).

A var. *lucida* ascosporis minoribus latioribusque differt.

Diagnostic features: *Thallus* continuous to marginally dispersed, medium-sized, smooth, yellowish grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* lens-shaped, with applanate top (Fig. 5D), 0.4-0.6 mm diam., often with a reddish tinge. *Ascospores* 7-septate, oblong, 30-38 × 5-6 µm, 6-7 times as long as broad (Fig. 6I). Pycnidia frequent, lens-shaped to hemispherical (Fig. 5D), 0.15 mm diam.; conidia simple, fusiform, 3-4 × 0.5-0.7 µm (Fig. 6I).

Notes: This new variety of *Porina lucida* was originally thought to represent the typical *P. lucida*, until the holotype material of the latter was examined. Var. *australiensis* covers individuals found in a restricted area in Northern Australia which differ from typical *P. lucida* by the broader, shorter ascospores and the often yellowish red, more applanate perithecia without any darker zone around the ostiole.

We have decided to describe this taxon as a variety of *P. lucida* since it is most similar to that species and is found within a very limited geographic range which partly overlaps with that of the nominal variety. It cannot be ruled out, however, that this variety is actually related to another species, and the similarities with *P. lucida* are mere analogies.

The conidia found in this taxon appear to be microconidia. They agree with those described for other species of *Porina* (Purvis & al. 1992; McCarthy 1993) and do not provide a good taxonomic character except for their presence, since they are regularly found in *P. lucida* var. *australiensis* but unknown in var. *lucida*.

#### Distribution and ecology

Known from lowland rain forest areas in northern Australia where it often occurs together with *Porina similis*.

#### Additional specimens examined

AUSTRALASIA: AUSTRALIA: Queensland, Atherton Tableland, 9.1983, *Henssen 29351, 29374, 29377* (herb. Lücking); Crediton State Forest, 21°19'S, 148°33'E, 840 m, forest dominated by *Argyrodendron trifoliatum* and *Syzygium* sp., 7.1986, *Streimann 37663* (herb. Lücking); Cape Tripulation, 16°05'S, 145°33'E, 5-20 m, lowland rain forest and coastal forest, 9.1992, *Kalb & Kalb s.n.* (herb. Kalb).

#### *Porina mazosioides*

*Porina mazosioides* Lücking & Vězda, **sp. nova**

Typus: Africa, Tanzania, N-Uluguru Mts., 1700-1850 m, mossy forest, 12.1972, *Pócs & al. 6851* (herb. Vězda, holotypus).

A *Porina epiphyloides* peritheciis et ascosporis maioribus differt.

Diagnostic features: *Thallus* dispersed, small to medium-sized, finely verrucose (Fig. 3D), greenish, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate rows. *Perithecia* young lens-shaped to hemispherical, mature ones hemispherical to wart-shaped (Fig. 3D), 0.4-0.6 mm diam., with a yellowish red tinge. *Ascospores* 7-septate, oblong, 40-50 × 5-6 µm, 7-8 times as long as broad (Fig. 7G).

Notes: *Porina mazosioides* is most closely related to *P. epiphyloides* but differs in the larger perithecia and the much larger ascospores. The shape of the perithecia is reminiscent of *P. lucida*, which has a non-verrucose thallus with non-radiate phycobiont and narrower ascospores. All known collections are very homogeneous. In one collection [Tanzania, *Pócs & al. 6259* (herb. Vězda)], the species was found overgrown by *Chroodiscus mirificus*, a commonly observed phenomenon in *Chroodiscus* and species of the *Porina epiphylla* group (Kalb & Vězda 1992).

#### Distribution and ecology

Thus far only known from tropical East Africa and Madagascar, and seemingly restricted to lower montane rain forests.

#### Additional specimens examined

AFRICA: KENYA: Taita District, Taita Hills, Mbololo Hill, 03°21'S, 38°27'E, 1525-1850 m, intermediate wet evergreen forest, 10.1970, *Faden & Githui 70* (herb. Vězda). — TANZANIA: Uluguru Mts., 2000-2100 m, 10.1970, *Pócs & al. 6297* (herb. Vězda); Rungwe volcano, 1950-2050 m, mossy forest, 8.1972, *Pócs 6763* (herb. Vězda); Tanga region, West-Usambara Mts., 1600-1700 m, 10.1986, *Borhidi & al. 86203* (herb. Vězda); *ibid.*, Ndelemai Forest Reserve, 1700 m, 3.1984, *Pócs 8429* (herb. Vězda); E-Usambara Mts., 1000 m, submontane rain forest, 12.1969, *Pócs & Pócs 6097* (herb. Vězda); Uluguru Mts., 1600-1700 m, montane evergreen forest, 2.1972, *Pócs 6536* (herb. Vězda). — MADAGASCAR: E of Antananarivo, 19°S, 48°30'E, Perinet Reserve, National Forest, 150 m, 12.1995, *Halda s.n.* (herb. Vězda).

***Porina minutissima****Porina minutissima* Henssen, Lücking & Vězda, **sp. nova**Typus: Australia, Queensland, Atherton Tableland, 9.1983, *Henssen 29401* (herb. Henssen, holotypus!).A *Porina epiphylla* peritheciis et ascosporis minoribus differt.

Diagnostic features: *Thallus* continuous, small, smooth, yellowish grey, matt to slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells-angular rounded (to rectangular), irregularly arranged. *Perithecia* young lens-shaped to hemispherical, mature ones hemispherical to wart-shaped, 0.2-0.25(-0.3) mm diam., often with a reddish tinge, numerous. *Ascospores* 7-septate, oblong, 20-25 × 2.5-3 µm, 8 times as long as broad (Fig. 6A).

Notes: We describe this taxon with some hesitation. Its separation from *Porina epiphylla* s.str. on account of the small perithecia and ascospores seems equally justified (or not) as that of *P. lucida* with its larger perithecia and ascospores. The presence of variational discontinuities, particularly in ascospore size, as well as the restricted distribution of *P. minutissima*, seem to support our view. The species was distinguished from *P. epiphylla* by other authors as well but identified as *P. epiphyloides* (Aptroot & Sipman 1991, Sipman 1991, 1993).

*Porina minutissima* is externally almost identical with *Porina albicera* but differs by the regularly 7-septate ascospores, thus providing a transition between *P. albicera* and *P. epiphylla*. The thallus structure of both *P. albicera* and *P. minutissima* is most reminiscent of that of *P. subepiphylla*.

## Distribution and ecology

Known only from a few collections from Australasia.

## Additional specimens examined

AUSTRALASIA: MALAYSIA: Sabah, Kinabalu National Park, 700 m, *Sipman & Tan 29532* (B); Longkawi Isl., Seven Falls, 3.1995, *Troneček s.n.* (herb. Lücking, herb. Vězda). — PAPUA NEW GUINEA: Monrobo, Boana, 1200 m, 6.1940, *Clemens s.n.* (UPS, filed under *P. epiphylla*). — AUSTRALIA: Queensland, Fitzroy Island, 16°56'S, 145°59'E, 50-100 m, 3.1988, *Aptroot & Aptroot 22298* (B).

***Porina mirabilis****Porina mirabilis* Lücking & Vězda, **sp. nova**Typus: America, Costa Rica, Caño Negro National Wildlife Refuge, 10°54'N, 84°47'W, 50 m, lowland rain forest, 2.1992, *Lücking 92-2874* (M, holotypus!).A *Porina lucida* peritheciis planioribus latioribusque ascosporis angustioribus bacilliformibusque differt.

Diagnostic features: *Thallus* continuous, small (to medium-sized), uneven-rugose (at the margins sometimes with slight radiate ridges), pale yellowish grey, slightly nitidous; no prothallus. Stalked, disciform isidia of the *Phyllophiale alba* type often present on the periphery of the thallus (Fig. 5H). *Phycobiont* a species of *Phycopeltis*, cells angular-rounded to rectangular, irregularly arranged or in very slightly radiate rows. *Perithecia* young applanately lens-shaped, mature ones lens-shaped to applanately wart-shaped, with broadly spreading base and hardly delimited from the thallus (Fig. 5G-H), 0.4-0.7 mm diam., often with an orange-reddish tinge. *Ascospores* 7-septate, bacillar (ends acute and proximal end slightly tapering), (35-)40-45 × 3-4.5 µm, 10-13 times as long as broad (Fig. 6K-L).

Notes: This new species has been misinterpreted as *Porina lucida* (Lücking 1992, Aptroot & Sipman 1993) but differs from the latter in various characters, particularly the broadly spreading perithecia and the narrow, bacillar ascospores with acute ends. *P. mirabilis* varies in the shape



of mature perithecia (sometimes slightly elevated and wart-shaped in the centre) and the colour around the ostiole, which usually has a reddish tinge (American specimens) but may sometimes, especially in Australasia, be dark brownish black [e.g. Papua New Guinea, *Sipman 24269c*; Australia, *Aptroot & Aptroot 22299b* (B)]. Due to its plane perithecia, *P. mirabilis* might be confused with species of the *P. applanata* group, particularly *P. applanata* itself, which differs by its perithecial anatomy (no crystals and horizontally projecting asci) and its much broader ascospores.

A particular feature of *Porina mirabilis* by which it differs from all other species of the *P. epiphylla* group is the frequent presence of isidia [e.g. Costa RICA, *Lücking 91-2653* (herb. Lücking); Guyana, *Sipman & Aptroot 19223h* (B); French Guiana, *Sipman 32334, 32684* (B)] of a type referred to as *Phyllophiale alba*, an imperfect taxon described by Santesson (1952). Smaller, brownish isidia described as *Phyllophiale fusca* R. Sant. are found on *Porina fusca* Lücking (1991). It has been repeatedly discussed whether these isidia are vegetative propagules of the corresponding *Porina* species or not (Lücking 1991, Aptroot & Sipman 1993). The observations supporting one view or the other are ambiguous, and a final solution must probably await molecular studies. That the disc-like isidia are vegetative propagules of the *Porina* species seems to be supported by the fact that they are regularly found on young thalli without perithecia and in mature thalli are restricted to the thallus periphery while perithecia are found in the centre. Lichenicolous taxa usually are restricted to certain areas of the host thallus and often suppress the formation of ascocarps (Matzer 1996). Furthermore, it would make little sense for a parasymbiotic species to disperse by diaspores which carry both fungal and algal elements, since a lichenicolous taxon makes use of the phycobiont of the host thallus.

On the other hand, we see some difficulties in the fact that the species of *Porina* producing *Phyllophiale* type isidia are only distantly related and even belong to different groups which recently have been recognized at generic level (Harris 1995). While *P. mirabilis* is a typical member of the *P. epiphylla* group (= *Porina* s.str. sensu Harris 1995), *P. fusca* belongs to the *P. rufula* group (= *Segestria* sensu Harris 1995). Even if generic separation of these groups is not well supported and not accepted by other authors (McCarthy & Malcolm 1997, Lücking 1998), the distance between the two species remains considerable. It is difficult to imagine that such a particular type of isidia had evolved independently in two different lineages. The relationships between the involved taxa appear even more complicate with *P. epilucida*, an interesting species described by Aptroot & Sipman (1993). We have studied the type material and collections from Guyana and Brazil and can confirm that *P. epilucida* is a lichenicolous taxon growing on thalli of a species originally identified as *P. lucida* (hence the epithet *epilucida*), but actually representing *P. mirabilis*. Morphologically and anatomically, *P. epilucida* is identical with *P. fusca* and differs only by its mostly 5-septate ascospores.

In view of these problems, we have adopted a conservative position and described the taxon treated here as a new species, while at the same time maintaining the individual status of *Phyllophiale alba*. Otherwise, the introduction of a new name would be superfluous and instead, the combination of the epithet *alba* into *Porina* would be necessary to cover the species in question, with both perithecia and isidia. In our view, such a progressive solution, although strongly supported, must await a definitive study using molecular methods.

#### Distribution and ecology

*Porina mirabilis* is a pantropical species but most common in tropical America. It is mainly found in lowland to submontane rain forests.

#### Additional specimens examined

AMERICA: COSTA RICA: Puntarenas, Corcovado National Park, 08°28'N, 83°35'W, 50-150 m, lowland rain forest, 7.1992, *Lücking 92-3546* (herb. Lücking, with *Phyllophiale* type isidia); Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-2653* (herb. Lücking, with *Phyllophiale* type isidia); Cartago, Centro Agronómico Tropical de Investigación y Enseñanza, near Turrialba, 09°53'N, 83°39'W, 600 m, lower montane rain forest, 3.1991,

*Lücking 91-3477* (herb. Lücking). — CUBA: Santiago, San Vicente valley, 140 m, 11.1974, *Pócs & Reyes 9050* (herb. Vězda); Oriente, Bayate, 1917, *Ekman L 128a* (UPS, filed under *P. epiphylla*). — COLOMBIA: Amazonas, Villazul, 00°45'S, 72° 06'W, 240 m, primary forest near river, 11.1988, *Sipman & Duivenvoorden 28121a* (B); Meta: Municipio Villavicencio, 600 m, 9.1984, *Aguirre & Sipman 5691b* (B). — GUYANA: Demerara, Mabura Hills, mixed forest (primary rain forest on poor soil), 3.1985, *Cornelissen & ter Steege 96a* (B); Upper Mazaruni: Trail from Kamarang river to Pwipwi mountain, 05°48'N, 60°47'W, 600 m, 25 m tall riverain forest, 2.-3.1985, *Sipman & Aptroot 19223h* (B, with *Phyllophiale* type isidia); *ibid.*, Kamarang, along trail to Waramadan, 05°52'N, 60°37'W, 500 m, 25 m tall, mixed forest, 2.1985, *Sipman & Aptroot 18942b* (B, filed under *P. andreana*). — FRENCH GUIANA: Sinnamary, Piste de St. Elie, 05°19'N, 53°02'W, 50 m, disturbed remnants of forest along road, 1.1988, *Sipman 32684* (B); Maripasoula, Saül, trail to Monts La Fumée, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32053* (B); *ibid.*, along Crique Limonade, 03°34'N, 53°13'W, 300 m, primary forest, 1.1988, *Sipman 32334* (B, with *Phyllophiale* type isidia). — BRAZIL: Amazonas, Rio Preto, 80 km E of Manaus, 03°10'S, 59°50'W, 40 m, 8. 1980, *Kalb s.n.* (herb. Lücking); *ibid.*, Rio Negro, 40 m, 10.1980, *Kalb 310* (herb. Vězda); Mato Grosso, Serra dos Coroados, 550 m, 8. 1980, *Kalb 279* (herb. Vězda, with *Phyllophiale* type isidia).

AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101181, 101195* (herb. Lücking). — CAMEROON: Bibundi, 1891, Jungner 51 a (UPS, filed under *P. epiphylla*). — CONGO: Haut-Zaïre, Ituri, Mt. Tatotudu, forêt primaire sur pente, 4.1976, *Lisowski 42590* (herb. Vězda). — GUINEA: Macenta, Ziama, 900 m, 3.1962, *Lisowski s.n.* (herb. Vězda, with *Phyllophiale*-type isidia). — TANZANIA: Morogoro region, Nguru Mts., Manyangu Forest Reserve, 560-680 m, 3.1989, *Farkas 89104* (herb. Vězda); *ibid.*, 5 km NW of Mhonda Mission, 800-850 m, 3.1989, *Farkas 89102* (herb. Vězda).

AUSTRALASIA: VIETNAM: Tonkin, Vinh-Phuc Prov., 4.1974, *Zsolt s.n.* (herb. Vězda). — PAPUA NEW GUINEA: Madang, Karkar Isl., 04°37'S, 145°55'E, 50 m, lowland rain forest, 1.1987, *Sipman 24269c* (B). — AUSTRALIA: Queensland, Fitzroy Isl. on Great Barrier Reef, 16°56'S, 145°59'E, 50-100 m, forest relict, 3.1988, *Aptroot & Aptroot 22299b* (B).

### ***Porina nucula***

*Porina nucula* Ach., Synops. Lich.: 112. 1814. — Typus: Africa, Guinea, s. loc., on bark, s.d., s.coll., s.n. (H-Ach 731-A, lectotypus fide Harris 1995, not seen; S, isotypus!).

Diagnostic features: *Thallus* continuous, medium sized (to large), coarsely verrucose (verrucae dense, 0.05-0.15 mm diam.), pale (yellowish) grey, matt (to slightly nitidous); *Phycobiont* a species of *Trentepohlia*, cells angular-rounded (near verrucae) to rectangular (between verrucae), irregularly arranged (near verrucae) or rows forming a regular net (between verrucae). *Perithecia* young lens-shaped, mature ones wart-shaped to almost subglobose with constricted base (Fig. 3F), 0.5-0.7 mm diam., with an irregular surface. *Ascospores* 7(-9)-septate, fusiform to ellipsoid and with gelatinous sheath, 40-55 × 10-12 µm, 4-5 times as long as broad (Fig. 7C).

Notes: *Porina nucula* is the type species of *Porina* (McCarthy 1993). The species is usually found on smooth bark in shaded habitats of dry evergreen forests, but occasionally foliicolous specimens are found which agree in most respects with the corticolous ones. The perithecia are usually wart-shaped but may reach the basally constricted shape typical of *P. nucula*, whose variation is given as hemispherical to subglobose (McCarthy 1994). Foliicolous specimens were partly identified as *P. mastoidea* by Aptroot & Sipman (1993: 31), who use an extremely broad concept of *P. mastoidea*: "The species is used here in a wider sense than usual ...", including taxa "... with or without black hypothallus and with a large range of ascospore dimensions." According to McCarthy (1993) and to our own observations on corticolous material, *P. mastoidea* s.str. is characterized by a usually nitidous, greenish grey, smooth thallus with a purplish black prothallus and by lens-shaped perithecia which often have a broad dark spot around the

ostiole, and hence differs considerably from *P. nucula*, while being related to *P. imitatrix*. Aptroot & Sipman (1993) correctly stated that their foliicolous specimens filed under *P. mastoidea* differed by the absence of a blackish prothallus and by the verrucose thallus, overlooking that these characters fit their own circumscription of *P. nucula*. Contrary to the latter, *P. mastoidea* s.str. is not known from leaves.

#### Distribution and ecology

Pantropical; mostly corticolous and not rare in open situations, foliicolous specimens being known from rain forest areas in tropical America and Asia.

Additional, foliicolous specimens examined

AMERICA: COSTA RICA: Cartago, Guayabo National Monument, 09°59'N, 83°43'W, 1400 m, montane rain forest, 5.1992, *Lücking 92-1742* (herb. Lücking); *ibid.*, secondary vegetation, 1.1991, *Lücking 91-3888* (herb. Lücking). — DOMINICA: Northern Forest Reserve, 600-700 m, rain forest, 7.1996, *Vězda s.n.* (herb. Vězda). — FRENCH GUIANA: Sinnamary, Piste de St. Elie, 05°19'N, 53° 02'W, 50 m, disturbed remnants of forest along road, 1.1988, *Sipman 32686a* (B). AUSTRALASIA: PAPUA NEW GUINEA: Monrobo, Boana, 1200 m, 6.1940, *Clemens s.n.* (UPS).

#### *Porina pocsii*

*Porina pocsii* Vězda in Folia Geobot. Phytotax. 19: 188. 1984. — Typus: America, Cuba, Santiago de Cuba, Sierra Maestra, 1000-1100 m, montane rain forest, 5.1979, *Pócs 9115* (herb. Vězda, holotypus!).

Diagnostic features: *Thallus* dispersed, small to medium-sized, finely verrucose, yellowish green, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate rows. *Perithecia* young hemispherical, mature ones wart-shaped, 0.5-0.7 mm diam., with a yellowish red tinge. *Ascospores* 7-septate, fusiform, 45-70 × 10-12 µm, 4-6 times as long as broad, with gelatinous sheath.

Notes: *Porina pocsii* is well distinguished by the combination of verrucose thallus with radiate phycobiont and large, fusiform ascospores with gelatinous sheath. It is probably related to *P. mazosioides* which has much narrower ascospores, but is also reminiscent of *P. nucula*, from which it differs mainly by the radiate phycobiont belonging to *Phycopeltis*. The presence of a gelatinous sheath around the ascospores is also known from other species of different affinity but also large ascospores, e.g. *P. nucula* and *P. imitatrix*, proving that this feature has no higher taxonomic significance but is probably correlated with ascospore size.

Harris (1995) has recently argued that within pyrenocarpous taxa, the same fungus may be involved in lichens with a different phycobiont, e.g. *Trentepohlia* or *Phycopeltis*, giving rise to different thallus morphology. Such a phenomenon is known from lichens where green algae and Cyanobacteria are involved, and has also been described for some Caliciales (Tibell 1982). In the present case, it remains to be proved but seems to be not entirely out of question.

Distribution: Only known from the type locality.

#### *Porina radiata*

*Porina radiata* Kalb, Lücking & Vězda, **nom. nov.**

≡ *Porina rugosa* Kalb & Vězda in Nova Hedwigia 55: 205. 1992, nom. illeg. (ICBN Art. 53.1) [non *P. rugosa* Ach., Synops. Lich.: 110. 1814]. — Typus: America, Brazil, Pará, Belem, 10 m, rain forest, 10.1980, *Kalb 311* (herb. Vězda, isotypus!).

Diagnostic features: *Thallus* dispersed but marginally confluent, small to medium-sized, with regular radiate ridges (Fig. 3A), greenish grey, (slightly) nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells rectangular, in distinctly radiate plates. *Perithecia* lens-shaped, 0.3-0.45 mm diam., sometimes with a brownish spot around the ostiole. *Ascospores* 7-septate, 28-35(-43) × 3.5-4.5 µm, 8-10 times as long as broad.

Notes: The existence of the validly published *Porina rugosa* Ach. was overlooked by Kalb & Vězda (1992), and therefore a new name has to be introduced for the present species. *P. radiata* is a characteristic species, easily distinguished by its radiate thallus ridges. African populations can be confused with *P. follmanniana*, which has appanately conical perithecia with a narrow, sharply delimited dark spot around the ostiole. The African populations are scarce, the thallus ridges being not very well developed, and the ascospores being longer on average (32-43 µm) than those of neotropical specimens.

Distribution: Known from tropical America, where it is very abundant, and from a few collections from tropical Africa. A typical lowland rain forest species, confined to primary vegetation.

#### Additional specimens examined

AMERICA: COSTA RICA: Puntarenas, Corcovado National Park, 08°34'N, 83°31'W, 50-200 m, lowland rain forest, 7.1992, *Lücking 92-3192* (herb. Lücking); Alajuela, Caño Negro National Wildlife Refuge, 10°54'N, 84°47'W, 50 m, lowland rain forest, 2.1992, *Lücking 92-2876* (herb. Lücking); Limón: Hitoy Cerere Biological Reserve, 09°41'N, 83° 02'W, 100-200 m, lowland rain forest, 3.1991, *Lücking 91-1356* (herb. Lücking). — COLOMBIA: Nariño, Munaco, Estación Forestal La Espriella, 01°25'N, 78°40'W, 35 m, moderately affected relicts of 30 m tall rain forest, 6.1986, *Sipman & al. 29633* (B); Amazonas, Villazul, Caquetá River, 00°42'S, 72° 07'W, 240 m, 11.1988, *Sipman & Duivenvoorden 28255* (B). — GUYANA: Demerara, Mabura Hills, mixed forest (primary rain forest on poor soil), 3.1985, *Cornelissen & ter Steege 107, 108* (B); Tumatumare, Potary River, 200 km SSW of Georgetown, 40 m, 5.1981, *Balazs 81-03* (herb. Vězda). — SURINAM, Jodensavanne, Mapane creek area, 9.1953, *Lindeman 4758s* (herb. Vězda); Lely Mts., SW plateau, 550-710 m, 9.1975, *Lindeman s.n.* (herb. Vězda). — FRENCH GUIANA: Sinnamary, Piste de St. Elie, 05°15'N, 53° 03'W, 50 m, disturbed primary forest along road, 1.1988, *Sipman 32635* (B); Maripasoula: Saül, Crique Limonade, 03°34'N, 53°13'W, 300 m, primary forest, 1.1988, *Sipman 32361* (B); *ibid.*, near Cambrouze, 03°38'N, 53°14'W, 300 m, primary forest, 1.1988, *Sipman 32456* (B); Roura, Montagne de Kaw, 04°41'N, 52°19'W, 200 m, moist primary forest, 1.1988, *Sipman 32516* (B). — BRAZIL: São Paulo, Serra da Cantareira, 950 m, 8.1978, *Kalb & Hannack 42* (herb. Vězda); Serra do Garrãozinho, 850 m, 7.1979, *Sipman s.n.* (herb. Vězda).

AFRICA: IVORY COAST: Tai National Park, 12.1975, *Aké Assi 13161* (herb. Vězda); *ibid.*, 05°52'N, 07°27'W, 200 m, 9.-10.1992, *Becker 101008, 101173* (herb. Lücking). — CAMEROON: Bibundi, 1891, *Jungner 51b* (UPS). — CONGO: Haut-Zaïre, Ituri, forêt primaire sur pente, 4.1976, *Lisowski 42590* (herb. Vězda); *ibid.*, 21 km N of Kisangani, margin of secondary forest, 11.1976, *Lisowski 43194* (herb. Vězda); *ibid.*, à l'W of Kisangani, forêt dense primaire, 6.1975, *Lisowski s.n.* (herb. Vězda). — MAGASCAR: Antsiranana, Reserve Integrale Nationale de Marojezy, 200-500 m, 3.1990, *Pócs & al. 90111* (VBI, herb. Lücking).

#### *Porina rudiuscula*

*Porina rudiuscula* (Nyl.) Müll. Arg. in *Hedwigia* 31: 287. 1892 ≡ *Verrucaria rudiuscula* Nyl., *Bull. Soc. Linn. Normand.*, ser. 2, 2: 124. 1868. – Typus: Australasia, New Caledonia, Loyalty Isl., Lifou, on bark, 1864, *Thiébaud* (H-Nyl 1928, holotypus, not seen).

Diagnostic features: *Thallus* continuous, large, coarsely verrucose, yellowish to brownish grey, matt. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded (near verrucae) to rectangular (between verrucae), irregularly arranged (near verrucae) or rows forming a regular net (between verrucae); *Perithecia* young lens-shaped, mature ones wart-shaped (to almost subglobose with constricted base), 0.5-0.7 mm diam., with an irregular surface. *Ascospores* 9-13-septate, fusiform and with gelatinous sheath, 65-80 × 15-20 µm, 4-5 times as long as broad (Fig. 7D).

Notes: Apart from the genuine *Porina nucula*, a further representative of that group of species is very rarely found on leaves. The taxon, which was identified with *P. mastoidea* by Aptroot &

Sipman (1993), differs from *P. nucula* by 9-13-septate ascospores being 65-80 × 15-20 μm in size. There is a number of non-foliicolous taxa which could be available as the home for this material [e.g. *P. americana* Fée, *P. guaranitica* Malme, *P. heterospora* (Fink) R. C. Harris, *P. simulans* Müll. Arg.], but according to the descriptions given in Malme (1929) and McCarthy (1993) and our observations on corticolous material housed in S, we believe that *P. rudiusscula* comes closest. This identification is of course preliminary and must await further studies since the taxonomy of this group of species is not yet settled.

#### Distribution and ecology

Probably pantropical but known by few collections only.

#### Additional, foliicolous specimen examined

AMERICA: FRENCH GUIANA: Maripasoula, Saül, route to Monts La Fumée, 03°38'N, 53°12'W, 300 m, tropical primary forest, 1.1988, *Sipman 32050* (B).

### *Porina similis*

*Porina similis* Kalb & Vězda in Nova Hedwigia 53: 225. 1991. – Typus: Australia, Queensland, Lamington National Park, 900 m, subtropical rain forest, 8.1988, *Kalb & Kalb s.n.* (herb. Kalb, holotypus!; herb. Vězda, isotypus!).

Diagnostic features: *Thallus* continuous but marginally dispersed, medium-sized, with an irregular surface and often with large (0.1-0.15 mm diam.), applanate verrucae containing crystals or undeveloped perithecial primordia, yellowish grey, matt, without visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young hemispherical, mature ones wart-shaped (Fig. 2E), 0.4-0.7 mm diam., top sometimes with a dark spot. *Ascospores* 7-septate, oblong, 32-45 × 3.5-5 μm, 8-9 times as long as broad.

Notes: *Porina similis* has only recently been separated from *P. epiphylla* (Vězda & Kalb 1991). It differs from the latter mainly by the larger, wart-shaped perithecia and larger ascospores, and the yellowish, often coarsely verrucose thallus. *Porina lucida* var. *lucida* and var. *australiensis* have similar sized ascospores and perithecia but the perithecia are lens-shaped. Further, in *P. lucida* var. *australiensis*, which often occurs together with *P. similis* (e.g. in the holotype of the former), the thallus is completely smooth and the ascospores are comparatively broader. Forms of *P. similis* may resemble *P. atriceps* and *P. atropunctata*, but the dark spot, if developed, is not as distinct as in the latter species, and the perithecia and ascospores are larger.

The large, applanate verrucae of *Porina similis* are very characteristic, although not always present, and very different from the fine verrucae found in species of the *P. epiphylloides* and *P. nucula* subgroup. They resemble pycnidia or perithecial primordia, but those checked so far only contained clusters of crystals.

#### Distribution and ecology

Rather common in (sub)tropical rain forests in Australia.

#### Additional specimens examined

AUSTRALASIA: AUSTRALIA: Queensland, D'Aguilar Range, 27°20'S, 152°46'E, 700 m, 8.1986, *Hafellner & Rogers s.n.* (B; *Plantae Graecensis*, Lich. 423, as *Porina epiphylla*); *ibid.* (B; *Lichenes Selecti Exsiccati* 2177, as *Porina epiphylla* var. *atriceps*); Crediton State Forest, 840 m, 6.1986, *Streimann 37663* (herb. Lücking; *Lichenes Selecti Exsiccati* 2327, as *P. lucida*); Lamington National Park, 900 m, 8.1988, *Kalb & Kalb s.n.* (herb. Lücking); Eacham Shire, Souita Falls, tropical rainforest, 17°35'S, 145°40'E, 8.1987, *Henssen 31243* (herb. Lücking, filed under *P. lucida* var. *australiensis*); New South Wales: Border Ranges National Park, 850 m, *Nothofagus moorei* forest, 8.1986, *Hafellner & al. s.n.* (herb. Vězda).

Incorrect records: PAPUA NEW GUINEA: Morobe, Busu River, 100 m, lowland rain forest, 6.1982, *Streimann s.n.* (CBG), is *Porina lucida* var. *lucida*. Western Highlands: Baiyer River

sanctuary, 1160 m, lower montane rain forest, 6.1982, *Streimann s.n.* (CBG), is *Porina lucida* var. *lucida*.

### ***Porina subepiphylla***

*Porina subepiphylla* Lücking & Vězda, **sp. nova**

Typus: America, Costa Rica, Heredia, La Selva Protection Zone, 10°26'N, 84°03'W, 50 m, lowland rain forest, 9.1991, *Lücking 91-5751* (CR, holotypus!).

A *Porina epiphylla* peritheciis verruciformis ascosporis maioribus fusiformibusque et thallo flavescente differt.

Diagnostic features: *Thallus* continuous, small to medium-sized, smooth, yellowish grey, matt, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young hemispherical, mature ones wart-shaped (Fig. 5A-B), 0.3-0.4 mm diam., often with a slight reddish tinge. *Ascospores* 7-septate, fusiform, 30-43 × 4.5-6 µm, 6-7 times as long as broad (Fig. 6F).

Notes: This new species is established with some hesitation, since its separation from *Porina epiphylla* s.str. is not always clear. However, the combination of characters, the distribution patterns and our field observations convinced us that this taxon is specifically different from *P. epiphylla* by its wart-shaped perithecia, its larger, fusiform ascospores, and its yellowish, matt thallus. The differences in colour is readily observed in the field but dried or not well-developed specimens might be difficult to distinguish. *P. subepiphylla* differs from *P. epiphylla* also in its ecology, being more abundant in semi-open situations. On the other hand, thallus and ascospore characters indicates a relationship between *P. subepiphylla* and *P. conica*, and the distribution of both species suggests that they are sister species originating from a common ancestor close to *P. epiphylla*.

Distribution: Thus far known from tropical America; the records from Africa (Lücking & al. 1998) are incorrect. *Porina subepiphylla* is the only foliicolous species of the group which is regularly found in more open situations while the other taxa are usually confined to the shaded understorey of the forest.

#### Additional specimens examined

AMERICA: COSTA RICA: Puntarenas, Corcovado National Park, 08°28'N, 83°35'W, 50-150 m, lowland rain forest, 7. 1992, *Lücking 92-3773* (herb. Lücking); Cartago: Guayabo National Monument, 09°59'N, 83°43'W, 1400 m, montane rain forest, 5.1992, *Lücking 92-1471* (herb. Lücking); Limón: Hitoy Cerere Biological Reserve, 09°41'N, 83°02'W, 100-200 m, lowland rain forest, 3.1991, *Lücking 91-4694* (herb. Lücking); Río Siquirres, 10°06'N, 83°31'W, 100 m, lowland rain forest, 3.1991, *Lücking 91-2870* (herb. Lücking). — FRENCH GUIANA: Maripasoula, Saül, route to Monts La Fumée, 03°38'N, 53°12'W, 300 m, primary forest, 1.1988, *Sipman 32050* (B, filed under *P. mastoidea*); Roura: Montagne de Kaw, 04°34'N, 52°14'W, 200 m, 1.1988, *Sipman 32586* (B, filed under *P. epiphylla*). — BRAZIL: Amazonas, Para, 1847, *Spruce s.n.* (B); Pernambuco, Dois Irmãos, 3.1998, *Cáceres & Lücking s.n.* (URM).

Incorrect records: Africa, Ivory Coast, Taï National Park, 05°52'N, 07°27'W, 200 m, lowland rain forest, 9.-10.1992, *Becker 101114, 101210* (herb. Lücking), are *Porina subnucula*.

### ***Porina subnucula***

*Porina subnucula* Lumbsch, Lücking & Vězda, **sp. nova**

Typus: Australia, Queensland, Cairns, wet sclerophyllous forest, 8.1987, *Lumbsch 5428j* (herb. Vězda, holotypus!).

A *Porina verruculosa* ascosporis 7-septatis maioribusque differt.

Diagnostic features: *Thallus* continuous, small, minutely and irregularly verrucose, yellowish grey, matt, without visible prothallus. *Phycobiont* a species of *Phycopeltis* or *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* young hemispherical, mature ones wart-shaped to almost subglobose, 0.25-0.4 mm diam., their top sometimes with a brownish spot. *Ascospores* 7-septate, fusiform, 30-40 × 5-6 µm, 6-7 times as long as broad (Fig. 7B).

Notes: This new species at first glance resembles a member of the *Porina epiphylla* subgroup, in particular *P. subepiphylla*, but on account of its thallus morphology must be included in the *P. nucula* subgroup. It is most similar and probably closely related to *P. verruculosa*, from which it differs by the slightly smaller perithecia and the larger, 7-septate ascospores. *P. subnucula* provides a transition between the *P. nucula* and the *P. epiphylla* subgroups and is an example how the latter might have evolved from the former.

According to the description given by Malme (1929) and McCarthy (1993), our new species resembles *Porina curtula* Malme. We have studied the type and a saxicolous specimen cited in McCarthy (1993) [Paraguay, Asunción, Lambaré, 8.1893, *Malme 1658* (S)] and found it to be different from *P. subnucula* but, on the other hand, similar to the foliicolous populations close to *P. tetracerae*, for which this name was adopted (see above).

#### Distribution and ecology

*Porina subnucula* is known from two rather distant but very homogeneous collections in tropical Africa and Australia.

#### Additional, foliicolous specimen examined

AFRICA: IVORY COAST: Taï National Park, 05°52'N, 07°27'W, 200 m, lowland rain forest, 9.-10.1992, *Becker 101114, 101210* (herb. Lücking).

### ***Porina tetracerae***

*Porina tetracerae* (Afz.) Müll. Arg. in Bot. Jahrb. Syst. 6: 401. 1885 ≡ *Verrucaria tetracerae* Afz. in Ach., Meth. Lich.: 121. 1803. – Typus: Sierra Leone, s. dat., *Afzelius s.n.* (H-Ach 838, holotypus, not seen; UPS, isotypus!).

Diagnostic features: *Thallus* continuous, medium-sized to large, uneven, greenish, nitidous, with a purplish black prothallus. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged. *Perithecia* hemispherical to wart-shaped, 0.4-0.7 mm diam. *Ascospores* 7-septate, narrowly fusiform, 30-45 × 4-6 µm, 7-8 times as long as broad (Fig. 4B).

Notes: *Porina tetracerae* differs from *P. imitatrix*, another common foliicolous species with dark prothallus, by the smaller perithecia and the much smaller ascospores without gelatinous sheath. It closely resembles *P. curtula*, but the perithecia and ascospores are larger than in that species, and the thallus is greenish and lacks minute verrucae.

#### Distribution and ecology

*Porina tetracerae* is pantropical and apparently rather commonly found on bark and rock (McCarthy 1993). A few foliicolous specimens are known at present.

#### Additional, foliicolous specimens examined

AMERICA: ECUADOR: Napo, Jatun Satcha Biological Station, 450 m, 6.1996, *Lücking 96-879* (herb. Lücking).

AUSTRALASIA: PAPUA NEW GUINEA: Kaiser Wilhelms Land, Simboug, 1899, *Nyman 57c* (UPS).

### ***Porina verruculosa***

*Porina verruculosa* Müll. Arg. in Flora 63: 197. 1890. – Typus: America, Brazil, Rio de Janeiro, Rio de Janeiro, s. dat., *Glaziou 18103* (G, holotypus!).

Diagnostic features: *Thallus* continuous, small, verrucose (verrucae dense, 0.05-0.15 mm diam.), pale yellowish grey, slightly nitidous. *Phycobiont* a species of *Trentepohlia*, cells angular-rounded, irregularly arranged or forming a net. *Perithecia* young hemispherical, mature ones wart-shaped to subglobose, 0.25-0.45 mm diam., usually with an irregular surface. *Ascospores* 5-septate, oblong to fusiform, 15-21 × 3-5 μm (Fig. 7A).

Notes: *Porina verruculosa* was related to corticolous species by Santesson (1952) but later used to include the typical and abundantly foliicolous taxon now separated as *P. guianensis* (Aptroot & Sipman 1993). *P. verruculosa* undoubtedly belongs to the *P. nucula* subgroup, being mainly separated by the smaller, less septate ascospores. It is known by a few, probably facultatively foliicolous specimens.

#### Distribution and ecology

Known from a few collections in the Neotropics. Statements on its ecology are difficult.

Additional, foliicolous specimens examined

AMERICA: COSTA RICA: Puntarenas, La Amistad International Park, *Greber 80* (ULM). — ST. VINCENT: St. Vincent, Bonhomme Woods, 1.1892, *Elliott 351* (UPS, filed under *Fellhanera elliotii*). — BRASIL: Rio Grande do Sul, Hamburgerberg, 10.1892, *Malme 636:1b* (S).

#### *Porina virescens*

*Porina virescens* (Kremp.) Müll. Arg. in Flora 66: 331. 1883 ≡ *Verrucaria virescens* Kremp., Lichenes Foliicol.: 21. 1874 [ & in Nuovo Giorn. Bot. Ital. 7: 53. 1875]. – Typus: Australasia, Malaysia, Borneo, Sarawak, *Beccari s.n.* (M, holotypus!).

= *Porina multiseptata* Müll. Arg. in Bot. Jahrb. 4: 57. 1883. – Typus: Australasia, Papua New Guinea, 1875, *Naumann s.n.* (G, holotypus!).

= *Porina pandanorum* Vain. in Ann. Acad. Sci. Fenn., ser. A, 15: 361. 1921. – Typus: Australasia, Philippines, Luzon, Mt. Bulusan, 1916, *Elmer 14915* (TUR, holotypus, not seen; BM, isotypus!).

Diagnostic features: *Thallus* continuous, (medium-sized to) large, smooth (to uneven), but sometimes furnished with cushions of soft hairs (Fig. 2G), yellowish grey, slightly nitidous, no visible prothallus. *Phycobiont* a species of *Phycopeltis*, cells angular-rounded, irregularly arranged. *Perithecia* young lens-shaped, mature ones lens-shaped to hemispherical, (0.35-)0.5-0.8 mm diam., with dense cushions of soft hairs. *Ascospores* 7-septate (“*virescens*” form) or irregularly 7-11(-15)-septate (“*multiseptata*” form), oblong to bacillar, 45-75 × 4-7 μm, × 10-12 times as long as broad (Fig. 4E-F).

Notes: *Porina virescens* is easily recognized by the dense cushions of soft hairs covering the perithecia and the adjacent thallus. The ascospores of this species are usually 7-septate. A form with more numerous septa has been described and accepted as *P. multiseptata* (Santesson 1952). We have seen several specimens and came to the conclusion that this form is more appropriately treated as a genetic modification of *P. virescens* not deserving taxonomic recognition, similar to the situation encountered in *P. guianensis*. The ascospores of the “*multiseptata*” form are of similar size range as those of typical *P. virescens*, and their septation is irregular, with 7-septate and up to 11(-15)-septate spores found in the same hymenium. Furthermore, both forms have the same distribution and often occur intermingled, with no ecomorphological differentiation. As in *P. guianensis*, they probably represent early stages of speciation.

#### Distribution and ecology

Known throughout Australasia, abundant in lowland to lower montane rain forests.

Additional specimens examined (“*virescens*” form)

AUSTRALASIA: VIETNAM: Tonkin, Ngoikoden Valley, 150 m, 1914, *Handel-Mazzetti 1168* (UPS). — SRI LANKA: Sabaragamuwe, Doluluwa Forest, 750 m, 11.1976, *Faden s.n.* (herb. Vězda). — INDONESIA: Java, Tjibodas, Primeval forest, 1898, *Nyman 3b* (UPS, filed under *P.*



*epiphylla*); Sumatra, Pisopiso, Lake Toba, 1200 m, 1926, *Palm 25e, 31* (UPS, ex Magn.). — MALAYSIA: Sabah, Kinabalu National Park, 06°05'N, 116°35'E, 1650 m, mossy oak forest, 5.1989, *Sipman & Tan 29469* (B); *ibid.*, Poring Hot Springs area, 06°05'N, 116°35'E, 750 m, tall forest, 5.1989, *Sipman & Tan 29574* (B). — PHILIPPINES: North Luzon, Kalinga-Apayao, 150 m, dense rain forest, 8.1983, *Kalb & Schrögl s.n.* (B); Palawan: Palawan Isl., Aborlan, 30-600 m, disturbed forest, 4.1992, *Tan 92-280h* (B); *ibid.*, Balabac Isl., Indalawan Sitio, 200 m, disturbed lowland forest, 4.1993, *Tan 93-235* (B); Luzon, Laguna, Los Banos, Mt. Makiling, 250 m, 1.1977, *Gruezo 2479* (herb. Vězda, filed under *P. atriceps*). — PAPUA NEW GUINEA: Madang, Wasabamal logging area, 04°50'S, 145°45'E, 25 m, logging area in lowland rain forest, 2.1987, *Sipman 24152* (B); *ibid.*, Balek Wildlife Reserve, 05°18'S, 145°43'E, 20 m, lowland rain forest, 3.1987, *Sipman 24287* (B); *ibid.*, Bunapas Mission, 04°13' S, 144°41'E, sea level, 2.1980, *Demoulin & Smeets 5915* (herb. Lücking); Morobe, Busom valley, 06°34'S, 146°58'E, 600 m, lowland rain forest, 3.1987, *Sipman 24539* (B); Central Province: Varirata National Park, 09°27'S, 147°22'E, 800 m, 3.1987, *Sipman 22428* (B). — AUSTRALIA: Queensland, Kurunda, 16°49'S, 145°38'E, 350 m, rain forest remnant, 3.1988, *Aptroot & Aptroot 22725* (B); *ibid.*, Bellenden Ker National Park, 17°20'S, 145°52'E, 50 m, rain forest, 3.1988, *Aptroot & Aptroot 22445d* (B); Atherton Tableland, 9.1983, *Henssen 29352* (herb. Lücking). (“multiseptata”-form): AUSTRALASIA: INDONESIA: Sumatra, Oostkust, Besitang, 30 m, 1926, *Palm 17e* (UPS, ex Magn.). — PAPUA NEW GUINEA: s.loc., 1875, *Naumann s.n.* (G). — AUSTRALIA: Atherton Tableland, 9.1983, *Henssen 29352* (herb. Henssen, herb. Lücking).

## Conclusions

In terms of species richness and abundance, the *Porina epiphylla* group is one of the most important groups of foliicolous lichens. It is also one of the most difficult with regard to species identification. In the present paper, we have tried to give a taxonomic survey and, although our results and conclusions are based on abundant worldwide material, much more remains to be done. In particular, some problems cannot be clarified without careful study of non-foliicolous species.

Of the 31 taxa treated in this survey (Fig. 8), *Porina distans* is most probably a synonym of another, isidia-producing species and thus far covers sterile forms of different taxa. Six species are probably mainly corticolous and rarely found on leaves: *P. conspersa*, *P. exasperatula*, *P. nucula*, *P. rudiusscula*, *P. tetracerae*, and *P. verruculosa*. Of the remaining 24 taxa, three species are quite restricted: *P. foliicola*, *P. longispora*, and *P. pocsii*. Three other species can be considered “microspecies”; two of them, *P. minutissima* and *P. lucida* var. *lucida*, are close to *P. epiphylla* and separated by variational discontinuities in quantitative measurements, while *P. follmanniana* is not very well separated from *P. radiata*. This leaves 18 well circumscribed, typically foliicolous taxa.

Contrary to the wide distribution of many foliicolous lichens (Lücking 1997), the *Porina epiphylla* group exhibits distinct distribution patterns (Tab. 1). Thus, the number of species to be expected in any tropical region is about 10-12, or 30-40 % of the total diversity. Besides the pantropical *P. epiphylla*, *P. imitatrix*, *P. lucida* var. *lucida*, and *P. mirabilis*, tropical America is characterized by the abundance of *P. atropunctata*, *P. curtula*, *P. guianensis*, *P. radiata*, and *P. subepiphylla*, accompanied by *P. andreana* and *P. atriceps*. Tropical Africa is dominated by pantropical taxa, while other species, like *P. albicera*, *P. conica*, *P. epiphyllodes*, *P. follmanniana*, *P. imitatrix*, *P. mazosioides*, *P. radiata*, and *P. tetracerae*, are comparatively rare. Apart from the pantropical species, in tropical Asia *P. albicera*, *P. atriceps*, *P. conica*, and *P. vire-scens* abound, while *P. atropunctata* and *P. minutissima* are rare. Tropical Australia is similar but differs in the presence of *P. lucida* var. *australiensis* and *P. similis*.

That the species of the *P. epiphyllodes* subgroup are restricted to tropical America and Africa is remarkable, especially as the *P. epiphylla* group as a whole seems to be most diverse in tropical

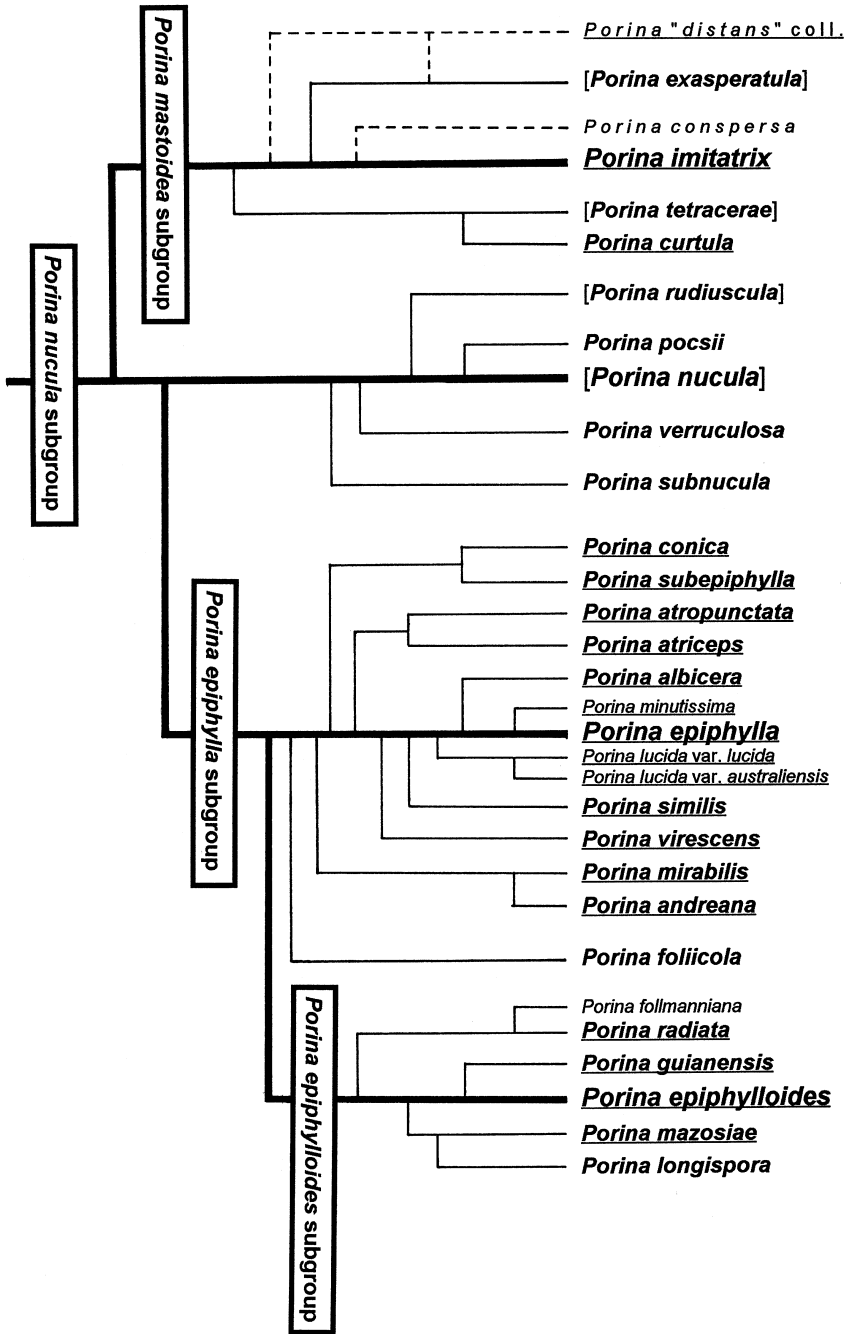


Fig. 8. Proposed subdivisions and empirical relationships in foliicolous species of the *Porina epiphylla* group. The *P. nucula* and *P. mastoidea* subgroup are incomplete since they are mainly formed by non-foliicolous species. Species in brackets [ ] are facultatively foliicolous, those underlined are common foliicolous taxa. *P. distans* and *P. conspersa* are uncertain in their biological status, while *P. minutissima*, *P. lucida* and *P. follmanniana* are considered “microspecies”.

Australasia. Obviously, there is a biogeographical separation between tropical America and Africa on one hand and tropical Asia and Australia on the other, with Africa also taking an intermediate position between America and Asia. This pattern is also obvious in other species of *Porina* and in foliicolous lichens in general (Farkas & Sipman 1997, Lücking & al. 1998).

The *Porina epiphylla* group can be divided into four entities: the *P. mastoidea*, the *P. nucula*, the *P. epiphylla*, and the *P. epiphylloides* subgroups (Fig. 8). Species of the *P. mastoidea* subgroup are characterized by a rather well-developed, nitidous, smooth thallus with dark prothallus and *Trentepohlia* as phycobiont, mostly large ascospores with a gelatinous sheath and the tendency towards muriform septation, and the frequent formation of isidiate thallus outgrowths. This group, which includes *Clathroporina eminentior* and its allies, is characteristic of the shaded understorey of humid tropical lowland forests and most commonly found on smooth bark. Its most typical foliicolous representative is *P. imitatrix*. The *P. nucula* subgroup is in many respects (ascospore variation!) similar to the preceding subgroup but differs in the absence of a dark prothallus, and the thallus is usually matt and provided with numerous crystalline verrucae. The species are more common in open situations, in drier habitats and in subtropical regions. There is no typical foliicolous representative but *P. nucula* itself is sometimes found on leaves.

The *Porina epiphylla* subgroup is entirely restricted to leaves. It is mainly characterized by a switch towards *Phycopeltis* as phycobiont and the narrower, elongate ascospores without gelatinous sheath. Most species are restricted to the shaded understorey of humid tropical lowland forests. *P. lucida* var. *lucida* and *P. virescens* extend into the lower montane forest belt. *P. atriceps* and *P. atropunctata* are particularly abundant in coastal or insular areas with high precipitation. *P. epiphylla* itself extends into evergreen dry forests. The only species which is also found in more open situations is *P. subepiphylla*. The lack of ecological diversification, which results in sympatric co-occurrence of closely related species, is also known in genera like *Mazosia* (Lücking & Matzer 1996).

Finally, in the *P. epiphylloides* group, the thallus exhibits a differentiation towards crystalline verrucae or ridges, while between these structures it lacks crystals, and the phycobiont maintains its original radiating cell arrangement. Some species in this group seem to prefer montane rain forests.

The successful colonization of the foliicolous habitat occurred several times in the *Porina epiphylla* group: two or more times in the *P. mastoidea* subgroup, e.g. in the distantly related *P. imitatrix* and *P. curtula*, and probably once in the *P. epiphylla* subgroup. The ancestor of the latter is unclear. While thallus characters suggest this subgroup to be derived from the *P. nucula* subgroup, its ecology is more similar to that of the *P. mastoidea* subgroup, which is also more successful in colonizing living leaves than the *P. nucula* subgroup. However, there might have been a very early evolution towards the foliicolous habitat in the *P. nucula* subgroup, resulting in the *P. epiphylla* subgroup, which reached its actual diversity through subsequent adaptive radiation. The *P. mastoidea* subgroup has probably evolved independently and, after conquering the understorey of humid tropical forests, some species secondarily extended into the foliicolous habitat. The *P. epiphylloides* subgroup is certainly derived from foliicolous representatives of the *P. epiphylla* subgroup. The reduced thallus morphology is a general phenomenon in foliicolous lichens growing in the shaded forest understorey, and the very restricted distribution patterns of this group suggest a young phylogenetic age. It must be pointed out that this group is not necessarily monophyletic, although with the species presently referred to it appears rather homogeneous.

Based on non-foliicolous collections, Harris (1995) separated the *Porina mastoidea* and *P. nucula* subgroups and accommodated them in the genera *Clathroporina* and *Porina* s.str., respectively. This separation was not accepted by McCarthy & Malcolm (1997), because of the numerous intermediate forms between these and other genera proposed by Hafellner & Kalb (1995) and Harris (1995). Our own observations confirm the statements of Harris (1995), but we follow McCarthy & Malcolm (1997) not recognizing them at generic level, not because of intergradations but because they seem too narrowly defined to receive generic status. For such cases, subgeneric divisions, almost unexplored in lichen systematics, are certainly appropriate.

Tab. 1. Distribution of foliicolous taxa in the *Porina epiphylla* group. Same arrangement as in Fig. 8; +++ = frequent, ++ = moderately common, + = rare. Statements in brackets [ ] indicate corticolous collections of facultatively foliicolous species.

Species	America	Africa	Asia	Australia
<b><i>Porina mastoidea</i> subgroup:</b>				
<i>P. "distans" coll.</i>	++	+	+	+
<i>P. exasperatula</i>	+			
<i>P. conspersa</i>	[+]	+		
<i>P. imitatrix</i>	+	+	+	
<i>P. tetracerae</i>	[++]	[+]	+	[+]
<i>P. curtula</i>	+++			
<b><i>Porina nucula</i> subgroup:</b>				
<i>P. rudiusscula</i>	+			
<i>P. pocsii</i>	+			[+]
<i>P. nucula</i>	+	[+]	+	[+]
<i>P. verruculosa</i>	+			
<i>P. subnucula</i>		+		+
<b><i>Porina epiphylla</i> subgroup:</b>				
<i>P. conica</i>		+	+++	+
<i>P. subepiphylla</i>	+++			
<i>P. atropunctata</i>	+++			
<i>P. atriceps</i>	+		+++	+
<i>P. albicera</i>		+	+	+
<i>P. minutissima</i>			+	+
<i>P. epiphylla</i>	+++	+++	+++	+++
<i>P. lucida</i> var. <i>lucida</i>	+++	+	+++	+
<i>P. lucida</i> var. <i>australiensis</i>				+
<i>P. similis</i>				+
<i>P. virescens</i>			+++	+
<i>P. mirabilis</i>	+++	+	+	+
<i>P. andreana</i>	+			
<i>P. foliicola</i>			+	
<b><i>Porina epiphylloides</i> subgroup:</b>				
<i>P. follmanniana</i>		+		
<i>P. radiata</i>	+++	+		
<i>P. guianensis</i>	+			
<i>P. epiphylloides</i>		+		
<i>P. mazosioides</i>		+		
<i>P. longispora</i>		+		

Judging from our own observations and the statements of Aptroot & Sipman (1993), Harris (1995), and McCarthy & Malcolm (1997), there seem to be great differences in foliicolous and non-foliicolous species (and specimens) of *Porina* as to their variation of thallus and ascospore characters. This is probably the main reason for the general disagreement on taxonomic and systematic concepts in the Trichotheliaceae. However, the discrepancy between foliicolous and non-foliicolous taxa is not a feature inherent to the Trichotheliaceae neither an artifact caused

by different workers, but probably explained by the following observation: Lichens are plastic, and the final appearance of a lichen thallus with all its characters is the result of interaction between genetic potential and environmental factors. The less the environmental influence, the more genetic potential will be expressed. In crustose lichens, thallus anatomy and surface structure depend to a large extent on the substrate. Saxicolous lichens are particularly variable due to the incorporation of substrate material into the thallus. In corticolous lichens, the thallus surface often reflects the structure of the bark. In foliicolous lichens, we have the other extreme: an influence of the substrate is practically absent. Characters such as verrucae or a prothallus are thus quite easily observed while in corticolous or saxicolous specimens they are not, which does not mean that they are not potentially present. Thus, foliicolous lichens are rather close to the genetic potential of a species and therefore appear more constant than non-foliicolous populations, as exemplified by *P. nucula*; this allows a narrower species concept as when based on non-foliicolous material alone.

This problem is particularly obvious in the genus *Porina*, where we have a large diversity of foliicolous, corticolous, and saxicolous taxa. Species switching between substrates, such as *P. nucula*, exhibit different magnitudes of thallus variation, with the effect that species concepts might not reflect natural entities but collective species, which secondarily exhibit a rather large “ascospore variation”. This problem can only be solved by cultivation of specimens from different substrates, which in practice is difficult, if not impossible, and beyond of the scope of any taxonomic treatment. On the other hand, these difficulties should not prevent from (sub)generic divisions, considering that saxicolous specimens cannot be taken as a rule for character variation but are rather the exception.

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