

Studies in lichenology with emphasis on chemotaxonomy, geography and phytochemistry
Festschrift Ch. Leuckert
Eds: Knoph, J.-G., Schriftner, K. & Sipman, H. J. M. — *Bibliotheca Lichenologica* 57: 161 — 186.
J. Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin-Stuttgart, 1995.

Studies in Trichotheliales *ordo novus*

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Abstract: The type species of the genera placed in the Trichotheliaceae in the most recent "Systema Ascomycetum" are revised. The family Trichotheliaceae is excluded from the Pyrenulales and placed in the new order Trichotheliales. The following genera of Trichotheliaceae are accepted and keyed: *Clathroporina*, *Porina*, *Pseudosagedia*, *Trichothelium* and *Zamenhofia*. *Pseudosagedia* subgen. *Pseudosagedia* is resurrected for the *Porina aenea* and *Porina nitidula* groups and *Pseudosagedia* subgen. *Limosagedia* is introduced for the *Porina linearis* group. *Arthopyrenia carpinea* is chosen as lectotype for *Arthopyrenia* sect. *Pseudosagedia*. Much attention is paid to acetone insoluble pigments in the perithecial walls. Besides BACHMANN's *Sagedia*-red and *Segestria*-brown, the pigments *Porina*-yellow and *Pseudosagedia*-violet are defined. The following new combinations are proposed: *Porina rubescens*, *Pseudosagedia aenea*, *P. atrocoerulea*, *P. boreri*, *P. byssophila*, *P. chlorotica*, *P. corruscans*, *P. curnowii*, *P. ginzbergeri*, *P. grandis*, *P. guentheri*, *P. impressa*, *P. interjungens*, *P. laticarpa*, *P. linearis*, *P. nitidula*, *P. obsoleta*, *P. oleriana*, *P. papillifera*, *P. rapaeformis*, *P. thaxteri*, *P. umbilicata*, *P. whinrayi* and *Strigula subsimplicans*. The terms crystallostratum, crystallocumuli and aeroclini are introduced to describe thallus structures of certain tropical crustose lichens.

Zusammenfassung: Die Typusarten der Gattungen, die im neuesten "Systema Ascomycetum" unter der Familie Trichotheliaceae genannt sind, werden revidiert. Diese Familie wird aus den Pyrenulales ausgliedert und in die neue Ordnung Trichotheliales gestellt. Sie umfaßt derzeit folgende Gattungen, die geschlüsselt sind: *Clathro-*

porina, *Porina*, *Pseudosagedia*, *Trichothelium* und *Zamenhofia*. *Pseudosagedia* subgen. *Limosagedia* umfaßt die *Porina linearis* Gruppe und *Pseudosagedia* subgen. *Pseudosagedia* die Arten aus der Verwandtschaft von *Porina aenea* und *Porina nitidula*. *Arthopyrenia carpinea* wird als Lectotypus für *Arthopyrenia* sect. *Pseudosagedia* ausgewählt. Große systematische Bedeutung wird den in Aceton unlöslichen Pigmenten in den Perithecienvänden beigemessen. Neben BACHMANN's Sagediarot und Segestriabrunn werden die Pigmente Porinagelb und Pseudosagediaviolett definiert. Folgende Neukombinationen werden vorgeschlagen: *Porina rubescens*, *Pseudosagedia aenea*, *P. atrocoerulea*, *P. borrieri*, *P. byssophila*, *P. chlorotica*, *P. corruscans*, *P. curnowii*, *P. ginzbergeri*, *P. grandis*, *P. guentheri*, *P. impressa*, *P. interjungens*, *P. laticarpa*, *P. linearis*, *P. nitidula*, *P. obsoleta*, *P. oleriana*, *P. papillifera*, *P. rapaeformis*, *P. thaxteri*, *P. umbilicata*, *P. whinrayi* und *Strigula subsimplicans*. Die Begriffe Kristallostratum, Kristallocumuli und Aeroclivien werden eingeführt, um Thallusstrukturen tropischer Krustenflechten zu kennzeichnen.

Introduction

Porina nom. cons. is one of the large genera of lichenized fungi. Because of species richness and of previous confusion with verrucose *Pertusaria* species, taxonomy and nomenclature is very complicated. Stability was achieved by conserving *Porina* Müll.Arg. over some earlier synonyms, following a proposal made by SANTESSON (1952).

Several attempts have been made to define smaller natural entities (MÜLLER ARGOVIENSIS 1883, BACHMANN 1929, VAINIO 1921, 1923, SCHILLING 1927, ZAHLBRUCKNER 1926). More information on these mostly subgeneric taxa can be read in SANTESSON (1952: 200 ff.) who wrote a detailed account on the history of *Porina*.

In recent times, although some important contributions to the knowledge of *Porina* have been made (SWINSCOW 1962, HARRIS 1975, POELT & VĚZDA 1977, LÜCKING 1991, McCARTHY 1993, McCARTHY & KANTVILAS 1993, APTROOT & SIPMAN 1994, UPRETI 1994), infrageneric classification has been little used.

Porina is placed in the family Trichotheliaceae (SCHILLING 1927). The group was originally proposed as a monotypic subtribe by MÜLLER ARGOVIENSIS (1885). In the most recent outline of Systema Ascomycetum (ERIKSSON & HAWKSWORTH 1993), the family is listed in the order Pyrenulales and seven genera are accepted. The inclusion in Pyrenulales seemed to be justified, because the *Trichothelium*-type ascus was thought to have directly evolved from clearly fissitunicate asci (JANEX-FAVRE 1971). HARRIS (1975) did not agree with JANEX-FAVRE in the interpretation of structural details of the ascus tip, but confirmed the presence of an external ring structure. Both, HARRIS (1975) and

ERIKSSON (1981) argued that the *Trichothelium*-type ascus is functionally unicellular. HARRIS (*loc. cit.*) saw similarities with the *Nectria*-type ascus, but ERIKSSON disagreed with this opinion.

For a long time, *Porina* was also confused with genera of Strigulaceae, e. g. *Phylloporis* (*i. e.* the former *Porina phyllogena* group), *Strigula* (the former *Porina affinis* group).

The survey presented here was undertaken mainly for two reasons. Firstly to point out clearly the heterogeneity of the Pyrenulales as accepted in ERIKSSON and HAWKSWORTH (1993) and secondly to apply a familiar concept derived from the investigation of the type-species *Trichothelium epiphyllum* to the genera, mentioned in this outline (ERIKSSON & HAWKSWORTH 1993: 113).

Material and methods

For this study, air dried herbarium specimens of the species cited below (under specimens investigated) have been used. External morphology was studied with a dissecting microscope (WILD M3, 6,4x-40x), anatomical studies of the thallus and the ascomata were carried out using a light microscope (REICHERT POLYVAR, 40x-1000x). Sectioning was performed with a freezing microtome (LEITZ, thickness of sections 12-15 µm) but squash preparations were also used especially for ascus analysis. Preparations were mounted in water. Where necessary, contrasting was performed by pretreatment with lactic acid-cotton blue (MERCK 13741). Chitinoid ring structures of ascus tips were stained with Congo Red (SIGMA C-6767). Sections and squash preparations were not pre-treated with KOH. Measurements refer to dimensions in ordinary water. Many species were screened by TLC (CULBERSON 1972, CULBERSON & AMMANN 1979, with improvements proposed by CULBERSON & JOHNSON 1982) to search for lichen substances.

Results and discussion

Characters

Thallus: All known Trichotheliaceae have a crustose, non-areolate thallus organisation with a rather simple anatomy as seen in sections. Usually the thallus is developed as an episubstratal crust, but among the corticolous and calcicolous species there are a few examples of a more or less complete endo-substratal thallus development (*e. g.* *Pseudosagedia linearis*). More or less distinct cortical layers (Fig. 1) are often found in tropical Trichotheliaceae where also large oxalate crystals embedded in the thallus are common. These oxalate crystals are arranged in two different ways causing different external appearances. They may form a continuous layer, for which the term "crystallostratum" is introduced here (Fig. 1). Such thalli have a smooth surface which may even be shiny (*desquamescens*-type). In many other species, however, the oxalate crystals are deposited in punctiform or elongate agglomera-

tions (crystallocumuli), which are dispersed over the whole thallus (Figs. 2, 3). These crustose thalli look minutely warted or ridged (*simulans*-type).

Thalli with small warts or ridges containing oxalate crystals or large amounts of lichen substances occur in a wide range of tropical lichens (e. g. *Porina simulans*, *Mazosia rubropunctata*, *Echinoplaca leucotrichoides*, *Calenia solarioides*, *Lecidea amazonica*, *Chroodiscus mirificus*). These minute protuberances are interpreted as an adaptation to humid climatic conditions. They prevent the thalli from getting completely soaked because the content of these structures is hydrophobic either by their crystalline structure or by chemical properties. Therefore, the morphological term "aeroclivi" (engl. aeroclives, germ. Aerocliven) is introduced here.

In Trichotheliaceae the mentioned thallus types are not correlated with other taxonomically relevant characters but seem to be useful at species level. In *Porina* species of temperate regions the thin overlying hyphal layer may be eroded so that the algal cells reach the thallus surface. The thallus of some *Porina* species is covered by free hyphae, resulting in a pilose appearance.

The photobiont of epiphyllous species is usually *Phycopeltis*, while the species growing on other substrata usually have other members of Trentepohliales. The occurrence of *Phycopeltis* instead of *Trentepohlia* coll. in foliicolous species is of no taxonomic significance, however, and can be observed in several other genera (e. g. *Chroodiscus*, *Enterographa*). Therefore, taxa based only on the presence or absence of *Phycopeltis*, have not been accepted in recent years (SANTESSON 1952).

Several species of Trichotheliaceae are able to produce isidia. Until now this capability is known in a few corticolous species of *Porina* where it seems not to be confined to one of the two thallus types mentioned above, and some foliicolous ones (e. g. *P. fusca*). Isidia are also known in *Clathroporina* (APTROOT & SIPMAN 1994: 12) and they are characteristic of all *Zamenhofia* species (see under *Zamenhofia*). Therefore, it is obvious that the genus *Zamenhofia* is not definable by the presence of isidia alone (COPPINS *et al.* 1992: 368).

Ascomata: The ascomata of *Porina* have been investigated thoroughly by JANEX-FAVRE (1971). They are true perithecia and different types can be distinguished. The perithecia are always partly or completely surrounded by an involucellum and are either naked or more or less covered by a thalline layer. As in the thallus, oxalate crystals may be present which are normally deposited in the thalline envelope. Presence or absence of a thallus layer upon the ascocarps has been used as a character at section level (e. g. ZAHLBRUCKNER 1926), but in our opinion an infrageneric classification based solely on this, does not lead to a natural arrangement (see also SANTESSON 1952: 201).

As it has been pointed out by several authors (MASSALONGO 1852, MÜLLER ARGOVIENSIS 1883, MALME 1929, SANTESSON 1952, SWINSCOW 1962) before, the nature of hyphal pigments deposited in the involucellum and partly in the peridium is a highly stable character. For characterisation of these pigments,

called *Porina*-yellow, *Pseudosagedia*-violet, *Sagedia*-red and *Segestria*-brown, see under chemistry further below. Under the dissecting microscope, the perithecia may be either yellowish to orange or black. A covering by a thalline layer is much more common in genera having *Porina*-yellow pigments in the perithecia. These pigments may even penetrate into algal cells found on the outside of the fruiting bodies (e. g. *Porina rufula*). The upper part of the perithecia of *Trichothelium* is provided with stiff setae composed of agglutinated hyphae. Similar structures are known in *Porina*. A tomentose cover may occur on the black perithecia of some Trichotheliaceae.

Commonly the perithecia are globose; lens-shaped perithecia are frequent among foliicolous species and are regarded as a kind of adaptation to the habitat. Depending on the substratum the perithecia can be sessile or immersed, but in some cases, this may also be a character at species level.

Hamathecium: Interascal unbranched filaments are always present in the perithecia. Commonly they are considered to be paraphyses. At least in mature ascomata, they are apically not attached to the peridial wall. In species of *Zamenhofia* and several species of *Clathroporina* a distinct persistent crown of periphyses can be observed. Distinct periphyses are also reported in *Porina ulceratula* by MCCARTHY (1993). However, short periphyses are also present at certain stages of development in all other Trichotheliaceae so far investigated, at least in the pore-region of the peridial wall. This type of short periphyses has also been observed by MCCARTHY (1993: 17).

Ascus: The *Trichothelium*-type ascus shows some peculiarities so far not observed in other groups of Ascomycotina. It is functionally unitunicate, has a truncate apical tip and is there provided with a chitinoid ring-structure incorporated in the outer part of the ascus wall. This ring-structure is neither externally nor internally protruding over the wall-surface and can be seen in LM as two black or bright dots (red, when stained with Congo Red), depending on the focus. (Figs. 7, 9, 11, 13). The asci open at dehiscence with an apical pore (Figs. 14, 15). In several species, especially in those with large ascospores, this ring-structure is partly reduced and may be visible only in young asci still having non-septate ascospores (Fig. 4). Only in two genera of Trichotheliaceae, the construction of the ascus wall shows some differences. In *Clathroporina*, (e. g. *C. olivacea*) the shape of the apical region of the ascus is different and no ring-structure could be observed. The *Clathroporina* ascus is slightly constricted in the subapical region (30-50 µm below apex) and the part above has an almost cone-like shape (Figs. 16-19, 22-24, 26). The typical shape of the ascus may be obscured by the internal pressure of mature ascospores (Figs. 21, 25, 27). Therefore, asci containing spore primordia should be studied. Because of the similarities in many other characters, these differences are interpreted as results of different functional needs in species having large ascospores with significantly lower length/width ratios. Ascii of *Zamenhofia* species still have a truncate apex, but we failed to observe the chitinoid ring (Fig. 12). *Zamenhofia*

is retained in Trichotheliaceae with some doubts. Thus the observations of HARRIS (1975) are fully confirmed.

Spores: Spores of Trichotheliaceae are hyaline and septate. Septation varies from three transverse septa to muriform. Reports of species with only one-septate spores (*Dichoporus schizospora* (Vain.) Clem. and *Diporina subsimplicans* (Nyl.) Clem.) proved to be erroneous because both species belong to *Strigula* (see excluded genera). Longitudinal septa are characteristic but not restricted to *Clathroporina*. Also in *Trichothelium* and *Pseudosagedia* species with (sub-)muriform spores are known (e. g. *Pseudosagedia interjungens*). So far, no dictyosporous *Porina* species are known. Species with submuriform spores, referred to *Porina* by MCCARTHY (1993) either belong to *Clathroporina* (*C. ocellata* and *C. sagedioides*) or to *Pseudosagedia* (*P. whinrayi*).

The presence of a perisporeal sheath is a characteristic feature of Trichotheliaceae ascospores (Figs. 6, 20). The thickness, however, varies greatly - even between closely related species. In quite a number of species, mature ascospores show no perispore at all in LM, but also in these cases it can be observed in premature ascospores still enclosed in the ascus. In late stages of spore ontogeny, the perispore may be highly condensed so as to look like a thick external wall layer (e. g. *Porina mastoidea*, *Clathroporina olivacea*).

Chemistry: The TLC of quite a number of different Trichotheliaceae revealed no secondary lichen products, and, so far, only few exceptions are known. However, *Clathroporina enteroxantha* produces an anthrachinone in the medulla (APTROOT & SIPMAN 1994: 12), replacing oxalate crystals, and this may be an adaptation to a very humid microclimate. Large oxalate crystals are common in many *Porina* and *Clathroporina* species and may also be present in other genera of the family. Such crystals are very common, both in the thallus and in the outer peridial wall. Concerning patterns of distribution of oxalate within the thallus, see further above.

Four hyphal pigments, not soluble in acetone, are known: *Porina*-yellow, *Pseudosagedia*-violet, *Sagedia*-red and *Segestria*-brown. Additional information on these pigments is given in Tab. 1.

Substrata: Trichotheliaceae occur on a wide range of different substrata, but are especially well represented on bark, acid rock and leaves. The foliicolous habitat was used to define the genus *Phylloporina*, which is here regarded as a heterogenous assemblage of species.

Distribution: Trichotheliaceae are distributed over all phytogeographical regions, but are best represented from the tropics to the oceanic extratropics. Only a few species are present in dry areas of the world. In the Holarctis different members of the family occur from sea level up to the alpine zone (e. g. *Porina mammillosa*).

Tab. 1. Colour-reactions of acetone insoluble perithecial hyphal pigments in Trichotheliales

Pigment	natural colour	colour in KOH	colour in H ₂ SO ₄	colour in HNO ₃	selected species
<i>Porina</i> -yellow	yellow to orange-red	intensifying to reddish-brown	light orange to brownish red	bright orange to reddish brown	<i>P. macula</i> , <i>P. epiphylla</i> , <i>P. lectissima</i> (outer part of involucellum), <i>P. rufila</i> , <i>P. mammillosa</i> (inner peridial wall)
<i>Pseudosagedia</i> -violet	dull brown to blackish with purple to violet tinge	darkening, purple to violet tinge disappearing	reddish brown	reddish brown	<i>P. aenea</i> , <i>P. chlorotica</i> , <i>P. mitchula</i> , <i>P. impressa</i> , <i>Trichothelium epiphyllum</i>
Sagedia-red (BACHMANN 1890: 34)	purple-red to dark violet	blue, then blackish	dark red	dark red	<i>P. mammillosa</i> (outer peridial wall) <i>P. linearis</i> (outer perithecial wall)
Segestria-brown (BACHMANN 1890: 34)	brownish	pale with pinkish tinge	violet	pale with violet tinge	<i>P. lectissima</i> (thallus and inner part of involucellum)

Taxonomical consequences

As members of Trichotheliaceae share a set of characters neither occurring in Pyrenulales nor in any other existing order, a new one is introduced here.

Trichotheliales Hafellner & Kalb *ordo novus*

Ascomycetes lichenisati; ascomata perithecia solitaria sunt; hamathecium bene evolutum; paraphyses simplices et periphyses plusminusve distinctae; ascii unitunicati, anulo chitinoideo instructi, rarius reducti, ascospores hyalinae, septatae.

Familia typica et adhuc unica: Trichotheliaceae (Müll.Arg.) Bitter & F.Schill.

Bas.: Tribus Pyrenuleae subtribus Trichothelieae Müll.Arg.

Lichenized ascomycetes, photobiont as far as known are trentepohlian algae. Ascomata solitary, perithecia with apical pore, perithecial wall thin, soft, naked or covered either by thallus or an involucellum, encrusted with acetone-insoluble pigments. Hamathecium well developed, consisting of unbranched paraphyses and more or less distinct periphyses. Ascii unitunicate, more or less cylindrical with truncate or obconical apex. A chitinoid ring structure on the outside of the ascus wall is commonly present but may be reduced. Ascii opening at maturity with an apical pore. Ascospores hyaline, phragmospored to muriform, perispore prominent to almost invisible in LM.

The differences between Trichotheliales and Pyrenulales of which the former are separated here, are summarized in Tab. 2. A broader concept is adopted by BARR (1979, 1990a), who included *Pyrenula* and related genera in Melanomatales, and this was followed by HARRIS (1989) and APTROOT (1991).

Furthermore the Trichotheliales differs from the non-lichenized Calosphaeraiales, Diaportales, Diatrypales, Hypocreales, Phyllachorales, Sordariales, Trichosphaeraiales and Xylariales by the unique position of the chitinoid ring structure. In all the mentioned orders but the Trichotheliales, ring structures, if present, are situated within or on the inner side of the ascus wall (BARR 1983, 1990b; HAWKSWORTH & ERIKSSON 1986). Almost external apical structures but of very different shape are found in the parasitic Clavicipitales. HARRIS (1975) saw similarities with the Hypocreales, but this was denied by ERIKSSON (1981).

Tab. 2. Differentiating characters of Trichotheliales and Pyrenulales

Character	Trichotheliales	Pyrenulales
hamathecial elements	unbranched paraphyses and periphyses; the latter often rudimentary	richly branched or unbranched, of different origin (ERIKSSON 1981, APTROOT 1991, HARRIS 1986, 1989)
ascus wall	one functional wall layer	two functional wall layers
apical structures	with external chitinoid ring structure, rarely reduced	without ring structures inner wall layer commonly with ocular chambers of different shape
ascus dehiscence	poroid	fissitunicate or degenerating
ascospores	hyaline, with thin septa	hyaline or pigmented, with internal wall thickenings
perithecial wall	encrusted with certain pigments (see Tab. 1)	with other pigments

Key to genera

- 1a Perithecia with a crown of stiff setae *Trichothelium*
- 1b Perithecia without stiff setae but small warts, loose hyphae, soft setae or isidia may be present 2
- 2a Perithecial wall at least partly with yellow to orange pigments, K+ orange-red 3
- 2b Perithecial wall without such pigments 4
- 3a Ascii of *Porina*-type *Porina*
- 3b Ascii without external chitinoid ring structure and with subapical constriction *Clathroporina*
- 4a Ascii without external chitinoid ring structure *Zamenhofia*
- 4b Ascii of *Porina*-type 5
- 5a Inner perithecial wall (peridium) with blackish-violet pigments (*Pseudosagedia*-violet), pigments of outer perithecial wall (involucellum) never K+ blue *Pseudosagedia* subgen. *Pseudosagedia*
- 5b Inner perithecial wall pale, outer perithecial wall at least externally K+ blue *Pseudosagedia* subgen. *Limosagedia*

Outline of accepted genera of Trichotheliaceae

Clathroporina Müll.Arg.

Flora 65: 517 (1882).

Typus generis: *Clathroporina olivacea* (lectotype, selected by JØRGENSEN et al. 1983: 53).

The genus *Clathroporina*, separated from *Porina* by MÜLLER ARGOVIENSIS (*l.c.*) basically on muriform ascospores, is kept here as distinct genus because of structural differences in the ascus tips (see above, and Figs. 16-19, 22-27). Of special interest is *Clathroporina ocellata*, occurring in the Southern hemisphere, with submuriform ascospores. The external appearance is quite similar to *Porina nucula* but the structure of the ascus wall is exactly as in *Clathroporina olivacea*. The presence of the perithecial pigment *Porina*-yellow shows the close relationship to *Porina* s. str. The genus seems to have a centre of radiation in Australasia but is present in other tropical areas, too.

Porina Müll.Arg. *nom. cons.*

Flora 66: 320 (1883).

Typus generis: *Porina nucula* Ach. (type)

= *Cryptopeltis* Rehm 1906.

Typus generis: *Cryptopeltis obtecta* (Rehm) Rehm (lectotype selected by SANTESSON 1952: 199) = *Porina epiphylla* (*fide* SANTESSON).

Phylloporina (Müll.Arg.) Müll.Arg. 1890.

Typus generis: *Phylloporina epiphylla* (Fée) Müll.Arg. (lectotype selected by SANTESSON 1952: 199).

Porophora Sprengel is cited as a further synonym of *Porina* by ERIKSSON and HAWKSWORTH (1993). However, SPRENGEL (1827: 241) clearly refers to *Porophora* Meyer (MEYER 1825: 326). No *Porina* species is mentioned in the protologue but *Pertusaria* species and *Ascidium* Fée is cited as synonym. As the latter genus is described as monotypic with the only species *Ascidium cinchonarum* Fée, *Porophora* Meyer is an illegitimate, superfluous name for *Ascidium* Fée.

Ophthalmidium Eschw. and *Segestria* Fr. are rejected names against *Porina* Müll.Arg. *nom. cons.* *Segestrella* Fr. and *Sphaeromphale* Reichenb. are superfluous names for *Segestria* Fr.

Notes: (1) SANTESSON (1952) arranged the foliicolous *Porina* species in five different groups. For the *Porina phyllogena* group the generic name *Phylloporis* is available and it belongs to Strigulaceae. The remaining species groups - as far as their members have been checked - belong to Trichotheliaceae. In the *Porina nitidula* group perithecial pigments of the *Pseudosagedia*-violet-type are common. These species are transferred here to *Pseudosagedia* (see below). Following SANTESSON (1952) the *P. epiphylla*- and *P. rufula*-group are regarded as belonging to *Porina*. Like the corticolous and saxicolous *Porina* species, the

members of these two groups are characterized by the presence of *Porina*-yellow-type pigments in the perithecial wall. The close relationship of *P. nucula* (generic type) with *P. epiphylla* is evident. Studying only selected species of the *P. rufula*-group one might get the impression that they merit a further genus in Trichotheliaceae. However, the two species groups are well linked by intermediate species (e. g. *P. albicera*, *P. pallescens*) combining characters of both species groups.

(2) *Porina mammillosa* contains the hyphal pigment *Porina*-yellow in the inner perithecial wall. In exposed parts of the perithecia the pigment *Sagedia*-red (BACHMANN 1890) is synthesized (for reactions see Tab. 1). However, protected parts of thalli and perithecia show that the species belongs to *Porina* s. str. We interpret therefore the occurrence of *Sagedia*-red in *Porina mammillosa* as a response to extreme habitats. For further species containing *Sagedia*-red see *Pseudosagedia* subgen. *Limosagedia*!

(3) The only type of vegetative diaspores so far known in *Porina* is the formation of isidia. Besides the peculiar *Phyllophiale*-type, occurring only on foliicolous species (SANTESSON 1952, LÜCKING 1991, APTROOT & SIPMAN 1994), cylindrical to coralloid isidia are occasionally developed (see under *Zamenhofia*).

(4) It is well known that the perithecia of *Porina* may be covered by tomentose hyphae (e. g. *P. virescens*). Perithecia of the recently described *Trichothelium rubescens* (LÜCKING 1991: 287) are provided with a crown of soft setae which is different from that of true *Trichothelium* species. The inner perithecial wall contains *Porina*-yellow. Already LÜCKING (*l. c.*) compared this species with *Porina octomera* and had doubts about the placement in *Trichothelium*. According to our generic concepts of Trichotheliaceae it must be transferred to *Porina*:

***Porina rubescens* (Lücking) Hafellner & Kalb comb. nova**

Bas.: *Trichothelium rubescens* Lücking, Nova Hedwigia 52: 287 (1991).

However most of the other *Trichothelium* species with pale perithecia and/or pale setae really belong to *Trichothelium*, as *Pseudosagedia*-violet is present at least in the inner perithecial wall (e. g. *Trichothelium pallescens*).

(5) The mediterranean calcicolous species, known as *Porina acrocordioides*, obviously does not belong to *Porina*, but is a member of Pyrenulales with hyaline ascospores. Although the majority of Pyrenulales do have pigmented ascospores, hyaline spores are also known, and this is interpreted by HARRIS (1989: 75) as a kind of neoteny. The species was transferred to *Plagiocarpa* by HARRIS (1989) and later to *Lithothelium* (APROOT 1991), who gave the correct name with *Lithothelium triseptatum* (Nyl.) Aptroot.

***Pseudosagedia* (Müll.Arg.) M.Choisy**

Bull. Mens. Soc. Linn. Soc. Bot. Lyon 18: 107 (1949).

Bas.: *Arthopyrenia* sect. *Pseudosagedia* Müll.Arg., *Mem. Soc. Phys. Hist. Nat.*

Geneve 16 (2): 428 (1862).

Typus sectionis: *Arthopyrenia carpinea* (Pers. ex Ach.) Müll.Arg. (lectotype, selected here).

= *Sagedia* sensu Massal. (1852), non Ach. (1809).

Pseudosagedia cerasi (Schrad.) M.Choisy is given as generic type in ING. However this species is not mentioned in the protologue (MÜLLER ARGOVIENSIS 1862) and therefore cannot be the type and would also be against the intention of MÜLLER ARGOVIENSIS (*l. c.*), while the type species proposed here reflects exactly the opinion of the original author. OKSNER (1956: 148) overlooked that CHOISY (1949) had already raised *Pseudosagedia* to generic rank and unnecessarily proposed the same combination once more. OKSNER (1956) as well as KOPACZEWSKAJA *et al.* (1977) used *Pseudosagedia* in the same sense as CHOISY. The genus is mainly characterized by the presence of non-crystallized pigments of *Pseudosagedia*-violet type in the perithecial wall. They are most easily visible in the upper part of the inner perithecial wall (peridium) but may also be frequently present in part of the outer perithecial wall (involucellum). The range of natural colours of *Pseudosagedia*-violet, as well as the reactions with common reagents, are given in Tab. 1. *Pseudosagedia*-violet is also the characteristic perithecial pigment of *Trichothelium* species. We therefore regard *Pseudosagedia* to be more closely related to *Trichothelium* than to *Porina* s. str. *Pseudosagedia rapaeformis* in some respect is an intermediate species, because its perithecia are ornamented with small warts around the ostiolum. No isidiate species are known in *Pseudosagedia*.

The following species have been checked and found to belong in *Pseudosagedia* subgen. *Pseudosagedia*:

Pseudosagedia aenea (Wallr.) Hafellner & Kalb comb. nova.

Bas.: *Verrucaria aenea* Wallr., *Fl. Crypt. Germ.* 3: 299 (1831).

Pseudosagedia atrocoerulea (Müll.Arg.) Hafellner & Kalb comb. nova.

Bas.: *Porina atrocoerulea* Müll.Arg., *Flora* 66: 336 (1883).

Pseudosagedia borreri (Trevisan) Hafellner & Kalb comb. nova.

Bas.: *Spermatodium boreri* Trevisan, *Consp. Verruc.*: 11 (1860).

Pseudosagedia chlorotica (Ach.) Hafellner & Kalb comb. nova.

Bas.: *Verrucaria chlorotica* Ach., *Lichenographia Univ.*: 283 (1810).

Pseudosagedia corruscans (Rehm) Hafellner & Kalb comb. nova.

Bas.: *Metasphaeria corruscans* Rehm, *Leafl. Philip. Bot.* 8: 2949 (1916).

Pseudosagedia curnowii (A.L.Sm.) Hafellner & Kalb comb. nova.

Bas.: *Porina curnowii* A.L.Sm., *J. Bot., London* 49: 44 (1911).

Pseudosagedia grandis (Koerb.) Hafellner & Kalb comb. nova.

Bas.: *Sagedia grandis* Koerb., *Parerga Lich.*: 355 (1863).

Pseudosagedia guentheri (Flot.) Hafellner & Kalb comb. nova.

Bas.: *Verrucaria guentheri* Flot., *Bot. Zeitung* 8: 575 (1850).

In the inner part of the peridium a pigment occurs which is presumably *Porina*-yellow (COPPINS, *in litt.*)

***Pseudosagedia impressa* (R.Sant.) Hafellner & Kalb comb. nova.**

Bas.: *Porina impressa* R.Sant., *Symb. Bot. Upsal.* **12** (1): 219 (1952).

***Pseudosagedia interjungens* (Nyl.) Hafellner & Kalb comb. nova.**

Bas.: *Verrucaria interjungens* Nyl., *Flora* **55**: 362 (1872).

***Pseudosagedia laticarpa* (Lücking) Hafellner & Kalb comb. nova.**

Bas.: *Porina laticarpa* Lücking, *Nova Hedwigia* **52**: 280 (1991).

***Pseudosagedia nitidula* (Müll.Arg.) Hafellner & Kalb comb. nova.**

Bas.: *Porina nitidula* Müll.Arg., *Flora* **66**: 336 (1883).

***Pseudosagedia obsoleta* (Oksner) Hafellner & Kalb comb. nova.**

Bas.: *Phylloporina obsoleta* Oksner, *J. Inst. Bot. Acad. Sci. RSS Ukraine* **21/22**: 309 (1939).

= *Porina oxneri* R.Sant.

***Pseudosagedia papillifera* (Stirt.) Hafellner & Kalb comb. nova.**

Bas.: *Verrucaria papillifera* Stirt., *Proc. Phil. Soc. Glasgow* **11**: 107 (1878).

***Pseudosagedia rapaeformis* (Vain.) Hafellner & Kalb comb. nova.**

Bas.: *Porina rapaeformis* Vain., *Acta Soc. Fauna Flora Fenn.* **7**: 225 (1890).

***Pseudosagedia thaxteri* (R.Sant.) Hafellner & Kalb comb. nova.**

Bas.: *Porina thaxteri* R.Sant., *Symb. Bot. Upsal.* **XII** (1): 218 (1952).

***Pseudosagedia umbilicata* (Müll.Arg.) Hafellner & Kalb comb. nova.**

Bas.: *Phylloporina umbilicata* Müll.Arg., *Bull. Soc. Bot. Belgique* **30**: 92 (1891).

***Pseudosagedia whinrayi* (P.M.McCarthy) Hafellner & Kalb comb. nova.**

Bas.: *Porina whinrayi* P.M.McCarthy, *Lichenologist* **22**: 195 (1990).

According to the description and drawings in the protologue, the species clearly belongs here.

For some further species a new subgenus is introduced here:

***Pseudosagedia* subgen. *Limosagedia* Hafellner & Kalb subgen. nov.**

Ascomycetes lichenisati. Differunt a speciebus generis *Porina* defectu pigmenti aurei (*Porina*-yellow) et a speciebus *Pseudosagedia* subgen. *Pseudosagedia* defectu pigmenti obscure violacei (*Pseudosagedia*-violet) in peridio interiore. Involucellum externe purpureum (*Sagedia*-red), KOH adito caeruleum tinctum. Habitans in saxis plusminusve calcareis.

Species holotypica: *Pseudosagedia linearis* (Leight.) Hafellner & Kalb

Lichenized ascomycetes. Thallus crustose, endolithic or epilithic, continuous to minutely rimose, not distinctly corticate; photobiont trentepohlioid. Perithecia black, partly immersed to almost sessile, naked; in vertical section peridium pale, at least in the upper part covered by a dark purplish involucellum.

Coloured part of involucellum K+ blue, then blackish (*Sagedia*-red *sensu* BACHMANN 1890) (see Tab. 1). Ascii of *Porina*-type, unitunicate, apically with chitinoid ring structure, in general 8-spored. Paraphyses mostly simple. Short periphyses in ostiolar region present. Ascospores colourless, transversally 3- to 7(-8)-septate, at least young ascospores with perisporal sheath. Pycnospores bacillar.

The subgenus *Limosagedia* so far seems to be restricted to different types of limestone. The prefix of the generic name refers to this ecological preference. The second part refers to *Sagedia* *sensu* A.Massal. because of the similar external appearance.

The following species belong to this subgenus:

Pseudosagedia byssophila (Koerb. ex Hepp) Hafellner & Kalb comb. nova.

Bas.: *Sagedia byssophila* Koerb. ex Hepp, Flechten Europas 12 (23/24): no. 695 (1860).

Pseudosagedia ginzbergeri (Zahlbr.) Hafellner & Kalb comb. nova.

Bas.: *Porina ginzbergeri* Zahlbr., Österr. Bot. Z. 53: 150 (1903).

Pseudosagedia linearis (Leight.) Hafellner & Kalb comb. nova.

Bas.: *Verrucaria linearis* Leight., Brit. Spec. Angiocarp. Lich.: 52 (1851).

Pseudosagedia oleriana (A.Massal.) Hafellner & Kalb comb. nova.

Bas.: *Sagedia oleriana* A.Massal., Symmicta Lich.: 95 (1855).

JANEX-FAVRE (1981) investigated the ontogeny of the perithecia of *Pseudosagedia byssophila* and found it to be very similar to *Porina*.

Trichothelium Müll.Arg.

Bot. Jahrb. 6: 418 (1885).

Typus generis: *Trichothelium epiphyllum* Müll.Arg. (holotype).

Syn.: see ERIKSSON & HAWKSORTH (1993: 114).

Within Trichotheliaceae the genus is mainly characterized by the presence of a crown of stiff setae (cf. SANTESSON 1952: 266) and the perithecial pigment *Pseudosagedia*-violet. The genus, restricted to tropical and subtropical regions, was thoroughly treated by SANTESSON (1952), but further species have been described by LÜCKING (1991), BARILLAS & LÜCKING (1992) and VĚZDA (1994).

Zamenhofia Clauzade & Cl.Roux

Bull. Soc. Bot. Centre-Ouest, Nouv. Sér., Num. Spéc. 7: 824 (1985).

Typus generis: *Zamenhofia coralloidea* (P.James) Clauzade & Cl.Roux (holotype).

Zamenhofia is retained in Trichotheliaceae with hesitation. As already pointed out, ascii of *Zamenhofia* species lack an external ring structure and perithecial pigments typical for Trichotheliaceae (*Porina*-yellow, *Pseudosagedia*-violet, *Sagedia*-red, *Segestria*-brown) are not present. Although all known *Zamenhofia*

species do have minute isidia this character cannot be used for generic delimitation. Isidiate species may also be found in *Porina*; these species are discernible by *Porina*-type ascci and the pigment *Porina*-yellow (e. g. *Porina conspersa*, *Porina isidiophora*). This is also the case with the crown of periphyses, which can be seen also in several species of *Clathroporina* and *Porina*.

Excluded genera

***Belonia* Koerb.**

Lich. Sel. Germ. 1-4: no. 79 (1856).

Typus generis: *Belonia russula* (holotype).

None of the perithecial pigments characteristic for Trichotheliaceae is produced in ascocarps of *Belonia russula*. The unitunicate ascii show a truncate apex but lack an external chitinoid ring structure. Because of the presence of carotenoid pigments in the paraphyses, etc., the genus was placed in Gyalectales by JØRGENSEN *et al.* (1983: 47).

***Clathroporinopsis* M.Choisy**

Icon. Lich. Univ. 4, t. 25 (1929).

Typus generis: no species mentioned by the author.

The genus was mentioned as a synonym of *Clathroporina* Müll.Arg. by ERIKSSON & HAWKSWORTH (1993), however CHOISY (*l. c.*) clearly had in mind a group of deeply urceolate discocarp lichenized fungi similar to *Topelia* M.Jørg. & Vězda (JØRGENSEN & VĚZDA 1984). Thus *Clathroporinopsis* cannot belong to Trichotheliaceae.

***Dichoporis* Clements**

Gen. Fungi: 40, 173 (1909).

Typus generis: *Dichoporis schizospora* (Vain.) Clements (holotype).

The correct name for the type species is *Strigula mediterranea* (ETAYO 1993). Thus *Dichoporis* is a later synonym of *Strigula*.

***Diporina* Clements**

Gen. Fungi: 40, 173 (1909).

Typus generis: *Diporina subsimplicans* (Nyl.) Clements (holotype).

= *Strigula subsimplicans* (Nyl.) R.C.Harris *comb. nova*.

Bas.: *Verrucaria subsimplicans* Nyl., Lich. Novae Zelandiae: 130 (1888).

The correct generic position of this species was first realized by HARRIS (see annotation slip on holotype!). *Diporina* therefore is a later synonym of *Strigula* Fr.

Pocsia Vězda

Folia Geobot. Phytotax. **10:** 401 (1975).

Typus generis: *Pocsia marattiae* Vězda (holotype).

The genus *Pocsia* was monotypically described for the foliicolous species *P. marattiae*. Shape and thickness of the ascal wall drawn by VĚZDA (1975: 403, fig. 7: 10, *Porinula tanzanica* ex errore) show clearly that the species does not belong to Trichotheliales.

Porinula Vězda

Folia Geobot. Phytotax. **10:** 399 (1975).

Typus generis: *Porinula tanzanica* Vězda (holotype).

The genus *Porinula* was monotypically described for the foliicolous species *P. tanzanica*. Shape and thickness of the ascal wall drawn by VĚZDA (1975: 401, fig. 6: 9, *Pocsia marattiae* ex errore) show clearly that the species does not belong to Trichotheliales.

Spermatodium Fée ex Trevisan

Conspectus Verrucarinarum: 10 (1860).

The generic name is illegitimate (ICBN Art. 63.1). TREVISAN cited among the synonyms of *Spermatodium* also the monotypic genus *Endophis* Norman which he should have adopted. *Endophis* is a rejected name versus *Leptorhaphis* Koerb. nom. cons. TREVISAN (*l. c.*) treated many *Pseudosagedia* species in *Spermatodium*.

Specimens examined

Belonia russula Koerb. ex Nyl.

Österreich, Salzburg: Kitzbüheler Schieferalpen, Maurerkogel W Schmittenhöhe über Zell am See, ca. 2000 m, 9.IX.1973, Steiner 13006 (GZU).

Clathroporina exocha (Nyl.) Müll.Arg.

Australien, Norfolk Island: Red Road Track to Mt. Bates, in dense subtropical rainforest, 220 m, 6.XII.1984, Elix 18624 & Streimann (GZU).

Clathroporina ocellata (Malme) Zahlbr.

Brasilien: Mato Grosso, etwa 35 km SE von Cuiaba, 120 m, 3.-4.VII.1980, Kalb 25665 (hb. Kalb).

Clathroporina olivacea Müll.Arg.

Australien, NSW: Bulahdelah District, Myall River State Forest, E Stroud, 150 m, 7.VII.1988, Kalb & Filson 17969 (hb. Kalb).

Lithothelium triseptatum (Nyl.) Aptroot

Frankreich, Provence: Vaucluse, Gorges du Régalon, an Kalk, 100 m, 13.VIII.1975, Kalb, Clauzade & Roux 3062 (hb. Kalb).

Porina albicerca (Kremp.) Overeem

Australien, Queensland: Daintree National Park, wenige km W von Mossman, in einem tropischen Regenwald, 250 m, 30.VIII.1988, Kalb 25400 (hb. Kalb).

Porina desquamescens Fée

Brasilien, São Paulo: Ilha de São Sebastião, Westhang des Morro das Tacas, 400 m, 6.VII.1979, Kalb (hb. Kalb).

Porina epiphylla (Fée) Fée

Costa Rica, Cartago: CATIE bei Turrialba, Urwald am Sendero de Espareles zwischen dem Hauptgebäude des CATIE und dem Rio Reventazon, 22.II.1990, Hiepko & Poelt (GZU).

Porina isidiophora Vain.

Indias occ. Insula St. Jan, Bordeaux-Hill, ad corticem arboris, 29.XI.1906, Raunkiaer (TUR).

Porina lectissima (Fr.) Zahlbr.

Österreich, Steiermark: Ostalpen, Koralpe, Sobot, Schlucht der Freistritz, 720-740 m, Aceri-Fraxinetum mit Schieferblöcken, 17.V.1983, Hafellner, Plant. Graec. Lich. 325 (GZU).

Porina leptalea A.L.Sm.

GB, Cornwall: Scilly Isles, Tresco, on the slope of the monument (S of Great Pool), on the trunk of a *Cupressus macrocarpa* in a very dark *Cupressus-Pinus radiata*-forest, 8.VII.1963, Santesson (GZU).

Porina leptosperma Müll.Arg.

Brasilien, São Paulo: Zwischen Osasco und Cabréuva, etwa 40 km WNW von São Paulo, in einem dichten Bergregenwald, 750 m, 22.III.1980, Kalb 25676 (hb. Kalb).

Porina mammillosa (Th.Fr.) Zahlbr.

Frankreich, Béarn: Pyrénées-Atlantiques, Pic de Ger, 40 km S von Pau, 2250 m, über Moosen, 4.VIII.1975, Kalb 3285 (hb. Kalb).

Porina nucula Ach.

Guatemala, Petén: Umgebung von Tikal, in feuchtem, düsterem Primärregenwald, 300 m, an Rinde, 9.-10.I.1979, Kalb & Plöbst 25660 (hb. Kalb). Brasilien, Minas Gerais: Serra da Mantiqueira, zwischen Vila Monte Verde und Camanducaia, 1300 m, 28.-29.XI.1980, Kalb (hb. Kalb).

Porina octomera (Müll.Arg.) F.Schill.

Venezuela, Mérida: La Mucuy oberhalb Tabay, E Mérida, 2200-2500 m, feuchter Wald in einem kleinen Tal, auf kultiviertem *Podocarpus rospigliosii*, III.1969, Oberwinkler & Poelt (GZU).

Porina pallescens R.Sant.

Nepal: S of Langtang Khola on way Lama Hotel - Sgabru, 20.IX.1986, Poelt N86-1348 (GZU).

Porina rubescens (Lücking) Hafellner & Kalb

Costa Rica, Puntarenas: Corcovado National Park, about 130 km SSE of San Jose, 50 km WSW of Golfito on the Osa peninsula, on leaves of dicotyledon, VII.1992, Lücking 92-3349 (GZU).

Porina rufula (Kremp.) Vain.

Brasilien, São Paulo: Ilha de São Sebastião (Ilha Bela), tropischer Regenwald an der Rua Castelhanor, 500 m, 6.VII.1979, Kalb & Poelt (GZU).

Porina simulans Müll.Arg.

Brasilien, Mato Grosso: Santo Antônio do Leverger, etwa 40 km S von Cuiaba, in einem hellen Galeriewald am Rio Cuiaba, 100 m, 5.VII.1980, Kalb & Marcelli, KALB, Lich. Neotrop. 68 (hb. Kalb).

Porina tijucana Vain.

Brasilien, São Paulo: Serra do Mar, Serra do Peruibe bei Ana Dias, etwa 120 km SW von São Paulo, an einem Laubbaum, in feuchtem, dunklem Regenwald, 50 m, 2.IV.1978, Kalb & Plöbst, KALB, Lich. Neotrop. 28 (hb. Kalb).

Pseudosagedia aenea (Wallr.) Hafellner & Kalb

Österreich, Burgenland: Umgebung von Güssing, Natzwald, kurz SW unter Hasendorf, ca. 230 m, an *Carpinus*, 18.IV.1989, Hafellner & Maurer 24987 (GZU).

Pseudosagedia atrocoerulea (Müll.Arg.) Hafellner & Kalb

Bolivia, Guayaramerin: 29.XI.1966, Mahunka (GZU).

- Pseudosagedia borri* (Trevis.) Hafellner & Kalb
 GB, Devon: Slapton, auf *Ulmus procera* im Garten des Fieldcenters, 12.IX.1971, Poelt (GZU).
- Pseudosagedia byssophila* (Koerb. ex Hepp) Hafellner & Kalb
 Tunesien: Kalkfelsbänke etwa 2 km SW Korba, an der Straße Nabeul - Temime, nahe der Küste, Kalksandstein, 10.IV.1968, Poelt (GZU).
- Pseudosagedia chlorotica* (Ach.) Hafellner & Kalb
 Sweden, Skåne: Oppmanna, Arkelstorp, 11.VII.1916, Malme & Vrang, MALME, Lich. succ. Exs. 624 (GZU).
- Pseudosagedia corruscans* (Rehm) Hafellner & Kalb
 Australien, Queensland: Oberhalb von Lake Placid, wenige km S von Kuranda (etwa 20 km NW von Cairns), in einem tropischen Regenwald, 450 m, 27.VIII.1988, Kalb 25637 (hb. Kalb).
- Pseudosagedia curnowii* (A.L.Sm.) Hafellner & Kalb
 Ireland, Cork: Castletownshend, Bawnlahan, Tragumna Bay, 13.VIII.1966, James, VĚZDA, Lich. Sel. Exs. 554 (GZU).
- Pseudosagedia ginzbergeri* (Zahlbr.) Hafellner & Kalb
 Griechenland: Kerkyra, unterhalb des Klosters Paläokastritsa, 20-30 m, 24.VIII.1970, Poelt 8913 (GZU).
- Pseudosagedia grandis* (Koerb.) Hafellner & Kalb
 Great Britain, V.C. 97 Westerness: Stream in wood on north shore of Loch Moidart, quartz-dolerite, 30.VI.1962, Swinscow (GZU).
- Pseudosagedia guentheri* (Flot.) Hafellner & Kalb
 Spanien, Asturias, Prov. Oviedo: Puerto de Leitariegos, ober der Laguna Arbas, 1650 m, Gneisblockwerk, 6.IX.1980, Hafellner (hb. Kalb).
- Pseudosagedia impressa* (R.Sant.) Hafellner & Kalb
 Australia, Queensland: Maleny Range, Mary Cairns Cross Park about 6 km S of Maleny, 26°47'S, 152°51'E, rainforest, 26.VI.1986, Hafellner & Stevens 19907 (GZU).
- Pseudosagedia laticarpa* (Lücking) Hafellner & Kalb
 Costa Rica, Puntarenas: Corcovado national park, about 130 km SSE of San Jose, 40 km WSW of Golfito, 50-200 m, on leaves of dicotyledon, VII.1992, Lücking 92-3185 (GZU).
- Pseudosagedia linearis* (Leight.) Hafellner & Kalb
 Spanien, Asturias: Prov. Oviedo, Playa San Antolin de Bedón E von Ribadesella, Kalkklippen an der Küste, 5-20 m, 31.VIII.1980, Hafellner 10987 (GZU).
- Pseudosagedia nitidula* (Müll.Arg.) Hafellner & Kalb
 Philippinen, Süd Luzon: Prov. Laguna, bei der Stadt Pagsanjan: In einem flussbegleitenden Regenwald, 200 m, 23.VIII.1983, Kalb & Schrögl 12067 (hb. Kalb).
- Pseudosagedia obsoleta* (Oksner) Hafellner & Kalb
 = *Porina oxneri* R.Sant.
 U.S.S.R.: Colchis (Caucasus), in valle rivi Jupsurskie vorota, 650-700 m, ad folia et ramulos *Buxi colchicae*, 17.VI.1989, Cuba (GZU).
- Pseudosagedia oleriana* (A.Massal.) Hafellner & Kalb
 Frankreich, Vaucluse: Montagne du Luberon, Gorges de Regalon bei Cheval Blanc, SO Cavaillon, schattige, steile bis überhängende Flächen der engen Schlucht, Kalk, 17.VII.1970, Poelt & Clauzade (GZU).
- Pseudosagedia papillifera* (Stirt.) Hafellner & Kalb
 Bolivia, Beni: Guayaremerin, 29.II.1966, Mahunka (GZU).
- Pseudosagedia rapaeformis* (Vain.) Hafellner & Kalb
 Brasilien: Rio de Janeiro, 1885, Vainio, VAINIO, Lich. Bras. Exs. 4 (TUR).
- Pseudosagedia thaxteri* (R.Sant.) Hafellner & Kalb
 Guadeloupe (Antilles), Île de Marie Galante: la gorge Calcaire creusée par la rivière de Saint Louis, à 30-50 m, épiphylle (*Palmae*), 14.IV.1991, Vivant (GZU).
- Pseudosagedia umbilicata* (Müll.Arg.) Hafellner & Kalb
 Venezuela, Mérida: La Mucuy oberhalb Tabay, östlich Mérida, 2200-2500 m, feuchter Wald auf kultiviertem *Podocarpus rospigliosii*, III.1969, Oberwinkler & Poelt 13888 (GZU).

Strigula subsimplicans (Nyl.) R.C.Harris
Nova Zelandia: Knight (H-NYL 1530).

Trichothelium epiphyllum Müll.Arg.

Brasilien, São Paulo: Ilha de São Sebastião, Westhang des Morro das Tacas, 600 m, 21.IV.1978, Kalb, KALB, Lich. Neotrop. 39 (hb. Kalb).

Trichothelium pallescens Lücking

Costa Rica, Limon: Hitoy Cerere biological reserve, about 120 km ESE of San Jose, Atlantic slope of the Cordillera de Talamanca, 100-200 m, on leaves of dicotyledon, III.1991, Lücking 91-248 (GZU).

Zamenhofia coralloidea (P.James) Clauzade & Cl.Roux

Italien, Latio: Prov. Roma, Tenuta di Caccia di Castel Porziano (SW Roma), 19.II.1991, Poelt (GZU).

Acknowledgements

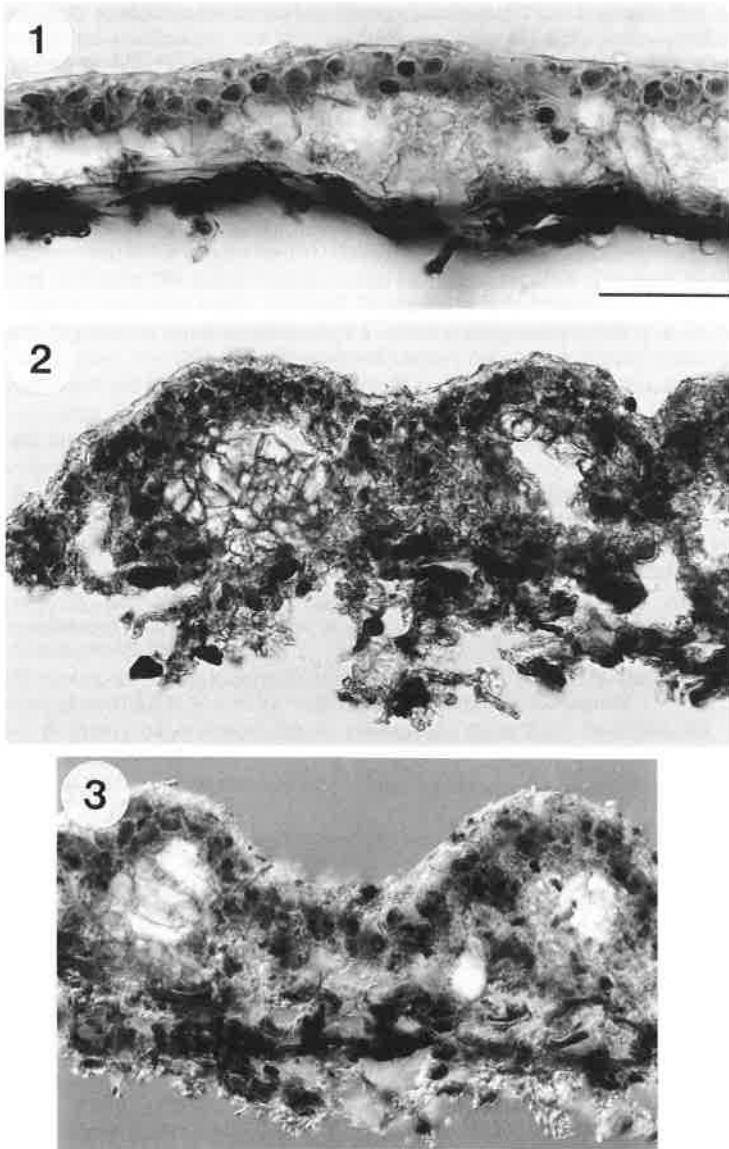
We have to thank Dr B. COPPINS for correcting the English, for making available some of his own observations on non-crystalline pigments and for valuable comments on the manuscript, Prof. Dr J. POELT for stimulating discussions, Dr H. SIPMAN for help with literature and the keepers of various herbaria, who made available lichen species, mentioned in the text.

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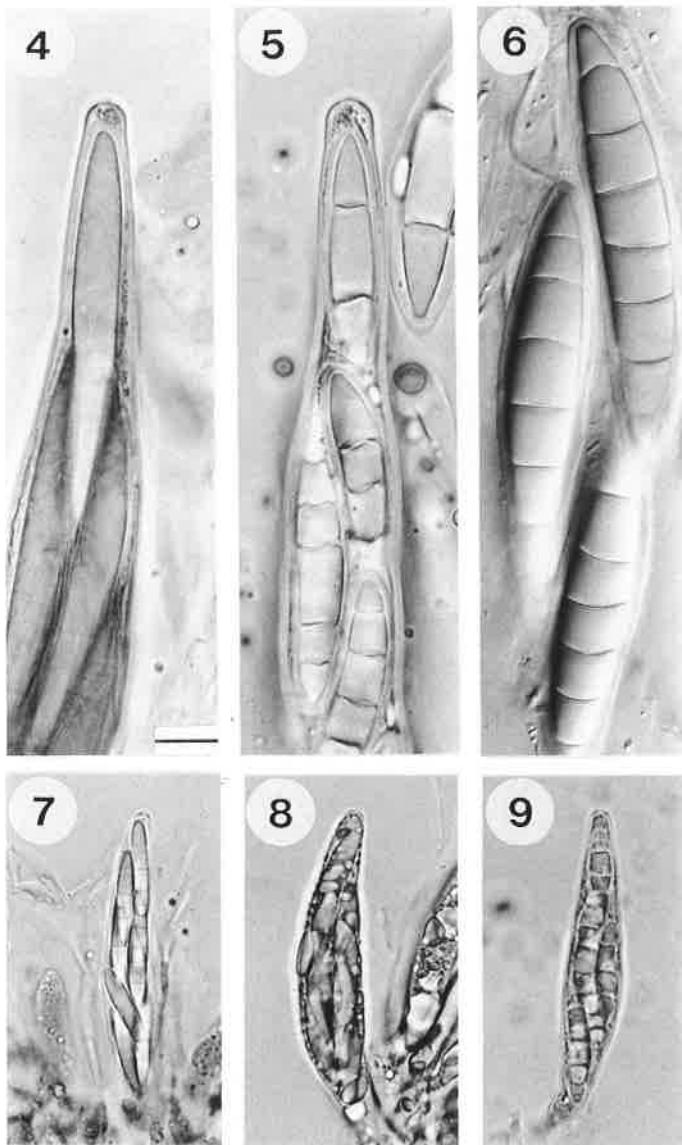
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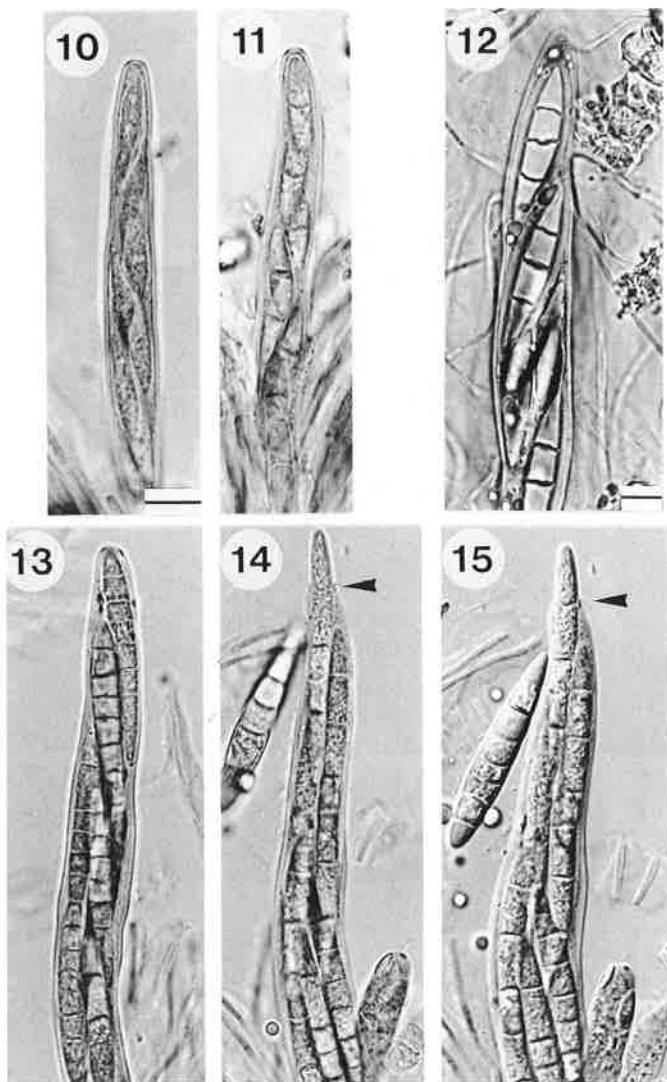
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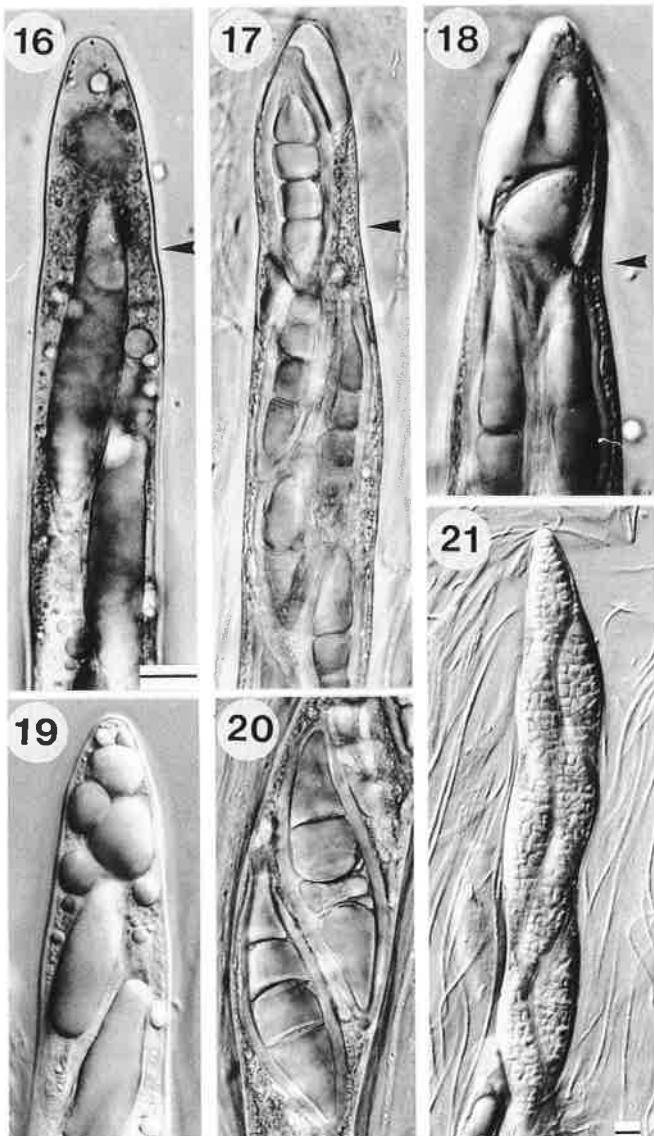
Figs. 1 - 3. Cross sections of *Porina* thalli. Fig. 1. *Porina desquamescens* (Brazil, Kalb), thallus with cristallostratum. Figs. 2 - 3. *Porina simulans* (KALB, Lich. neotropicici 68), thallus with cristallocumuli. Fig. 3. View in interference contrast. (Staining used in Figs. 1 - 3: lactophenol cotton blue, scale = 25 µm, for Figs. 1 - 3 on Fig. 1).



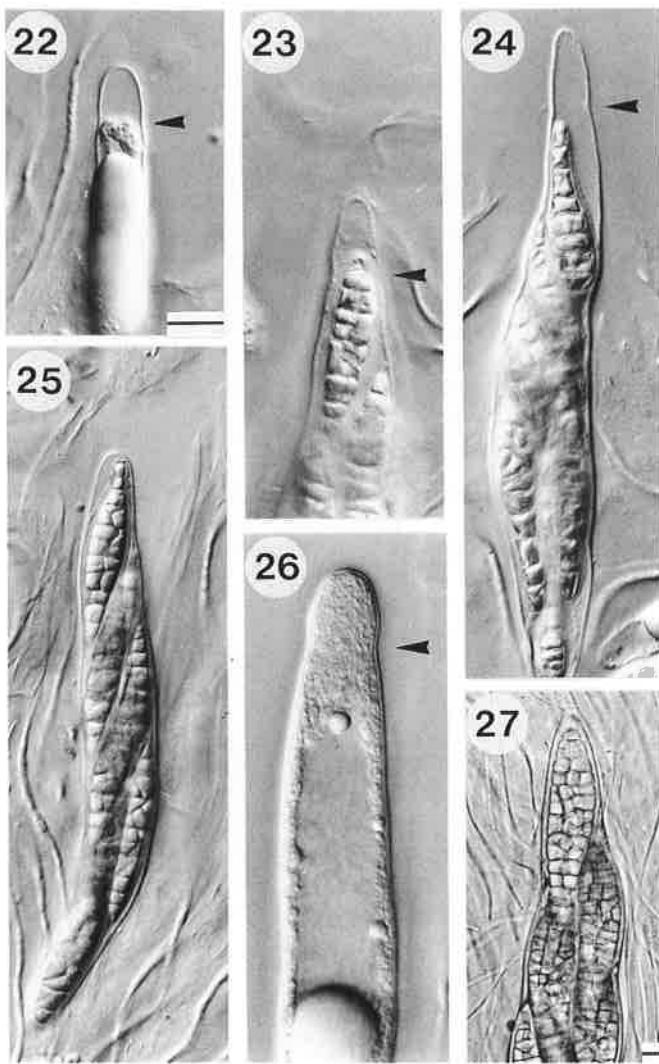
Figs. 4 - 9. Ascii and ascospores of Trichotheliaceae. Figs. 4 - 6. *Porina tijucana* (KALB, Lich. neotropicici 28). Fig. 4. Tip of young ascus. Fig. 5. Upper part of semimature ascus. Fig. 6. Mature ascospores. Fig. 7. *Porina albicera* (Kalb 25400), mature ascus. Figs. 8 - 9. *Pseudosagedia aenea* (Hafellner 24987). Fig. 8. Young ascus. Fig. 9. Mature ascus. (Staining used in Figs. 4 - 9: Congo Red, scale = 10 µm, for Figs. 4 - 9 on Fig. 4).



Figs. 10 - 15. Asci of Trichotheliaceae. Figs. 10 - 11. *Pseudosagedia linearis* (Hafellner 10987). Fig. 10. Young ascus. Fig. 11. Semimature ascus. Fig. 12. *Zamenhofia coralloidea* (Italy, Poelt), upper part of semimature ascus. Figs. 13 - 15. *Trichothelium epiphyllum* (KALB, Lich. neotropici 39). Fig. 13. Mature ascus. Fig. 14. Ascus at dehiscence. Fig. 15 same as 14. Interference contrast, the arrow points to the stained ring-structure. (Staining used in Figs. 10 - 15: Congo Red, scale = 10 µm, for Figs. 10 - 11, 13 - 15 on Fig. 10).



Figs. 16 - 21. *Clathroporina olivacea* (Kalb 17969) Figs. 16 - 19. Ascus tips in different stages of development, the arrows point to the characteristic subapical constrictions. Fig. 20. Young ascospores. Fig. 21. Ascus with mature ascospores. (Staining used in Figs. 16 - 21: Congo Red, scale = 10 μm , for Figs. 16 - 20 on Fig. 16).



Figs. 22 - 27. Asci and ascospores of *Clathroporina* species. Figs. 22 - 25. *Clathroporina ocellata* (Kalb 25665). Fig. 22. Tip of very young ascus. Figs. 23 - 24. Tips of semimature asci. Fig. 25. Mature ascus. Figs. 26 - 27. *Clathroporina exocha* (ELIX, Lich. australasici 79). Fig. 26. Tip of very young ascus. Fig. 27. Tip of mature ascus. (Staining used in Figs. 22 - 27: Congo Red, scale = 10 µm, for Figs. 22 - 26 on Fig. 22).