Generic classification of the Verrucariaceae (Ascomycota) based on molecular and morphological evidence: recent progress and remaining challenges

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Recent molecular phylogenetic analyses and morphological studies have shown that it is necessary to revise the present morphology-based generic delineation of the lichen family Verrucariaceae in order to account for evolutionary relatedness between species. Consequently, several genera were recently described or resurrected, and others were re-circumscribed. As an additional step toward this generic revision, three new genera (Hydropunctaria, Parabagliettoa, Wahlenbergiella) and eleven new combinations are proposed here. A summary of the current taxonomic and morphological circumscription of all genera investigated so far is also presented. Several monophyletic groups are identified for which further taxonomical changes will be required, but for which taxon and gene sampling is presently viewed as insufficient. Clear morphological synapomorphies were found to be rare for newly delimited genera. In some cases (reduced morphology or plesiomorphism), even the combinations of slightly homoplasious phenotypic characters do not allow a clear morphological generic circumscription. Molecular features are envisioned as characters for delimiting these taxa.

KEYWORDS: generic delineation, Lichens, taxonomy, Verrucariales

INTRODUCTION

Verrucariaceae is a large family of mostly lichenized species including 45 genera and about 750 species (Hawksworth & al., 1995; Eriksson, 2006). Members of this family are ecologically quite diverse, with species colonizing many different substrates (rock, soil, wood, bark, mosses and lichens) and living in various habitats (on arid and exposed rock surfaces, on permanently immersed boulders in streams, on rocky shores in the intertidal zone). They are found at different latitudes, from the tropics to the polar regions. Morphologically, species within Verrucariaceae are characterized by perithecial ascomata, bitunicate asci (Janex-Favre, 1971) with a dehiscence occurring by gelatinization of the apical part of the outer ascus wall (Grube, 1999), a hamathecium...
formed by periphyces located in the upper part of the ostiolar collar and short pseudoparaphyses located below and in the ostiolar collar (Fig. 1B; Janex-Favre, 1971), the lack, at least at maturity, of long interascal sterile hyphae (Fig. 1E, F)—which separate them from the Ade-lococeae, the other family of Verrucariaceae, in which long interascal sterile hyphae are persistent (Matzer & Hafellner, 1990; Triebel, 1993)—and a blue reaction of the hymenial gel to potassium-iodine (Henssen & Jähns, 1974).

Traditionally, three main morphological characters were used to define genera within this family (Zahlbruckner, 1903–1908, 1926; Zschacke, 1933–1934): spore septation, thallus structure and the presence or absence of algae in the hymenium (for a more complete history of the taxonomy of this family, see Gueidan & al., 2007; Savić & al., 2008). However, this generic delimitation has been considered artificial by many authors (Servit, 1946; Fröberg, 1989; Nimis, 1993, 1998; Poelt & Hinteregger, 1993; Halda, 2003). One of the major issues was the use of spore septation (Fig. 1H–K) to circumscribe genera within this family. For example, the occasional appearance of longitudinal septa in some spores in specimens with otherwise only transverse septa (pauciseptate muriform spores) led to a great deal of confusion in attributing these specimens to a genus. In some cases, spore septation varies within species (e.g., Orange, 1991) and is, therefore, also potentially problematic at the generic level. Similarly, thallus structure (Fig. 2) and the presence of hymenial algae (Fig. 1C) were believed to be of limited use as synapomorphies, because of possible convergent evolution. Nevertheless, the generic concepts in the Verrucariaceae remained unchanged, with only one attempt (Servit, 1953) to propose a radically different system. Servit (1953) revised the generic classification of the Verrucariaceae mainly based on characters of the involucrellum, a dark pigmented structure covering the perithecia (Fig. 1A), but other authors rarely adopted this new system. The scarcity of additional morphological characters available for proposing a new generic system prevented the proposal of important changes in the classification. It is only recently, with the development of molecular techniques, that a new set of data became available for assessing the generic circumscription and the relevance of morphological characters in classifying species from this family.

During the past two decades, contributions to fungal classification based on molecular data have led to major changes in our understanding of the evolution of fungi and of their phylogenetic affinities (see Hibbett & al., 2007 for a review). The first molecular studies to include molecular data on the family Verrucariaceae aimed at finding the phylogenetic placement of high-rank taxa within the ascomycetes (Lutzoni & al., 2001, 2004; Lumbsch & al., 2002, 2004, 2005; Liu & Hall, 2004; Geiser & al., 2006; Spatafora & al., 2006), and showed that the order Verrucariales was sister to an order of non-lichenized fungi, the Chaetothyriales. Other molecular studies have mostly addressed phylogenetic relationships at the infrageneric level (Heiðmarsson, 2003 and Amtoft & al., 2008 for the genus Dermatocarpon), and two recent molecular phylogenetic studies have presented new results that have challenged the traditional morphology-based generic delimitation of this family (Gueidan & al., 2007; Savić & al., 2008). They confirmed that spore septation cannot be used as the main generic character by showing that none of the crustose genera Verrucaria (simple spores), Polyblastia (muriform spores), and Thelidium (transversally pauci- to multiseptate spores) were monophyletic. Moreover, a squamulose thallus was shown to have evolved from a crustose thallus several times independently in this family, and hymenial algae were also acquired in distantly related groups (Gueidan & al., 2007).

Morphological studies and molecular phylogenetic analyses now suggest that taxonomical changes are needed in the Verrucariaceae. As a first step towards a more comprehensive taxonomic treatment of this family, specialists met in Akureyri, Iceland, for the second workshop on Verrucariales in 2007. Among other subjects, the generic classification of the family Verrucariaceae and some taxonomically related issues were discussed. The scope of this paper is to (1) summarize the recent systematic work done on taxa within Verrucariaceae, as well as the conclusions reached during this workshop, (2) propose taxonomic changes when the data available are considered sufficient, and (3) point out taxa on which further work is needed before a taxonomic revision can be proposed. This revision integrates both the morphological and molecular data available at this time and represents a starting point for subsequent taxonomic studies on Verrucariaceae.

MATERIALS AND METHODS

Material. — A total number of 110 described species of Verrucariaceae was included to this study (Appendix 1). Voucher information and GenBank accession numbers for taxa included in this study are available in Amtoft & al. (2008), Gueidan & al. (2007), Navarro-Rosinés & al. (2007), and Savić & al. (2008). The taxonomy refers to Breuss (1966a) for the catapyrenioid taxa, Orange (2004) for the Verrucaria fuscella group, Navarro-Rosinés & al. (2007) for the genera Verrucula and Verruculopsis, Savić & al. (2008) for Polyblastia and related taxa, Heiðmarsson (1998, 2001) and Amtoft & al. (2008) for Dermatocarpon, Nimis (1993), Clauzade & Roux (1985) and Santesson & al. (2004)
for lichen floras and catalogues, as well as diverse other publications that are mentioned throughout the article.

**Phylogenetic methods.** — The main phylogenetic tree presented in Fig. 3 was obtained using a Bayesian approach with the two markers nucLSU and RPBI (details available in Savić & al., 2008). Other phylogenetic analyses, highlighted using dark boxes in Fig. 3, were carried out independently with different methods and gene sampling: the phylogeny of *Dermatocarpon* was obtained from a Maximum Parsimony (MP) analysis using ITS (details in Amtoft & al., 2008); the phylogenies of *Verrucula* and of the clade including *Verruculopsis* and *Placopyrenium* were obtained using a Bayesian approach (MB) and ITS (details in Navarro-Rosinês & al., 2007). The phylogeny of the clade E was obtained from a MP analysis using ITS and nucLSU (details in Savić & Tibell, 2008a). Finally, the phylogeny of *Hydropunctaria* was obtained from a MP analysis using nucLSU. In the latter, out of the 1,667 characters available, 1,536 were excluded since constant and 71 were parsimony informative. A tree search of 100 random addition sequences (RAS) found, for each sequence, a single most parsimonious reconstruction of 162 steps (CI = 0.8889; RI = 0.7955). A bootstrap of 1,000 replicates and 2 RAS was then carried out to obtain support values. Branch lengths and support values for each of these independent analyses are shown in Fig. 3.

**RESULTS**

Genera investigated in this study are listed below alphabetically. Three new genera are described (*Hydropunctaria*, *Parabagliettoa*, *Wahlenbergiella*), and the delineations of many other genera were re-assessed. For the clades including paraphyletic taxa for which taxonomic changes were not proposed in this article because of lack of data, taxa can be found under their group names as used by Gueidan & al. (2007) and Savić & al. (2008). Phylogenetic relationships between investigated taxa are summarized in Fig. 3.

1. **Bagliettoa**


**Diagnostic characters**

- Calciicolous endolithic thallus, usually with outline of the thallus well visible on the rock surface.
- Upper cortex differentiated into a lithocortex (Pinna & al., 1998; Gueidan & Roux, 2007).
- Perithecia immersed, with or without an involucrelum (Fig. 2L).
- Involucrellum, when present, shield-shaped and with a radially split aperture.
- Oil cells (macrospheroids sensu Zukal, 1886) often present in the lower part of the medulla, laterally or terminally branching and often with a basal swelling (Gueidan & al., 2007).
- Ascospores absent or deformed in several species for which short pseudoparaphyses are numerous, without a gelatinous matrix but with detachable apical cells (Gueidan & al., 2007).

**Comments.** — *Bagliettoa* is sister to the endolithic genus *Parabagliettoa*, from which it differs mostly by its immersed perithecia and lithocortex. Unfortunately, the type of *Bagliettoa* (*B. limborioides*) was not included in our study. Because it is a rare species, no recent collections seem to be available (Halda, 2003: 16). However, according to the morphology of *B. limborioides* (thallus and perithecia endolithic, presence of oil cells and radially split involucrellum), the species studied here are undoubtedly congeneric with this species.


2. **Clade C**

(as delineated in Savić & al., 2008)

*Trimmatothela perquisita* is strongly supported as sister to a currently unidentified species of *Verrucaria* (C. Gueidan 742, DUKE; Savić & al., 2008). Both species have small perithecia and a distinct involucrellum. However, *T. perquisita* differs from this species of *Verrucaria* by having polysporous and much smaller spores. Ertz & Diederich (2004) argued (by analogy with other fungal genera including species with both octosporous and...
polysporous asci, such as Buellia s.l. and Candelariella) that since only polysporous asci distinguish Trimmatotile from Verrucaria, these genera should be united. Consequently, they proposed the combination V. perquisita (Norman) Ertz & Diederich. Because the type of Verrucaria is only remotely related to Trimmatotile perquisita, this combination was subsequently not accepted (Savić & al., 2008).


Diagnostic characters
- Thallus thin, with a smooth upper surface.
- Perithecia small, semi-immersed, with a well-developed involucrellum.
- Asci polysporous.
- Ascospores small, simple.


3. Clade E
(see Savić & al., 2008)

Clade E, as defined by Savić & al. (2008), includes the genera Atla, Henrica, Sporodictyon and Verrucaria, as well as an unknown species of Thelidium (S. Savić 3157, UPS). The resurrected genus Sporodictyon and its sister group, the new genus Atla, were recently segregated based on both morphological and molecular data (Savić & Tibell, 2008a; Savić & Tibell, in press). The type of Verrucaria, V. rupestris, forms a monophyletic group together with Henrica, a genus well supported by molecular data and emended in Savić & Tibell (2008b). The phylogenetic placement of Thelidium sp. (S. Savić 3157, UPS) is still unclear, as it received only weak support.

Atla S. Savić & Tibell in Lichenologist 40: 273. 2008.–


Diagnostic characters
- Saxicolous or terricolous, on calcareous substrates.
- Thallus crustose, immersed to diffusely areolate.
- Perithecia medium size to large, sessile to immersed, with well-developed involucrellum.
- Ascospores muriform, medium-sized to large, hyaline to dark brown when mature.

Comments. – The genus Atla was recently described to accommodate Polyblasia wheldonii and three new species (Savić & Tibell, 2008a). This genus is sister to Sporodictyon, another genus within Clade E, which has similar morphological characteristics. However, both genera can easily be differentiated based on molecular data, as Sporodictyon shows some characteristic indels in ITS1 and ITS2 (Savić & al., 2008). Moreover, Sporodictyon also differs by often having additional cyanobacterial photo-bionts within cephalodia.

Literature. – Savić & Tibell (2008a, new genus).


Diagnostic characters
- Saxicolous, on siliceous and calcareous substrates.
- Thallus crustose, smooth to verrucose or peltate with subcrenulate margin.
- Perithecia medium-sized to rather large, sessile to semi-immersed, with well-developed involucrellum.
- Ascospores muriform, medium-sized to large, medium to dark brown when mature.

Comments. – Morphologically, Henrica differs from the endolithic simple-spored Verrucaria by having pigmented muriform spores and an epilithic thallus. Like Sporodictyon, another member of clade E, Henrica has
a well-developed involucrellum and muriform spores. However, unlike *Sporodictyon*, *Henrica* does not seem to form cephalodia and their perithecia generally lack a thalline cover.


*Sporodictyon* A. Massal. in Flora 35: 326. 1852 – Type: *Sporodictyon schaereriänum* A. Massal. in Flora 35: 326. 1852. Type: ‘Ad saxa arenar. aqua suffusa in M. Gurnigel’ (as Parmelia aträ v. areolata-verrucosa), collector unknown s.n. Schäerer, Lich. Helv. exs. 538 (probably kept in VER, not seen; but material of Schäerer, Lich. Helv. exs. 538 in UPS was studied).

**Diagnostic characters**
- Thallus crustose, smooth to rimose or areolate or sometimes almost missing.
- Perithecia medium-sized to rather large, hemispherical, with a thalline cover at least in the lower part.
- Ascospores muriform, large, yellowish to medium or dark brown when mature.
- Photobiont a green alga, but cyanobacteria (*Nostoc* sp.) occur as an additional symbiont in cephalodia.

**Comments.** – *Sporodictyon* was recently resurrected to accommodate a group of species often referred to as *Polyblástia*, characterized by having large spores, perithecia often at least partially covered by the thallus, and cephalodia (Savić & Tibell, in press, including a historical review of *Sporodictyon*). Most species are epilithic and prefer humid and often shaded habitats along streams or on lakeshores, except for *S. terrestre*, which may occasionally grow on soil or mosses. They are sometimes found in temporarily inundated localities. They occur in Northern Europe, North America, the Arctic and also in the mountains of mainland Europe and the British Isles. The species are morphologically quite plastic and several species formerly recognized are now considered taxonomic synonyms (Savić & Tibell, in press).


**Diagnostic characters**
- Thallus endolithic.
- Perithecia ½ immersed to superficial, with dimidiate involucrellum.
- Exicum pale.
- Spores simple, colorless.

**Comments.** – Once the largest genus within Verrucariaceae, *Verrucaria* is here restricted to its type *V. rupestris*. However, further morphological and molecular studies will most probably find closely related species to *V. rupestris*, and this genus will not stay monotypic for long. Preliminary analyses did not confirm the currently accepted synonymy between *V. muralis* Ach., a mostly epilithic species, and *V. rupestris*, a strictly endolithic species with similar range of spore sizes, although the distinction was made by previous authors, including Zschacke (1934). A molecular analysis including a typical specimen of *V. muralis* provided by Keller (W139, WSL) suggests that this species belongs to the *Staurothele* group, and is more closely related to *V. praetermissa*. Specimens studied in Gueidan & al. (2007) and Savić & al. (2008), both strictly endolithic, more likely belong to *V. rupestris*, the type of *Verrucaria*. The phylogenetic placement of this genus is, therefore, considered here as part of Clade E, and sister to *Henrica*. The examination of the type specimen of *V. rupestris* will however be necessary to confirm the identity of the two specimens of *V. rupestris* investigated with molecular data (Gueidan & al., 2007; Savić & al., 2008) and the phylogenetic affiliation of the genus *Verrucaria*.

**Fig. 3.** Phylogenetic relationships between and within the main genera of Verrucariaceae. The main tree was obtained using a Bayesian approach (MB) with nuclLSU and RPB1 (Savić & al., 2008; support values posterior probabilities (PP)/ML bootstrap). Dark boxes highlight phylogenetic analyses conducted independently. The genus *Dermatocarpon* was analyzed using MP and ITS (Amtoft & al., 2008; support value MP bootstrap). *Verrucula* and the clade including *Verruculopsis* and *Placopyrenium* were analyzed using MB and ITS (Navarro-Rosínés & al., 2007; support values PP/ML bootstrap). Clade E was analyzed using MP and ITS-nucLSU (Savić & Tibell, 2008a; support values PP/MP bootstrap). *Hydropunctaria* was analyzed using MP and nuclLSU (support values MP bootstrap). Species that were represented by more than one specimen in the original analyses have a triangle at the top of the terminal branches. A dot indicates branches with support value(s) of 100%. Branch lengths are indicated by scale bars for each of the independent analyses. A star indicates generic types. New genera are highlighted in red. Genera that have been recently re-circumscribed are indicated in blue. Grey boxes show monophyletic groups for which additional taxonomical changes will be necessary. The distributions of six morphological characters are depicted across our taxon sampling. The three first columns correspond to characters traditionally used for generic classification (A: thallus structure; B: spore septation; C: hymenial algae), and the tree last columns to newly investigated characters (D: structure of the upper cortex; E: black thallus inclusions; F: pycnidium type). Character states were color-coded as indicated in the figure.
4. Dermatocarpon


Diagnostic characters
- Thallus foliose umbilicate (Fig. 2A).
- Lower cortex of Dermatocarpon-type (Harada, 1993a).
- Perithecia immersed in the thallus, almost entirely pale.
- Ascospores simple, 8 per ascus.
- Pycnidia of Dermatocarpon-type (Janex-Favre & Wagner, 1986).

Comments. – In the past, Dermatocarpon included, in addition to its foliose species, the squamulose species of Catapyrenium s.l. (Zahlbruckner, 1926; Zschacke, 1934) and several crustose species (a short review of the historical delimitation of the genus can be found in Heiðmarsson, 2001). Currently, Dermatocarpon forms a well-supported monophyletic clade within the Verrucariaceae, and includes species that can be easily recognized by their foliose umbilicate thallus (Fig. 2A). This genus has recently been treated in the Nordic countries where eleven species were found (Heiðmarsson, 2001) and in the Ozarks (U.S.A.) where seven species and one variety occur (Amtoft & al., 2008). Other recent revisions of the genus are from the British Isles (Orange, 1998) and Japan (Harada, 1993a). Apart from these revisions, the genus stays insufficiently known in the rest of the world, and a molecular study by Heiðmarsson (2003) on the D. minutum-complex indicates that species boundaries remain to be defined in many cases.


5. Endocarpon group
(as defined in Gueidan & al., 2007)

The Endocarpon group includes the genera Endocarpon (a squamulose genus with muriform spores and hymenial algae) and Neocatapyrenium (a squamulose genus with simple spores and without hymenial algae), as well as six species of ‘Verrucaria’ (all crustose with simple spores and without hymenial algae). Together with the Staurothele group, it is a group in which paraphyletic species of ‘Verrucaria’ make the generic circumscription problematic (Fig. 3). Two options are possible to accommodate this paraphyletic assemblage of species. The first option would be to include all species from the Endocarpon group into one large genus. However, the resulting genus would be morphologically diverse and difficult to characterize. The second option would be to describe a new genus for each of the paraphyletic entities. This option also has drawbacks, as it might potentially lead to a multiplication of monotypic or small genera. Because of the poor taxon sampling for this group, it was decided to not propose taxonomic changes at this time.


= Willeyæ Müller in Flora 66: 345. 1883 – Type: W. diffractella (Tuck.) Müller Arg.


Diagnostic characters
- Thallus squamulose, occasionally crustose.
- Upper cortex usually well differentiated.
- Photobiont often arranged in columns in the algal layer.
- Hymenium with algal cells.
- Ascospores muriform, often pigmented and 1–4 per ascus (Fig. 1G).
- Pycnidia of Endocarpon-type.

Comments. – In the past, this genus comprised only squamulose species, but a molecular study by Gueidan & al. (2007) showed that Endocarpon diffractellum, a crustose epilithic species previously included in the genus Staurothele, belongs to Endocarpon. The generic concept of Endocarpon was therefore slightly broadened to include both crustose epilithic and squamulose species. Crustose epilithic species from this genus can be mistaken for species of Staurothele. However, it has been observed that many species of Endocarpon have algal cells arranged in columns in the algal layer (Gueidan & al., 2007). To our knowledge, this trait has not been observed in Staurothele. Another important character to distinguish Staurothele from the Endocarpon group is the pycnidium type (Gueidan & al., 2007). Species in the Endocarpon group have typical Endocarpon-type pycnidia (Fig. 3), which can be commonly observed on specimens. In Staurothele, the pycnidia are often lacking, but they were shown to be of the Dermatocarpon-type in S. fissa.

6. Heteroplacidium


Diagnostic characters

- Thallus crustose-areolate to squamulose, entirely paraplectenchymatous or subparaplectenchymatous.
- Perithecia immersed in the thallus, lacking an involucrellum.
- Ascospores simple, 8 per ascus, rounded to ellipsoid.
- Pycnidia of Dermatocarpon-type.

Comments. – Heteroplacidium was described by Breuss in an attempt to account for morphological diversity in the genus Catapyrenium s.l. (Breuss, 1996a). The crustose parasitic species Verrucaria fuscula Nyl. was included in the genus Heteroplacidium in a subsequent study (Gueidan & al., 2007). Based on morphology, two other parasitic lichens, Verrucaria compacta (A. Masal.) Jatta (found as a saxicolous lichen or as an epiphyte on crustose or non-crustose allied lichens) and Verrucaria zamenhofiana Clauzade & Cl. Roux (a parasite on Staurotheca areolata), were also suggested to belong to Heteroplacidium (Gueidan & al., 2007; Roux, 2008).

7. Hydropunctaria

Hydropunctaria Keller, Gueidan & Thüs, gen. nov. [MB 512878].


Description. – Aquatic and amphibious saxicolous species, colonizing either marine or freshwater habitats. Thallus crustose, continuous to rimose or areolate, yellow-brown-green, dark grayish olive to black, subgelatinous. Upper cortex weakly differentiated, formed by cortical cells of a diameter usually relatively smaller than the fungal cells from the algal layer. Uppermost layer of cortical cells, when present, often with yellowish to brown or olive-blackish pigments, but also sometime colorless (especially in specimens from shaded sites). Black punctae sometimes visible at the surface of the thallus, at least in wet thalli. Algal layer not clearly delimited from the upper cortex, with algal cells usually arranged in vertical columns, sometimes interrupted by black punctae or columns. Medulla paraplectenchymatous, sometimes very thin or absent, often replaced by a black carbonaceous layer, interrupted by isolated black punctae or columns, but never forming black ridges. Perithecia immersed to half-immersed. Black involucrellum apical to dimidiate or entire, with upper surface often uneven-rough. Excipulum either pale with a brown ostiule or entirely pigmented.
**Hydropunctaria rheitrophila**

Conidiospores: simple, bacilliform, 3–4.5 × 1–1.5 μm.

Type: **Hydropunctaria maura** (Wahlenb.) Keller & al.

**Diagnostic characters**

- Hydrophilic species, restricted to sites with periodic inundation or strong influence by water spray.
- Thallus crustose, subgelatinous when wet, often interrupted by black punctae or columns (Fig. 1D).
- Upper cortex weakly differentiated.
- Medulla not differentiated or forming a black basal layer.
- Algal layer with algal cells usually arranged in vertical columns.
- Involucrellum with upper surface often uneven-rough.
- Ascospores simple, with a median length usually in the range of 10–18 μm.


**Hydropunctaria maura** (Wahlenb.) Keller, Gueidan & Thüs, **comb. nov.** [MB 512882] = *Verrucaria maura* Wahlenb. in Acharius, Methodus, Suppl.: 19. 1803 – Type: ‘Finmarkiae Norvegicae in saxis potrisque maritimis aqua marina interdum perfusis per insulas promontoriae vulgaris;’ **collector unknown s.n.**

(UPS!, lectotype; designated here; see Appendix 2).


**Hydropunctaria scabra** (Věžda) Keller, Gueidan & Thüs, **comb. nov.** [MB 512884] = *Verrucaria scabra* Věžda in Folia Geobot. Phytotax. 5: 308. 1970 – Type: Slowakei, Carpathen, Niedere Tatra; in declivi orientali montis ‘Kosariska’ dicti, in parte supriore valvis ‘Biela voda’, alt. 1300 m, ad lapides schistosos siliceos in torrente minore, 7 October 1966, **collector unknown s.n.**

**Comments.** – Two marine (*V. maura*, *V. adriatica*) and two freshwater (*V. scabra*, *V. rheitrophila*) species of *Verrucaria* form a well-supported monophyletic group. They are here included in the new genus *Hydropunctaria*. The most typical character of this genus of amphibious species with small to medium sized ascospores is the frequent formation of carbonaceous structures in the thallus with punctiform to column-like appearance. These structures can also originate directly from the involucrellum, which often has a distinctly rough and uneven upper surface. Black carbonaceous structures in the thalli of other amphibious species with small sized ascospores (e.g., *Wahlenbergiella striatula*) tend to fuse and form elongated ridges and sometimes ramified structures, giving a fingerprint like appearance if viewed from above. These fingerprint-like structures are never found in *Hydropunctaria* where the carbonaceous structures appear punctiform if viewed from above. *Wahlenbergiella striatula* can develop similarly isolated punctae but in this species, the upper surface of the involucrellum is always smooth, and not irregularly roughened as often observed in *Hydropunctaria*.


### 8. Parabagliettoa


**Thallus** crustaceus endolithicus de continuo ad rimosum, de cinereoviridibus ad cinereofuscis, saepe limitatus atrofusca hypothallina linea, thallum quoque dividente in partem superficiali et algalis, cellulis subcoloratis in culmine aliquando stratis. *Algosum stratum* non distincte delimitatum, cum algosis cellulis glomerulis. *Medulla* prosoplectenchymatium sine macrospheroidibus formata. *Perithecium* de superficiales ad ½ aut ¾ immersum, de globulo ad planum in apice, 0.1–0.4 mm diametro, cum nigro involucro, de dimidiato ad integrum; excipulum de incolore ad pallidofuscum. *Hymenium* incoloratum, K⁺/I⁻ caeruleum.
Ascus claviformis, cum 8 sporis, bitunicatus. Ascosporae incoloratae, ellipsoidales, plurumque simplices, sed aliquando unisepctae. Conidia aliquando in thalli margine observata. Conidiosporae simplices, bacilliformes, 3.5–4.5 × 0.5–1.5 μm. Habitat: saxatiles et calcicolae species, plus minusve sciaphiles.

Description. – Saxicolous calcicolous species, more or less sciaphilous. Thallus crustose endolithic, continuous to rimose, grey-green to grey-brown, frequently delimited by a brown dark hypothalline line, also subdividing the thallus in some species. Upper cortex formed by a thin prosoplectenchyma intermingled with microcrystals, sometimes with one layer of slightly pigmented cortical cells at the top. Algal layer not clearly delimited, with algal cells in clusters. Medulla formed by a prosoplectenchyma, lacking oil cells. Perithecium superficial to ½ or ¾ immersed, globose to flat on the top, 0.1–0.4 mm in diameter, with black involucrellum dimidiate to reaching the base of the excipulum; excipulum colorless to pale brown. Hymenium colorless, K/I + blue. Hamathecium consisting of paraphyses and short pseudoparaphyses, the latter abundant or not, but never spreading and detachable as in some species of Bagliettoa. Ascus clavate, 8-spored, bitunicate. Ascospores colorless, ellipsoid and mostly simple (but sometimes some uniseptate spores present). Conidia sometimes observed at the thallus margin. Conidiospores simple, bacilliform, 3.5–4.5 × 0.5–1.5 μm.

Type: Parabagliettoa dufourii (DC.) Gueidan & Cl. Roux

Diagnostic characters

- Calcicolous endolithic species (Fig. 2M).
- Upper cortex not well differentiated (pseudocortex).
- Medulla lacking oil cells.
- Perithecium superficial or semi-immersed, with well developed and not radially split involucrellum.
- Short pseudoparaphyses relatively abundant, but never spreading and detachable as in Bagliettoa.

Comments. – Parabagliettoa is sister to Bagliettoa.

It differs from this genus mainly by the thallus having a pseudocortex (in opposition to the well differentiated lithocortex in Bagliettoa), and superficial perithecia with an involucrellum not radially split.


1805 – Type: France, ‘on stones of a wall in Meudon,’ collector unknown s.n. (probably kept in G, but missing).


9. Placidium


Diagnostic characters

- Thallus squamulose (Fig. 2B–C), with a well-differentiated upper cortex.
- Perithecia immersed in the thallus, without involucrellum.
- Ascii clavate to cylindrical, containing 8 simple ascospores (Fig. 1E).
- Pycnidia of Dermatocarpon-type.

Comments. – Together with five other genera (Anthracocarpus, Catapyrenium, Involucropyrenium, Neocatapyrenium, Scleropyrenium), Placidium, Heteroplacidium and Clavasicidium were described or resurrected in an attempt to account for morphological diversity in Catapyrenium s.l. (Breuss, 1996a). The distinction between some of these genera was confirmed using molecular data (Catapyrenium s.str., Heteroplacidium, Neocatapyrenium), but the separation of Placidium and Clavasicidium was shown to be more problematic (Gueidan & al., 2007). The type of Clavasicidium, C. umbrinum, as well as an undescribed Clavasicidium-like species from the Ozarks in North America (R.C. Harris 46789, NY) are nested within a group of Placidium (Fig. 3). The two genera Placidium and Clavasicidium differ by the shape of their young asci and by the ascospore arrangement. Clavasicidium has clavate ascii with biseriate ascospores, whereas Placidium has asci, which are, at least at the beginning of their development, cylindrical and with uniseriate ascospores (Fig. 1E; Breuss, 1996a). However, in our molecular phylogenetic analysis, two species of Placidium are more closely related to Clavasicidium than to the other species of Placidium, and, together with Clavasicidium sp. (R.C. Harris 46789, NY), they form a monophyletic group (Fig. 3). To our knowledge, no morphological characters seem to characterize these two monophyletic groups (Clavasicidium spp., Placidium sp. [K. Knudsen 733, DUKE] and P. lacinulatum versus other Placidium spp.). Therefore, the simplest solution to maintain the monophyly of Placidium is to unite Clavasicidium with Placidium.
DNA extraction from available specimens of the generic type, Placidium michelii, failed because the material was too old. As this species is rare, no recently collected specimens were found for molecular work. However, morphological study of this type species gave no doubt as to its close relationship with species of Placidium s.l. Whether P. michelii is more closely related to Clavascidium/Placidium or to the other species of Placidium is of no importance because the two genera Clavascidium and Placidium are united. The resulting group of Placidium is still monophyletic and the type P. michelii has the priority over the type species of Clavascidium. Therefore, we propose to include Clavascidium in Placidium. A new combination for the type Clavascidium umbrinum is proposed here. Taxonomic changes for the three remaining species of Clavascidium, C. liratum (Breuss) Breuss, C. antillarum (Breuss) Breuss, and C. kisovense (Zahlbr.) Breuss will be undertaken in a future study, if molecular data confirms their placement in the genus Placidium (Prieto, unpub.).


10. Placocarpus

• Juvenile parasite on Lecanora muralis var. versicolor.
• Thallus thick, areolate to placodioid (Fig. 2H), with subumbilicate areoles.
• Medulla prosoplecticenchymatous, I+ (blue), interspersed with small colorless crystals.
• Ascospores simple, halonate (particularly visible in young spores), 8 per ascus.
• Pycnidia of Dermatocarpon-type.

Comments. – Breuss reinstated Placocarpus to accommodate Verrucaria schaereri, for which the generic attribution has always been problematic (Breuss, 1985). The remaining species originally included by Trevisan in Placocarpus were transferred to other genera, so that it is now monotypic. According to molecular results, Placocarpus is sister to the parasitic genus Verrucula (Gueidan & al., 2007).


11. Placopyrenium

• Often parasitic on diverse crustose species (Fig. 2G).
• Thallus crustose areolate to placodioid (Fig. 2E, G).
• Areoles often with black borders and subdividing lines.
• Perithecia immersed, with or without a rudimentary involucellum.
• Black basal layer present or not.
• Ascospores colorless, simple to uniseptate.
• Pycnidia of Dermatocarpon-type.

Comments. – The genus Placopyrenium, represented in our study by its type P. bucekii, also includes some species previously placed in Verrucaria, and often found as parasites on other lichens (Navarro-Rosínés & al., 2007). These crustose species related to the placodioid Placopyrenium are characterized by an epilithic thallus (Fig. 2G), black-bordered areoles and by having immersed perithecia (‘V.’ fuscella, ‘V.’ canella, but with the exception of ‘V.’ polysicta, which is nested in the Endocarpus group, and ‘V.’ liceoides, now in Verruculopsis). Placopyrenium fuscellum and P. canellum have been the subject of a recent detailed study in Great Britain and Ireland by Orange (2004), where their taxonomy was clarified. According to Roux (unpub.), the hamathecium of P. bucekii is composed, as in all Verrucariceae, of periphyses (very difficult to observe and not seen in Ménard & Roux, 1995) and of short pseudoparaphyses (mistaken for periphyses in Ménard & Roux, 1995). Short pseudoparaphyses were shown to be present in the primordial stage of the development of perithecia in Verrucariceae (Janex-Favre, 1971, 1975), and, at maturity, are located in the upper part of the perithelial cavity, below and in the ostiolar collar (Fig. 1B). Periphyses are only formed during the development of the ostiole, and are, at maturity, located in the upper part of the ostiolar collar (Fig. 1B).

12. Polyblastia


**Diagnostic characters**
- Species crustose endo- to epilithic, or growing on soil and mosses.
- Thallus immersed to continuous, verrucose to areolate.
- Perithecia sessile to immersed, with or without involucrellum.
- Ascospores colorless, muriform, small to mediumsized.

**Comments.** – *Polyblastia* s.str. is supported as sister to the *Thelidium* group. This genus, as delimited in this study, is well characterized based on molecular data, and differs morphologically from most of the other members of the *Thelidium* group in spore size and septation. However, three species of *Polyblastia* nested within the *Thelidium* group (‘P.’ abscondita, ‘P.’ clandestina, ‘P.’ lutosae) are morphologically and anatomically quite similar to *Polyblastia* s.str. A remaining nomenclatural problem in *Polyblastia* s.str. is that the type specimen of *P. cupularis* was not available for study. Consequently, the connection between the type and the material representing *P. cupularis* in molecular studies (Gueidan & al., 2007; Savić & al., 2008) needs confirmation.

**Literature.** – Zschacke (1914, 1934, revisions), Servit (1954, revision), Swinscow (1971, revision), Savić & al. (2008, molecular phylogeny).

13. Staurothele group

The *Staurothele* group is one of the clades, together with the *Endocarpon* group, where paraphyletic species of ‘Verrucaria’ make the generic circumscription problematic (Fig. 3). Two main options seem possible for accommodating three paraphyletic species of ‘Verrucaria’ (*V. caerulea, V. praetermissa, V. tristis*). One could describe a new genus for each of these species. The taxon sampling of this study being quite limited compared to the species diversity of this family, it is very likely that none of these three genera will stay monotypic in the future. Alternatively, one could also decide to transfer these three species into a large genus including both *Catapyrenium* and *Placidiopsis*. Amongst other characters, the paraphyletic species of *Verrucaria* differ from *Catapyrenium* and *Placidiopsis* by having a crustose thallus. An undescribed species collected in California and parasitized by *Verrucaria subdivisa* Breuss (K. Knudsen 5333, DUKE) is sister to all of the other taxa from the *Staurothele* group, and might also constitute a new genus. Unfortunately, the data available so far is probably not sufficient to make nomenclatural changes for these taxa. Further morphological and molecular work is needed to delineate genera in this group.


**Diagnostic characters**
- Thallus crustose epithilic, continuous to areolate.
- Upper cortex weakly differentiated (pseudocortex).
- Perithecia immersed in areole to partially superficial, with hymenial algal cells (Fig. 1C).
- Ascospores muriform, pigmented, 2–8 (or rarely 1) per ascus (Fig. 1K).

**Comments.** – *Staurothele* is quite well accommodated within the *Staurothele* group, and includes exclusively epitheilic species. Gueidan & al. (2007) showed that a species of *Staurothele* with a palisade algal layer belonged to *Endocarpon*. Further morphological and molecular studies will be necessary to see if other species of *Staurothele* also have to be transferred to the genus *Endocarpon*. Moreover, two endolithic species of *Staurothele*, *S. immersa* and *S. rupifraga*, were shown to be nested within the *Thelidium* group (Gueidan & al., 2007; Savić & al., 2008). Additional work is also needed in order to confirm the phylogenetic affiliation of the other endolithic species of *Staurothele*.


**Catapyrenium** Flot. in Bot. Zeitung (Berlin) 8: 361. 1850
previous attempts to locate the type material have failed).  
**Diagnostic characters**  
- Thallus squamulose, with relatively small squamules (Fig. 2D).
- Upper cortex a cinereum-type pseudocortex (Breuss, 1996a).
- Perithecia immersed.
- Ascospores usually simple, but not uncommonly one-septate.

Comments. – Recent molecular analyses showed that *Catapyrenium* is sister to the genus *Placidiopsis* (Gueidan & al., 2007; Savić & al., 2008). Although both *Catapyrenium* and *Placidiopsis* appear to be monophyletic (but only two species of each genus were included; see Fig. 3), the recognition of these two genera has already been criticized in the past (Breuss & Hansen, 1988; Breuss, 1996b). The only character separating them is the presence of a transversal septum in the spores of *Placidiopsis*. Observations show that the septation is rarely either totally absent or always present, and that some specimens of *Catapyrenium* can have some uniseptate spores. Therefore, the division into *Catapyrenium* for non-septate taxa and *Placidiopsis* for uniseptate taxa seems arbitrary, and the fusion of these two genera can be envisaged. However, Breuss & Hansen (1988) also noticed that the septation in *Placidiopsis* (“true” septa) was different than the one in *Catapyrenium* (pseudosepta). The monophyly of both genera *Catapyrenium* and *Placidiopsis* is, therefore, still an open question.

Pycnidia were unknown for a long time in this genus and in the closely related *Placidiopsis*, in spite of exhaustive revisions (Breuss, 1990; Breuss, 1996a, b). A recent description of a new species of *Catapyrenium* from New Mexico, *C. dactylinum* Breuss, shows that pycnidia are of Dermatocarpon-type in this genus (Breuss, 2000). This pycnidial type has already been found in several other genera in the Verrucariaceae (Fig. 3): Dermatocarpon, Heteroplacidium, Placidium, Placocarpus, Placopyrenium, Staurothele, Verrucula and Verruculopsis. However, a recent study suggested that *C. dactylinum* might not belong to *Catapyrenium* (Prieto & al., 2008).


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**Diagnostic characters**  
- Thallus squamulose, with relatively small squamules.
- Upper cortex a pseudocortex, similar to the cinereum-type (Breuss, 1996a, b).
- Perithecia immersed.
- Ascospores mostly one-septate (Fig. 1I).

Comments. – See the previous section “Catapyrenium”.


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14. **Thelidium group**  
(as defined in Savić & al., 2008)

The *Thelidium* group contains many species with a surprising variation in thallus structure (endolithic to superficial), perithecial anatomy (with or without involucellum and with and without hymenial algae), spore pigmentation (hyaline to dark brown), and spore septation (non-septate to muriform; Fig. 1H, J). The poor resolution obtained for this group calls for additional molecular markers, and more representatives from the large genus *Thelidium*, as well as from related genera. At this time, few conclusions are evident. As pointed out earlier (Gueidan & al., 2007; Savić & al., 2008), *Polyblastia* is not monophyletic and the ‘*Polyblastia*’ species in the *Thelidium* group will have to be transferred to a different genus in the future. Likewise, *Staurothele immersa* and *S. rupifraga* cannot be kept in *Staurothele* (see “*Staurothele*” section).


**Diagnostic characters**  
- Saxicolous, mostly calcicolous.
- Thallus endo- to epilithic.
- Perithecia immersed to superficial.
- Ascospores transversally septate (Fig. 1J).

Comments. – Recent molecular studies (Gueidan & al., 2007; Savić & al., 2008) have cast a doubt on the monophyly of the genus *Thelidium*. Although *T. papulare*, *T. pyrenophorum* and *T. umbilicatum* form a monophyletic group, *T. decipiens* appears to be more closely related to *Staurothele immersa*, and *T. incavatum* to ‘*Polyblastia*’ nidulans. Molecular data will be necessary for the type of *Thelidium*, *T. amylaceum*, in order to further recircumscribe this genus.

Literature. – Zschacke (1934, revision), Servít (1954, revision), Savić & al. (2008, molecular phylogeny).
15. Verrucula


**Diagnostic characters**
- Parasitic on _Caloplaca_ spp. with anthraquinones and _Xanthoria elegans_.
- Thallus areolate to squamulose-areolate (Fig. 2F), sometimes reduced.
- Upper cortex weakly differentiated (pseudocortex).
- Medulla I+ (blue) or I–.
- Excipulum pale except for the part around the ostiole, which is pale to pale brown.
- Ascospores simple, colorless, simple to rarely unisepitate.
- Pycnidia of _Dermatocarpon_-type.

**Comments.** _Verrucula_ is sister to the monotypic genus _Placocarpus_. Both genera only include parasitic species. Young thalli of _Placocarpus schaereri_ often parasitize _Lecanora muralis_, and species of _Verrucula_ are parasitic on _Caloplaca_ with anthraquinones and _Xanthoria elegans_. _Verrucula_ was recently resurrected to include some but not all species of ‘Verrucaria’ found as parasites on _Caloplaca_ with anthraquinones (Navarro-Rosinés & al., 2007), with the remaining taxa belonging to _Verruculopsis_, a genus sister to _Placopyrenium_. Species of both _Verrucula_ and _Verruculopsis_ are morphologically quite similar, probably as a result of a convergence to parasitism. Only few characters help in distinguishing them. In _Verrucula_, the excipulum is pale (except for the part around the ostiole, which is pale to pale brown). In _Verruculopsis_, the excipulum is, at maturity, pale brown at the base and dark brown in the upper part. Moreover, the medulla in _Verrucula_ is I+ (blue) to I–, whereas _Verruculopsis_ has an I– medulla.

**Literature.** Navarro-Rosinés & al. (2007, monograph), Ménard & Roux (1991, _V. irubescentis_).

17. Wahlenbergiella

_Wahlenbergiella_ Gueidan & Thüs, _gen. nov._ [MB 512880] – Type: _Wahlenbergiella mucosa_ (Wahlenb.) Gueidan & Thüs

_Thallus_ crustosus, continuus, laevissimus, subgelatinosus, viridis, in sicco helvolus vel cinereovirens, interdum cristas atris carbonaceis interruptus. _Cortex superus_ saxae nullus. _Stratum algarum_ hyphis verticalis formatum, cellularae algarum interdum paliformes. _Medulla_ absens vel praesens. Punctae et aliae in pagina thalli desunt. _Persithecia_ immersa vel superficialia, 0.08–0.2 mm diametro, involucello dimidiato vel deminuto; excipulum pallidum vel omnino atrum. _Hymenium_ incolore, K/I + caeruleum. _Hamathecium_ peripherico et pseudoparaphysibus brevibus formatum. _Asci_ claviformes, 8-spori, bitunicati. _Ascospores_ simplices, subrotundatae ad ellipsoidales, generatim breves (medium < 12 μm). _Conidia_ unilocularia, ostiolo nigro, cellularae conidiogenae elongatae parieti pyenidi direkte affixae. _Conidiosporae_ simplices, bacilliformes, 3–4. 5 × 1–2 μm. _Habitat_ in petris marinis.

**Description.** _Marine saxicolous lichens growing in the intertidal zone, periodically immersed. Thallus_ crustose epilithic, smooth and continuous, subgelatinous, green to grayish yellow green when dry, transparent green when wet (at least at the margins of young and thin thalli), sometimes interrupted by black carbonaceous ridges. **Upper cortex** often absent; algal layer reaching the uppermost...
part of the thallus. *Algal layer* formed by vertically oriented hyphae, with algal cells arranged in columns or not. *Medulla* absent or when present with hyphae not differentiated from the algal layer and some sparse algal cells. Carbonaceous ridges sometimes present, but black punctae absent. *Perithecia* immersed to superficial, small (0.08-0.2 mm diam.), with involucellum from reduced to dimidiate (Fig. 1A), and excipulum from pale to entirely black. *Hymenium* colorless, K+/I− blue. *Hamathecium* consisting of periphyses and short pseudoparaphyses. *Asci* clavate, 8-spored, bitunicate. *Ascospores* simple, colorless, subglobose to ellipsoid, with a median length usually shorter than 12 μm. *Conidia* with a single cavity (although nearby cavities can sometimes be connected laterally), a dark pigmented ostiole, and elongated conidiogenous cells bordering directly a rudimentary pycnidium wall (*mucosa*-type). *Conidiospores* simple, bacilliform, 3-4.5 × 1-2 μm.

**Diagnostic characters**

- Marine species with green to olive-green subgelatinous thalli (Fig. 2J).
- Upper cortex often absent.
- Medulla thin and not differentiated, or absent.
- Ascospores simple, generally with a median length shorter than 12 μm.
- Conidia of *mucosa*-type, only observed in *W. mucosa* so far.

**Comments.** – The new genus *Wahlenbergiella* is described here to accommodate the two marine species *V. mucosa* (Fig. 2J) and *V. striatula* (Fig. 2I). The name *Wahlenbergiella* was given after the author of these two species, Göran Wahlenberg. *Wahlenbergiella* is quite similar to another genus also including marine species, *Hydropunctaria*. They both are characterized by a subgelatinous thallus, and the black ridges of *W. striatula* could easily be compared to the black punctae present in the thallus of *Hydropunctaria*. However, *Wahlenbergiella* differs from *Hydropunctaria*, as well as from other amphibious species traditionally placed in the genus *Verrucaria*, by the following combination of characters: small ascospores (median length generally shorter than 12 μm), subgelatinous thallus, smooth surface of the involucellum, greenish thallus color, and the general absence of an upper cortex or a differentiated medulla.

**Wahlenbergiella mucosa** (Wahlenb.) Gueidan & Thüs, **comb. nov.** [MB 512888] ≡ *Verrucaria mucosa* Wahlenb. in Acharius, Methodus, Suppl.: 23. 1803 – Type: Norway, ‘Finnmark: Finmarkiae Norvegicae, peninsula juxta Pásekop, in rupe littore maris,’ 25 April 1802 and 20 May 1802. *G. Wahlenberg* s.n. (UPS!, lectotype; designated here; see Appendix 2).


**DISCUSSION**

The generic classification within Verrucariaceae traditionally relied on three main morphological characters, the thallus structure, the spore septation, and the presence or absence of hymenial algae. Although this system had been criticized in the past (Servít, 1946; Fröberg, 1989; Poelt & Hinteregger, 1993; Nimis, 1993, 1998; Halda, 2003), no major revisions were proposed and adopted for the genera in this family for a long time, mostly because of the lack of discriminating morphological characters. With the recent contribution of molecular phylogenetic studies, the knowledge on evolutionary relationships between species and genera in this family has greatly improved these last few years. Molecular results confirmed that the generic classification was in need of a revision, by showing that *Verrucaria*, the largest genus of the family (with about 250 species), was mostly characterized by plesiomorphic states and, therefore, highly polyphyletic (Gueidan & al., 2007; Savić & al., 2008). Moreover, other species-rich genera (*Polyblastia, Thelidium and Staurothele*) were also found to be polyphyletic.

**Recent progress in the revision of genera in Verrucariaceae.** — Because molecular data helped in understanding the phylogenetic relationships between main species and genera of Verrucariaceae, it was possible to carry out some taxonomical changes within this family in order to reconcile phylogeny and classification. Most of these changes were necessary to accommodate species previously belonging to *Verrucaria* and other non-monophyletic taxa into newly delimited or described genera. *Verruculopsis*, a genus exclusively parasitic on other lichens, was recently described for a group of species previously belonging to *Verrucaria* (Navarro-Rosinés & al., 2007), and *Atla*, a genus including crustose calcicolous species, was described for some species previously referred to as *Polyblastia* (Savić & Tibell, 2008a). Other genera have been recently resurrected or emended, such as *Verrucula*, (Navarro-Rosinés & al., 2007), *Sporodictyon* (Savić & Tibell, in press), and *Henricia* (Savić & Tibell, 2008b). The delineations of the squamulose genera *Endocarpon* and *Heteroplacidium* were broadened to also include crustose species (Gueidan
Bagliettoa, a genus previously defined by the presence of an involucrellum with a star-shaped aperture (Fig. 2L), now also comprises species lacking an involucrellum (Gueidan & al., 2007; Gueidan & Roux 2007). Finally, the delimitation of the placodii (crustose with peripheral lobes) genus Placopyrenium was also broadened to include species that do not have lobate margins (Fig. 2E, G; Navarro-Rosinés & al., 2007). In this study, three additional genera are described to accommodate species of Verrucaria that were not found to be related to its type V. rupestris: Parabagliettoa, a close relative to the strictly endolithic genus Bagliettoa, and the two aquatic (marine and freshwater) genera Wahlenbergiella and Hydropluntaria. New generic delimitations of currently valid genera are also proposed. The squamulose genus Clavascidum is here subsumed within Placodium, with which it is morphologically very similar. The genus Staurothele is shown to be restricted to its epilithic members, the endolithic species being found in Clade E. The genera Polyblastia and Verrucaria are also now restricted to a narrower generic concept, especially for the later genus, which currently, but most probably temporarily, includes only a single species.

Remaining problems of the generic classification. — Two main problems remained that made this taxonomical work at the generic level difficult, and sometimes prevented us from proposing changes. First, it is not always possible to delimitate genera using morphological characters. The new monophyletic groups, inferred from molecular data and taken into consideration to delineate new generic entities or to re-delineate existing genera, were only sometimes supported by clear morphological synapomorphies. Because many of the available morphological character states are symplesiomorphic or homoplastic, clear (unique) morphological synapomorphies were rare. It has been previously suggested that, instead of clear synapomorphies, combinations of slightly homoplastic characters could be used to define taxa (Miller & Huhndorf, 2005). However, even by combining different characters, it is not always possible to morphologically delineate all genera recognized here. For example, the two highly specialized genera Verrucula and Verruculopsis, which include species that are extremely reduced, possibly as a result of their parasitic lifestyle, cannot be clearly delimited using morphological data.

Secondly, many species of Verrucaria have a paraphyletic and basal phylogenetic placement in regard to other genera, as for example in the Staurothele and Endocarpon groups. The three character states that defined the genus Verrucaria (crustose thallus, simple spores, absence of hymenial algae) were most likely present in the ancestor of the family Verrucariaceae (Gueidan & al., 2007). While this family diversified, derived character states evolved in some lineages (such as the squamulose thallus, the muriform spores and the hymenial algae in Endocarpon), but plesiomorphic states were also retained in many distantly related groups within Verrucariaceae. All the species characterized by plesiomorphic states have been included in Verrucaria, which, therefore, in its traditional usage is highly polyphyletic. The taxonomic treatment of these species of Verrucaria, paraphyletic to otherwise morphologically well defined genera (such as Endocarpon and Staurothele), constitute a real problem. Two options seemed to be possible. The paraphyletic species of Verrucaria could be included in genera to which they are most closely related. This first option has the disadvantage of broadening the concept for genera previously morphologically well circumscribed. The second option would be to describe new genera for each of these paraphyletic groups. With our present limited taxon sampling, many of these newly described genera would be monotypic.

Next steps towards a more comprehensive revision of the generic classification. — Some problems remain to be addressed for a more practical and comprehensive generic classification of the Verrucariaceae. The lack of morphological characters to define some of the genera will be seen as a problem by many users of taxonomy. In such cases, molecular data may be taken into consideration as a source of synapomorphies. Strong signals from phylogenetic analyses of molecular data—corresponding to numerous synapomorphies and comparatively low levels of homoplasy—seem to us to be a substantial argument for evolutionary distinctiveness, particularly if a similar pattern is found in functionally independent parts of the genome. Sporodictyon, a recently resurrected genus (Savić & al., 2008), is an interesting example of a morphologically reasonably well-characterized genus (usually recognizable in the field) that has distinctive molecular features (Savić & Tibell, in press). When an alignment of the ITS-region of Polyblastia s.str., Thelidiun group, Sporodictyon and Clade C and E is studied, a number of synapomorphies, occurring in single positions, are found for Sporodictyon (Savić & al., 2008). In addition, there are also very distinctive indels in the Sporodictyon sequences, which are not alignable with the other sequences, and form ‘motifs’ characteristic at the generic level. If we want our classification to strongly reflect our evolutionary hypotheses, we would argue that genera might be recognized also in cases when easily observed morphological synapomorphies cannot be demonstrated, provided that they obtain strong support in phylogenetic analyses and from other molecular features (such as the indel ‘motifs’ mentioned)—ideally from independent parts of the genome.

The multiplication of monotypic genera for the paraphyletic species of Verrucaria is probably the most important issue remaining to be addressed. However,
considering the high species diversity within Verrucariaceae (about 730 species) and within Verrucaria (about 250 species), this problem might be an artifact of our still limited taxon sampling. It is very likely that none of the potentially new genera would remain monotypic using a broader taxon sampling. Moreover, the multiplication of the number of genera was to be expected when studying a family with one large genus including all species characterized by pleisomorphic traits.

Although some problems remain, significant progress has been made in the generic classification of the Verrucariaceae. Several new genera were described or resurrected, and concepts were either broadened or restricted for others. Many changes no doubt remain to be proposed, but they need further investigations based on additional taxon and gene samplings, as well as morphological and ecological studies. However, the main genera of Verrucariaceae and their phylogenetic relationships are now starting to be discernable, and these will, hopefully, help lichenologists to establish a more natural generic classification of this family.

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LITERATURE CITED


Appendix 1. Names of investigated species as accepted in this study and their citations. Recently proposed synonymies are also indicated.

Bagliettoa

Trimmatotele
- *T. periquista* (Norman) Norman ex Zahlbr. 1903.

Atla (Clade E)

Henrica (Clade E)

= *H. ramosula* B. de Lesd.

Sporodictyon (Clade E)
- *S. cruentum* (Körb.) Körb., Parerga Lichenol.: 332. 1863.
- *S. schaereri* A. Massal. în Flora 35: 326. 1852.
- *S. minutum* S. Savić & Tiöffl în Taxon 2009 în press.

Verrucaria (Clade E)

Dermatocarpon

Endocarpon (Endocarpon group)
- *E. pallidulum* (Nyl.) Nyl. în Lich. Exot.: 278. 1892.

Neocatapyrenium (Endocarpon group)

Other species investigated in the Endocarpon group

Heteroplasticum

Hydropunctaria
- *H. adriatica* (Zahlbr.) Keller & Gueidan, comb. nov.
- *H. maura* (Wahlenb.) Keller, Gueidan & Thüs, comb. nov.
- *H. rheiophila* (Zschacke) Keller, Gueidan & Thüs, comb. nov.
- *H. scabra* (Vězda) Keller, Gueidan & Thüs, comb. nov.

Parabagliettoa
- *P. cyanea* (A. Massal.) Gueidan & Cl. Roux, comb. nov.
- *P. dufourii* (DC.) Gueidan & Cl. Roux, comb. nov.

Placidium
- *P. umbrinum* (Breuss) Prieto & Breuss, comb. nov.

Placocarpus

Placopyrenium
Appendix 1. Continued.


**Polyblasia**
- *S. frustulenta* (Servít) (ined.).
- *P. sendtneri* Kremp. in Flora 38: 67. 1855.

**Staurothele (Staurothele group)**
- *S. areolata* (Ach.) Lettau in Hedwigia 52: 84. 1912.
- *S. fissa* (Taylor) Zwackh in Flora 45: 552. 1862.

**Catapyrenium (Staurothele group)**
- *C. daedaleum* (Kremp.) B. Stein in Cohn, Krypt.-Fl. Schlesien, 2, 2: 312. 1879.

**Placidipsis (Staurothele group)**
- *P. castanea* (A. Massal.) Körber, Parerga Lichenol.: 305. 1863.

**Other species investigated in the Staurothele group**

**Verrucula**
- *V. bryophila* Lönnr. in Flora 39: 631. 1858.
- *V. bryophila* Wahlenbergiella (Wahlenb.) Gueidan & Thüs, comb. nov.
- *V. striatula* (Wahlenb.) Gueidan & Thüs, comb. nov.

**Other species investigated in the Thelidium group**
- *T. fusca* Arnold in Flora 68: 147. 1885.
Appendix 2. Lectotypifications proposed in this study.

**Hydropunctaria maura** (Wahlenb.) Keller, Gueidan & Thüs, **comb. nov.** ≡ *Verrucaria maura* Wahlenb. in Ach., Methodus, Suppl.: 19. 1803 – Type: ‘Finnmarkiae Norvegicae in saxis petrisque maritimis aqua marina intermedium perfusis per insulas promontoriaque vulgaris,’ *collector unknown* s.n. (UPS!, lectotype; designated here).

This species was in need of a lectotypification. The type material of *Verrucaria maura* Wahlenb. (1803) includes 13 homoneous rock fragments, all collected in the same locality. The label indicates, for all fragments, ‘Finnmarkia Norvegia in insula sinus Altensis, 11 May 1802’. One of the fragments was designated as the lectotype. The other fragments, obviously coming from the same collection, can be considered as islectotypes. Because this species is known to be quite variable, a short description of the type material is provided below.

Thallus crustose-areolate, effigurate, dark brown to black. Areoles (0.2)0.4–0.6(0.8) × (0.1)0.3–0.4(0.5) mm, angular. Thallus margin sometimes paler and rimose-areolate. Upper cortex weakly differentiated, thin (10–15 μm), the upper most layer of cells dark pigmented. Algal layers 50–60 μm high, with algal cells arranged in vertical columns (palisade). Algal cells 7.5–10.0 μm in diameter, often in pairs or tetrads. Medulla absent. Dark basal layer present, with dark columns reaching up to the upper cortex. Areole margins also dark pigmented, continuous with the dark basal layer. Perithecium (0.2–0.3 mm in diameter), immersed in the thallus to slightly prominent. Excipulum dark-brown to black. Involucellum black, dimidiate, often appearing continuous with the black basal layer.

Hymenium I+ (blue) in Lugol. Short pseudoparaphyses 20.0–30.0 × 1.5–3.0 μm. Asci ca. 70 × 20 μm, 8-spored. Ascospores simple, colorless, 11.0–17.0 × 6.5–8.7 μm.


The lectotype had been selected by Breuss in 1990, but not subsequently published. It is designated here.


No lectotype has been designated in the past for *Staurothele clopima* (Wahlenb.) Th. Fr. Wahlenberg described this species as *Verrucaria clopima* in Acharius (1803, Suppl.: 20). The protologue included the following information: ‘Habitat Finnmarkiae Norvegicae in rupibus alpium saepeirrigatis umbrosisque ad Altenfjord menos copiosae, Wahlenberg. In Ostro-Gothia, Westring’. Original material collected by Wahlenberg included 17 numbered specimens, among which number 6 was chosen as a lectotype. The specimen information for the lectotype is: ‘Finnmarkia Norvegicae In parietibus rupiem montis Konsamfjället ad Altenfjord. 7 Maji 1802. Verrucaria clopima’, Wahlenberg (in Wahlenberg’s handwriting). The locality probably refers to Komsafjellet in Alta. The lectotype is a well-developed specimen with numerous perithecia, a very dark brown, thin, rimose thallus, the hymenial algal cells are cylindrical and the spores brown, 2 per ascus. Glued to the same sheet are also additional specimens of the same species plus another species, identified as *S. frustulenta* by Santesson in 1959. For the specimens in the upper part of the sheet another collecting date is indicated. Because of the mixed material in this collection, Santesson considered *V. clopima* to be a nomen dubium, and adopted the later name *S. fuscocuprea* (Nył.) Zschacke for this species (Santesson & al., 2004). Here we choose to lectotypify *Verrucaria clopima* on specimen 6, and hence also the type of *Staurothele*. As a consequence, *S. clopima* becomes the legitimate name for *S. fuscocuprea*.

**Wahlenbergiella mucosa** (Wahlenb.) Gueidan & Thüs, **comb. nov.** ≡ *Verrucaria mucosa* Wahlenb. in Acharius, Methodus, Suppl.: 23 (1803). Type: Norway, ‘Finnmark: Alten, adest *Verrucaria striatula*,’ 1802. *G. Wahlenberg* s.n. (UPS!, lectotype; designated here).

The type material of *Verrucaria mucosa* is kept in UPS and includes one unique specimen corresponding to a fragment of rock collected in ‘Alten, Finnmark’ by Wahlenberg in 1802. This fragment of rock is covered in part by a large thallus of *V. mucosa*, which is here designated as the lectotype, and by several small thalli of *V. striatula*.


The type material of *Verrucaria striatula* is kept in UPS and includes two specimens. The first specimen contained three fragments collected in *Finnmarkia* by G. Wahlenberg, and the second contained 22 homogeneous fragments collected in *Finnmarkia Norvegica in rupe ad litores maris peninsulæ juxta Pásekop* by Wahlenberg in 1802. The original diagnosis by Wahlenberg in Acharius (1803, Suppl.: 23) mentioned: ‘Finnmarkiae Norvegicae in petris marinis sub fluxus semper aqua immersis ubique vulgaris’. Therefore both specimens could be chosen for lectotype. Among the 22 fragments of the second specimen, the one bearing the largest thallus was selected as the lectotype. In the type material of *W. striatula*, specimens show carbonaceous structures, areole-like in the center of the thallus and lobe-like at the margin, instead of the typical ridge-like structures more commonly observed in this species. According to Santesson (1939), and also confirmed by Thüs (unpub.), an areole-like or almost lobate appearance of *W. striatula* is characteristic for specimens growing at the margins of their ecological amplitude, but differs from the morphology of the vast majority of the specimens growing under more suitable conditions.