

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

Cécile Gueidan^{1,16}, Sanja Savić², Holger Thüs³, Claude Roux⁴, Christine Keller⁵, Leif Tibell², Maria Prieto⁶, Starri Heiðmarsson⁷, Othmar Breuss⁸, Alan Orange⁹, Lars Fröberg¹⁰, Anja Amtoft Wynns¹¹, Pere Navarro-Rosinés¹², Beata Krzewicka¹³, Juha Pykälä¹⁴, Martin Grube¹⁵ & François Lutzoni¹⁶

¹ *Centraalbureau voor Schimmelcultures, P.O. Box 85167, 3508 AD Utrecht, the Netherlands. c.gueidan@cbs.knaw.nl (author for correspondence)*

² *Uppsala University, Evolutionary Biology Centre, Department of Systematic Botany, Norbyvägen 18D, 752 36 Uppsala, Sweden*

³ *Botany Department, Natural History Museum, Cromwell Road, London, SW7 5BD, U.K.*

⁴ *Chemin des Vignes vieilles, 84120 Mirabeau, France*

⁵ *Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland*

⁶ *Universidad Rey Juan Carlos, ESCET, Área de Biodiversidad y Conservación, c/ Tulipán s/n, 28933 Móstoles, Madrid, Spain*

⁷ *Icelandic Institute of Natural History, Akureyri division, P.O. Box 180, 602 Akureyri, Iceland*

⁸ *Naturhistorisches Museum Wien, Botanische Abteilung, Burggring 7, 1010 Wien, Austria*

⁹ *Department of Biodiversity and Systematic Biology, National Museum of Wales, Cathays Park, Cardiff CF10 3NP, U.K.*

¹⁰ *Botanical Museum, Östra Vallgatan 18, 223 61 Lund, Sweden*

¹¹ *Institute for Ecology, Department of Zoology, Copenhagen University, Thorvaldsensvej 40, 1871 Frederiksberg C, Denmark*

¹² *Departament de Biologia Vegetal (Botànica), Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain*

¹³ *Laboratory of Lichenology, Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland*

¹⁴ *Finnish Environment Institute, Research Programme for Biodiversity, P.O. Box 140, 00251 Helsinki, Finland*

¹⁵ *Karl-Franzens-Universität Graz, Holteigasse 6, 8010 Graz, Austria*

¹⁶ *Duke University, Biology Department, Box 90338, Durham, North Carolina 27708, U.S.A.*

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

TAXONOMY

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¹ Centraalbureau voor Schimmelcultures, P.O. Box 85167, 3508 AD Utrecht, the Netherlands. *c.gueidan@cbs.knaw.nl* (author for correspondence)

² Uppsala University, Evolutionary Biology Centre, Department of Systematic Botany, Norbyvägen 18D, 752 36 Uppsala, Sweden

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⁶ Universidad Rey Juan Carlos, ESCET, Área de Biodiversidad y Conservación, c/ Tulipán s/n, 28933 Móstoles, Madrid, Spain

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⁸ Naturhistorisches Museum Wien, Botanische Abteilung, Burgring 7, 1010 Wien, Austria

⁹ Department of Biodiversity and Systematic Biology, National Museum of Wales, Cathays Park, Cardiff CF10 3NP, U.K.

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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 periphyses 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 Adlococaceae, the other family of Verrucariales, 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 & Jahns, 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 (Servít, 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 (Servít, 1953) to propose a radically different system. Servít (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 (1996a) 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 nuLSU 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-Rosinés & al., 2007). The phylogeny of the clade E was obtained from a MP analysis using ITS and nuLSU (details in Savić & Tibell, 2008a). Finally, the phylogeny of *Hydropunctaria* was obtained from a MP analysis using nuLSU. 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*

Bagliettoa A. Massal., Mem. Lichenogr.: 146. 1853 – Type: *Bagliettoa limborioides* A. Massal., Mem. Lichenogr.: 147. 1853. Type: Italy, ‘Vive sulle roccie calcaree nel

Bosco Bagato presso Genova,’ *F. Bagliettoa* s.n. (VER, holotype, not seen; see Halda, 2003).

Diagnostic characters

- Calcicolous 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 involucrellum (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.

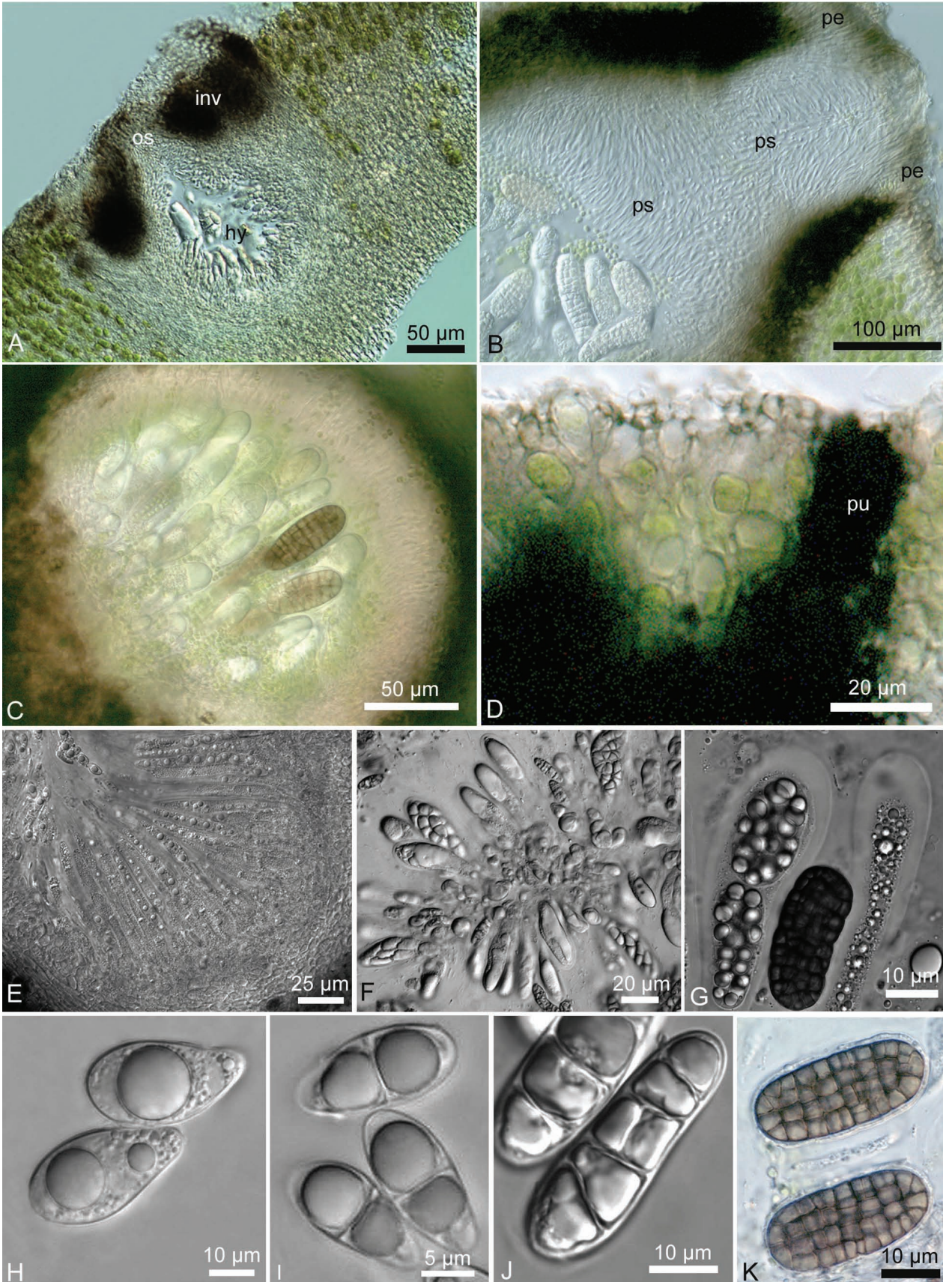
Literature. – Gueidan & Roux (2007, neotypification of *Verrucaria calciseda*), Gueidan & al. (2007, oil cells), Halda (2003, revision), Pinna & al. (1998, anatomy), Servit (1939, revision), Tretiač & Geletti (1997, physiology).

2. Clade C

(as delineated in Savić & al., 2008)

Trimmatothele 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 asci and much smaller spores. Ertz & Diederich (2004) argued (by analogy with other fungal genera including species with both octosporous and

Fig. 1. Main anatomical characters of species in Verrucariaceae [photos by C. Gueidan]. A, cross-section of a perithecium of *Wahlenbergiella mucosa* showing an apical involucrellum (hy: hymenium; inv: involucrellum; os: ostiole); B, cross-section of the ostiole of a perithecium of *Endocarpon adscendens* showing the short pseudoparaphyses (ps) and the paraphyses (pe); C, cross-section of the perithecium of *Staurothele areolata* showing small photobiont cells in the hymenium; D, cross-section of the thallus of *Hydropunctaria maura* showing a black punctum (pu); E, cross-section of a perithecium of *Placidium arboreum* showing cylindrical and uniseriate asci; F, squash mount of the hymenium of ‘*Polyblastia viridescens*’ showing clavate and biseriate asci; G, thick bitunicate ascus wall in *Endocarpon pusillum*; H, simple spores in ‘*Verrucaria hochstetteri*’; I, transversally uniseptate spores in *Placidopsis cinerascens*; J, transversally multiseptate spores in *Thelidium* sp.; K, brown muriform spores in *Staurothele frustulenta*.



polysporous asci, such as *Buellia* s.l. and *Candelariella*) that since only polysporous asci distinguish *Trimmatothele* 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 *Trimmatothele perquisita*, this combination was subsequently not accepted (Savić & al., 2008).

Trimmatothele Norman ex Zahlbr. in Engler & Prantl, Nat. Pflanzenfam. 1(1): 56. 1903 – Type: *Trimmatothele perquisita* (Norman) Norman ex Zahlbr. in Engler & Prantl, Nat. Pflanzenfam. 1(1): 56. 1903 (*Coniothete perquisita* Norman in Bot. Not. 1868: 192. 1868). Type: Norway, Nordland, Stegen, on calcareous rocks, *J.M. Norman s.n.* (O, lectotype, designated by Ertz & Diederich, 2004; not seen).

Diagnostic characters

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

Literature. – Ertz & Diederich (2004, taxonomy), Nash (2002, Sonoran desert), Savić & al. (2008, molecular phylogeny).

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.– Type: *Atla alpina* S. Savić & Tibell in Lichenologist

40: 273. 2008. Type: Sweden, Härjedalen, Ljusnedal par., Mittåkläppen, 1.8 km NNW of Djupdalsvallen, 62°43'56" N 12°27'11" E, 1170 m altitude, on vertical slate rocks facing SW, 2006, *Savić 3129* (UPS!), lectotype, designated by Savić & Tibell, 2008a).

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 *Polyblastia 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 photobionts within cephalodia.

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

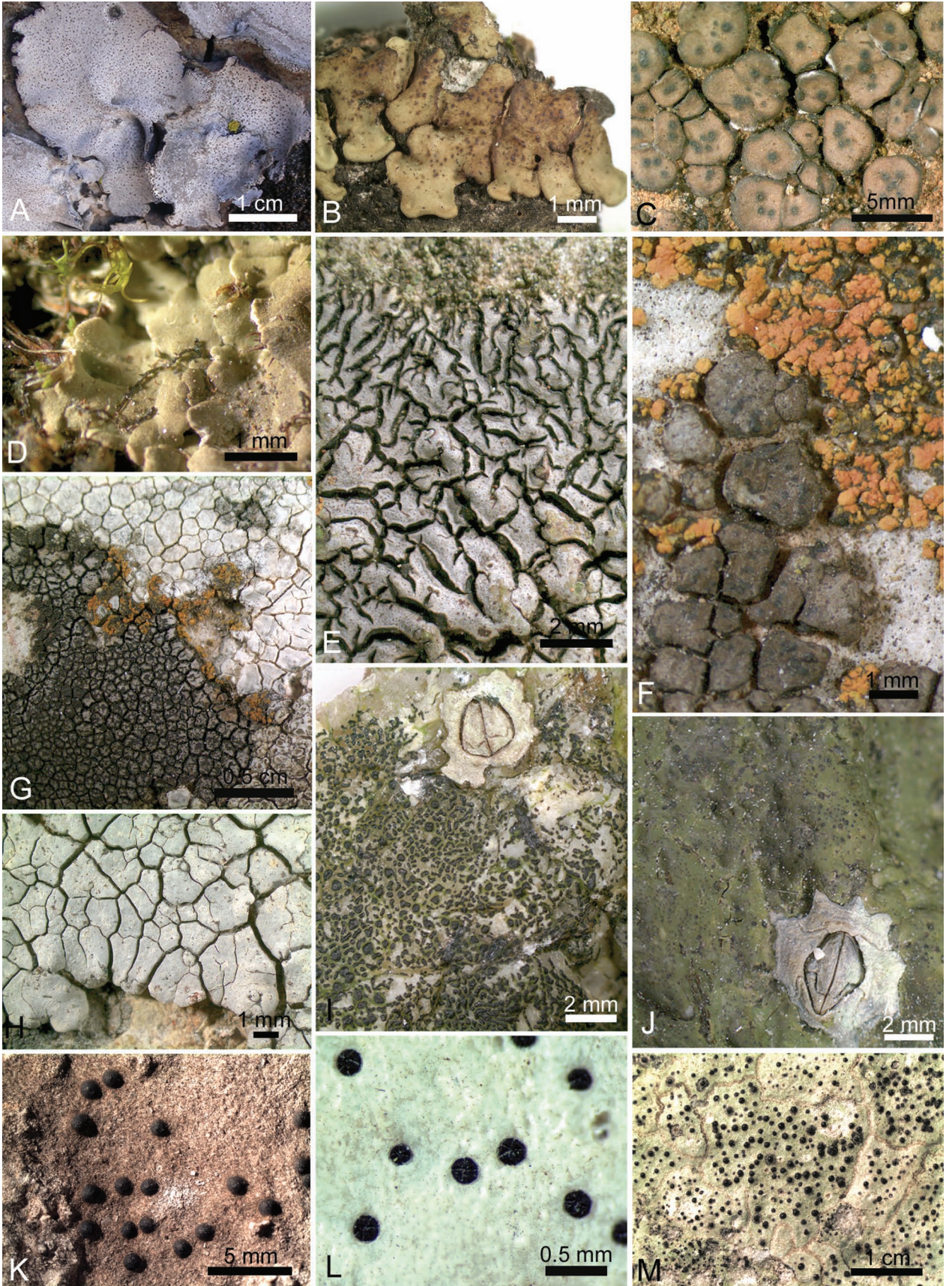
Henrica B. de Lesd. in Bull. Soc. Bot. France 68: 206. 1921 – Type: *Henrica ramulosa* B. de Lesd. in Bull. Soc. Bot. France 68: 206. 1921. Type: Spain, Cataluña, Lleida, Valle de Aran, 1990, *Hladun & Navarro-Rosinés s.n.* (BCC, neotype; designated by Navarro-Rosinés & Hladun, 1992: 129).

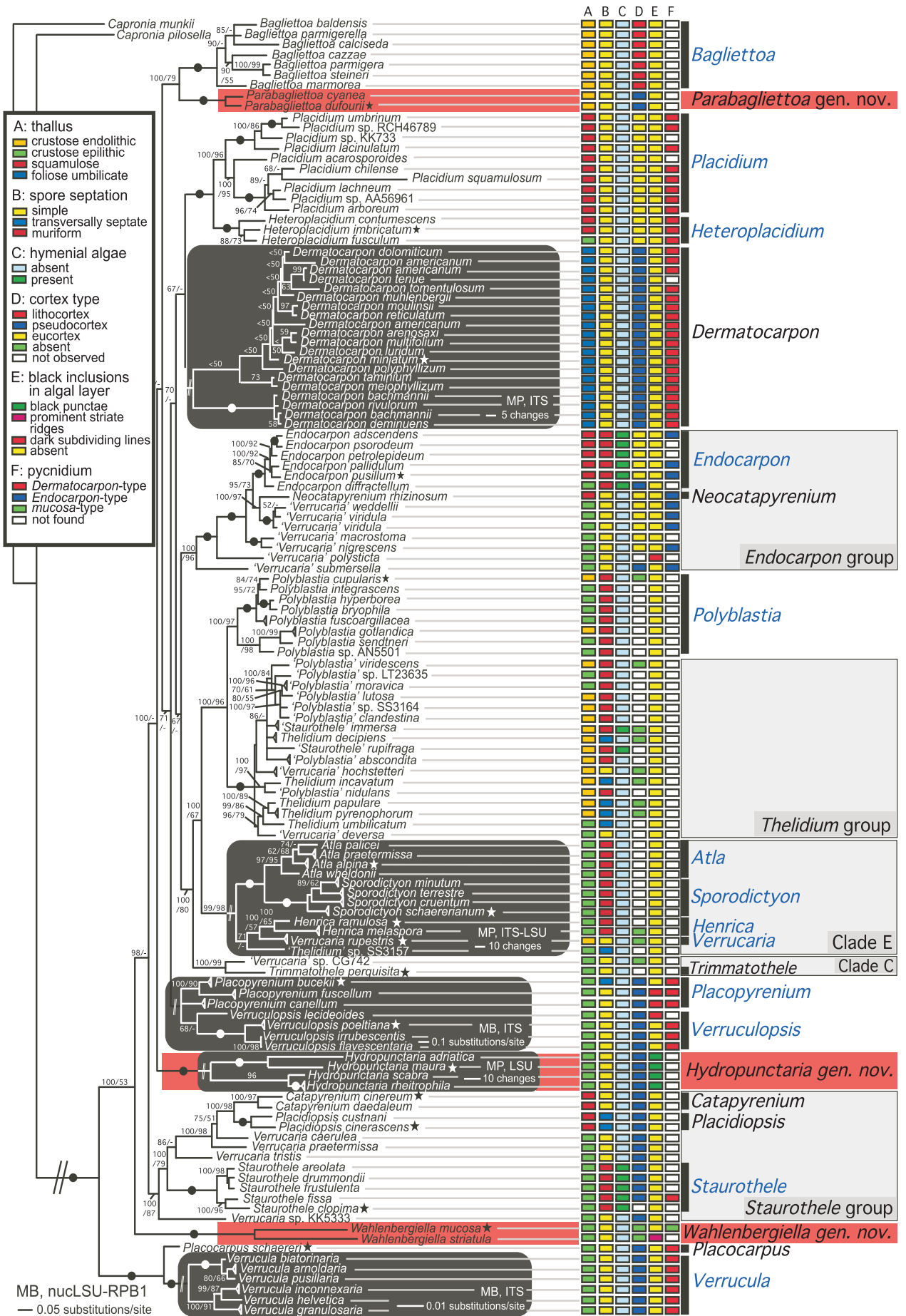
Diagnostic characters

- 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

Fig. 2. Main habits of species of Verrucariaceae. **A**, foliose umbilicate thallus of *Dermatocarpon* [photo F. Kauff]; **B**, squamulose and corticolous species *Placidium arboreum*; **C**, squamulose and terricolous species *Placidium umbrinum*; **D**, small squamulose thallus for *Catapyrenium daedaleum*; **E**, crustose placodioid species *Placopyrenium bucekii*; **F**, crustose species *Verrucula granulosa*, parasitic on *Caloplaca granulosa*; **G**, crustose species *Placopyrenium fuscillum*, parasitic on *Aspicilia calcarea*; **H**, crustose epilithic species *Placocarpus schaefereri*; **I**, marine species *Wahlenbergiella striatula*; **J**, marine species *Wahlenbergiella mucosa*; **K**, semiendolithic species *Verrucaria weddellii*; **L**, endolithic species *Bagliettoa baldensis*, with radially-split involucrellum; **M**, crustose endolithic species *Parabagliettoa cyanea*, with superficial perithecia [photos B–M by C. Gueidan].





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.

Literature. – Navarro-Rosinés & Hladun (1992, *Henrica ramulosa*), Savić & Tibell (2008b, Northern Europe).

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

Literature. – Savić & Tibell (in press, revision), Swinscow (1971, revision), Zschacke (1914, 1934, revisions).

Verrucaria Schrad., Spic. Fl. Germ. 1: 108. 1794, nom cons. –Type: *Verrucaria rupestris* Schrad., Spic. Fl. Germ. 1: 109. 1794. Type: ‘Ad saxa calcarea; passim etiam in lapidibus arenariis provenit,’ collector unknown s.n. (probably kept in GOET, not seen).

Diagnostic characters

- Thallus endolithic.
- Perithecia $\frac{3}{4}$ immersed to superficial, with dimidiate involucrellum.
- Excipulum 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 nuLSU 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-Rosinés & al., 2007; support values PP/ML bootstrap). Clade E was analyzed using MP and ITS-nuLSU (Savić & Tibell, 2008a; support values PP/MP bootstrap). *Hydropunctaria* was analyzed using MP and nuLSU (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*

Dermatocarpon Eschw., Syst. Lich.: 21. 1824 – Type (designated by Clements & Shear, Gen. Fungi: 289. Jun-Dec 1931): *Dermatocarpon miniatum* (L.) W. Mann, Lich. Bohemia: 66. 1825 (*Lichen miniatus* L., Sp. Pl.: 1149. 1753). Lectotype (designated by Jørgensen & al., 1994: 378): illustration in Dillenius 1742: 223, tab. 30, fig. 127; epitype (designated by Jørgensen & al., 1994: 378): Dillenius herbarium (OXF), tab. 30, no. 127B.

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. miniatum*-complex indicates that species boundaries remain to be defined in many cases.

Literature. – Amtoft & al. (2008, Ozarks), Breuss (1995, *Polyrhizion* section; 2003, Canada), Harada (1993a, Japan), Heiðmarsson (1996, pruina; 1998, species delimitation; 2001, Nordic countries; 2003, *miniatum* complex), Heiðmarsson & Breuss (2004, Sonoran desert), Orange (1998, British Isles).

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.

Endocarpon Hedw., Descr. Micr.-Anal. Musc. Frond. 2: 56. 1789 – Type: *Endocarpon pusillum* Hedw., Descr. Micr.-Anal. Musc. Frond. 2: 56. 1789. Type: 'circa Lipsiam obviam suit Schoenfeldi supra murum antiquum argilaceum, et ad declivitatem aggeris praestructi piscinae, in sylvia lindenthalensi', collector unknown s.n. (probably kept in G, not seen; in need of a lectotypification).

= *Willeya* Müll. Arg. in Flora 66: 345. 1883 – Type: *W. diffractella* (Tuck.) Müll. Arg.

= *Phalostauris* Clem., Gen. Fungi: 39, 173. 1909 – Type: *P. diffractella* (Tuck.) Clem.

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*.

Literature. – Breuss (2002a, Sonoran desert), Gueidan & al. (2007, pycnidia), Harada (1993b, Japan; 1997, Micronesia), McCarthy (1991, 2001a, Australia), Singh & Upreti (1984, India), Wagner (1987, perithecium ontogeny), Wagner & Letrouit-Galinou (1988, thallus ontogeny).

Neocatapyrenium H. Harada in Nat. Hist. Res. 2: 129. 1993 – Type: *Neocatapyrenium cladonioideum* (Vain.) H. Harada in Nat. Hist. Res. 2: 129. 1993 (*Siphula cladonioidea* Vain. in Bot. Mag. Tokyo 35: 47. 1921). Type: Japan, Honshu, Gunma-ken (as Prov. Kozuke), Mt. Myôgi, on rock, 19 April 1916, A. Yasuda 142 (TUR, holotype, not seen; see Harada, 1993a: 129).

Diagnostic characters

- Thallus squamulose.
- Squamules with dark rhizines (Breuss, 1996a).
- Upper cortex usually well differentiated (Gueidan & al., 2007).
- Ascospores simple.
- Pycnidia of *Endocarpon*-type.

Comments. – The catapyrenioid genus *Neocatapyrenium*, described by Harada (1993a) for species of *Catapyrenium* s.l. with *Endocarpon*-type pycnidia and dark rhizines as the only attachment structure, seems to belong to the *Endocarpon* group. However, the type of this genus, *N. cladonioideum*, was not sampled in our study. Therefore, further morphological and molecular work is necessary to confirm the proper use of the name *Neocatapyrenium*.

Literature. – Breuss (1990, monograph; 1996a, revision; 2005, *N. disparatum*), Gueidan & al. (2007, upper cortex), Harada (1993a, new genus).

6. *Heteroplacidium*

Heteroplacidium Breuss in Ann. Naturhist. Mus. Wien, B, 98 (Suppl.): 40. 1996 – Type: *Heteroplacidium imbricatum* (Nyl.) Breuss in Ann. Naturhist. Mus. Wien, B, 98 (Suppl.): 40. 1996 (*Endocarpon imbricatum* Nyl. in Bot. Not. 1853: 161. 1853). Type: France, Hérault, ‘ad Mireval prope Monspelium,’ W. Nylander s.n. (H-NYL 3985, lectotype; designated by Breuss, 1990: 73).

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. Massal.) 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 *Staurothele areolata*), were also suggested to belong to *Heteroplacidium* (Gueidan & al., 2007; Roux, 2008).

Literature. – Breuss (1990, monograph; 1996a, new genus; 2001a, Australia).

7. *Hydropunctaria*

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

Thallus crustosus, continuus ad rimosus vel areolatus, subgelatinosus. *Cortex superus* infirme evolutus. *Punctae* atrae in pagina thalli interdum visibiles. *Stratum algarum* e cortice supero non clare delineatum, cellulae algarum vulgo paliformes. *Medulla* paraplectenchymata, interdum tenuis vel destituta, saepe strato atro carbonaceo substituta. *Perithecia* immersa vel semi-immersa, involucrello nigro, dimidiato vel integro, cum pagina exasperata; excipulum pallidum ostiolo fusco vel omnino atro-pigmentosum. *Hymenium* incoloratum, K/I + caeruleum. *Hamathecium* periphysis et pseudoparaphysis brevibus formatum. *Asci* claviformes, 8-spori, bitunicati. *Ascosporae* simplices, rotundatae ad ellipsoidales, generatim longae (medium > 12 µm). *Conidia* aliquando observata. *Conidiosporae* simplices, bacilliformes, 3–4.5 × 1–1.5 µm. *Habitat* in petris aquae marinae et dulcis.

Description. – Aquatic and amphibious saxicolous species, colonizing either marine or freshwater habitats. *Thallus* crustose, continuous to rimose or areolate, yellowish-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 ostiole or entirely pigmented.

Hymenium colorless, K/I+ blue in Lugol's solution. *Hamathecium* consisting, at maturity, of periphyses and short pseudoparaphyses. *Asci* clavate, 8-spored, bitunicate. *Ascospores* simple, rounded to ellipsoid, of size variable between species or populations, but, in general, characterized by a median length greater than 12 µm and a length/width ratio greater than 2. *Conidia* sometimes present. *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 adriatica (Zahlbr.) Keller & Gueidan, **comb. nov.** [MB 512881] ≡ *Verrucaria adriatica* Zahlbr. in Denkschr. Kaiserl. Akad. Wiss., Wien Math.-Naturwiss. Kl. 92: 303. 1915 – Type: locality unknown, *collector unknown s.n.* (probably kept in W, not seen).

Hydropunctaria maura (Wahlenb.) Keller, Gueidan & Thüs, **comb. nov.** [MB 512882] ≡ *Verrucaria maura* Wahlenb. in Acharius, Methodus, Suppl.: 19. 1803 – Type: 'Finmarkiae Norvegicae in saxis petrisque maritimis aqua marina interdum perfusis per insulas promontoriaque vulgaris,' *collector unknown s.n.* (UPS!, lectotype; designated here; see Appendix 2).

Hydropunctaria rheitrophila (Zschacke) Keller, Gueidan & Thüs, **comb. nov.** [MB 512883] ≡ *Verrucaria rheitrophila* Zschacke in Verh. Bot. Vereins Prov. Brandenburg 64: 108. 1922 – Type: In einem Bächlein unter dem Meiseberge, Nordost-Harzes, 20 July 1920, Zschacke *s.n.* (B!, lectotype; designated by Harada, 1996b: 317; see Thüs, 2002: 99).

Hydropunctaria scabra (Vězda) Keller, Gueidan & Thüs, **comb. nov.** [MB 512884] ≡ *Verrucaria scabra* Vězda in Folia Geobot. Phytotax. 5: 308. 1970 – Type: Slowakei, Carpathen, Niedere Tatra: in declivi orientali montis 'Kosariska' dicti, in parte superiore vallis 'Biela voda', alt. 1300 m, ad lapides schistosos

siliceos in torrente minore, 7 October 1966, *collector unknown s.n.* Vězda Lich. Sel. exs. 876 (W and M, isotypes; see Thüs, 2002: 106).

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*.

Literature. – Brodo & Santesson (1997, key), Fleniken & Gibson (2003, Cape Ann, MA), Fletcher (1975, key), Grummann (1937, ecology), Harada (1996a, b, taxonomy), Lewis (1964, 1965, ecology), Renobales & Noya (1991, Costa Vasca), Thüs (2002, revision).

8. *Parabagliettoa*

Parabagliettoa Gueidan & Cl. Roux, **gen. nov.** [MB 512879] ≡ *Verrucariomyces* Thomas ex Cif. & Tomas. in Ist. Bot. Univ. Lab. Crittog. Pavia Atti ser. 5. 10(1): 31, 58. 1953, nom. illeg. (see Lücking & Hawksworth, 2007) – Type: *V. dufourii* (DC.) Thomas ex Cif. & Tomas.

Thallus crustaceus endolithicus de continuo ad rimosum, de cinereoviridi ad cinereofuscum, saepe limitatus atrofusca hypothallina linea, thallum quoque dividente in quibusdam speciebus. *Cortex superus* constitutus prosoplectenchymati tenui et minutis crystallis sparso, corticalibus cellulis subcoloratis in culmine aliquando stratis. *Algosum stratum* non distincte delimitatum, cum algosis cellulis glomerulis. *Medulla* prosoplectenchymati sine macrospheroidibus formata. *Perithecium* de superficiali ad ½ aut ¾ immersum, de globuloso ad planum in apice, 0.1–0.4 mm diametro, cum nigro involucrello, de dimidiato ad integrum; excipulum de incolorato ad pallidofuscum. *Hymenium* incoloratum, K/I + caeruleum. *Hamathecium* formatum periphysis et brevibus pseudoparaphysis, eis posterioribus copiosis aut non, sed nunquam expansis nec unquam disjunctis ut in quibusdam *Bagliettoae* speciebus.

Ascus claviformis, cum 8 sporis, bitunicatus. *Ascosporae* incoloratae, ellipsoidales, plerumque simplices, sed aliquando uniseptatae. *Conidia* aliquando in thalli margine observata. *Conidiosporae* simplices, bacilliformes, $3.5\text{--}4.5 \times 0.5\text{--}1.5 \mu\text{m}$. *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 dark brown 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 $\frac{1}{2}$ or $\frac{3}{4}$ 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 periphyses 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, $3.5\text{--}4.5 \times 0.5\text{--}1.5 \mu\text{m}$.

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

Diagnostic characters

- Calcicolous endolithic species (Fig. 2M).
- Upper cortex not well differentiated (pseudocortex).
- Medulla lacking oil cells.
- Perithecia 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.

Parabagliettoa cyanea (A. Massal.) Gueidan & Cl. Roux, **comb. nov.** [MB 512886] \equiv *Verrucaria cyanea* A. Massal., Mem. Lichenogr.: 144. 1853 – Type: ‘Vive sulle roccie nummoliche del Paese di Garda (Rocca) nel Veronese,’ collector unknown s.n. (probably kept in VER, not seen).

Parabagliettoa dufourii (DC.) Gueidan & Cl. Roux, **comb. nov.** [MB 512885] \equiv *Verrucaria dufourii* DC. in Candolle & Lamarck, Fl. Franç., ed. 3, t. 2: 318.

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

Literature. – Khodosovtsev (2003, Crimea), Clauzade & Roux (1985, occidental Europe).

9. *Placidium*

Placidium A. Massal., Symm. Lich. Nov.: 75. 1855 – Type (designated by Massalongo, Sched. Crit. 5: 100. 1856): *Placidium michelii* A. Massal., Sched. Crit. 5: 100. 1856 – Type: ‘Ad terram ubique in prov. Veronensi.—in nemore *Mantico* (78–80 metr. supra mare), in Mont. *Belocca* prope Tremniacum 700–900 metr. supra mare.’ Massalongo s.n. Massalongo, Lich. exs. Ital. 161 (W, lectotype; designated by Breuss, 1990: 95).

Diagnostic characters

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

Comments. – Together with five other genera (*Anthracocarpon*, *Catapyrenium*, *Involucropyrenium*, *Neocatapyrenium*, *Scleropyrenium*), *Placidium*, *Heteroplacidium* and *Clavascidium* 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 *Clavascidium* was shown to be more problematic (Gueidan & al., 2007). The type of *Clavascidium*, *C. umbrinum*, as well as an undescribed *Clavascidium*-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 *Clavascidium* differ by the shape of their young asci and by the ascospore arrangement. *Clavascidium* has clavate asci 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 *Clavascidium* than to the other species of *Placidium*, and, together with *Clavascidium* 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 (*Clavascidium* 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 *Clavascidium* 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.).

Placidium umbrinum (Breuss) Prieto & Breuss, **comb. nov.** [MB 512889] ≡ *Catapyrenium umbrinum* Breuss in Linzer Biol. Beitr. 22(1): 78–79. 1990 – Type: Jugoslawien: Dalmatien, Nordseite der Svilaja-Planina zwischen Sinj und Vrlika, Kalk, ca. 1400 m, 14.5.1906, *J. Baumgartner s.n.* (W!, holotype) ≡ *Clavascidium umbrinum* (Breuss) Breuss in Ann. Naturhist. Mus. Wien. B, 98 (Suppl.): 41. 1996.
Literature. – Breuss (1990, monograph; 1996a, key; 2002b, Sonoran desert).

10. *Placocarpus*

Placocarpus Trevis., Consp. Verruc.: 19. 1860 –Type (designated by Breuss, 1985: 314): *P. schaeferi* (Fr.) Breuss in Pl. Syst. Evol. 148: 314. 1985 (*Parmelia schaeferi* Fr., Lichenogr. Europ. Reform.: 106. 1831). Type: Gallia, Lozera, sub *Parmelia schaeferi*, *Dufour s.n.* E.M. Fries, Lichenogr. Europ. Reform. exs. 106 (UPS!, lectotype; designated here; see Appendix 2).
Diagnostic characters

- Juvenile parasite on *Lecanora muralis* var. *versicolor*.
- Thallus thick, areolate to placodioid (Fig. 2H), with subumbilicate areoles.
- Medulla prosoplectenchymatous, 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 schaeferi*, 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).

Literature. – Breuss (1985, resurrected genus), Gueidan & al. (2007, molecular phylogeny).

11. *Placopyrenium*

Placopyrenium Breuss in Stud. Geobot. 7 (Suppl.): 182. 1987 – Type: *Placopyrenium bucekii* (Nádv. & Servít) Breuss in Stud. Geobot. 7 (Suppl.): 182. 1987 (*Dermatocarpon bucekii* Nadv. & Serv. in Beih. Bot. Centralbl. 55B: 267. 1936). Type: Bulgarien, Rhodope, Karlik Batak, 1800 m, Silikatgestein, *J. Buček s.n.* (M, lectotype; designated here; see Servít, 1936: 267).

Diagnostic characters

- 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 involucrellum.
- 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-Rosinés & 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. polysticta*, which is nested in the *Endocarpon* group, and *V. lecideoides*, now in *Verruculopsis*). *Placopyrenium fuscillum* 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 Verrucariaceae, 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 Verrucariaceae (Janex-Favre, 1971, 1975), and, at maturity, are located in the upper part of the perithecial 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).

Literature. – Breuss (1987, new genus; 2002c, Sonoran desert; 2009, key), Khodosovtsev (2005, Crimea), Ménard & Roux (1995, *P. bucekii*), Navarro-Rosinés & al. (2007; new combinations), Orange (2004, *fuscella* group), Zehetleitner (1978, parasitic *Verrucaria*).

12. *Polyblastia*

Polyblastia A. Massal., Ric. Auton. Lich. Crost.: 147. 1852 –Type: *Polyblastia cupularis* A. Massal., Ric. Auton. Lich. Crost.: 148. 1852. Type: ‘Vive sulle rocce arenacee della Provincia Veronese, specialmente nel paese di Tregnago (Zengiè),’ collector unknown s.n. (probably kept in VER, not seen).

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 medium-sized.

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.* *lutosa*) 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), Servít (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.

Staurothele Norman, Conat. Praem. Gen. Lich.: 28. 1852, nom. cons. – Type: *Staurothele clopima* (Wahlenb.) Th. Fr., Lich. Arct.: 263. Mai-Dec 1860 (*Verrucaria clopima* Wahlenb. in Kongl. Vetensk. Akad. Nya Handl.: 152. 1809). Type: ‘Finmarkia Norvegicae In parietibus rupiem montis Konsamfjället ad Altenfjord.’ 7 May 1802. *G. Wahlenberg 6* (UPS!, lectotype; designated here; see Appendix 2).

Diagnostic characters

- Thallus crustose epilithic, continuous to areolate.
- Upper cortex weakly differentiated (pseudocortex).
- Perithecium 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 epilithic 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*.

Literature. – Harada (1992, taxonomy), Janex-Favre (1975, anatomy and ontogeny), McCarthy (2001b, Australia), Swinscow (1963, Great-Britain), Thomson (1991, North-America; 2002, Sonoran desert).

Catapyrenium Flot. in Bot. Zeitung (Berlin) 8: 361. 1850 – Type (designated by Flotow, 1850: 361): *Catapyrenium cinereum* (Pers.) Körb., Syst. Lich. Germ.: 325. 1855 (*Endocarpon cinereum* Pers., Neue Annal. Bot. 1: 28. 1794). Type: ‘Reperi hanc speciem prope Schanzfeld: circa die alte Kirche & prope montem Meisner,’ collector unknown s.n. (in need of lectotypification);

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).

Literature. – Breuss (1990, revision; 1996a, generic concept; 2000, pycnidia; 2001b, Australia; 2002d, Sonoran desert); Breuss & Hansen (1988, Greenland).

Placidiopsis Beltr., Lich. Bassan.: 212. 1858 – Type: *Placidiopsis grappae* Beltram., Lich. Bassan.: 212. 1858 (= *Placidiopsis cinerascens* (Nyl.) Breuss). Type: Italy, Prov. Venezia, ‘In terra fra *Lecidea decipiens* a 1500–1600 m sul Grappa,’ *V. Trevisan* 929 (FI, lectotype, designated by Breuss, 1996b: 79).

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*”.

Literature. – Breuss (1983, *P. pseudocinerea*; 1994, North-Africa; 1996b, revision; 2002e, Sonoran desert), Breuss & Hansen (1988, Greenland), Etayo & Breuss (1994, *P. cavicola*), Harris (1979, *P. minor*), Thomson (1987, North-America).

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), perithecium anatomy (with or without involucrellum 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).

Thelidium A. Massal., Framm. Lichenogr.: 15. 1855 – Type (designated by Clements & Shear, 1931: 288): *Thelidium amylaceum* A. Massal., Symm. Lich. Nov.: 103. 1855. Type: ‘Ad saxa eonica in opp. Velo (M. Purga) Prov. Veronens. et potiss. in opp. Campofontana ad saxa oolitica (M. Alba),’ *A. Massalongo* (probably kept in VER, not seen; in need of a lectotypification).

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 circumscribe this genus.

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

15. *Verrucula*

Verrucula J. Steiner in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 105 (1): 444. 1896 – Type: *Verrucula aegyptiaca* (Müll. Arg.) J. Steiner in Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 105 (1): 444. 1896 (*Verrucaria aegyptica* Müll. Arg. in Rev. Mycol. 8: 82. 1880). Type: ‘Egypt, Wüste [Wüste] Wadi Cheresa in Aegyptem (between Cairo and Suez).’ 1877. *J. Schweinfurth s.n.* (G, lectotype; see Navarro-Rosinés & al., 2007).

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 colorless, simple to rarely uniseptate.
- Pycnidia of *Dermatocarpon*-type.

Comments. – *Verrucula* is sister to the monotypic genus *Placocarpus*. Both genera only include parasitic species. Young thalli of *Placocarpus schaeereri* 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), Zehetleitner (1978, parasitic *Verrucaria*).

16. *Verruculopsis*

Verruculopsis Gueidan & al. in Bull. Soc. Linn. Provence 58: 139. 2007 – Type: *Verruculopsis poeltiana* (Clauzade & Cl. Roux) Gueidan & al. in Bull. Soc. Linn. Provence 58: 139. 2007 (*Verrucaria poeltiana* Clauz. & Cl. Roux in Nova Hedwigia 79: 194. 1984). Type: ‘Francio, Provenco, Bouches-du-Rhône, Mouriès, Alpilles, Le Destet, sur krutaĵo el kalkopetro kompakta

kaj tre kohera, el supra rognacio, orient.: de U ĝis N, dekl.: 10–90°, 100 m.’ 19 October 1982. *G. Clauzade & C. Roux 22640* (MARSSJ, holotype; see Navarro-Rosinés & al., 2007).

Diagnostic characters

- Non-parasitic, or parasitic on *Caloplaca* with anthraquinones.
- Thallus areolate to squamulose-areolate, sometimes reduced.
- Upper cortex weakly differentiated (pseudocortex).
- Medulla I–.
- Excipulum, at maturity, with pale brown base, the upper part being dark brown.
- Ascospores simple, colorless.
- Pycnidia of *Dermatocarpon*-type.

Comments. – *Verruculopsis* is sister to the genus *Placopyrenium*. Like *Placopyrenium* (as newly circumscribed by Navarro-Rosinés & al., 2007), *Verruculopsis* includes mostly—but not only—species parasitic on other lichens. Species of *Verruculopsis* are morphologically and anatomically very similar to species of *Verrucula* (see previous section “*Verrucula*”).

Literature. – Clauzade & Roux (1984, *V. poeltiana*), Navarro-Rosinés & al. (2007, monograph), Ménard & Roux (1991, *V. irrubescentis*).

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 cristis atris carbonaceis interruptus. *Cortex superus* saepe nullus. *Stratum algarum* hyphis verticalis formatum, cellulae algarum interdum paliformes. *Medulla* absens vel praesens. *Punctae atrae* in pagina thalli desunt. *Perithecia* immersa vel superficialia, 0.08–0.2 mm diametro, involucrello dimidiato vel deminuto; excipulum pallidum vel omnino atrum. *Hymenium* incoloratum, K/I + caeruleum. *Hamathecium* periphysis et pseudoparaphysis brevibus formatum. *Asci* claviformes, 8-spori, bitunicati. *Ascosporae* simplices, incoloratae, subrotundatae ad ellipsoidales, generatim breves (medium < 12 µm). *Conidia* unilocularia, ostiolo nigro, cellulae conidiogenae elongatae parieti pycnidii directe 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 involucrellum 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 \times 1–2 μm .

Diagnostic characters

- Marine species with green to olive-green subgelatinous thalli (Fig. 2I, J).
- 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 involucrellum, greenish thallus color, and the general absence of an upper cortex or a differentiated medulla.

Wahlenbergiella mucosa (Wahlenb.) Gueidan & Thüs, **comb. nov.** [MB 512888] \equiv *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; see Appendix 2).

Wahlenbergiella striatula (Wahlenb.) Gueidan & Thüs, **comb. nov.** [MB 512887] \equiv *Verrucaria striatula*

Wahlenb. in Acharius, Methodus, Suppl.: 21. 1803 – Type: Norway, ‘Finnmark: Finmarkiae Norvegi-cae, peninsula juxta Påsekop, in rupe littores maris,’ 25 April 1802 and 20 May 1802. *G. Wahlenberg s.n.* (UPS!, lectotype; designated here; see Appendix 2).

Literature. – Brodo & Sloan (2005, Queen Charlotte Islands), Flenniken & Gibson (2003, Cape Ann, MA), Fletcher (1975, key), Ried (1969, physiology), Dethier & Steneck (2001, growth).

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 *Henrica* (Savić & Tibell, 2008b). The delineations of the squamulose genera *Endocarpon* and *Heteroplacidium* were broadened to also include crustose species (Gueidan

& al., 2007). *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 placodioid (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 *Hydropunctaria*. New generic delimitations of currently valid genera are also proposed. The squamulose genus *Clavascidium* is here subsumed within *Placidium*, 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., *Thelidium* 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 plesiomorphic 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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Appendix 1. Names of investigated species as accepted in this study and their citations. Recently proposed synonymies are also indicated.

Bagliettoa

- *B. baldensis* (A. Massal.) Vězda in Biblioth. Lichenol. 16: 363. 1981.
- *B. calciseda* (DC.) Gueidan & Cl. Roux in Bull. Soc. Linn. Provence 58: 187. 2007.
- *B. cazzae* (Zahlbr.) Vězda & Poelt in Biblioth. Lichenol. 16: 363. 1981.
- *B. marmorea* (Scop.) Gueidan & Cl. Roux in Mycol. Res. 111: 1157. 2007.
- *B. parmigera* (J. Steiner) Vězda & Poelt in Biblioth. Lichenol. 16: 363. 1981.
- *B. parmigerella* (Zahlbr.) Vězda & Poelt in Biblioth. Lichenol. 16: 363. 1981.
- *B. steineri* (Kušan) Vězda in Biblioth. Lichenol. 16: 363. 1981.

Trimmatothele

- *T. perquisita* (Norman) Norman ex Zahlbr. 1903.

Atla (Clade E)

- *A. palicei* S. Savić & Tibell in Lichenologist 40: 277. 2008.
- *A. praetermissa* S. Savić & Tibell in Lichenologist 40: 279. 2008.
- *A. alpina* S. Savić & Tibell in Lichenologist 40: 273. 2008.
- *A. wheldonii* (Travis) S. Savić & Tibell in Lichenologist 40: 280. 2008.

Henrica (Clade E)

- *H. melaspora* (Taylor in Hook.) S. Savić & Tibell in Nordic J. Bot. 26: 243. 2008.
 - *H. theleodes* (Sommerf.) S. Savić, Tibell & Nav.-Ros. in Nordic J. Bot. 26: 244. 2008.
- = *H. ramulosa* B. de Lesd.

Sporodictyon (Clade E)

- *S. cruentum* (Körb.) Körb., Parerga Lichenol.: 332. 1863.
- *S. schaeerianum* A. Massal. in Flora 35: 326. 1852.
- *S. minutum* S. Savić & Tibell in Taxon 2009 in press.
- *S. terrestre* (Th. Fr.) S. Savić & Tibell in Mycol. Res. 112: 1311. 2008.

Verrucaria (Clade E)

- *V. rupestris* Schrad., Spic. Fl. Germ. 1: 109. 1794.

Dermatocarpon

- *D. americanum* Vain. in Dansk Bot. Ark. 4(11): 25. 1926.
- *D. aenosaxi* Amtoft in Bryologist 111(1): 24. 2008.
- *D. bachmannii* Anders in Hedwigia 63: 271. 1922.
- *D. deminuens* Vain. in Acta Soc. Fauna Fl. Fenn. 49(2): 15. 1921.
- *D. dolomiticum* Amtoft in Bryologist 111(1): 27. 2008.
- *D. luridum* (Dill. ex With.) J.R. Laundon in Lichenologist 16: 222. 1984.
- *D. meiophyllizum* Vain. in Acta Soc. Fauna Fl. Fenn. 49(2): 16. 1921.
- *D. miniatum* (L.) W. Mann, Lich. Bohemia: 66. 1825.
- *D. moulinsii* (Mont.) Zahlbr. in Engler & Prantl, Nat. Pflanzenfam. 1(1): 60. 1903.
- *D. mühlenbergii* (Ach.) Müll. Arg. in Bot. Jahrb. Syst. 6: 377. 1885.
- *D. multifolium* Amtoft in Bryologist 111: 36. 2008.
- *D. polyphyllizum* (Nyl.) Blomb. & Forsell, Enum. Plant. Scand.: 96. 1880.
- *D. reticulatum* H. Magn. in Ann. Cryptog. Exot. 5: 18. 1932.
- *D. rivulorum* Dalla Torre & Sarnth., Fl. Tirol: 504. 1902.
- *D. taminium* Heiðmarsson in Mycol. Res. 107: 466. 2003.
- *D. tenue* Heiðmarsson in Mycol. Res. 107: 467. 2003.

- *D. tomentulosum* Amtoft in Bryologist 109: 182. 2006.

Endocarpon (Endocarpon group)

- *E. adscendens* (Anzi) Müll. Arg. in Bull. Murith. Soc. Valais. Sci. Nat. 10: 58. 1881.
- *E. diffractellum* (Nyl.) Gueidan & Cl. Roux in Mycol. Res. 111: 1157. 2007.
- *E. pallidulum* (Nyl.) Nyl. in Hue, Lich. Exot.: 278. 1892.
- *E. petrolepideum* (Nyl.) Nyl. in Hue, Lich. Exot.: 278. 1892.
- *E. psorodeum* (Nyl.) Th. Fr. in Blomb. & Forsell, Enum. Plant. Scand.: 97. 1880.
- *E. pusillum* Hedw., Descr. Micr.-Anal. Musc. Frond. 2: 56. 1789.

Neocatapyrenium (Endocarpon group)

- *N. rhinosum* (Müll. Arg.) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 41. 1996.

Other species investigated in the Endocarpon group

- ‘*Verrucaria*’ *macrostoma* Dufour ex DC., in Candolle & Lamarck, Fl. Franç., ed. 3, t. 2: 319. 1805.
- ‘*Verrucaria*’ *nigrescens* Pers. in Bot. Mag. (Römer & Usteri) 15: 36. 1795.
- ‘*Verrucaria*’ *polysticta* Borrer in Hook. & Sowerb., Engl. Bot. Suppl. 2: plate 2741. 1834.
- ‘*Verrucaria*’ *submersella* Servít, Česk. Lišejníky Čel. Verrucariaceae: 142. 1954.
- ‘*Verrucaria*’ *viridula* (Schrad.) Ach., Methodus, Suppl.: 16. 1803.
- ‘*Verrucaria*’ *weddellii* Servít in Stud. Bot. Českoslov. 7: 80. 1946.

Heteroplacidium

- *H. contumescens* (Nyl.) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 40. 1996.
- *H. fusculum* (Nyl.) Gueidan & Cl. Roux in Mycol. Res. 111: 1157. 2007.
- *H. imbricatum* (Nyl.) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 40. 1996.

Hydropunctaria

- *H. adriatica* (Zahlbr.) Keller & Gueidan, comb. nov.
- *H. maura* (Wahlenb.) Keller, Gueidan & Thüs, comb. nov.
- *H. rheitrophila* (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. acarosporoides* (Zahlbr.) Breuss in Bull. California Lichen Soc. 7(2): 39. 2000.
- *P. arboreum* (Schweinitz) Lendemer in Mycotaxon 90(2): 320. 2004.
- *P. chilense* (Räsänen) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 38. 1996.
- *P. lachneum* (Ach.) de Lesd. in Ann. Cryptog. Exot. 5: 100. 1932.
- *P. lacinulatum* (Ach.) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 39. 1996.
- *P. squamulosum* (Ach.) Breuss in Ann. Naturh. Mus. Wien, B, 98 (Suppl.): 39. 1996.
- *P. umbrinum* (Breuss) Prieto & Breuss, comb. nov.

Placocarpus

- *P. schaeereri* (Fr.) Breuss in Pl. Syst. Evol. 148: 314. 1985.

Placopyrenium

Appendix 1. Continued.

- *P. bucekii* (Nádv. & Servít) Breuss in Nimis & Poelt, Stud. Geobot. 7 (Suppl.): 182. 1987.
 - *P. canellum* (Nyl.) Gueidan & Cl. Roux in Bull. Soc. Linn. Provence 58: 174. 2007.
 - *P. fuscillum* (Turner) Gueidan & Cl. Roux in Bull. Soc. Linn. Provence 58: 174. 2007.
- Polyblastia**
- *P. bryophila* Lönnr. in Flora 39: 631. 1858.
 - *P. cupularis* A. Massal., Ric. Auton. Lich. Crost.: 148. 1852.
 - *P. fuscoargillacea* Anzi in Comment. Soc. Crittog. Ital. 2: 26. 1864.
 - *P. gotlandica* (Servít) (ined.).
 - *P. hyperborea* Th. Fr., Lich. Arct.: 266. 1860.
 - *P. integrascens* (Nyl.) Vain. in Acta Soc. Fauna Fl. Fenn. 49: 104. 1931.
 - *P. sendtneri* Kremp. in Flora 38: 67. 1855.
- Staurothele (Staurothele group)**
- *S. areolata* (Ach.) Lettau in Hedwigia 52: 84. 1912.
 - *S. clopima* (Wahlenb.) Th. Fr., Lich. Arct.: 263. Mai–Dec 1860.
 - = *S. fuscocuprea* (Nyl.) Zschacke in Hedwigia 54: 187. 1913—vide Santesson & al. 2004.
 - *S. drummondii* (Tuck.) Tuck., Gen. Lich.: 257. 1872.
 - *S. fissa* (Taylor) Zwackh in Flora 45: 552. 1862.
 - *S. frustulenta* Vain. in Acta Soc. Fauna Fl. Fenn. 49(2): 93. 1921.
- Catapyrenium (Staurothele group)**
- *C. cinereum* (Pers.) Körb., Syst. Lich. Germ.: 325. 1855.
 - *C. daedaleum* (Kremp.) B. Stein in Cohn, Krypt.-Fl. Schlesien, 2, 2: 312. 1879.
- Placidiopsis (Staurothele group)**
- *P. custmani* (A. Massal.) Körber, Parerga Lichenol.: 305. 1863.
 - = *P. cartilaginea* (Nyl.) Vain. in Acta Soc. Fauna Fl. Fenn. 49(2): 23. 1921.
 - *P. cinerascens* (Nyl.) Breuss in Pl. Syst. Evol. 148: 315. 1985.
- Other species investigated in the Staurothele group**
- ‘*Verrucaria caerulea* DC. in Candolle & Lamarck, Fl. Franç., ed. 3, t. 2: 318. 1805.
 - ‘*Verrucaria praetermissa* (Trevis.) Anzi in Comment. Soc. Crittog. Ital. 2(1): 24. 1864.
 - ‘*Verrucaria tristis* (A. Massal.) Kremp. in Flora 40: 376. 1857, nom. illeg., non *V. tristis* Hepp in Zoll., Syst. Verz., heft. 1-2: 8. 1854.
- Thelidium (Thelidium group)**
- *T. decipiens* (Hepp) Kremp. in Denkschr. K. Bayer. Bot. Ges. 4(2): 246. 1861.
 - *T. incavatum* (Nyl.) Mudd, Man. Brit. Lich.: 295. 1861.
 - *T. papulare* (Fr.) Arnold in Flora 68: 147. 1885.
 - *T. pyrenophorum* (Ach.) Mudd, Man. Brit. Lich.: 294. 1861.
 - *T. umbilicatum* Th. Fr., Bot. Not.: 112. 1865.
- Other species investigated in the Thelidium group**
- ‘*Polyblastia abscondita* (Nyl.) Arnold in Flora 46: 141. 1863.
 - ‘*Polyblastia clandestina* (Arnold) Jatta, Syll. Lich. Ital.: 567. 1900.
 - ‘*Polyblastia lutosa* Zschacke, Rabenh. Krypt.-Fl. 9(1): 467. 1934.
 - ‘*Polyblastia moravica* Zschacke in Preslia 5: 3. 1927.
 - ‘*Polyblastia nidulans* (Stenh.) Arnold in Ber. Naturhist. Vereins Augsburg 14: 64. 1861.
 - ‘*Polyblastia viridescens* Zschacke, Rabenh. Krypt.-Fl. 9(1): 416. 1934.
 - ‘*Staurothele immersa* (A. Massal.) Dalla Torre & Sarnth., Fl. Tirol: 553. 1902.
 - ‘*Staurothele rupifraga* (A. Massal.) Arnold in Verh. Zool.-Bot. Ges. Wien 30: 149. 1880.
 - ‘*Verrucaria deversa* Vain. in Acta Soc. Fauna Fl. Fenn. 49(2): 49. 1921.
 - ‘*Verrucaria hochstetteri* Fr., Lichenogr. Eur. Reform.: 435. 1831.
- Verrucula**
- *V. arnoldaria* Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 152. 2007.
 - *V. biatorinaria* (Zehetl.) Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 153. 2007.
 - *V. granulosa* (Clauzade & Zehetl.) Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 157. 2007.
 - *V. helvetica* (B. de Lesd.) Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 158. 2007.
 - *V. inconnexaria* Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 160. 2007.
 - *V. pusillaria* Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 165. 2007.
- Verruculopsis**
- *V. flavescentaria* Gueidan, Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 166. 2007.
 - *V. irrubescentis* (Ménard & Cl. Roux) Gueidan, Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 168. 2007.
 - *V. lecideoides* (A. Massal.) Gueidan & Cl. Roux in Bull. Soc. Linn. Provence 58: 174. 2007.
 - *V. poeltiana* (Clauzade & Cl. Roux) Gueidan, Nav.-Ros. & Cl. Roux in Bull. Soc. Linn. Provence 58: 168. 2007.
- Wahlenbergiella**
- *W. mucosa* (Wahlenb.) Gueidan & Thüs, comb. nov.
 - *W. striatula* (Wahlenb.) Gueidan & Thüs, comb. nov.

Appendix 2. Lectotypifications proposed in this study.

Hydropunctaria maura (Wahlenb.) Keller, Gueidan & Thüs, **comb. nov.** \equiv *Verrucaria maura* Wahlenb. in Ach., Methodus, Suppl.: 19. 1803 – Type: ‘Finmarkiae Norvegicae in saxis petrisque maritimis aqua marina interdum 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 homogeneous rock fragments, all collected in the same locality. The label indicates, for all fragments, ‘Finmarkia 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 isoelectotypes. 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) \times (0.1)0.3–0.4(0.5) mm, angular. Thallus margin sometimes paler and rimose-areolate. Upper cortex weakly differentiated, thin (10–15 μ m), the upper most layer of cells dark pigmented. Algal layer 50–60 μ m high, with algal cells arranged in vertical columns (palisade). Algal cells 7.5–10.0 μ m 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. Perithecia (0.2–0.3 mm in diameter), immersed in the thallus to slightly prominent. Excipulum dark-brown to black. Involucrellum black, dimidiate, often appearing continuous with the black basal layer. Hymenium I+ (blue) in Lugol. Short pseudoparaphyses 20.0–30.0 \times 1.5–3.0 μ m. Asci ca. 70 \times 20 μ m, 8-spored. Ascospores simple, colorless, 11.0–17.0 \times 6.5–8.7 μ m.

Placocarpus schaereri (Fr.) Breuss in Pl. Syst. Evol. 148: 314. 1985 \equiv *Parmelia schaereri* Fr., Lichenogr. Europ. Reform. 1831: 106. 1831 – Type: Gallia, Lozera, sub *Parmelia schaereri*, *Dufour s.n.* E.M. Fries, Lichenogr. Europ. Reform. exs. 106 (UPS!, lectotype; designated here).

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

Staurothele clopima (Wahlenb.) Th. Fr., Lich. Arct.: 263. Mai–Dec 1860 = *Staurothele fuscocuprea* (Nyl.) Zschacke, Hedwigia 54: 187. 1913—fide Santesson & al. (2004) – Type: ‘Finmarkia Norvegicae In parietibus rupiem montis Konsamfjället ad Altenfjord.’ 7 May 1802. *G. Wahlenberg 6* (UPS!, lectotype; 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 Finmarkiae Norvegicae in rupibus alpium aqua nivali saepeirrigatis umbrosisquae ad Altenfjord minus copiose, 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: ‘Finmarkia 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* (Nyl.) 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.** \equiv *Verrucaria mucosa* Wahlenb. in Acharius, Methodus, Suppl.: 23 (1803). Type: Norway, ‘Finmark: 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*.

Wahlenbergiella striatula (Wahlenb.) Gueidan & Thüs, **comb. nov.** \equiv *Verrucaria striatula* Wahlenb. in Acharius, Methodus, Suppl.: 21. 1803 – Type: Norway, ‘Finmark: Finmarkiae Norvegicae, peninsula juxta Påsekop, in rupe littores maris,’ 25 April 1802 and 20 May 1802. *G. Wahlenberg s.n.* (UPS!, lectotype; designated here).

The type material of *Verrucaria striatula* is kept in UPS and includes two specimens. The first specimen contained three fragments collected in ‘Finmarkia’ by G. Wahlenberg, and the second contained 22 homogeneous fragments collected in ‘Finmarkia Norvegica in rupe ad littores maris peninsulae juxta Påsekop’ by Wahlenberg in 1802. The original diagnosis by Wahlenberg in Acharius (1803, Suppl.: 23) mentioned: ‘Finmarkiae 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.