16 Basidiolichens

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I. Introduction

This is an updated version of my previous review on basidiolichens (Oberwinkler 2001).

Originally the basidiolichens were considered to be exclusively tropical lichens, best represented by the genera *Cora* and *Dictyonema*. In his monograph of *Clavaria* and allied genera, Corner (1950) treated several phycophilous clavarioid fungi from temperate zones in the genus *Clavulinopsis* and *Lentaria*. Mycofloristic studies initiated a breakthrough in further recognitions of basidiolichens. *Clavaria mucida* was considered to be an extratropical basidiolichen by Geitler (1955). Poelt (1959) reported *Clavulinopsis septentrionalis* from the Alps and *Lentaria* (*Clavaria*) *mucida* from Bavaria (1962). Finally, Gams (1962) recognized the association of *Botrydina* and *Coriscium* thalli with *Omphalina* basidiocarps, and Poelt and Oberwinkler (1964) analysed their anatomical structures. A remarkable lichenized clavarioid species has been found in the Sierra de Santa Marta, Colombia, and described as *Lepidostroma terricolens* (Mägdefrau and Winkler 1967). *Pseudocraterellus leptoglossoides* (Corner 1966) was transferred as a basidiolichen into a new genus, *Semiomphalina*, by Redhead (1984). A comparative morphology of all known basidiolichen genera, known at that time, has been published by Oberwinkler (1970). In a study on new or interesting clavarioid fungi from Yunnan, Petersen and Zang (1986) reported on *Multiclavula fossicola*, and *Multiclavula sinensis*, both “with film of algae”. Redhead and Kuyper (1987) studied fully lichenized arctic alpine *Omphalina* species and proposed nomenclatorial changes for them in *Botrydina*, *Coriscium*, *Omphalina*, and *Phytoconis*. Jørgensen (1989) erected a new basidiolichen species

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without basidiocarps from the Venezuelan Andes, *Omphalina foliacea*, a taxon that was transferred into its own genus, *Marandiomphalina*, by Diederich and Lawrey (2007). Another anamorphic basidiolichen, also from the Andes had been also described as a new genus, *Acantholichen*, by Jørgensen (1998). From Costa Rica, two *Dictyonema* species (Chaves et al. 2004), and *Multiclavula ichthyiformis* (Lawrey et al. 2007) were introduced as new taxa.

Based on transmission electron microscopic studies, Roskin (1970) reported on the ultrastructure of the host–parasite interaction in *Cora pavonia* (*Dictyonema glabratum*). Detailed ultrastructural analyses were carried out by Oberwinkler (1980, 1984) for representatives of most basidiolichen genera. Three main types of fungus–alga interactions in basidiolichens were found and documented.

Cora pavonia was the favoured basidiolichen for ecophysiological studies (Lange 1965; Feige 1969; Coxson 1987a, b, c; Larcher and Vareschi 1988; Lange et al. 1994; Trembley et al. 2002a, b).

The axenic culture of mycobionts of basidiolichens is very difficult. Experiments of Langenstein (1994) were successful to separate myco- and photobionts, to synthesize *Botrydina*, and to characterize essential steps in the ontogeny of the thallus globules.

Lichenized *Omphalina* species and related non-lichenized ones were used as a model for understanding coevolution and the influence of lichenization on evolutionary rates (Lutzoni and Vilgalys 1995a, b; Lutzoni 1997; Lutzoni and Pagel 1997).

Figure 16.1 is used as a guideline for this chapter. The scheme is considered to facilitate various comparative interpretations in the following text. It comprises and compares structural components (cellular interactions, thalli, basidiocarps) with taxonomic units on the generic level (*Athelia*, *Athelopsis*, *Dictyonema*, *Cora*, *Cyphellostereum*, *Lepidostroma*, *Multiclavula*, *Semiomphalina*, *Lichenomphalia*). The anamorphic genera *Acanthonema* and *Marchandiomphalina* cannot be included in accurate positions in this overview because basidiocarps are not yet known.

II. Morphology of the Lichen Thalli

In basidiolichens exclusively members of the Agaricomycetes (Fig. 16.2) are lichenized. They are obligatorily associated with cyanobacteria and/or green algae. The morphological expression of this symbiontic association is the lichen thallus (Figs. 16.1, 16.3, 16.4a, b, 16.5, 16.6a–c, 16.7c, f, 16.8a, b, 16.9a, b, e, f).

The most conspicuous basidiolichen thalli are those of *Cora pavonia* (*Dictyonema glabratum*, Fig. 16.3h, i). Some morphological and anatomical observations of this species were reported by Tomaselli and Caretta (1969). The cellular composition of the thallus and the fungus–alga compartmentation was studied and illustrated by Oberwinkler (1970). He also compared *Cora* with *Dictyonema* species and discussed the considerable differences in thallus architecture of both taxa. In his comparative morphological study also *Corella* and *Vainiocora* were included. The thallus of these taxa is identical and determined by the fungus, forming leaf-like structures with upper and lower pseudoparenchymatous layers and central compartments in which *Rhizonema* trichomes are densely packed as photosynthetic units. In *Dictyonema* the *Rhizonema* trichomes are long filaments ensheathed with mantles of densely longitudinally oriented hyphae which are shortly bent in a wave-like manner (Figs. 16.3f, 16.7a, b). The same structural characters are present in *Rhipidonema*, a taxon which cannot be separated from *Dictyonema*.

A new genus and species, *Acantholichen pannarioides*, has been proposed by Jørgensen (1998). It is based on sterile thalli composed of clampless hyphae with acanthohyphidia and *Rhizonema* trichomes (Fig. 16.7e, f). Thallus architecture and hyphae–algae interactions are very similar to those of the *Dictyonema*–*Cora* group. The lichen grows *Pannaria*-like on debris, mosses, and other lichens.

Also some *Athelia* species are associated with *Rhizonema* and/or coccomyxoid green algae (Oberwinkler 1970). There are no macroscopically distinct thalli. The fungus–alga interaction occurs in basal layers of the basidiocarp (Fig. 16.5b). As shown by Oberwinkler (1970), in

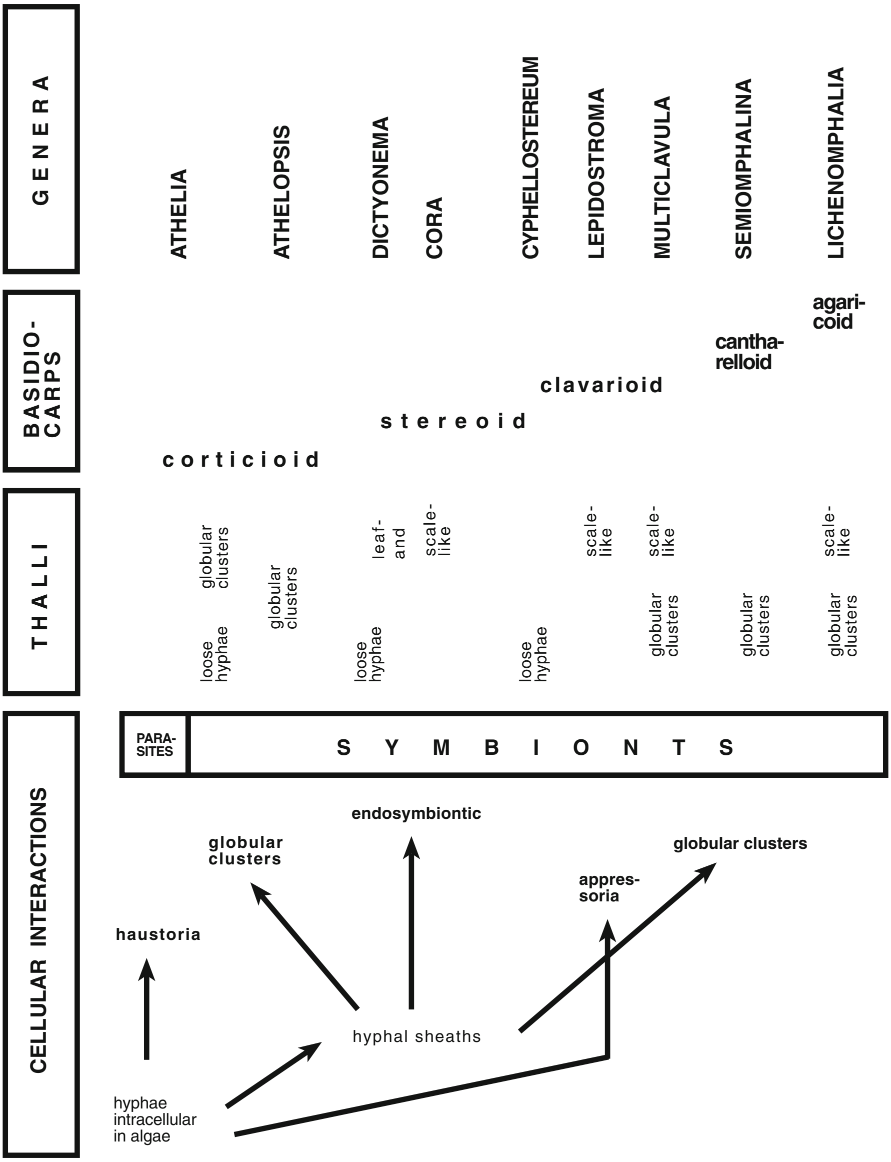

Fig. 16.1. Scheme of basidiolichen genera and their most important structural features, modified after Oberwinkler (2001). Because basidiocarps are not known, *Acanthonema* and *Marchandiomphalina* could not be included in this overview. The arrangement of genera reflects increasing complexity of basidiocarps, i.e. corticioid–stereoid–clavarioid–agaricoid, thus corresponding with the general structures in homobasidiomycetes. The distribution of types of lichen thalli is intermixed. Loose hyphae, globular clusters, and scaly thalli occur convergently. The cellular interactions show an informative distribution pattern: *Athelia* can be parasitized with haustoria but also hyphae can surround algae in globular clusters. Hyphal sheaths in the *Dictyonema* group are always associated with endosymbiontic hyphae of the *Scytonema* (= *Rhizonema*) symbionts. Appressoria occur only in *Lepidostroma*. Comparatively simple globular clusters and scale-like thalli are formed by *Multiclavula* species. Complex globular structures of the *Botrydina* type, and associations of globules in scale-like thalli (*Coriscium*) are present in *Lichenomphalia*

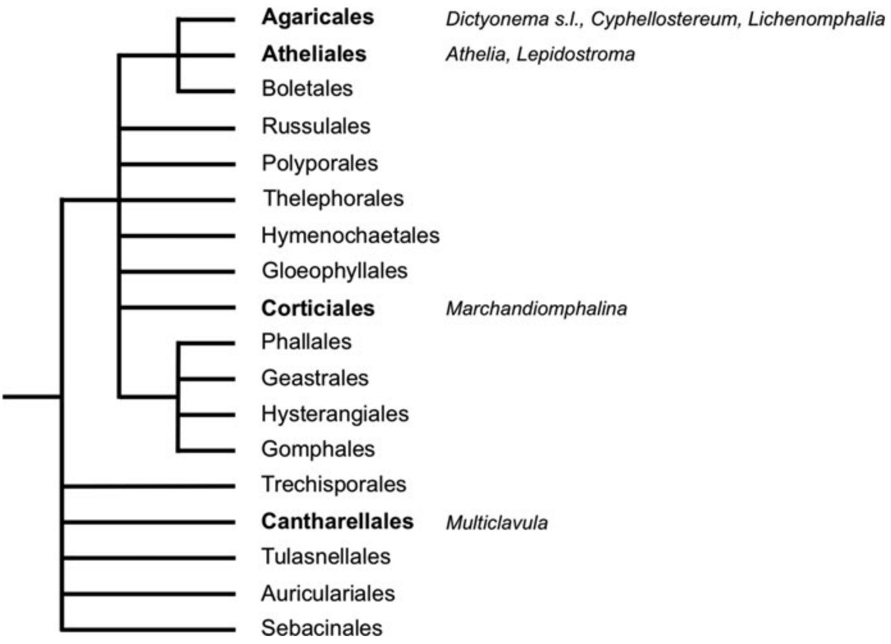

Fig. 16.2. Simplified phylogenetic dendrogram indicating the orders (in *bold*) in which lichenized species occur. They are restricted to Agaricomycetes. The dendrogram is in agreement with generally accepted phylogenies of Agaricomycotina and is modified after Hibbett et al. (2007)

one fungal fructification, both cyanobacteria and green algae can serve as photobionts. In contrast, the closely related *Athelia arachnoidea* and *A. epiphylla* are strong parasites of algae and lichens (Poelt and Jülich 1969b; Oberwinkler 1970; Arvidsson 1979; Gilbert 1988; Parmasto 1998), penetrating the host algal cells with haustoria (Fig. 16.5a).

Elias Fries (1820) was among the first to recognize green material at the basis of *Agaricus ericetorum*, which in fact is the assemblage of tiny lichenized globules (Fig. 16.3k, l), later named as *Botrydina vulgaris* by Brébisson (1844). Because of simple globose thallus structures, *B. vulgaris* has been considered a primitive lichen (Acton 1909). Observations in the field led Gams (1962) to propose specific connections between the sterile lichen thalli *Botrydina* and *Coriscium* with basidiomycetes of the agaricoid genus *Omphalina* (Figs. 16.3k–p, 16.9a–c, e, f). Poelt and Oberwinkler (1964) and Oberwinkler (1970) studied the micromorphology of the thalli and of the associated *Omphalina* basidiocarps and were able to provide structural evidence for lichenization of *Omphalina* species. Dolipores with perforated parenthesomes in hyphae of *Coriscium* were found by Henssen and Kowallik (1976) and Oberwinkler (1980, 1984); and they were also independently documented in *Botrydina* by Boissière (1980) and Oberwinkler (1980, 1984). The globose *Botrydina* thalli have a most complex cell architecture in which algal compartments are inserted within a compact, pseudoparenchymatous hyphal system (Fig. 16.9b, c). This was analysed with the light microscope by Poelt and Oberwinkler (1964) and Oberwinkler (1970) and with the transmission electron microscope by Oberwinkler (1980, 1984). Haustoria are lacking, but there is a dense cell to cell contact of myco- and photobionts. The *Botrydina* globules are dynamic structures which undergo a strongly regulated ontogeny. During this process, photobionts are able to reproduce mitotically to build up more and more algal compartments, but still within the solid pseudoparenchymatous hyphal structure of the enlarging globules. *Botrydina*-like thalli occur also in *Semiomphalina leptoglossoides* (Redhead 1984).

Globular clusters of fungus–alga interactions are also present in *Athelopsis* (Coste and Royaud 1994). The globules are formed in the basal layer of the thin corticioid basidiocarps

(Fig. 16.5d, e), thus not representing macroscopically visible thalli.

Rather conspicuous thallus layers are found in several *Multiclavula* species. In *M. mucida* irregular globose thalli (Oberwinkler 1970, 1984; Figs. 16.3a, 16.4b) are embedded in a gelatinous matrix on wet and decaying wood. Soil-inhabiting *Multiclavula* species have various types of thalli, some appear as uniform crustous layers, others are more separated in granular or scale-like units. These species have not yet been studied comparatively. Nelsen et al. (2007) described *M. ichtyiformis* from Costa w?>Rica. Their light microscopic photographs indicate a thallus structure similar to that in *M. mucida*. However, cellular details of fungus–alga interactions cannot be seen in these illustrations. Originally, two new *Multiclavula* species were proposed from Rwanda (Fischer et al. 2007). Comparing them with *Multiclavula calocerum* (= *Lepidostroma calocerum*), their interpretations of the cellular thallus architecture are rather misleading. The presence of upper and lower pseudopyrenchymatous layers in a scale-like to foliose thallus is a general prerequisite, and not at all a "unique feature amongst the clavarioid lichenized basidiomycetes" (Fischer et al. 2007). In addition, the *Coriscium* thallus is quite different from the *Lepidostroma* thallus, as can easily be seen in the illustrations of Poelt and Oberwinkler (1964) and Oberwinkler (1970, 1980, 1984, 2001). Molecular data indicated that these Rwandan clavarioid species belong in the genus *Lepidostroma* (Ertz et al. 2008).

The scale- and leaf-like types of basidiolichen thalli are rather diverse in architecture and do not occur in closely related taxa. The best known of these is *Coriscium viride* (Figs. 16.3m, o, p, 16.9e, f), described as a sterile lichen by Vainio (1890). The thalli are morphologically distinct and anatomically highly structured (Fig. 16.5f). There are upper and lower pseudoparenchymatous epidermis-like fungal layers and central loose hyphae with globular chambers for the phytobionts, surrounded by hyphal sheats. The gross morphology varies specifically.

Also the thallus of *Lepidostroma calocerum* (Mägdefrau and Winkler 1967) is scaly with distinct and dense hyphal pseudoparenchyms and loose inner hyphae, but the overall cellular composition is totally different from the *Coriscium* type (Fig. 16.6c). This is another example for the multiple convergent evolution of structurally similar and functionally identical photosynthetic organs which are not homologous. According to the description and light microscopic photos of *Multiclavula rugaramae* (Fischer et al. 2007), the thallus is *Lepidostroma*-like. Based on molecular data, this species and *Multiclavula akaragae* were transferred to the genus *Lepidostroma* by Ertz et al. (2008).

III. Associations of Mycobionts and Photobionts and Ultrastructure of Fungus–Alga Interactions

Three main types of fungus–alga interactions occur in basidiolichens (Fig. 16.1): (1) hyphal sheaths from which haustoria-like endosymbiontic hyphae originate, (2) appressoria, and (3) solid globular clusters formed by densely arranged hyphae surrounding green algae without haustoria.

1. *Rhizonema* trichomes are enveloped by hyphae and penetrated by haustoria, originating from the mantle hyphae in *Dictyonema, Cora* and *Acantholichen* (Fig. 16.7a–c, e–g). This interactive system, which has been misinterpreted as a dual fungal symbiosis with the algal host (Slocum and Floyd 1977), is different from all others known in basidio- and ascolichens. Because of the vitality of the photobiont and the lack of any signs of significant structural changes, the mycobiont–photobiont relationship has been interpreted as an endosymbiontic interaction (Oberwinkler 1980; Slocum 1980). Tschermak-Woess (1983) records a strong compression of the lichenized trichomes and a lack of cyanophycin in *Dictyonema moorei* studied with the light microscope. Yet, there is no proof that these changes are due to mutualistic interactions. The interaction of myco- and photobiont in *Acantholichen pannarioides* has also been studied by light microscopy by Oberwinkler (1980; Fig. 16.7e, f). It was

Fig. 16.3. Basidiocarps and thalli of basidiolichens. All photographs by F. Oberwinkler; (**a–d**, **j**, **k**, **m**, **n**) *bar* 5 mm; (**e**) *bar* 1 cm; (**f**, **l**, **p**) *bar* 0.5 mm; (**g–i**) *bar* 1 cm; (**o**) *bar* 2 mm. (**a**) *Multiclavula mucida*, Wertach, Germany, 4 Oct 1996. (**b**) *Multiclavula corynoides*, Oberjoch, Germany, 3 Oct 2004. (**c**) *Multiclavula* sp., Zamora, Ecuador, 15 July 2004. (**d**) *Multiclavula sinensis*, Nan Nou Shan, Yunnan, China, 15 Aug 1995. (**e**) *Lepidostroma calocerum*, Sierra de Santa Marta, Colombia, 20 June 1978. (**f**) *Dictyonema interruptum*, Levada de Portela, Madeira, 28 Mar 1984. (**g**) *Dictyonema sericeum*, El Valle, Mérida, Venezuela, 11 Mar 1969. (**h**) *Cora pavonia*, upper side of thallus, Laguna Negra, Mérida, Venezuela, 18 Apr 1969. (**i**) *Cora pavonia*, underside of thallus with fresh hymenium, Laguna Negra, Mérida, Venezuela, 18 Apr 1969. (**j**) *Cyphellostereum pusiolum*, basidiocarp, Mérida, Venezuela, 15 June 1969. (**k**) *Lichenomphalia umbellifera*, basidiocarp and thallus, Bschiesser, Oberjoch, Germany, 4 July 1984. (**l**) *Lichenomphalia umbellifera*, thallus, Bschiesser, Oberjoch, Germany, 4 July 1984. (**m**) *Lichenomphalia velutina*, basidiocarp and thallus, Paramo de Mucubaji, Mérida, Venezuela, 4 Oct 1968. (**n**) *Lichenomphalia hudsoniana*, basidiocarp and thallus, Bschiesser, Oberjoch, Germany, 25 July 1979. (**o**) *Lichenomphalia hudsoniana*, basidiocarp and thallus, Bschiesser, Oberjoch, Germany, 3 Sept 1984. (**p**) *Lichenomphalia hudsoniana*, thallus, Bschiesser, Oberjoch, Germany, 3 Sept 1984

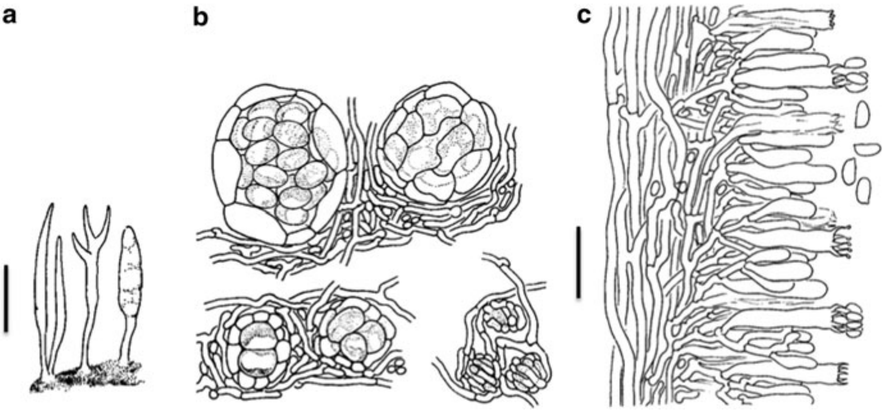

Fig. 16.4. *Multiclavula mucida* (after Oberwinkler (1970, 2001)). (**a**) Basidiocarps with basal lichen thalli; *bar* 5 mm. (**b**) Interactive globular units of hyphae and *Coccomyxa* in different developmental stages; *bar* 20 μm. (**c**) Section through the subhymenium and hymenium with basidia of different ages and basidiospores; note clamped hyphae; *bar* 20 μm

found that it is essentially the same as in *Cora* and *Dictyonema*.

2. In *Lepidostroma calocerum* hyphae become attached to the algal cells and develop into morphologically distinct appressoria (Oberwinkler 1980, 1984). The attached algae degenerate and collapse (Fig. 16.6c, d), non-attached ones in the thallus are vital and obviously capable for cell division. Such details cannot be seen in the illustrations by Fischer et al. (2007) of *L. akaragae* (as *Multiclavula a.*) and *L. rugaramae* (as *Multiclavula r.*).
3. Globose hyphal–algal associations are characteristic of *Multiclavula* species (Oberwinkler 1980, 1984; Fig. 16.4b) and of *Botrydina vulgaris* (Boissière 1980, Oberwinkler 1980, 1984; Fig. 16.9b, c). Comparable globular clusters of fungal and algal cells develop inside the thalli of *Coriscium viride* (Oberwinkler 1980, 1984; Fig. 16.9f). Though densely packed, the algal cells are only surrounded by hyphae, and are not penetrated by haustoria. The globular thallus with clustered green algae has also been found in *Athelopsis* (Coste and Royaud 1994; Fig. 16.5d, e), and in otherwise differently lichenized species of *Athelia* (Oberwinkler 1970; Fig. 16.5b), *Cyphellostereum* (as *Clavaria* sp. by Oberwinkler 1970; Fig. 16.8b), and *Lepidostroma* (Oberwinkler 1970). In *Sistotrema brinkmannii* (Oberwinkler 1970) the association of myco- and photobiont certainly is facultative because the fungus normally grows on wood without algae. The common *Resinicium bicolor* also is not lichenized but quite often grows together with green algae (Poelt and Jülich 1969b; Oberwinkler 1970).

To my knowledge, no additional detailed studies on fungus–alga interactions in basidiolichens have been published.

IV. Fungi

All fungal partners of basidiolichens are members of the Agaricomycetes (Fig. 16.2). No lichenized Pucciniomycotina, Ustilaginomycotina, Tremellomycetes or Dacrymycetes are known. Thus, basidiolichens belong to one large relationship with a high number of nonlichenized species and few lichenized ones.

A. *Multiclavula*

Multiclavula (Petersen 1967) is a taxonomic segregate of *Clavaria* s.l., *Lentaria*, and *Clavulinopsis* sensu Corner (1950, 1956). Species of the genus were considered to share a special hyphal morphology as a unifying characteristic, and often basidia can have more than four sterig-

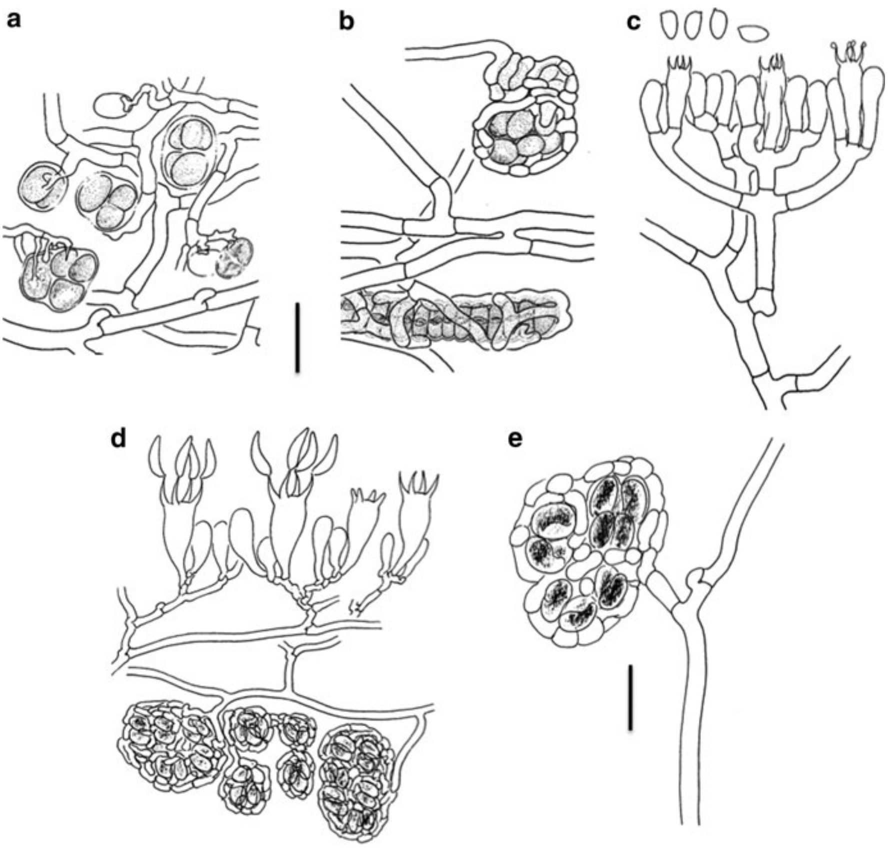

Fig. 16.5. *Athelia* (**a–c**) and *Athelopsis* (**d**, **e**) (rearranged after Oberwinkler (1970, 2001)); (**a–d**) *bar* 20 µm, (**e**) *bar* 10 µm. (**a**) Hyphae and haustoria of *Athelia epiphylla* parasitic on unicellular green algae. (**b**) Hyphae of *Athelia andina* partly ensheathing *Scytonema* (= *Rhizonema*). Note central hypha in *Rhizonema* (*below*) and unicellular green algae (*above*). (**c**) Section of basidiocarp of *Athelia andina* with loose subhymenial hyphae and non-thickening hymenium with basidia of different developmental stages and basidiospores. (**d**) Section through *Athelopsis* with lichenized lower part and whole basidiocarp showing the total cellular construction of the basidiolichen in the sporulating stage with basidia in different developmental stages and basidiospores. (**e**) *Athelopsis* hyphae ensheathing *Coccomyxa* algae; note clamped hypha

mata. Originally, also *Clavaria* (*Lepidostroma*) *calocera* was included in *Multiclavula* by Petersen (1967), but *Lepidostroma* is distinctly separate from *Multiclavula* in the micromorphology of the basidia and thalli, and in phylogenetic hypotheses, based on molecular data (Fig. 16.2).

The phylogenetic analysis of several *Multiclavula* (Nelsen et al. 2007), *Clavulina*, *Sistotrema* species, and *Hydnum rufescens*, groups *S. brinkmannii* and *Multiclavula* in one clade. *S. brinkmannii* can be associated with algae, occasionally forming *Botrydina*-like globules, however, apparently not as lichenized structures (Oberwinkler 1970).

B. *Marchandiomphalina*

The genus *Marchandiomphalina* was proposed for an anamorphic Basidiolichen (Diederich and Lawrey 2007), originally described as *Omphalina foliacea* (Jørgensen 1989). The lichen resembles a large *Leptogium* but has green photobionts and basidiomycete hyphae (Jørgensen 1989). Basidiocarps are still unknown.

In a molecular analysis, Palice et al. (2005) confirmed the fungal partner in *O. foliacea* as a basidiomycete. However, the phylogenetic position is not in the omphalinoid group. It was considered to belong eventually to the

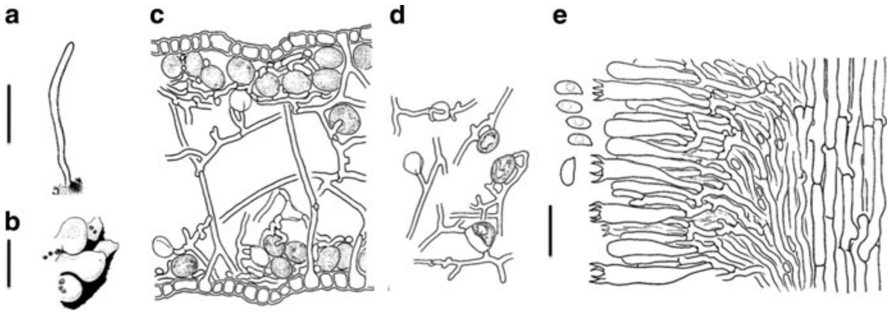

Fig. 16.6. *Lepidostroma calocerum* (rearranged after Oberwinkler (1970, 2001)); (**a**) *bar* 5 mm; (**b**) *bar* 1 mm; (**c**–**e**) *bar* 20 µm. (**a**) Basidiocarp. (**b**) Lichen thalli. (**c**) Section of thallus with upper and lower pseudoparenchymatic hyphae, neighbouring algal layers, and loose interconnecting hyphae. (**d**) Fungus–alga interactions by appressoria; note different numbers of appressoria per algal cell and different developmental stages of algae, including dead ones without cytoplasm. (**e**) Section through the subhymenium and hymenium with basidia of different ages and basidiospores; note clamped hyphae

hymenochaetoid clade. Finally, Binder et al. (2005) found, that the species is a member of the cortioid clade, a position that was confirmed by Diederich and Lawrey (2007) and Lawrey et al. (2008).

C. *Athelia*, *Athelopsis*

Athelia species are corticioid homobasidiomycetes with loose subhymenial hyphae and non-thickening, pellicular hymenia (Fig. 16.5c). Basidia are short-cylindrical to slightly clavate with 2–4 sterigmata. As in all basidiolichens, spores are smooth, thin-walled, hyaline, and inamyloid. *Athelia* species often grow together and over algae and lichens. Oberwinkler (1970) reported and illustrated fungus–alga interactions with parasitic (haustoria) and apparently symbiontic structures, similar to initial *Botrydina* granules. Additional reports on lichenized *Athelia* species mostly lacked essential details to document lichenization. The species delimitation in *Athelia* is still difficult and needs careful revisions as that for non-lichenized ones of Northern Europe by Eriksson and Ryvarden (1973). A study like this, combined with molecular data, is desirable.

The athelioid clade (Larsson et al. 2004; Binder et al. 2005, 2010) has finally been recognized as its own order, Atheliales, but was named as such already by Boidin et al. (1998).

Athelopsis was proposed "*ad interim*" by Oberwinkler (1965) and validated by Parmasto (1968). It differs from *Athelia* by clavate basidia (Fig. 16.5e). Often basidiocarps are very thin with a dense subhymenium, but loosely interwoven hyphae also can occur, as in the example illustrated here. Two species, *A. glaucina* and *A. subinconspicua* group in the phylogenetic clade of Atheliales but appear not to be congeneric (Binder et al. 2010).

D. *Lepidostroma*

The fungal partner of *Lepidostroma calocerum* has been studied in detail by Oberwinkler (1970; Fig. 16.4h, i). Macroscopically, the clavarioid basidiocarps resemble *Calocera* species. The micromorphology is similar to that of *Multiclavula*, i.e. there is a simple, monomitic hyphal system, septa with clamps, a dense subhymenium, and a thickening hymenium. In contrast to *Multiclavula* the basidia are not suburniform and 4-6-(8)-spored, but clavate-cylindrical and four-spored.

Two species from Rwanda, originally placed in *Multiclavula* (Fischer et al. 2007), were included in *Lepidostroma*: *L. akagerae* and *L. rugaramae* (Ertz et al. 2008). This treat-

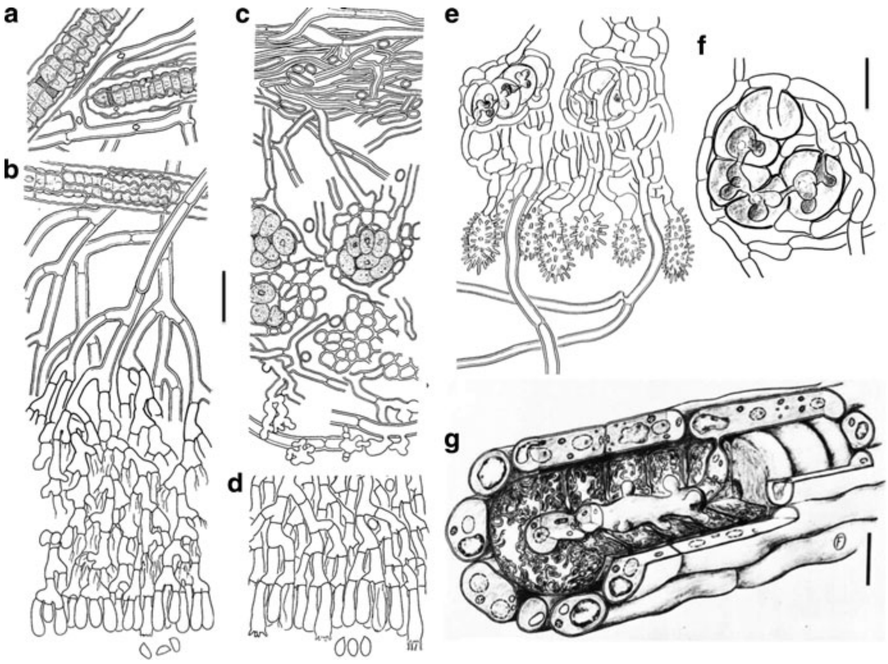

Fig. 16.7. *Dictyonema* (**a**, **b**, **g**), *Cora* (**c**, **d**), *Acantholichen* (**e**, **f**) (rearranged after Oberwinkler (1970, 1980, 1984, 2001)); (**a–e**) *bar* 20 µm, (**f**) *bar* 10 µm, (**g**) *bar* 5 µm. (**a**) Fungus–alga interaction in *Dictyonema irpicinum*; note clamped hyphae, dense hyphal mantles, and faint structures of central hyphae in *Rhizonema* trichomes. (**b**) Fungus–alga interaction and basidiocarp of *Dictyonema sericeum*; note clampless hyphae, loose subhymenium with thick-walled hyphae, and thickening hymenium, one young basidium and basidiospores. (**c**) Section through thallus of *Cora pavonia* (*Dictyonema glabratum*); note leaf-like architecture of the thallus with upper and lower hyphal layers and central compartments of coiled *Rhizonema* trichomes, densely surrounded by hyphae; parts of central hyphae in *Rhizonema* are indicated by darker areas. (**d**) Thickening hymenium of *Cora pavonia* with basidia of different age and basidiospores. (**e**) Detail of the *Rhizonema–Acantholichen* interactive system; note the intracellular hypha in *Rhizonema* and its origin from an external hypha. (**f**) Lower part of the thallus of *Acantholichen pannarioides* with hyphae connecting the thallus to the substrate (*below*), acanthohyphidia of the lower surface of the thallus, and two algal chambers with short *Rhizonema* trichomes surrounded by hyphae; note the central hypha in *Rhizonema* in the left trichome. (**g**) Fungus–alga interaction of *Dictyonema sericeum*

ment is based on molecular data. Though light microscopic photos were published, these did not show clear details of the micromorphology of thalli and basidiocarps necessary for a substantial comparison with those in *L. calocerum*, the type of the genus.

E. *Cora*, *Dictyonema*, *Acantholichen*

Cora and *Dictyonema* basidiocarps have been studied by Oberwinkler (1970) and Parmasto (1978). They agreed that the fungi are very similar, representing one genus which appears closely related to *Byssomerulius* (*Meruliopsis*) with saprobic species. This interpretation was based on comparative micromorphological features, like thick-walled and loose subhymenial hyphae and thickening hymenia in mature basidiocarps (Fig. 16.7b, d). However, molecularly based phylogenies place *Cora* and *Dictyonema* as well as *Lichenomphalina* in the Hygrophoraceae (Lawrey et al. 2009), a basal family in the Agaricales. In contrast, *Byssomerulius* and *Meruliopsis* fall in a cluster together with *Gloeoporus, Ceriporia* and *Candelabrochaete* inside the Polyporales, according to Larsson (2007).

Parmasto (1978) proposed *Cora* as a synonym of *Dictyonema*, a taxonomy appearing meaningful considering the micromorphology of fungi. Molecular phylogenies (Lawrey et al.

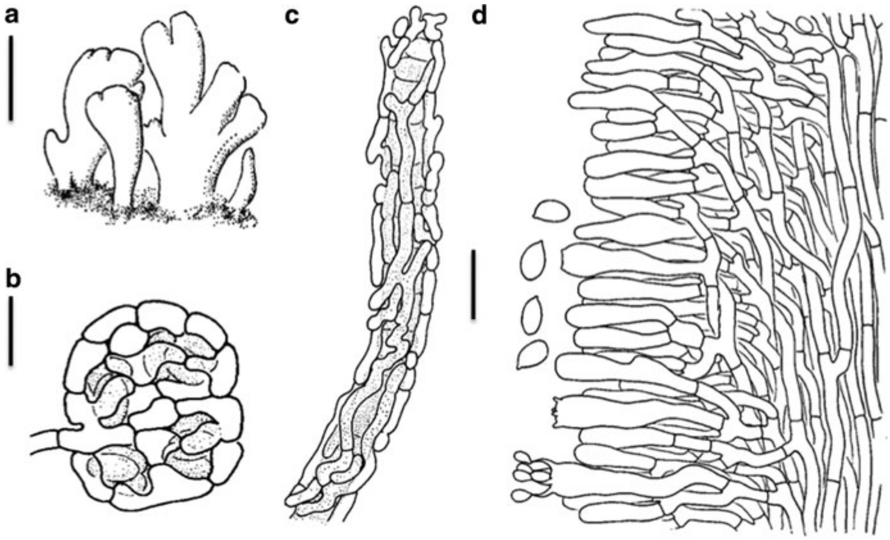

Fig. 16.8. *Cyphellostereum pusiolum* (rearranged after Oberwinkler (1970, 2001)); (**a**) *bar* 5 mm, (**b**) *bar* 10 µm, (**c, d**) *bar* 20 µm. (**a**) Basidiocarps with basal lichen thalli. (**b**) Cluster of green algae enveloped by *Cyphellostereum* hyphae. (**c**) *Rhizonema* trichome surrounded by *Cyphellostereum* hyphae. (**d**) Section through the subhymenium and hymenium with basidia of different ages and basidiospores; note unclamped hyphae

2009) can be used to support this taxonomy, with the result that also *Acantholichen* and *Cyphellostereum* belong into *Dictyonema*. Another, also acceptable interpretation with molecular support, would be, to keep *Cora*, *Dictyonema*, *Cyphellostereum*, and *Acantholichen* as very closely related, but separate genera. This makes sense considering the macromorphology and molecular phylogenies based on adequate sampling.

The genus *Acantholichen* (Jørgensen 1998) is monotypic and based on sterile thalli with clampless hyphae terminating with acanthophyphidia (Fig. 16.7e, f). Acanthohyphidia are known from corticioid, stereoid, and cyphelloid basidiomycetes, e.g. *Aleurodiscus* s.l. and *Stereum* s.l. However, they are diverse and not always homologous. Terminal cells of the thallus underside in *Cora pavonia* are irregularly shaped (Fig. 16.7c). *Acantholichen* has also the *Dictyonema*-type of fungus–alga interaction (Oberwinkler 2001; Fig. 16.7e, f). The fungal relationship cannot be derived from the hyphal system of the thallus. In *Cora* and *Dictyonema* basidiocarps develop on the underside of the lichen thalli. This can be expected also for *Acantholichen*. However, it is technically very difficult to examine the underside of the tiny scales in a search for basidiocarps.

F. *Cyphellostereum*

Cyphellostereum pusiolum has small and stout, upright growing, simple or split basidiocarps, a monomitic hyphal system, and clavate-cylindrical, slightly bent holobasidia (Figs. 16.3j, 16.8a, d). Substrate hyphae of *Cyphellostereum* can be closely attached to green algae and to *Rhizonema* trichomes (Fig. 16.8b, c). The latter fungus–alga interaction is very similar to the *Cora–Dictyonema* type concerning the cyanobacterial partner (Fig. 16.7g). However, detailed studies for the close cellular interaction are still lacking.

Cyphellostereum appeared not to be monophyletic. The lichenized *C. pusiolum*, the type of the genus, as shown by Lawrey et al. (2009), is inside the *Dictyonema—Acantholichen—Cora* cluster, while the saprobic *C. laeve* falls into the Hymenochaetales (Larsson 2007). To clarify the nomenclature, Redhead, Lücking, and Lawrey (Lawrey et al. 2009) proposed the new genus *Muscinupta* for *C. laeve*.

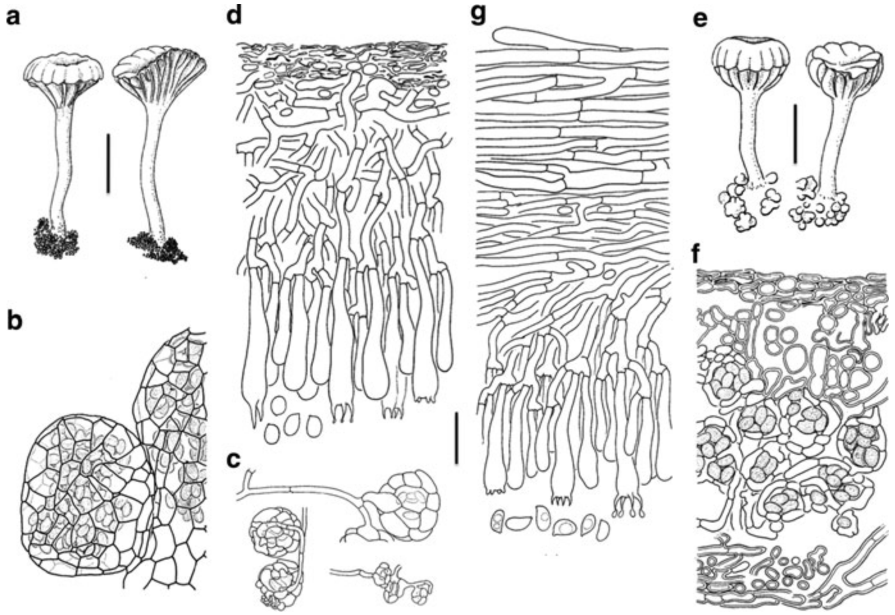

Fig. 16.9. *Lichenomphalia umbellifera* (**a–d**) and *L. hudsoniana* (**e–g**) (after Oberwinkler (1970, 2001)); (**a, e**) *bar* 5 mm, (**b–d, f, g**) *bar* 20 µm. (**a**) Basidiocarps of *L. umbellifera* (*Omphalina ericetorum*) with basal lichen thalli. (**b**) Mature thalli (*Botrydina*). (**c**) Ontogenetic stages of the *Botrydina* thalli. (**d**) Transverse section in between lamellae of *L. umbellifera* in an older developmental stage; note collapsed hyphae of the outer pileus layer (*above*) and basidia with various numbers of sterigmata. (**e**) Basidiocarps of *L. hudsoniana* (*Omphalina luteolilacina*) with basal *Coriscium* thalli. (**f**) Section of the thallus of *L. hudsoniana* (*Coriscium viride*); note the leaf-like architecture of the thallus with upper and lower marginal hyphae and central algal chambers; also note the photobionts, densely surrounded by hyphae. (**g**) Intralamellar radial section of the pileus of *L. hudsoniana* with cutical hyphae, trama layers, subhymenium, hymenium with basidia of different ages, and basidiospores; note the uniform hyphal system

G. *Lichenomphalia*

Lichenomphalia species are small agarics with a characteristic macromorphology (Figs. 16.3k, m, n, 16.9a, e), i.e. with central stipes, convex to umbilicate pilei, and decurrent lamellae. The micromorphology is also very distinct, but prominent features are lacking (Fig. 16.5c, e). The hyphae are simple, comparatively loosely interwoven and therefore rather distinct, not gelatinous, with parietal or intrahyphal bright pigments, and without clamps. Trama hyphae are not or only slightly swollen, there are no cystidia in the hymenium and on the pileus. Also subhymenial hyphae are normally loosely interwoven, the hymenium is not much thickening, and basidia are basally slightly tapering and apically inconspicuously swollen, normally with four, but also with two sterimgata. Basidiospores lack any special characters, i.e. they are short cylindrical to subglobos, thin-walled, smooth, and inamyloid. Karyological studies of *L. umbellifera* (as *Omphalina ericetorum*) by Lamoure (1968), and Poelt and Jülich (1969a) of *L. velutina* (as *O. grisella*, Fig. 16.3m) demonstrated apomictic ontogenies.

Redhead and Kuyper (1988) considered fully lichenized omphaloid agarics distinct from their non-lichenized allies in *Omphalina*. The differentiating characters focussed on lichen thalli, and noticeably thickened basal mycelium in mutualistic species. These distinctions have not been accepted as generically valuable by workers at that time. However, after molecular phylogenies became available, the monophyly of lichenized *Omphalina* species became obvious, and taxonomic conclusions then followed.

Lutzoni and Vilgalys (1995a) used 17 morphological characters and nuclear ribosomal

DNA large subunit sequences to analyse four lichenized *Omphalina* and three non-lichenized ones and *Arrhenia lobata*. The dendrogram based on morphological characters as well as the one based on a combined data sets clustered the lichenized species in one group. Also in a study with four molecular data sets from 30 species of *Omphalina* and related taxa, Lutzoni (1997) demonstrated that the lichen-forming *Omphalina* species represent a monophyletic group, thus confirming the taxonomic conclusions of Redhead and Kuyper (1987) and Norvell et al. (1994).

A molecular investigation based on combined data sets of 25S, 5.8S, ITS1, and ITS2 from the nuclear ribosomal DNA of lichenized fungi and fungi associated with *Marchantia* and *Blasia* and non-mutualist fungi revealed four independent transitions to mutualism (Lutzoni and Pagel 1997). Two of these transitions refer to *Gerronema marchantiae* and *Rickenella pseudogrisella* associated with liverworths. The others are two lichenized *Multiclavula* species and a monophyletic group of five lichen-forming *Omphalina* species. The authors demonstrated "a highly significant association between mutualism and increased rates of nucleotide substitions in nuclear ribosomal DNA" and that "a transition to mutualism preceded the rate acceleration of nuclear ribosomal DNA in the lineages. The generalized genomic acceleration in the lichen-forming *Omphalina* lineage is mostly due to selection of mutations that disrupt the potential formation of thymine dimers" (Lutzoni and Pagel 1997).

The phylogenetic hypotheses of Hibbett and Thorn (2001) and Redhead et al. (2002) gave further support for a generic separation of lichenized species. The omphalinoid taxa, including *Lichenomphalia* are now grouped in the Hypgrophoraceae (Lawrey et al. 2009; Seitzman et al. 2011), including also *Dictyonema* s.l.

H. *Semiomphalina*

Corner (1966) described *Pseudocraterellus leptoglossoides* from Papua New Guinea, and accurately illustrated macro- and micromorphology of the species. It has a clear omphalinoid hyphal system with a thickening hymenium, clamps are lacking, basidia and basidiospores are exactly of the *Omphalina* type.

Restudying the type material, Redhead (1984) found *Botrydina*-like bulbils on the substrate that were clearly connected with the basidiocarps. Therefore the new basidiolichen genus, *Semiomphalina*, was proposed. Until now the species has not been studied molecularly.

I. *Marasmiellus affixus*

Singer (1970) mentions "*Marasmiellus affixus* (Berk.) Sing. is also lichenized and grows in association with a crustaceous lichen on the surface of *Eucalyptus* saplings in Australia". A little more information he gave in a note on *M. affixus* (Singer 1973) is "crustaceous organism consisting of *Coccomyxa* imbedded in basidiomycetous hyphae".

To my knowledge, *M. affixus* has never been studied in detail morphologically or molecularly. In a website article on basidiolichens, Lepp (2011) discusses *M. affixus* at some length but without conclusions about the lichenization status.

V. Photobionts

In ascolichens and in basidiolichens the two major lichen-forming partners, cyanobacteria and green algae, serve as photobionts.

Unanimously the long trichomes of the photobiont in *Dictyonema* species have been identified as *Scytonema* (e.g. Bornet 1873; Oberwinkler 1970, 1980, 1984; Parmasto 1978; Tschermak-Woess 1983). The cyanobacteria in *Cora pavonia* have earlier been assigned to *Chroococcus* (Bornet 1873; Mattirolo 1881; Ahmadjian 1958). In realty they are short coiled trichomes of the *Scytonema* type (Vainio 1890; Räsänen 1943; Oberwinkler 1970, 1980, 1984; Roskin 1970; Tschermak-Woess 1983).

The photobiont of *Acantholichen pannarioides* was reported as *Scytonema* by Jørgensen (1998). A microscopic re-study (Oberwinkler 2001) showed that it is very similar to the *Cora* photobiont inclusive of the fungus–alga interaction type (Fig. 16.7e, f).

Lücking et al. (2009) analysed 16S rDNA sequences to determine the phylogenetic positions of *Scytonema* in cyanolichens of the Asco- and Basidiomycota. The lichenized scytonematoid cyanobacteria of both Asco- and Basidiolichens, form a clade different from the one of free living *Scytonema* s.str. For this clade the name *Rhizonema*, erected by Thwaites (in Smith and Sowerby 1849) for *Calothrix interrupta*, can be used.

Most of green algal photobionts, including *Coccomyxa* species, belong to the Trebouxiophyceae (Beck and Persoh 2009). The association of coccomyxoid green algae with *Lentaria (Multiclavula) mucida* has been described by Geitler (1955). He also found that the algae of the lichenized globules are larger than free living ones. This was interpreted as a possible retardation of the algal division frequency caused by the mycobiont (Geitler 1956).

In a phylogenetic study of *Coccomyxa*, Zoller and Lutzoni (2003) detected "three main lineages within this genus, corresponding to free-living *Coccomyxa*, individuals isolated from basidiolichens *Omphalina* (*Lichenomphalia*) and *Coccomyxa* isolated from ascolichens belonging to the Peltigerales". The genetic changes in *Lichenomphalia* are 27.5 times higher than those of their *Coccomyxa* photobionts. Six *Lichenomphalia* species share the same *C. subelliptica.*

In a phylogenetic tree of Trebouxiophyceae, including free-living, endophytic, symbiontic, and parasitic species (Rodrigéz et al. 2008), a monophyletic *Coccomyxa* comprises *C. pringsheimii*, *C. glaronensis*, photobionts of *Nephroma arcticum* and *Peltigera britannica*, *Paramecium bursaria* endobionts, endophytes of *Ginkgo biloba*, and green algae in mussels.

Langenstein (1994) isolated *Coccomyxa* from *Botrydina* and *Coriscium* and characterized algal cells in axenic culture. They reproduce asexually by autospores. A comparison of strains from *Omphalina* thalli with *Coccomyxa* isolated from the ascolichen *Icmadophila ericetorum* as well as authentic substrains of *Coccomyxa pringsheimii* and *C. subellipsoidea* showed high identity of morphological and reproductive characters. Also the growth of colonies of the various strains was remarkably similar.

VI. Physiology

Because of its big and more or less flat thallus, *Cora pavonia (Dictyonema glabratum)* is a suitable lichen for ecophysiological experiments. Already in 1965 Lange investigated the temperature dependance of photosynthesis, and Coxson (1987a) reported on a chilling stress which was considered to be an important factor in the limitation of distribution. Coxson (1987b, c) found an unexpected breadth of photosynthetic response under prevailing cloud conditions on La Soufrière (Gouadeloupe). The species shows no depression in net photosynthesis at saturated thallus water content in contrast to most other lichens. Extensive ecophysiological field investigations in *C. pavonia*, carried out by Lange et al. (1994) in a premontane tropical rainforest in Panama confirmed the observation of Coxson (1987c). The authors found that net photosynthesis was adapted to high temperatures, and when the thalli were fully hydrated, the CO_2 uptake was not reduced. Desiccation of the thalli caused a decrease of net photosynthesis and influenced apparent photon yield of CO_2 fixation. Though there were days with a negative carbon balance, the total carbon gain was extremely high and estimated at 228 % per year.

Pioneer populations of *Cora pavonia* on La Soufrière lahar flows showed high nitrogenase activities during rehydration (Fritz-Sheridan 1988). The author suggests that under full hydration a high supply of nitrogen compounds would support growth and membrane repair.

The C-metabolism of *Cora pavonia* has been investigated by Feige (1969) who found that in contrast to all other lichens with cyanobacterial phytobionts, pentitol was synthesized and accumulated as pentitolgalactosid. The main excretory product was glycolic acid after bicarbonate incubation in liquid phase.

Larcher and Vareschi (1988) studied the variation in morphology and functional traits of *C. pavonia* from various habitats in the Venezuelan Andes. They found optimally developed thalli in the lower Paramos around 3,500 m which exhibit the highest photosynthetic capacity. Specimens growing in very high altitudes up to 4,300 m have strongly reduced thalli, but the same respiration intensity as specimens from the lower Paramo, reflecting a homeostatic adjustment to the prevailing temperature regime. Thalli which grow in lower altitudes of the montane forest have approximately half the size and barely half the net photosynthetic rate in comparison to those growing in optimal Paramo regions. Thus, the increasingly unfavourable carbon budget may delimit the altitudinal distribution. Lange et al. (1994) explained the reduction of population densities of macrolichens in tropical lowland rainforests by the negative carbon balance caused by increased nocturnal temperatures at lower elevations.

The wide temperature range in photosynthetic activity is a general feature in lichens (Lange 1965). A distinct adaptation to low temperature was found in *Botrydina* and *Coriscium* by Heikkilä and Kallio (1966).

VII. Phytochemistry

Higher fungi including the basidiomycetes are very rich in specific chemical compounds (Gill and Steglich 1987) that often are of taxonomic importance. Likewise, secondary metabolites of ascolichens (lichen substances) are widely distributed and have been studied intensively (e.g. Huneck and Yoshimura 1996; Eisenreich et al. 2011). The taxonomic use of metabolic data in lichen-forming fungi has been summarized by Lumbsch (1998); however, basidiolichens could not be included because of lacking data.

In a study on antibiotic active substances of *Cora pavonia* (*Dictyonema glabratum*; Mitidieri et al. 1964) no chemical substances were mentioned. Iacomini et al. (1987) isolated and characterized β-ᴅ-glucan, heteropolysaccharides, and trehalose components also from *C. pavonia*. Again, from the same species atranorin and tenuiorin, as well as ergosterol and ergosterol peroxide were reported by Piovano et al. (1995). *Dictyonema* was also included in a chemical study on secondary metabolites in lichens from Bario highlands, Borneo, by Din et al. (1998). Jørgensen (1998) found no lichen acids in the new basidiolichen genus *Acantholichen*. The polysaccharides pseudonigeran, a (1–4)-linked β-xylan, and a new(1–6)-linked β-mannan were discovered in *C. pavonia* by Carbonero et al. (2002).

VIII. Ecology

In his field studies, Johow (1884) observed that *Cora pavonia* appears to be confined to higher altitudes in the tropical islands of Dominica and Trinidad. His transplantation experiments to lowlands failed within a few days. Thus, the species appeared to be adapted to cool, humid, and bright conditions of tropical mountain regions. In standings with disturbed or scarce higher plant vegetation, *C. pavonia* can occur in remarkably rich, ground-covering populations.

Acantholichen pannarioides is a species of moist montane regions in Central America and northern South America, where it grows on debris of vegetation, bark, bryophytes, and other lichens (Jørgensen 1998).

Multiclavula species display a remarkably diverse adaptation to ecological niches. Wet wood of huge logs is the most suitable substrate for *M. mucida*. In Central Europe preferably coniferous wood is colonized, but the species occurs also in such subtropical and tropical regions where gymnosperms are lacking. Other *Multiclavula* species grow on bare soil under different climatic conditions in arctic-alpine regions, temperate and tropical zones.

Lepidostroma species are sofar only known from tropical regions, *L. calocerum* from Colombia and Costa Rica, and *L. akagerae* and *L. rugaramae* from Rwanda (Ertz et al. 2008).

Lichenomphalia species are common agaricoid lichens in arctic-alpine vegetations where they are mostly protected by a winter snow cover (Heikkilä and Kallio 1966). They also occur fully exposed in high alpine regions of tropical mountains with often extreme day and night temperature differences.

IX. Dispersal

Similar to ascolichens only the fungal partners of basidiolichens are able to propagate sexually. In most species, basidiocarps are developed sporadically so that production of basidiospores is limited in time. However, enormous quantities of spores are produced during the sporulation phase, also from tiny basidiocarps like those of a small *Athelia*. The high amount of basidiospores is an essential prerequisite for effective dispersal in basidiolichens, as in basidiomycetes in general.

Dispersal by mitotic progagules is limited to few basidiolichens. Poelt and Obermayer (1990) considered thallus bulbils in *Multiclavula vernalis* as distinctive vegetative diaspores. They consist of inflated hyphae, a thin cortical layer and contain one or a few groups of algal cells. Fischer et al. (2007) confirmed this finding and reported on similar, but bigger bulbils in *M. akagerae*, transferred to *Lepidostroma* later (Ertz et al. 2008). It is tempting to hypothesize that *Botrydina* globules also can serve as vegetative propagules in *Lichenomphalia*. However, normally *Botrydina* is quite solidly attached to the substrate by hyphae.

Structures resembling soredia occur in *Acantholichen*, and isidioid appendages are known from thalli of *Dictyonema melvinii* and *D. ligulatum* (Chaves et al. 2004).

X. Distribution

Two main geographical distribution patterns can be found in basidiolichens: (1) cosmopolitan to subcosmopolitan ranges with restrictions to specific ecological niches (certain species of *Athelia*, *Dictyonema*, *Multiclavula*, and *Lichenomphalia*), and (2) regional to continental distributions (*Lepidostroma*, *Cyphellostereum*, *Acantholichen*, *Cora*, *Dictyonema*).

According to Petersen and Kantvilas (1986), *Multiclavula* seems to include several species which are truly cosmopolitan, e.g. *M. mucida* and *M. vernalis*.

Dictyonema sericeum is reported from all continents with tropical and subtropical regions (Parmasto 1978). In contrast, *D. ligulatum* is known only from southeastern Asia and Oceania (Parmasto 1978). Besides all previous records of *D. moorei* from Japan (Parmasto 1978), the species was also recorded from Chile (Henssen 1963), Western Australia, and Queensland (Lepp 2011). *Dictyonema interruptum* was originally described from England and was additionally reported from the Azores (Coppins and James 1979) and from the Pyrenees (Etayo et al. 1995).

Cora pavonia (*D. glabratum*) is known to occur from South Florida to Cape Horn (Parmasto 1978). Thus, the species seems to be restricted to subtropical and tropical America with an extension into temperate and cool regions of South America.

Acantholichen pannarioides is known from Costa Rica to the northern Andes in Venezuela and Ecuador, as well as from the Galapagos Islands (Jørgensen 1998).

Semiomphalina leptoglossoides (*Pseudocraterellus l.*) has been collected only once in the Wau area of Papua New Guinea (Corner 1966; Redhead 1984).

The extensive fieldwork of Heikkilä and Kallio (1966, 1969) gave a substantial basis to document that *Botrydina* and *Coriscium* have circumpolar distributions in artic and subarctic regions. Some *Lichenomphalia* species appear to be cosmopolitan, e.g. *L. umbellifera* (*Omphalina ericetorum*) has a circumpolar distribution and has been recorded also from New Zealand (Galloway 1985) and Australia (Lumbsch and Ewers 1992), and *L. chromacea* is geographically restricted to southern Australia (Lepp 2011).

XI. Culture Experiments

Heikkilä and Kallio (1966) were unsuccessful to obtain axenic cultures of the fungal partners in lichenized *Omphalina* species. However, in living cultures of *Botrydina* and *Coriscium* several times *Omphalina* basidiocarps were developed. In contrast to the fungus, the photobiont of *Botrydina* was easily cultivated on agar and in liquid media. Shape and size of the algal cells varied widely in culture. The photobiont isolated from *Coriscium* appeared very similar.

Langenstein (1994) was successful in isolating phyco- and mycobionts of *Botrydina*, to grow them in axenic culture, and to synthesize *Botrydina* thalli in the laboratory. This was a remarkable progress in experimental lichenology. When *Coccomyxa* is present, hyphae originating from basidiospores contact the algal cells and surround them. Original compartments with single algae develop into multicellular ones by autospore production and ingrowth of fine hyphal branches into the photobiont colony. Unfortunately this study has not been published in a journal, but it was cited in the above phrasing by Oberwinkler (2001). This may explain that Lawrey et al. (2007) hoped that: “it may also be possible to experimentally synthesize basidiolichens using cultures of the bulbil-forming fungi and photobionts to see the extent to which bulbil formation leads to formation of basidiomycete thallus structures”.

A circadian rhythm was found in the mycobiont culture of an unidentified *Omphalina* sp., considered to be a basidiolichen by Kalangutkar and Kamat (2010). However, there is no documentation of mycobiont–photobiont interactions in this pre-publication document.

XII. Phylogenetic Systematics and Evolution

A. Origin and Evolution of Thalli

Lichenization in Basidiomycota is only known from Agaricomycetes and originated at least in four different clades (Fig. 16.2). The multiple origin of basidiolichens is apparent in several molecularly based dendrograms, the first of them using small subunit rDNA data (Gargas et al. 1995).

The convergent evolution of lichenized structures within bulbilliferous fungi was discussed by Lawrey et al. (2007). Lichenized bulbils are considered as ancestral states in the evolution of basidiolichens. Examples can be found in the *Multiclavula* relationship (Figs. 16.3a, b, 16.4b), the *Marchandiomphalina* group, in lichenized *Athelia* (Fig. 16.5b) and *Atheliopsis* (Fig. 16.5d, e), *Cyphellostereum pusiolum* (Fig. 16.8b), and *Lichenomphalia* (Figs. 16.3k, l, 16.9a–c).

B. Evolution of Basidiocarps

Based on comparative morphology, Oberwinkler (1970) distinguished three main groups within the basidiolichens: (1) the *Athelia–Dictyonema* complex including *Cora*, (2) the *Multiclavula–Lepidostroma* group with clavarioid basidiocarps, and (3) the agaricoid, lichenized *Omphalina* species. These taxa were considered of distant relationship because of their different micromorphological characters, a view largely in agreement, at that time, with a classification based on basidiocarp morphology.

Actually accepted molecularly based phylogenetic hypotheses can be summarized as in Fig. 16.2: *Multiclavula* falls in Cantharellales as a sister group to Clavulinaceae, *Marchandiomphalina* belongs to the Corticiales, the Atheliales comprise *Athelia* and *Atheliopsis*, and *Lepidostroma* is a sister taxon. Finally, most of the basidiolichens are members of the Hygrophoraceae (Lawrey et al. 2009), a basal family of the Agaricales. They include *Dictyonema*, *Cora*, *Acantholichen*, *Cyphellostereum*, and *Lichenomphalia*.

1. Cantharellales and Clavulinaceae

Clavarioid basidiolichens have been assigned to different genera, e.g. *Clavaria*, *Clavulinopsis*, *Lentaria*, *Lepidostroma*, and *Multiclavula*. These have been analysed morphologically and discussed comparatively by Oberwinkler (1970) with the result that lichenized *Lentaria* spp. cannot be separated generically from *Multiclavula* spp. Because of the unique thallus and the peculiar fungus–alga interaction, *Lepidostroma* was recognized as a separate lichen genus.

A phylogenetic analysis of four *Multiclavula* species (*M. corynoides*, *M. mucida*, *M. vernalis*, and the newly described *M. ichthyiformis*; Nelsen et al. 2007) resulted in a monophyletic group of these taxa with a basally positioned *Sistotrema brinkmannii*. The sister group is a monophylum of *Clavulina* species. Both clades are highly supported (bootstrap 100 %) and considered by the authors to represent Clavulinaceae in an emended sense.

2. Corticiales

Corticiales is a taxon based on a clade in Agaricomycetes, found in several molecular phylogenetic studies (Larsson et al. 2004; Binder et al. 2005; DePriest et al. 2005; Hibbett et al. 2007;

Lawrey et al. 2007), and formally erected by K-H Larsson (in Hibbett et al. 2007). This clade includes a single, lichenized species, *Marchandiomphalina foliacea* Diederich and Lawrey (2007), for which basidiocarps are not yet known. The species was originally described as *Omphalina foliacea* by Jørgensen (1989), though sterile, and assigned to the agaricoid genus *Omphalina*. The thallus macromorphology is obviously different from known lichenized *Omphalina* (*Lichenomphalia*) species, and also its micromorphology appears to be intermediate between *Botrydina* and *Coriscium* Jørgensen (1989).

The species included at present in the molecularly defined Corticiales are more or less crustouse or bulbil-like, clavarioid and agaricoid ones are lacking. Therefore, it would be very surprising if the mycobiont of *Marchandiomphalina foliacea* turned out to be agaricoid, as implied by the generic names so far used.

3. Atheliales

In a cladistic study of corticioid fungi by Parmasto (1995), *Athelia* and *Athelopsis* fell within a group “arbitrarily named at this stage Atheliaceae”. Boidin et al. (1998) used the ribosomal internal transcribed spacer sequences (ITS1-5.8S-ITS2) to evaluate the phylogenetic relationships within the Aphyllophorales. They recognized an order Atheliales with *Athelia*, *Amyloathelia*, *Fibulomyces*, and *Leptosporomyces*. In the analysis of Larsson et al. (2004), the athelioid clade includes species of *Amphinema*, *Athelia*, *Athelopsis*, *Byssocorticium*, *Piloderma*, and *Tylospora*. Also Binder et al. (2005) found an athelioid clade, because of limited sampling represented only by *Athelia arachnoidea* and *A. fibulata*. None of the species in the studies mentioned above were recognized as being associated with algae or even lichenized.

The ecological diversity of species in the Atheliales, as defined by molecular hypotheses, is surprisingly high. They include saprobes, parasites of algae and lichens, ectomycorrhizal fungi, and lichenized species (Fig. 16.5).

In contrast, all taxa mentioned and actually assembled in the Atheliales have thin and pellicular basidiocarps with loose subhymenia, rarely with hymenial cystidia as in *Amphinema*, and thin-walled, hyaline spores. Such micromorphological traits do not give any indication for a closer relationship with Boletales and/or Agaricales. However, in all phylogenetic overviews of Agaricomycetes, Atheliales cluster with Boletales and Agaricales.

4. Lepidostromataceae

Surprisingly, the Lepidostromataceae with the single genus *Lepidostroma* are close to the Atheliales or may even be included in this order as indicated by molecularly based hypotheses (Ertz et al. 2008). Morphological characters of thalli and basidiocarps show distinct differences to those in *Multiclavula* spp., supporting a generic separation. However, an affiliation with taxa of the athelioid clade cannot be based on morphological characters of basidiocarps. Eventually, parasitism of algae in *Athelia* (Fig. 16.5a) and *Lepidostroma* (Fig. 16.6c) can be considered as a similar interaction type.

5. Hygrophoraceae

In the Agaricomycetes, the stereoid cyanolichen *Dictyonema* s.l. and the omphalinoid chlorolichen *Lichenomphalia* appear to be closely related members of the Hygrophoraceae in molecular phylogenetic hypotheses (Lutzoni and Vilgalys 1995b; Lutzoni 1997; Redhead et al. 2002; Lodge et al. 2006; Ertz et al. 2008; Lawrey et al. 2009; Seitzman et al. 2011).

The micromorphology of homologous hyphal systems, like subhymenia and hymenia, characteristics of the basidia and basidiospores (Figs. 16.7b, d, 16.9g, d) of these taxa are very similar, thus supporting the results of molecular phylogenies. These characteristics are also present in *Cyphellostereum pusiolum* (Fig. 16.8), a species that belongs in the *Dictyonema* clade according to molecular data, as does *Acantholichen pannarioides* (Lawrey et al. 2009). Accordingly, systematic conclusions would either to include *Acantholichen*, *Cora*, and *Cyphellostereum* in *Dictyonema* s.l., or to keep these taxa generically separate.

Considering the mycobiont–photobiont interactions, species of *Dictyonema* s.l. are associated with cyanobacteria *(Rhizonema)* and have a unique haustorial apparatus (Oberwinkler 1980, 1984, 2001; Fig. 16.7e–g), certainly a synapomorphy of high systematic and evolutionary importance. In contrast, *Lichenomphalia* species are chlorolichens, forming globose hyphal sheats around *Coccomyxa* algae (*Botrydina*; Fig. 16.9a–c), even when these are enclosed in squamulose thalli, like in *Coriscium* (Fig. 16.9e, f).

XIII. Comparison with Ascolichens

The number of lichenized Ascomycetes may be as high as of the non-lichenized ones. In Basidiomycetes the majority of mutualistic species is associated with certain groups of seedplants as ectomycorrhizal fungi. The number of known basidiolichens, however, is very small.

One of the most striking and unique features of ascolichens is the independent and convergent evolution of the thalli to morphological structures which have not been developed in fungi and algae. Such thallus evolution did not occur in basidiolichens. Their thallus macromorphologies are comparatively simple. However, the fungus–alga interaction is remarkably diverse, comprising three main types. One of them, the *Dictyonema* type, is unique for all lichens.

The transition to lichen symbiosis in Agaricomycetes is demonstrated as an accelaration of nucleotide substitutions (Lutzoni and Pagel 1997). This acceleration had yet no influence on species radiation.

Multiple independent losses of lichen symbioses as in Ascomycota (Lutzoni et al. 2001) are not known in Agaricomycetes.

Because of the limited number of species and their restriction to special niches, basidiolichens have been overlooked for a long time. However, *Cora pavonia* can occur in dense populations in neotropical mountain areas, and in arctic alpine vegetations *Lichenomphalia* species, recognizable without basidiocarps as *Botrydina* and *Coriscium*, may develop in considerable quantities on suitable acidic substrates.

XIV. Conclusion

Though basidiolichens represent only a very small group of all obligately lichenized fungi, they are highly diverse. This is reflected by: (1) structural and functional adaptations of the lichen thalli, (2) the different structures of basidiocarps which are developed by the fungal partners, (3) the cellular interactions of myco- and photobionts, (4) the world-wide distribution in specialized ecological niches, (5) some unique ecophysiological properties, and (6) several convergent phylogenies.

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