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# Biodiversity of bryophilous ascomycetes

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Up to now, about 300 species of ascomycetes are known to grow obligately on the gametophytes of mosses or hepatics; these belong to more than 80 ascomycete genera, some of them unknown elsewhere, and at least nine orders. They vary greatly in relation to the mode of nutrition (necrotrophic, biotrophic and gall-inducing parasites), the host organs infected, host specificity, and geographical distribution. Diversity of these fungi is illustrated by spore outlines of 36 species. Hyphae growing superficially, inter- or intracellularly, and various types of appressoria and haustoria are illustrated. Adaptations to the unique substratum, such as the formation of minute reduced ascomata containing gelatinous material, a preference for moist microhabitats such as the interlamellar spaces of leaves in Polytrichales, and phototropic reactions are discussed. Convergent evolution leading to similar morphological features is rather common. The colonization of mosses and hepatics by ascomycetes is a very frequent though generally neglected phenomenon. Some bryophytes seem to grow always with their specific parasites. It is supposed that species diversity among the bryophilous ascomycetes is as high as among the lichenicolous ones. Numerous new taxa remain to be described, but only a small fraction of bryophytes has been proved to be infected so far.

*Keywords*: biodiversity; bryophilous ascomycetes; bryophytes as hosts; spore types;
hyphal characters; adaptive features.

## Introduction

Bryophilous fungi grow on gametophytic or sporophytic organs of bryophytes, muscicolous species infecting mosses (Musci), and hepati(ci)colous species colonizing liverworts (Hepaticae). These fungi are defined by their ecology as are lichenicolous or coprophilous species, and their systematic positions, modes of nutrition and biological peculiarities may be quite different. Literature on fungi living on the haploid stage of bryophytes is reviewed by Felix (1988). Pyrenocarpous ascomycetes as well as mitosporic fungi present on both generations are compiled by Racovitza (1959) in a monographic study. For bryophilous lichenized ascomycetes see Faegri (1980), Kalb (1994), Obermayer and Poelt (1994), and Poelt (1986). Sterile intracellular fungal hyphae frequently form endomycorrhiza-like associations in numerous hepatics (Paul, 1916; Pocock *et al.*, 1984; Pocock and Duckett, 1985a, b; Duckett and Renzaglia, 1988; During and Van Tooren, 1990). Symbiotic associations between endophytic hyphae and hepatics are refered to as 'mycothalli' by Boullard (1979, 1988). In this paper, I will concentrate on fruit-body-forming ascomycetes which develop on the haploid, gametophytic stage of mosses or hepatics.

Bryophytes are unique host plants in numerous ways. One of the most important features 'is a life cycle that involves an alternation of generations with a dominant, free-living gametophyte' (Wyatt, 1982). Vegetative multiplication by various modes is frequent and reveals an enormous capacity for regeneration. Very important for the establishment of interactions with fungi seems to be the small size of mosses and hepatics, which means a limited availability of the substratum, their indefinite growth in the form of dense colonies, mats and cushions without periodic leaf-fall, and an often pronounced poikilohydric organization. Successful fungal colonization requires morphological and physiological adaptation to these special conditions.

Bryophytes are generally considered as phylogenetically ancient plants with a slow rate of evolution over at least 300 million years (Szweykowski, 1984a, b). Miller (1982) regards them as the oldest extant terrestrial plants which represent the level of evolution associated with transmigration to the land. Frey (1977) argues that the origin of the large groups of mosses must date back to before the late Palaeozoic age. Therefore, 'fungi growing on living parts of mosses and ferns are considered to be the most ancient plant parasites' (von Arx, 1985). Savile (1968; p. 651) points out that 'obligate parasitism in the fungi is not a belated evolutionary bypath, but a fundamental attribute of primitive groups'. This is supported by the fact that some rather archaic insects are present in bryophytes (Gerson, 1982, p. 320).

Bryophilous fungi do not receive much attention, and are not even mentioned in the relevant bryological literature (Schuster, 1966, 1983, 1984; Smith, 1982; Schofield, 1985). The situation in mycology is comparable. This is certainly a result of their often extremely small, sometimes light-coloured or hyaline ascomata hidden between host organs. Even for a keen and experienced observer it is a time-consuming and troublesome task to detect them. In addition, the overlap between bryology and mycology is very small in contrast to the situation in lichenicolous fungi. Lack of known economic importance is also an important factor. According to the general view, 'bryophytes, even herbarium specimens, are hardly ever attacked by microorganisms' (Ando and Matsuo, 1984, p. 181). In reality, both mosses and hepatics represent excellent hosts for fungi.

What should be the purpose of studies on bryophilous fungi? Of course, they are part of the still mostly unknown biological diversity of our planet, which is not only of taxonomic interest. Analyses of morphological and ecological features of the moss-inhabiting fungi, their relationship with non-bryophilous fungi, host interactions, specificity, geographical distribution, and decomposition enlarge our ideas and concepts of the systematics and biology of fungi in general, and the parasitic ascomycetes in particular. These are remarkable and unique interactions between members of two different kingdoms of organisms. Relatively simple anatomical structures of mosses and hepatics easily allow host and parasite to be distinguished at the cellular level. A further argument is that these fungi, when better known, can be expected to contribute to the clarification of taxonomic problems and evolutionary relationships of their hosts, having co-evolved in close relationships with them.

The goal of this article is to draw attention to a highly diverse, widespread, unquestionably successful and intriguing group of ascomycetes, which undoubtedly occupies one of the least explored ecological niches for fungi today.

## Methods

Under field conditions it is rather difficult, if not impossible, to detect bryophilous ascomycetes, although necrotrophic species often causing distinct decolorized patches within green colonies of mosses and hepatics can attract attention. However, not all the whitish, yellowish or brownish spots in bryophytes yield ascomata. Randomly collected samples of potential hosts must be screened in the laboratory with a stereomicroscope for the presence of fungi. In most cases, it is recommendable or even indispensable to wet the plants thoroughly. Bryophytes covered by soil particles and detritus should be cleaned with flowing tap water. Unabsorbed water has to be soaked up to avoid inconvenient light reflections. Ascomata can easily be confused with air bubbles, all kinds of detritus, colonies of cyanobacteria and algae, pollen grains, parts of the host itself (e.g. brotes, gemmae) or the cysts and eggs of small animals. It is easier to count the number of basidiomes of the bracket-fungi in a forest than to know the number of ascomata in a handful of *Hylocomium splendens*. I fear some mycologists will even look in vain for fruit-bodies of certain species in material in which I have ascertained they are indeed present.

A very effective method for obtaining access to material from different and remote geographical regions, is the examination of potentially infected specimens in bryological collections. Bryophytes present in biosystematic collections ('herbaria') represent a rich source of accidentally gathered fungal parasites, unknown to their collectors, curators and more significant, often unknown to science. The same applies to ascomycetes on algae (Kohlmeyer, 1975) and to fungi growing on lichens (lichenicolous fungi). Nevertheless, necrotrophic species are apparently underrepresented in bryological herbaria, as collectors prefer healthy green mosses and hepatics.

Fungal infections in colonies of different species of bryophytes deserve special attention. These colonies constitute natural infection experiments, by which host specificity often can be demonstrated easily and conclusively.

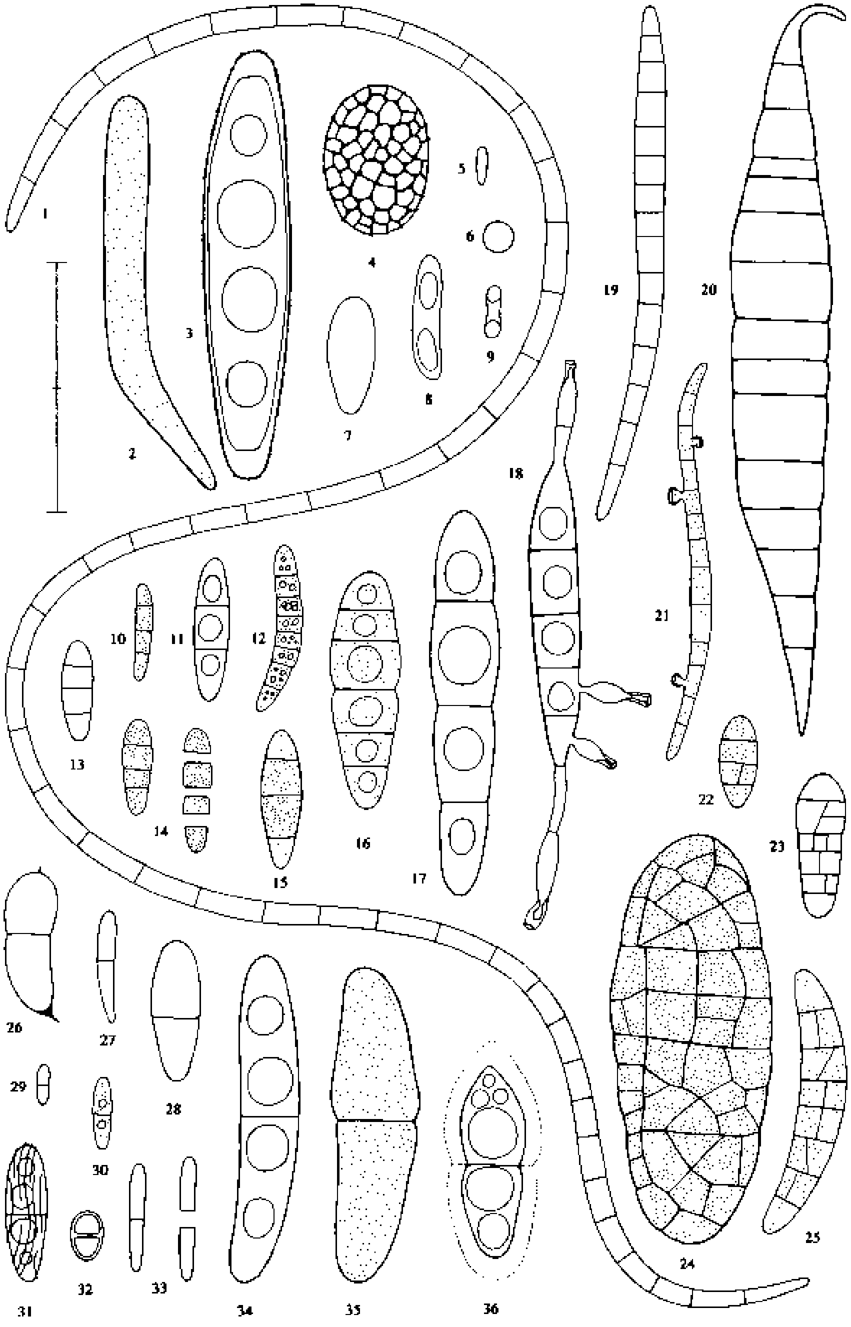
It is useful to have at least a basic knowledge of bryophyte morphology and living habits. Without knowing the capacity of acrocarpous mosses to innovate from subterranean rhizoids (Meusel, 1935; Wigglesworth, 1947), the ecology of *Octospora* would remain unclear.

Over the last 20 years, I have carefully examined tens of thousands of individual plants of mosses and hepatics, and thousands of collections in order to obtain an idea of their fungus biota. However, in almost every case I feel that we still know only a very small fraction of the total systematic, biologic and geographic diversity of the bryophilous fungi.

## Systematics

Up to the present, about 300 species (including ca 50 of *Octospora*) in more than 80 genera of ascomycetes have been described as growing on the gametophytes of mosses and hepatics. Their systematic position is quite diverse since no less than nine orders are involved: Dothideales, Hypocreales, Leotiales, Pezizales, Verrucariales and, to a more marginal extent, Arthoniales, Lecanorales, Ostropales and Sordariales. The genera *Acrospermum* and *Dactylospora* remain in families *incertae sedis*. The heterogenity of the bryophilous fungi is reflected at least partially by the diversity of their ascospore-types, which vary greatly in size, shape, septation, colour, and other features (Fig. 1).

Several genera are known exclusively from mosses and hepatics (obligate bryophilous genera), e.g. *Bryodiscus, Bryoscyphus, Bryosphaeria, Epibryon, Hypobryon, Octospora* and *Potriphila*. They apparently represent independent phylogenetic lineages, in which speciation occurred *after* attaining the bryophilous habit. However, some non-bryophilous genera do exist which include obligate parasites of mosses and hepatics, for instance *Dactylospora heimerlii, Muellerella frullaniae* and several species of *Hymenoscyphus* and *Nectria*. The 'waste basket' genus *Epibryon* with about 35 species is the largest bryophilous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'genus'. *Octospora* and related genera form a biologically defined isolated group within the terrestrial Pezizales morphologically characterized by elaborate infecting structures. These fungi should be separated taxonomically as they represent a 'class of discomycete similar to the Erysiphaceae' postulated more than 65 years ago (Corner, 1929).

The appropriate systematic position of a bryophilous ascomycete is often difficult to ascertain, as the tiny and reduced fruit-bodies are *a priori* poor in characters and convergent evolution has often led to surprisingly similar morphological features. Fortunately, hyphal characters offer a rich source of valuable additional information for the definition of taxa, though this has generally been neglected by other authors.

## Infected host organs

*Octospora libussae* is the only macromycete species known to grow on the algal-like protonemata of mosses (Döbbeler and Itzerott, 1981). However, there is no essential difference between rhizoids and protonematal filaments (Goode *et al.*, 1992). Several species of *Octospora* attack the subterranean vital rhizoids of acrocarpic mosses (Döbbeler, 1979b, 1993; Itzerott, 1983b; Senn-Irlet, 1988), thus being somewhat spatially independent from the leafy part of the gametophyte. Only few ascomycetes, such as *Bryoscyphus conocephali* and *B. marchantiae*, parasitize thalloid hepatics (Spooner, 1984). Several species of *Riccia* are recorded as hosts for different ascomycetes (Srinivasan, 1939; Stephens, 1939; Bapna, 1962; Bonar, 1965; Singh and Pavgi, 1979). However, the overwhelming majority of ascomycetes infects leaves or stems of mosses or leafy hepatics.

The hepaticolous *Nectria egens* develops perithecia mainly on the distal part of the host leaves, where the photosynthetic activity is highest (Corner, 1935). Microhabitats protected against rapid moisture loss are often prefered or even exclusively selected for fruit-body formation, while hyphae also colonize other parts of the host plant. Ascomata of *Bryorella semiimmersa* are partly immersed in the stems of Lophoziaceae. *Teichospora jungermannicola* and related species form individual fruit-bodies in the leaf-axils of foliose hepatics, sometimes resulting in a regular zigzag line of ascomata decreasing in size towards the plant apex. However, even from these moisture retaining places ascospore discharge into the open air still has to be possible. This may be the reason why ascomata are not developed other than on the generally favoured lower leaf side but at the leaf margins, as in *Nectria praetermissa*.

*Epibryon hypophyllum* on *Radula* forms fruit-bodies in which the delicate hymenium is on the protected ventral leaf surface. The leaf blade is perforated by an apical papilla, so

**Figure 1.** Different types of ascospores of bryophilous ascomycetes (all drawn to same scale = 30 μm). Coloured spores are indicated by stippling. 1, *Acrospermum adeanum*; 2, *'Lizonia' sphagni*; 3, *Octosporella ornithocephala*; 4, *Lamprospora retispora*; 5, *Dawsicola neglecta*; 6, *Pitya madothecae*; 7, *Gloeopeziza interlamellaris*; 8, *Grimmicola parasiticus*; 9, *Pseudonectria brongniartii*; 10, *Muellerella frullaniae*; 11, *Nectria racomitrii*; 12, *Epibryon perrumpens*; 13, *Protothelenella polytrichi*; 14, *Bryosphaeria epibrya* (spores desintegrating into single cells already in the asci); 15, *Hypobryon bicolor*; 16, *Bryosphaeria cinclidoti*; 17, *Bryostroma trichostomi*; 18, *Belonioscyphella hypnorum* (germinating spores with conidiogenous cells); 19, *Bryodiscus hepaticarum*; 20, *Trichonectria pellucida*; 21, *Epibryon filiforme* (germinating spores with conidiogenous cells); 22, *Epibryon cryptosphaericum*; 23, *Bryorella cryptocarpa*; 24, *Pleosphaeria* sp.; 25, *Epibryon diaphanum*; 26, *Bryomyces caudatus*; 27, *Potriphila navicularis*; 28, *Dactylospora heimerlii*; 29, *Dawsophila callichroma*; 30, *Philobryon anuliferum*; 31, *Nectria sanramonensis*; 32, *Nectria lankesteri*; 33, *Nectria brenesii* (spores desintegrating into single cells already in the asci); 34, *Bryostroma rhacomitrii*; 35, *Lizonia emperigonia*; 36, *Bryostroma halosporum*.

that the ostiole is situated on the dorsal surface of the leaf. Perforation occurs only in the distal part of leaves which are not covered by a leaf beneath, allowing unhindered ascospore liberation. Several ascomycetes on hepatics with differently overlapping leaves exhibit the same strategy.

Hepaticolous species such as *Calonectria fullaniae* and *Nectria perianthicola* are confined to young sporophytes still enclosed by the perianth. When mature, the apices of the perithecia perforate the perianth wall to achieve ascospore liberation. Infected sporophytes do not develop further and decompose.

*Bryostroma trichostomi* forms ascomata in the leaf axils of pottiaceous mosses, and *Epibryon muscicola* on the adaxial leaf side of diverse *Tortella* species. A similar behaviour is known from the leotialian *Grimmicola parasiticus* on *Grimmia* (Döbbeler and Hertel, 1984). *Bryorella acrogena* selects the leafy shoot apices of pleurocarpous mosses for fruit-body formation (Döbbeler, 1984), as does *Bryostroma rhacomitrii* on *Rhacomitrium lanuginosum*. *Lizonia* species form densely aggregated ascomata in the antheridial cups of *Polytrichum*. Exactly the same niche is occupied by the systematically unrelated *Durella polytrichina* (Racovitza, 1940, 1946).

The longitudinal spaces between the photosynthetic leaf-lamellae of Polytrichales represent one of the most favoured microhabitats. There are more than twenty species of different systematic positions known to colonize these phylogenetically ancient and stable niches. They offer striking examples of convergent evolution, for example the formation of compressed, sometimes extremely small, and reduced ascomata. Even heavy infections with hundreds of fruit-bodies in a single leaf of *Dawsonia superba* do not lead to any visible symptoms (Döbbeler, 1981). Certain species of leaf-inhabiting ascomycetes on polytrichaceous mosses show distinct distribution patterns on that host, prefering apical, basal or lateral parts of the host leaves (Döbbeler, 1986).

## Modes of nutrition

Necrotrophic species, such as *Acrospermum adeanum, Belonioscyphella hypnorum, Bryostroma necans,* all species of *Lizonia*, and several of *Nectria*, cause necrotic and often conspicuously discoloured lesions among healthy green plants of the host colony. Centrifugally expanding and clearly zonated infections are characteristic of *Nectria muscivora* destroying acrocarpous mosses on walls in wet winter months. This is one of the most frequent muscivorous species in the city of Munich. Comparable but larger infections can form spectacular fairy rings or ring-like systems in arctic and antarctic moss communities (Hawksworth, 1973; Longton, 1973, 1988; Fenton, 1983; Gamundí and Spinedi, 1988; p. 476); one of the fungi present has been identified as *Thyronectria hyperantarctica* (Pegler *et al.*, 1980). The hyphae of all bryophyte-destroying ascomycetes hitherto analysed grow *within* their host cells (Fig. 2, number 6). *Acrospermum adeanum* and *Nectria muscivora* attack mosses with an additional superficial mycelium; this is visible to the naked eye as a small whitish zone at the periphery of expanding infections.

Most species on bryophytes are biotrophic parasites which do not or just slightly damage their hosts. Hyphae of these species grow superficially on the host organs (Fig. 2, numbers 1 and 2) or within the cell walls irregularly (Fig. 2, number 4) or in a regular manner (Fig. 2, number 5). Superficial hyphae prefer to grow along the anticlinal walls, often following exactly the host cell reticulum. The mycelium of *Bryochiton perpusillus* develops subcuticularly or within the outermost part of the host cell wall (Fig. 2, number 3). In general terms, biotrophic parasitism is correlated with a superficial and/or intercellular mycelium, and necrotrophic parasitism with an intracellular mycelium.

Systemic infections with the fungal mycelium following the, at least theoretically, unlimited growth of the host colony are frequent. Only the growing points and adjacent tissues are free from hyphae. Several pyrenocarpous and discocarpous parasites reflect this developmental process by presenting differently aged fruit-bodies along the axis of the host plant. The distal younger parts contain primordia, while the proximal older parts carry mature ascomata. Vegetative propagules of the host infected by fungal hyphae probably represent combined distribution units of the host and its parasite. This could be an effective way for an ascomycete to become established on epiphyllous hepatics in rainforests, which often propagate by large, disc-shaped gemmae (Thiers, 1988). Redhead (1980) indicates that the hepaticolous agaric *Gerronema pseudogrisella* is frequently dispersed as mycelium established on gemmae of the liverwort *Blasia pusilla*.

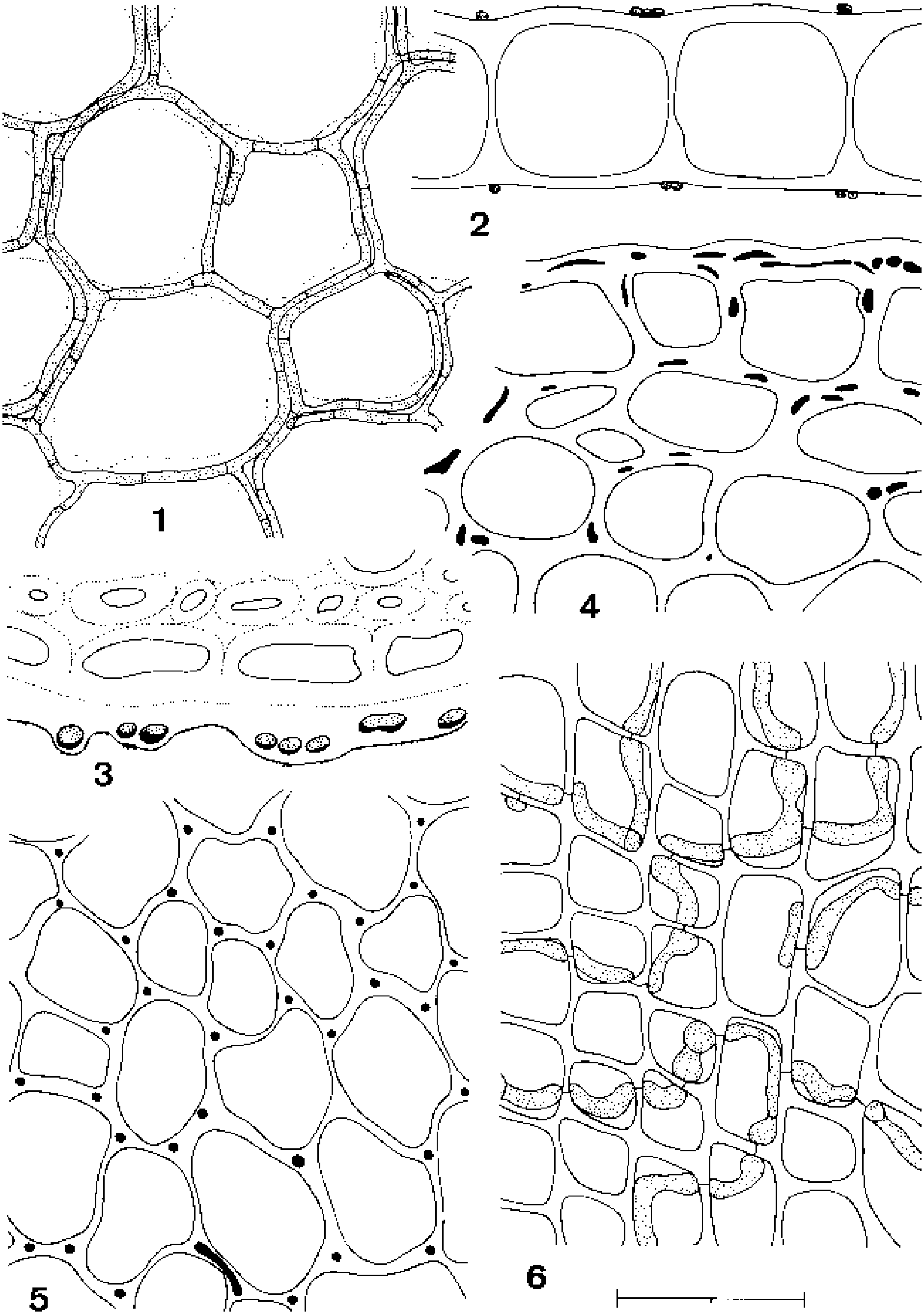
The only known gall-inducing species of bryophilous ascomycetes belong to the genus *Octospora*. Galls are formed by meristematic regions of the subterranean rhizoids of mostly acrocarpous mosses. These hypertrophies sometimes resemble rhizoid gemmae, which are also known from certain acrocarpous mosses (Whitehouse, 1966; Risse, 1987). Several gall types can be distinguished, belonging to at least six species of *Octospora*. The always one-celled, globular galls differ depending on their position on the rhizoids, and micromorphological characters such as the number of appressoria produced (Döbbeler, 1979b; Döbbeler and Itzerott, 1981; Itzerott and Döbbeler, 1982; Itzerott, 1983a; Senn-Irlet, 1988). A careful analysis of the contact zone between *Octospora* species and their hosts will certainly reveal further gall-forming species.

Several bryophilous ascomycetes develop preferentially on older, dying parts of the plant, for example several species of the genus *Epibryon* in the interlamellar spaces of Polytrichales. Bates (1979) points out that in *Pleurozium schreberi* there is no sharp limit between the dead and vital regions, the ageing parts only showing certain decreased physiological processes. The occurrence of obligate, true saprophytes on the gametophyte of mosses and hepatics seems doubtful.

## Appendages of the mycelium

Hyphae of many bryophilous fungi form sessile or stalked appendages (Fig. 3). Together with other hyphal features, they are most useful for species description and the definition of higher taxa. Appressoria, haustoria, or a combination of both, are related to attachment and absorption, whereas conidiogenous cells play a role in asexual reproduction or spermatization.

*Nectria hylocomii* and related species develop appressoria more or less irregularly on their host cells (Fig. 3, number 2). The appressoria of *N. egens* are located at the cell junctions (Corner, 1935), and the elaborate appressoria of the two species of *Dawsomyces* exclusively occupy the periclinal walls of single host cells (Fig. 3, number 1). Complex appressoria-like structures at the internal apical side of the mucilage cells of *Sphagnum* are produced by *Discinella schimperi* (Fig. 3, number 3; Redhead and Spicer, 1981). The surprising regularity by which some fungi select particular sites of the host surface for appressorium formation is evidence of the importance of specific microhabitats (Emmett and Parbery, 1975, p. 158).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Haustoria originating directly from a superficial mycelium without the formation of appressoria may be intraparietal or intracellular. Peg-like haustoria confined to the host cell walls are typical of *Bryomyes hemisphaericus* and other congeneric species (Fig. 3, number 5). *Potriphila navicularis* develops haustoria within individual cells of the hair-like leaf trichomes of *Polytrichum alpinum* (Fig. 3, number 4), while *Gloeopeziza cuneiformis* infects the cells of the leaf blade of several species of *Polytrichum* with intracellular haustoria (Döbbeler, 1996a). The combination of appressoria and intraparietal haustoria characterizes the genus *Hypobryon* (Döbbeler, 1983). Conspicuous appressoria and intracellular haustoria occur in *Octospora* and related genera (Fig. 3, number 6; Corner, 1929; Racovitza and Racovitza, 1945; Racovitza, 1946; Döbbeler 1979b, 1980b).

In several cases, conidiogenous cells have been observed on the hyphae. Small phialidic cells are typical for *Hypobryon* (Döbbeler, 1983) and *Epibryon filiforme* (Döbbeler and Menjívar, 1992). Similar anamorphs seem to be more frequent, but are difficult to detect.

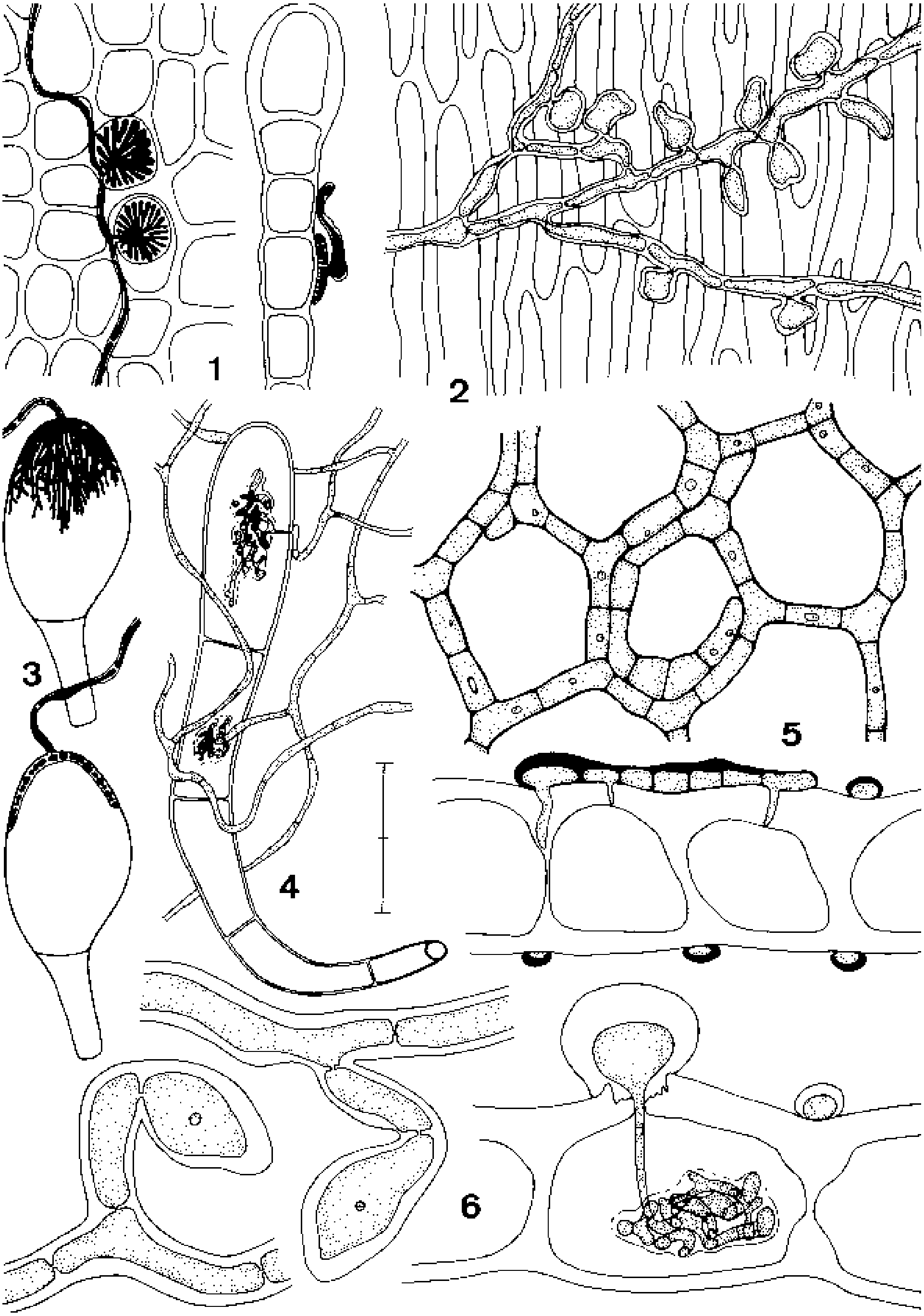
## Adaptations

The colonization of bryophytes by fungi requires biochemical adaptations to the host metabolism, as in other fungal parasites. In addition, extreme environmental conditions in ecological niches such as late snow-lie areas in arctic regions or the phyllosphere in tropical rainforests are reflected by specific adaptations of both hosts and parasites. Some of the fungal features related to their bryophilous habit are discussed here. A phenological synchronization between host and parasite is demonstrated by the *Polytrichum*-inhabiting species of *Lizonia;* the ascomata develop only when uninfected plants produce antheridia.

Perhaps the most striking adaptation of the bryophilous fungi is the small size of their fruit-bodies. Many ascomata are smaller than 100 μm in diameter. Those of *Bryochiton monascus* and *B. perpusillus*, hardly reach 50 μm in diameter, and, spectacularly, *Epibryon endocarpum* has ascomata only 25–35 μm in diameter obligately formed *within* individual cells of *Plagiochila asplenioides* (Döbbeler, 1980a). These fungi are among the smallest fruit-body-forming ascomycetes. The reduced size may be interpreted as a response to the limited size of the substratum and to the small amount of available nutrients. Redhead (1984) points out that bryophilous members of *Omphalina* and other genera are normally smaller than their non-bryophilous relatives, interpreting the reduced size of the basidiomata as a response to a limited availability of nutrients.

Mechanisms assuring survival in dry conditions are very important for bryophilous fungi, and a preference for moist microhabitats on the host plants has been mentioned

**Figure 2.** Positions of hyphae in relation to the host cells (scale = 25 μm). 1, *Epibryon plagiochilae* on *Plagiochila porelloides*: superficial hyphae following the anticlinal walls of the host cells (Germany, Bavaria, Kreuzeck, 24 July, 1980, Poelt & Döbbeler 3484, M); 2, The same leaf in section; 3, *Bryochiton perpusillus* on *Polytrichum piliferum*: transverse section through a leaf showing subcuticular hyphae at the abaxial side of the leaf (Austria, Tyrol, Fimbertal, 28 July, 1979, Döbbeler 3548, M); 4, *Dactylospora heimerlii* on *Plagiochila asplenioides* s. l.: transverse section through the outer part of the stem; hyphae grow irregularly within the cell walls (Germany, Bavaria, Jachenau, 1 November, 1978, Döbbeler 3164, M); 5, *Punctillum hepaticarum* on *Plagiochila* sp.: transverse section through the stem, hyphae growing in the angles of the cell walls nearly exclusively in the longitudinal direction of the axis (Tasmania, Mt Barrow, without date, Jarman 1477, M); 6, *Nectria muscivora* on *Didymodon rigidulus*: hyphae within cells of the basal part of the leaf, note the fine hyphal pegs perforating the anticlinal cell walls (Germany, North Rhine-Westphalia, Olpe, 7 January, 1978, Döbbeler 2852, M).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above. Perithecia or perithecia-like ascomata are more frequently developed than apothecia-like ones; the latter are less xerophytic than perithecia (Eckblad, 1968, p. 151). The fruit-bodies of the hepaticolous *Octosporella jungermanniarum* (Pezizales), which resemble perithecia, are interpreted by Corner (1929) as modified apothecia consequent to depauperation and xerophily.

As in lichen-forming ascomycetes, gelatinous material may be produced in the hymenium and/or ascomatal wall as a water storing substance (Ingold, 1959; Pfister, 1976). Mucilage in the hymenium often reacts with Lugol's solution resulting in either a reddish or a bluish colour after pretreatment with potassium hydroxide (Döbbeler, 1978, p. 12). Baral (1987) terms this conspicuous reaction 'hemiamyloid'. It is regarded as one of the diagnostic characters for the genera *Epibryon, Hypobryon* and some other bryophilous taxa.

Discomycetes with reviving ascomata which are closed when dry and open when moist in order to expose the hymenium (Haines and McKnight, 1977; Sherwood *et al.*, 1980; Sherwood, 1981; Kropp and Carpenter, 1984) are to be expected among the bryophilous fungi.

Phototropic movements of different parts of ascomata towards the incident light have been sporadically observed in different bryophilous ascomycetes. They are typical in those on *Polytrichum sexangulare*, which grows in dense carpets (Döbbeler, 1987). The formation of fruit-bodies mainly in the upper halves of leaves and a positive phototropism facilitates ascospore discharge into the open air. The phototropic reaction is achieved in different ways: by the whole ascomata, by ascomatal necks (as in *Protothelenella polytrichi*), by laterally orientated ostioles (e.g. certain *Bryochiton* species), or by the ascus apices (e.g. *Gloeopeziza interlamellaris* of Leotiales). The phototropic curving of asci has previously been reported mainly in Pezizales (Ingold, 1971, p. 14).

Species such as *Epibryon diaphanum* occurring mostly on Hypnaceae, or as parasites of epiphyllous hepatics like *E. deceptor* (sp. nov. ined.) on *Radula flaccida* show a remarkable tendency towards reduced fertility. Scattered ascomata contain few asci with large spores, and anamorphs are unknown. These fungi apparently occupy stable niches in which a high reproductive potential does not yield a selective advantage. The same phenomenon occurs in the coprophilous genus *Sordaria* and in the Laboulbeniales (Raper, 1968). We face the

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**Figure 3.** Hyphae with appressoria and/or haustoria (scale = 20 µm). 1, *Dawsomyces mirabilis* on *Dawsonia superba*: appressoria without haustoria covering single periclinal walls of cells of leaf-lamellae; on the left side two appressoria in surface view, on the right side section through an infected leaf lamella (Tasmania, Castra Road, 24 June, 1891, Burchard, M–holotype); 2, *Nectria hylocomii* on *Hylocomium splendens*: irregularly oriented appressoria without haustoria on the cells of a leaf in surface view (Germany, Bavaria, Spitzingsee, 8 October, 1977, Döbbeler 2788, M); 3, *Discinella schimperi* (sterile infection) on *Sphagnum squarrosum*: infected mucilaginous cells of the apical parts of the stem with an intracellular appressorium closely appressed to the internal cell wall; above in surface view, below optical section (Canada, Ontario, Nipigon, 1 July, 1956, Heinrich, M); 4, *Potriphila navicularis* on *Polytrichum alpinum*: intracellular haustoria in cells of trichomes arising from the leaf-lamellae, without appressoria (Austria, Tyrol, Fimbertal, 28 July, 1979, Döbbeler 6759, M–holotype); 5, *Bryomyces hemisphaericus* on *Plagiochila porelloides*: hyphae grow superficially and follow strictly the anticlinal cell walls, develop peg-like haustoria into the cell walls, and lack appressoria; above seen from above, below section (Germany, Bavaria, Rossstein, 7 October, 1978, Döbbeler 3351, M); 6, *Octosporella ptilidii* on *Ptilidium ciliare*: appressoria with haustoria; on the left side two stalked appressoria seen from above, to the right section through an appressorium with peg-like perforation-tube and intracellular haustorium (Switzerland, Lower Engadine, Lavin, 1 September, 1984, Müller & Döbbeler 5925, M–holotype).

paradoxical situation that the delicate and short-lived epiphyllous hepatics, the 'biological nomads' of the rainforest (Richards, 1984), represent stable niches for hepaticolous fungi.

## Host specificity

The choice of hosts has to be carefully considered because 'the host is part of the parasite's environment and must be part of the species circumscription' (Savile, 1993, p. 270). Indeed, nearly all bryophilous fungi exhibit a certain degree of host specificity. Notwithstanding the fact that many species are known only from the original collection, there are rather well – documented examples of species depending on single host species and others infecting a wide range of hosts. Between these extremes intermediate types occur. *Epibryon metzgeriae* is known only from *Apometzgeria pubescens* (Döbbeler, 1985), and *Pseudonectria brongniartii* is recorded exclusively from *Frullania dilatata* (Döbbeler, 1984). The very common *Epibryon plagiochilae* is specific to *Plagiochila asplenioides* and the closely related *P. porelloides* and does not infect *Pedinophyllum interruptum* (syn. *Plagiochila interrupta*), a member of the only additional genus of the Plagiochilaceae in Europe. *Pedinophyllum interruptum* is easily confused with *Plagiochila porelloides* (Grolle, 1969). I checked more than 60, mostly Central European, specimens of *Pedinophyllum interruptum* in the Botanische Staatssammlung München (M) without finding any infection. The presence of *Epibryon plagiochilae* is a useful way of determining *Plagiochila asplenioides* s.1.

After studying hundreds of polytrichaceous mosses, I consider *Potriphila navicularis* to be specific for *Polytrichum alpinum* in Central Europe. The infection of *Pogonatum urnigerum* (syn. *Polytrichum urnigerum*) by this parasite has never been observed, though the moss can be confused with *Polytrichum alpinum*. On the other hand, the extremely common *Epibryon pogonati-urnigeri* on *Pogonatum urnigerum* does not attack *Polytrichum alpinum*. These examples show that the *Polytrichum*-inhabiting ascomycetes are excellent taxonomists, sometimes knowing their hosts better than bryologists (Döbbeler, 1996b).

The four accepted species of *Lizonia* are known exclusively from polytrichaceous mosses. European populations of *Polytrichum commune*, *P. formosum* and *P. sexangulare* are frequently infected. These hosts, and *P. piliferum* have specific parasites, defined by host selection and anatomical characters. Mosses only once recorded as hosts for *Lizonia* are *Pogonatum* sp. from Nepal (Döbbeler, 1978), *Oligotrichum aligerum* from Alaska (Parriat and Moreau, 1954) and *Dendroligotrichum dendroides* from Chile (Döbbeler, unpubl.).

*Dactylospora heimerlii* is known to grow on nine different host genera of the Jungermanniales, most commonly on *Plagiochila asplenioides,* which has received special attention as a rich host for unusual fungi. However, until now neither *Frullania* nor *Radula*, which both belong to the same order, are documented as hosts for *Dactylospora*, though many specimens of these hepatics were examined (Döbbeler and Triebel, 1985).

A very wide host range characterizes *Acrospermum adeanum*, with most of the infected bryophytes belonging to the Hypnobryales, growing on bark of trees or on calcareous rocks (Döbbeler, 1979a). *Sphagnum* supports, unsurprisingly in view of its relationships, a mycobiota of its own with several genus- or species-specific parasites, for example *Epibryon turfosorum*, *Discinella schimperi*, and diverse species of *Lasiosphaeria*. *Bryochiton perpusillus* is frequently recorded from hepatics such as *Ptilidium* and the moss *Polytrichum* (Döbbeler, 1978). In this case, conspecificity should be re-investigated carefully.

*Didymosphaeria marchantiae* on *Marchantia polymorpha* is now regarded as a synonym of the cosmopolitan *Phaeodothis winteri*, which occurs on an astonishingly wide range of hosts, including fungi as well as lignified and non-lignified phanerogams (Aptroot, 1995a, b). If the conspecificity is proved, this is one of the very few examples of a facultative bryophilous species.

Members of the systematically isolated Polytrichaceae (including *Dawsonia*) are nearly always infected by fungi. More than 40 ascomycetes are known to be associated with them (Döbbeler, 1986). These large or even gigantic mosses with long-lived gametophytes are characterized by a structural complexity in kind or degree which is achieved by no other group of bryophytes (Smith, 1971, p.76). They provide many different microhabitats. In addition, the antiquity of *Polytrichum* and allied genera has probably favoured the evolution of a large number of parasites restricted to them. The lichen genus *Peltigera* is also considered to be particularly old, partly because of the many obligately lichenicolous fungi known only from this host genus (Hawksworth, 1980, 1982; Hawksworth and Santesson, 1988).

## Frequency and geographical distribution

To understand the frequency and the geographical distribution of the fungi on bryophytes, two facts should be taken into consideration. First, the presence of a fungus is recorded by the presence of its *fertile* structures, i.e. ascomata. However, mosses or hepatics growing under natural conditions are actually never free from hyphae, i.e. non-sporing fungal infection. Normally, hyphal features do not permit the distinction of taxa at a lower level, an exception being some fungi with characteristic hyphal appendages. *Discinella schimperi*, a highly specialized parasite of *Sphagnum squarrosum*, is very frequent in the northern circumpolar region. The presence of sterile mycelia with unique appressoria (Fig. 3, number 3) indicates that the infection rate may be higher than 50 % (Redhead and Spicer, 1981). From a sterile mycelium with characteristic appressoria and haustoria on the hepatic *Schistochila aligera* I can recognize an *Octosporella*-like fungus from Sri Lanka (Döbbeler, 1978, p. 107). Ascomata of *Octosporella*, and the recently separated genus *Filicupula* (Yao and Spooner, 1996), are until now recorded only from Europe, Costa Rica and Venezuela.

Second, the presence or absence of fruit-bodies in a host population depends on the size of the collection. Infections are often randomly distributed in patches within mosses or hepatics. The investigation of more individual host plants, or larger cushions, increases the probability of discovering parasites. In general terms, bryophilous fungi are much more frequent than records indicate.

Döbbeler (1987) concluded that about half of the collections of *Polytrichum sexangulare* deposited in reference collections are inhabited by at least one of the six species of ascomycetes which attack this host. Several parasites of the tropical epiphyllous *Radula flaccida* occur regularly in the whole American as well as the African area of the host (Döbbeler, unpubl.). *Epibryon pogonati-urnigeri* on *Pogonatum urnigerum* is known from Europe, North America and Asia (Döbbeler, 1985), and has been recorded recently from Zaire in Africa (Döbbeler, unpubl.). *Potriphila navicularis* has a bipolar distribution, as does its host *Polytrichum alpinum* (Döbbeler, 1996b). *Bryochiton perpusillus* is extremely widespread because it seems to be constantly present on *Polytrichum piliferum*, which is almost cosmopolitically distributed (Long, 1985) and infects also other polytrichaceous mosses, including *Dawsonia*.

## The actual situation

Several examples clearly demonstrate that our knowledge of the bryophilous ascomycetes is in an almost Linnean situation, especially outside Central Europe. Five of the six species of *Hypobryon* are known exclusively from their type collections (Döbbeler, 1983; Döbbeler and Menyivar, 1992). Four new species of *Nectria* on epiphyllous hepatics are known only from Costa Rica (Döbbeler and Carranza, 1993). Actually, the genus *Frullania* is the 'best' host genus of the hepatics, with 15 species of associated ascomycetes which are nearly exclusively known from *F. dilatata* and *F. tamarisci*, though the genus contains perhaps over 500 species (Schuster, 1988). Ten species are known on *Plagiochila*, nearly always recorded from *P. asplenioides* s. l., yet, *Plagiochila* is by far the largest genus of the Hepaticae with hundreds of species (Schuster, 1980). The situation is similar in large genera like *Porella* and *Radula*, in which only very few, mostly European, species have been demonstrated as substrata for fungi.

A single collection of the epiphyllous hepatic *Radula flaccida* from Africa (Tanzania, Amani, 1911, Braun, M) yielded seven parasitic non-lichenized species, whereas up to now only four bryophilous ascomycetes are known from the whole continent (Döbbeler, unpubl.).

Polytrichaceous mosses are relatively well studied, but the approximately 20 species recorded as hosts represent only 5% of the 354 species of the Polytrichidae (Walther, 1983).

Schofield (1985) indicates that there are about 18 000 species of bryophytes, 10 000 Musci and 8000 Hepaticae. They all constitute *potential* hosts, though by no means all of them may harbour specific parasites. Until now only a very small fraction has been proved to be a substratum for fungi. Remarkably, the number of bryophyte species is comparable to that of the estimated world total of 17 000 to 20 000 lichens postulated to exist (Galloway, 1992), although only around 13 500 lichenized fungi are as yet described (Hawksworth *et al*., 1995). Mosses and hepatics share several important ecophysiological characters with lichens, though they are evolutionarily unrelated (Nash and Egan, 1988). Hawksworth (1991) points out that there may be at least 2000 species of obligately lichenicolous fungi. I am convinced that species diversity among bryophilous fungi is at least as high as among the lichenicolous ones.

The first clear and accurate descriptions and illustrations of bryophilous ascomycetes were published by the bryologist Johann Hedwig in 1789, introducing the generic name *Octospora* for several muscicolous species (Müller, 1977). More than two hundred years later we realize that within the bryophilous fungi more remains to be discovered and described than in many other ecological groups. Bryomycology urgently needs more attention from both bryologists and mycologists!

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