Notes RBG Edinb. 44(3):549–560 (1987)

OBSERVATIONS ON THREE ALGICOLOUS MICROFUNGI

D. L. HAWKSWORTH*

ABSTRACT. Studies on three microfungi forming symbiotic associations with algae are reported. The nomenclature of the marine hyphomycete *Blodgettia* Wright and its type species *B. bornetii* Wright is examined and the correct generic and species names found to be *Blodgettia* Harvey and *B. confervoides* Harvey; this fungus forms a mutualistic symbiosis with *Cladophora*. A pyrenocarpous fungus collected on a freshwater *Lemanea* from France conspecific with *Sphaeria lemaneae* Cohn ex Woronin is found to be most appropriately placed in *Phaeospora* Hepp ex B. Stein as *Phaeospora lemaneae* (Cohn ex Woronin) D. Hawksw. The new hyphomycete genus *Velutipila* D. Hawksw. is introduced for the single species *V. poeltii* D. Hawksw. from Austria; this associates with a chlorococcalean alga (?*Gyroeffyana humicola*) and forms lichen-like patches in decaying moss cushions in Austria.

In the course of the preparation of a survey of the variety of symbiotic relationships between algae and fungi (Hawksworth, in press) three algicolous fungi came to my attention which merited separate consideration because of nomenclatural confusion, uncertain position, or for being previously undescribed. These cases are reported on here.

Blodgettia Harvey in Smithson. Contrib. Knowl. 10:46 (1858).
Syn.: *Blodgettia* Wright in Trans. R. Irish Acad. 28:25 (1881); nom. illegit. (Arts. 63.1, 64.1).
Blodgettiomyces Feldmann in Revue Bryol. Lichén. 11:157 (1938); nom. illegit. (Art. 63.1).

Blodgettia confervoides Harvey in Smithson. Contrib. Knowl. 10:48 (1858). Fig. 1.
Syn.: *Blodgettia bornetii* Wright in Trans. R. Ir. Acad. 28:25 (1881); nom. illegit. (Art. 63.1).
Blodgettiomyces bornetii (Wright) Feldmann in Revue Bryol. Lichén. 11:157 (1938); as '*borneti*'; nom. illegit. (Art. 63.1).
For descriptions see Harvey (1858), Feldman (1938), and Kohlmeyer & Kohlmeyer (1979).
USA. Florida, Key West, on *Cladophora* sp., *F. W. Hooper* [Farlow, Anderson & Eaton, *Algae Exs. Am. Bor.* no. 44] (IMI 296815).

This widespread hyphomycete, which occurs on marine *Cladophora* Kütz. species, forms an apparently mutualistic symbiotic association in which the fungus grows within the algal cell walls. The alga is consequently the 'exhabitant' and the fungus the 'inhabitant' in the terminology of Law & Lewis (1983); the association is a 'mycophycobiosis' as understood by Kohlmeyer & Kohlmeyer (1972).

This association was first described by Harvey (1858) who did not appreciate its composite nature and thought he was dealing with a novel alga. The biological situation was clarified by Wright (1881) who rejected

*CAB International Mycological Institute, Ferry Lane, Kew, Surrey TW9 3AF.

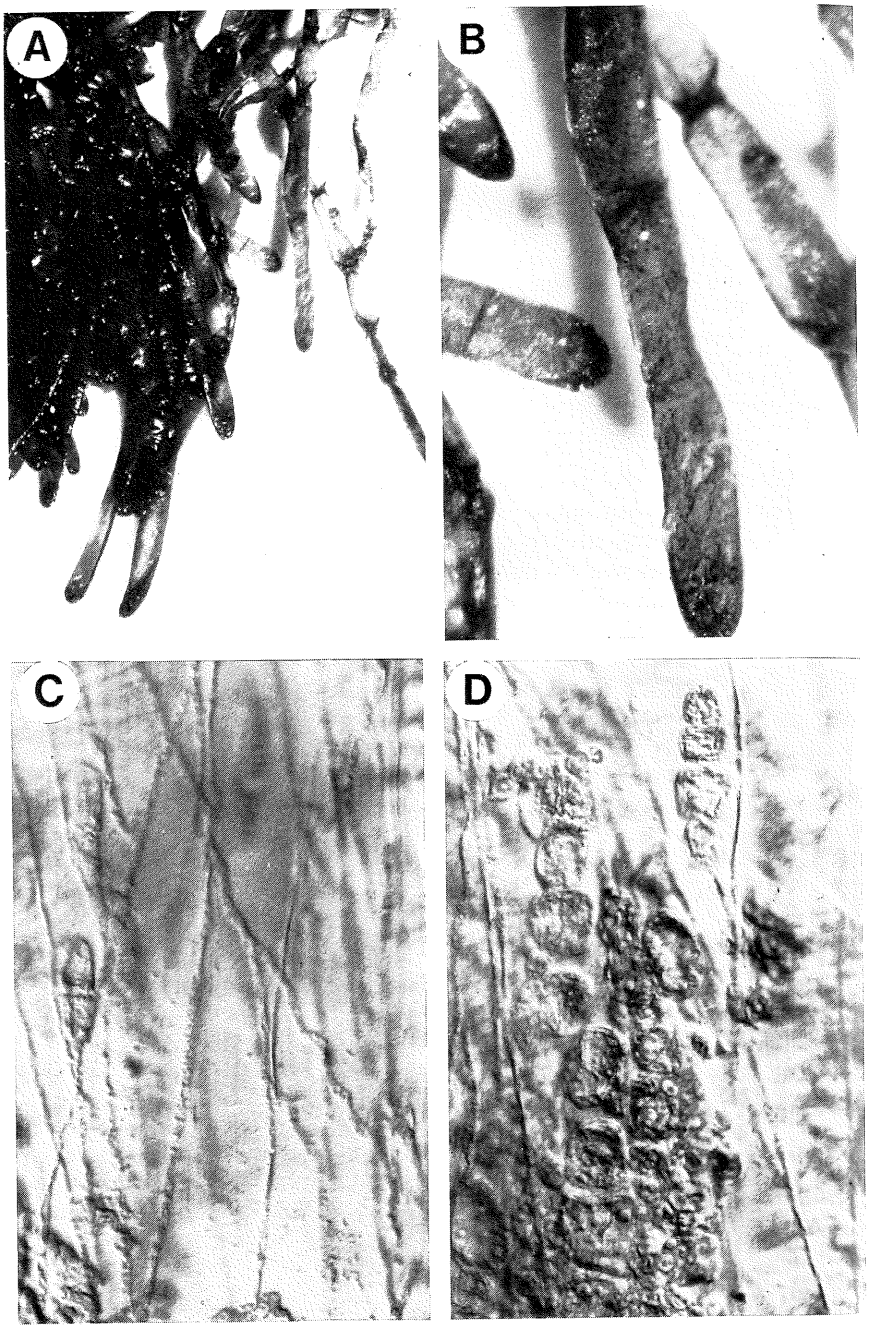


FIG. 1. *Blodgettia confervoides* (IMI 296815). A, infected *Cladophora* thallus (×2); B, lobe showing conidia as speckles (×6·5); C, developing conidium and hyphae immersed in the walls of the host (×400); D, conidia still attached to the conidiogenous cells (×400).

Harvey's names as they were based on discordant elements and described a new genus, *Blodgettia* Wright, with *B. bornetii* Wright as the only species. *Blodgettia* Wright, however, could not be accepted as it was a later homonym of Harvey's validly published name. Feldmann (1938), correctly under the then operative Code, coined the new generic name *Blodgettiomyces* Feldmann for the fungal component and transferred Wright's specific epithet into it. Kohlmeyer & Kohlmeyer (1979) adopted the genus '*Blodgettia* Wright' and '*B. bornetii* Wright', citing Art. 70 of the Code which stated that names based on discordant elements were to be rejected.

Unfortunately, Art. 70 of the Code was deleted at the 1975 Leningrad International Botanical Congress and has not been reinstated. Under the currently operative Code adopted at the Sydney Congress in 1981, one of the elements of such mixed material must be selected as lectotype for such names. The principle diagnostic features for Harvey's (1858) generic and specific names were those of the fungal component and so this is the natural lectotype which must now be adopted. This generic lectotypification was in effect implied by Wright (1881) in retaining '*Blodgettia*' for the fungal partner.

Under the currently operative Code, the correct generic citation is *Blodgettia* Harvey and the current name of the type species is *B. confervoides* Harvey. A synopsis of the nomenclature is presented above.

Phaeospora lemaneae (Cohn ex Woronin) D. Hawksw., **comb. nov.** Figs 2–4.

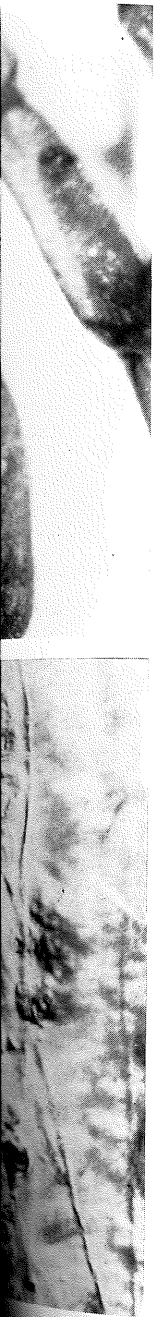
Syn.: *Sphaeria lemaneae* Cohn ex Woronin, in de Bary & Woronin, Beitr. Morph. Phys. Pilze 1(3):1 (1870).

Leptosphaeria lemaneae (Cohn ex Woronin) Sacc., Syll. Fung. 2:84 (1883).

Sphaeria fluviatilis Phillips & Plowright in Grevillea 10:73 (1881).

Leptosphaeria fluviatilis (Phillips & Plowright) Sacc., Syll. Fung. 2:84 (1883).

Mycelium immersed, composed of richly branched colourless hyphae 2·3–3·5μm wide ramifying between the cortical cells of the host and also later in the central lumen of the filaments between the sporangiospores. *Ascomata* perithecia, arising singly or 1–2 compressed in vertical sections, immersed, only the tip of the ostiole reaching the surface, black, subglobose to obpyriform, lacking a distinct neck, 50–75(–90)μm diam. in surface view, 75–115μm tall and 60–110μm wide in vertical section; ascoma walls 10–14μm thick throughout, composed of 3–4 irregularly arranged layers of pseudoparenchymatous cells, textura angularis, brown to almost colourless towards the base, always dark brown in at least the upper two-thirds; individual cells subglobose to angular, 5–7μm diam., the outer and upper cells most deeply pigmented; centrum tissues not turning blue in Lugol's iodine (after pre-treatment with KOH). *Hamathecium* absent; colourless thin-walled pseudoparenchymatous cells present between developing asci in young ascomata but disappearing as these mature. *Asci* broadly cylindrical, short-stalked, thick walled, especially at the apex which has a small internal apical beak, bitunicate in structure, discharge fissitunicate, (50–)55–60 × 9–12μm, (6–)8-spored. *Ascospores*



us (×2); B, lobe
immersed in the
×400).

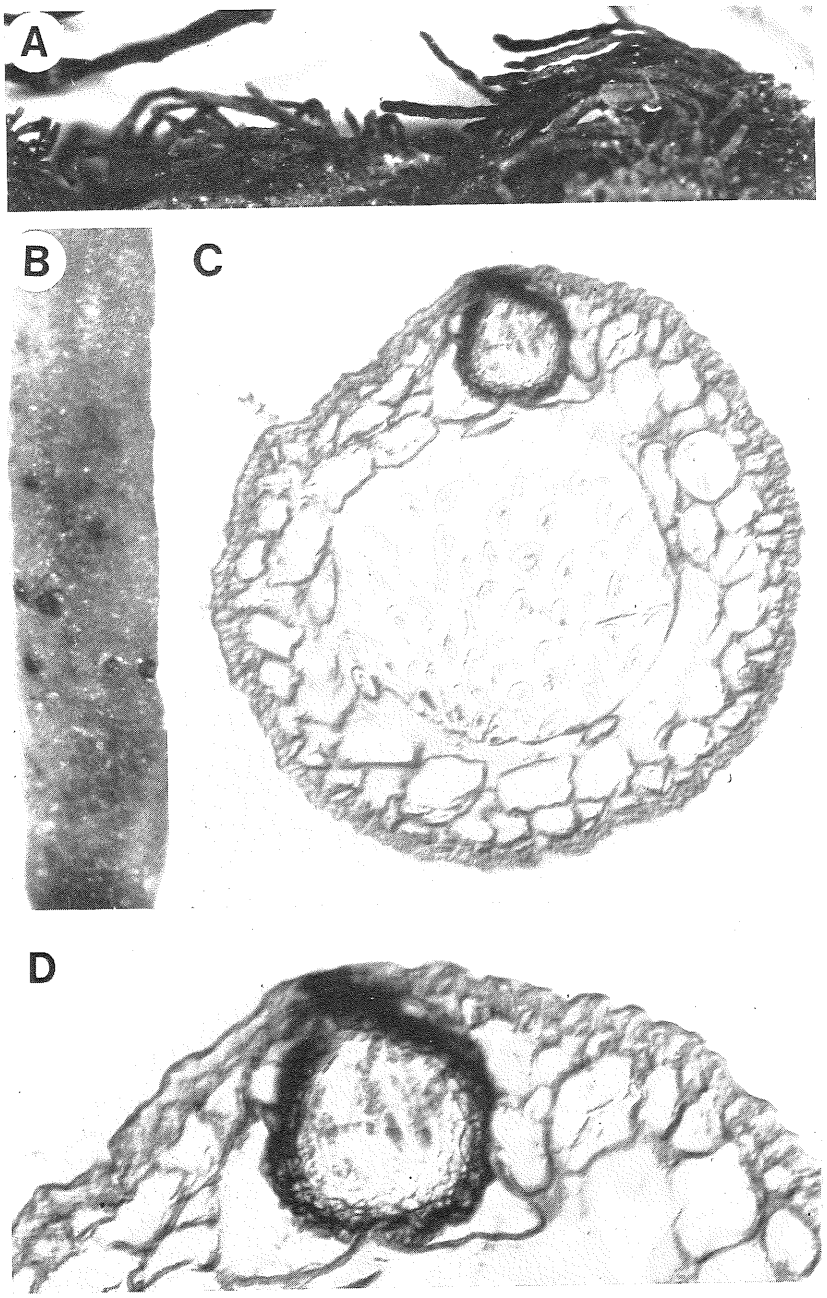


FIG. 2. *Phaeospora lemaneae* (IMI 312670). A, infected *Lemanea* thallus (×2·5); B, filament with immersed ascomata (×13); C, vertical section of filament with immersed ascoma (×200); D, vertical section of ascoma (×400).



FIG. 3. *Phaeospora lemaneae* (IMI 312670). A, vertical section of ascoma (×800); B, asci with 3-septate (left) and 1-septate (right) ascospores (×2200); C, mature 3-septate ascospores (×2200).

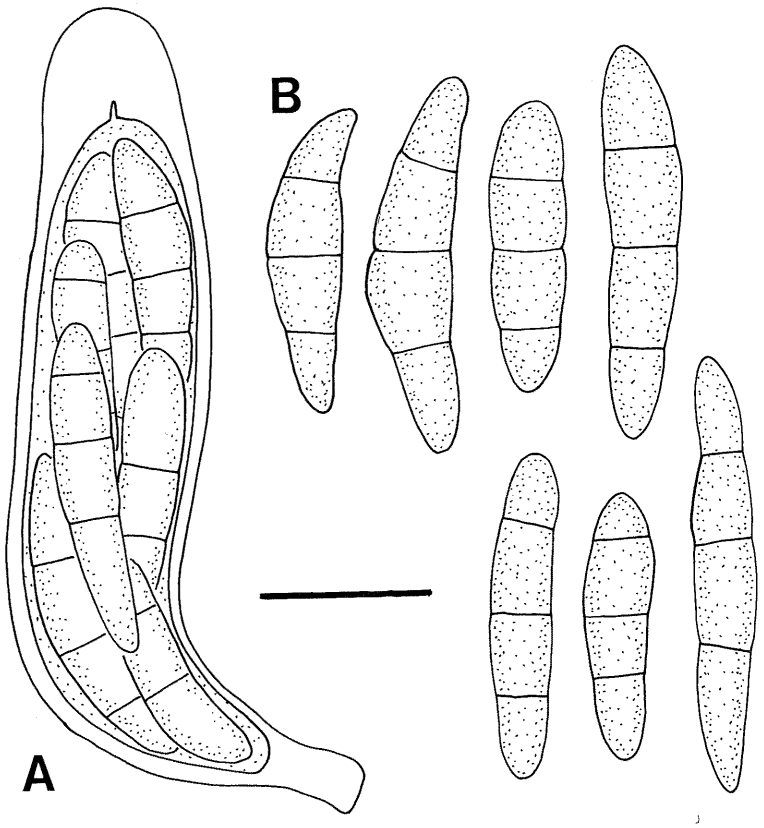


FIG. 4. *Phaeospora lemaneae* (IMI 312670). A, ascus; B, ascospores. Scale = 10μm.

irregularly arranged in the ascus, elongate-ellipsoid to broadly fusiform, straight to slightly curved, 3-septate when mature, not or slightly constricted at the septa, colourless to pale yellowish-brown when mature, smooth-walled, lacking any distinct gelatinous sheath, (18–)19–23(–25) × 4–4·5(–5)μm.

ENGLAND. Shropshire, Long Mynd, 'on submerged aquatic plant' [*Lemanea* Bory sp.], [ex-herb. M. C. Cooke 1865], *?W. Phillips* (K; ? holotype of *Sphaeria fluviatilis*).

FRANCE. Cévennes, near St Jean du Gard, Sanmane, on *Lemanea* sp. on schists by stream, 15–30cm above water level, vii 1986, *D. J. Hill* (IMI 312670).

GERMANY. Freiburg, Brisgov., on *Lemanea fluviatilis,* viii 1863, *M. Woronin* [Rabenhorst, *Fungi Eur.* no. 640] (K).

This species was first discovered on *L. fluviatilis* (L.) C. Agardh collected near Bonn in 1854, and then in Freiburg in 1863–64. According to the excellent illustrations provided by Woronin (1870: Tab. 1 figs 1–23) and material distributed in Rabenhorst's *Fungi Europaei* no. 640 (K), there is no doubt that the fungus collected in France is conspecific with

Cohn and Woronin's fungus. Phillips & Plowright (1881) gave the ascospores as 20–22 × 5μm, but ones down to 19 × 4μm were found in what is presumed to be the Phillips's collection in K.

Ingold (1955) stated that the ascospores were normally 2-celled, but 3-septate ones were regularly seen inside asci in all three collections examined here (Figs 3B, 4A); 1-septate ascospores appeared to be immature (Fig. 3B).

The ascomata are abundantly produced along the length of the filaments of the alga. The filaments appear to be essentially unharmed and the alga continues to sporulate abundantly. Brierley (1913) studied the life history in detail and noted that in older filaments haustoria could penetrate the algal cells. However, the hyphae also ramify through the central canal of the algal filaments and, as noted by Hudson (1986), the general impression is of a symbiotic association parallel to that between *Mycosphaerella ascophylli* Cotton and *Pelvetia canaliculata* (L.) Dcne & Thuret. However, the alga can apparently occur without this fungus, so the extent of any mutualism is less than in that case. It seems most probable that the association is at first commensalistic but tends to become parasitic as the algal filaments age.

Brierley (1913) already recognized that as the ascomata lacked any hamathecial filaments *Leptosphaeria* Ces. & de Not. was not an appropriate genus for this fungus. The uncertain *Metasphaeria* Sacc. is also inappropriate as it is generally used for species with hamathecial filaments and colourless ascospores. In the heterogeneous *Sphaerulina* Sacc. the ascospores remain entirely hyaline also. I cannot, however, find any valid reason why this fungus should not be placed in *Phaeospora* Hepp ex B. Stein, a genus hitherto exclusively of lichenicolous fungi with aparaphysate ascomata and generally 3-septate subhyaline to pale brown ascospores. The necessary new combination is therefore made here.

A further pyrenomycete described from *Lemanea* is *Metasphaeria aquatica* Pat.; this was said to have ascospores 30–38 × 9–10μm (Patouillard, 1908) and so would not appear to be conspecific with *Phaeospora lemaneae*.

Velutipila D. Hawksw., **gen. nov.**

Genus algicola, ad Hyphomycetes pertinens. Stromata, setae et hyphopodia absentia. Conidiophora micronematata. Cellulae conidiogenae e mycelio immerso exorientes, holoblasticae, cicatricae, subcylindricae vel ad elongato-ampulliformes, hyalinae, laeves. Conidia anguste subcylindrica, basi attenuata, hyalina, 1–3-septata, laevia.

Species holotypica, adhuc unica, est *Velutipila poeltii* D. Hawksw.

Genus algicolous, belonging to the Hyphomycetes. *Stromata,* setae and hyphopodia absent. *Conidiophores* micronematous. *Conidiogenous cells* arising from the immersed mycelium, holoblastic, bearing scars formed by the cessation of conidia near the apex, subcylindrical to elongate-ampulliform, often rather geniculate apically, colourless, smooth. *Conidia* narrowly subcylindrical, tapered at the base, hyaline, 1–3 septate, smooth.

This new genus most strongly resembles *Vermispora* Deighton & Piroz., introduced for *V. grandispora* Deighton & Piroz. known from a single collection overgrowing *Irenopsis aciculosa* (Winter) Stevens in Sierra Leone (Deighton & Pirozynski, 1972). Type material of this fungus was

examined (Sierra Leone, Bumpe, on leaves of *Sida urens* L., 30 x 1949, *F. C. Deighton* M3296B, IMI 40258b–holotype) and found to be distinguished from *Velutipila* by the massive and somewhat sigmoid conidia with an almost acuminate apex, the presence of septate conidiophores, and particularly the raised denticulate conidial scars.

The generic name *Velutipila* recalls the velvety pile-like appearance of the infested algal colonies.

Velutipila poeltii D. Hawksw., **sp. nov.** Figs 5, 6.

Fungus algicola. Mycelium immersum, hyalinum, hyphis 0·75–1μm latis compositum. Conidiophora micronemata. Cellulae conidiogenae e mycelio immerso exorientes, holoblasticae, cicatricae, subcylindricae vel elongato-ampulliformes, hyalinae, 11–20 × 3–5μm, laeves. Conidia anguste subcylindrica, hyalina, (0–)1–3-septata, laevia, (11–)14–23(–30) × 1·5–2μm, basi attenuata et 1·5–2 × 0·5μm.

Typus: Austria, Koralpe, Steiermark, Soboth, Wey St. Leonhard-Nedwed-Gaschitzbach, symbiotic with a chlorococcalean alga (? *Gyroeffyana humicola* Kol. & Chodat) on *Ditrichum pusillum* (Hedwig) Hampe, alt. 1180–1300m, 10 viii 1986, *J. Poelt* (IMI 309488—holotypus; GZU P6–86—isotypus).

Colonies developing in moss cushions on the ground, forming dark greenish to green-black nitidous patches 1–3cm diam., comprising irregular areas of algae and moss fragments matted together with fungal hyphae in a gelatinized matrix to form an uneven crust. *Mycelium* ramifying between the algal cells and decayed moss fragments, hyaline, smooth, septate, irregularly branched, 0·75–1μm wide, becoming enlarged to 1·5–2μm wide in the vicinity of algal cells to which they may adhere. *Conidiophores* micronematous. *Conidiogenous cells* arising directly from the mycelium, erumpent through the algal colonies giving the surface a velvety appearance at low magnification (× 20–50), integrated, mono- or rarely polyblastic, elongate-ampulliform, hyaline, thin-walled, smooth-walled, 11–20μm tall, 3–5μm wide at the base but becoming somewhat geniculate and tapering to 1–1·5μm wide near the apex; conidial scars distinct, refractive, scarcely protruding, 0·5μm diam., extension of the conidiogenous cell taking place behind the most recently formed scar which is then forced into a lateral position. *Conidia* arising singly from the apex of the conidiogenous cell, developed holoblastically by growth of the outer and inner wall layers of the conidiogenous cells, dry, elongate cylindrical-fusiform, straight to slightly curved, hyaline, (0–)1–3-septate, smooth-walled, lacking a gelatinous sheath, (11–)14–23(–30)μm long, mainly 1·5–2μm wide but the lowermost 1·5–2μm narrowing to 0·5μm wide at the point of secession.

This fungus, which has been noted by Professor J. Poelt in various localities in the Austrian alps, appears to form a stable association with the alga present. The algal cells do not appear to be killed (Fig. 5B) and a mutualistic or at least commensalistic symbiosis is evidently developed. The biological situation is, however, evidently complex in view of the intimate association with moss colonies and it is conceivable that the fungus is initially parasitic on the moss, later capturing the algae to form a separate lichen-like symbiosis. The situation may parallel that seen in certain species of *Vezdaea* Tsch.-Woess & Poelt (Tschermak-Woess & Poelt, 1976) and particularly *Epigloea* Zukal (Döbbeler, 1984). Döbbeler (1984) interpreted *Epigloea* species as highly adapted parasites of the algal

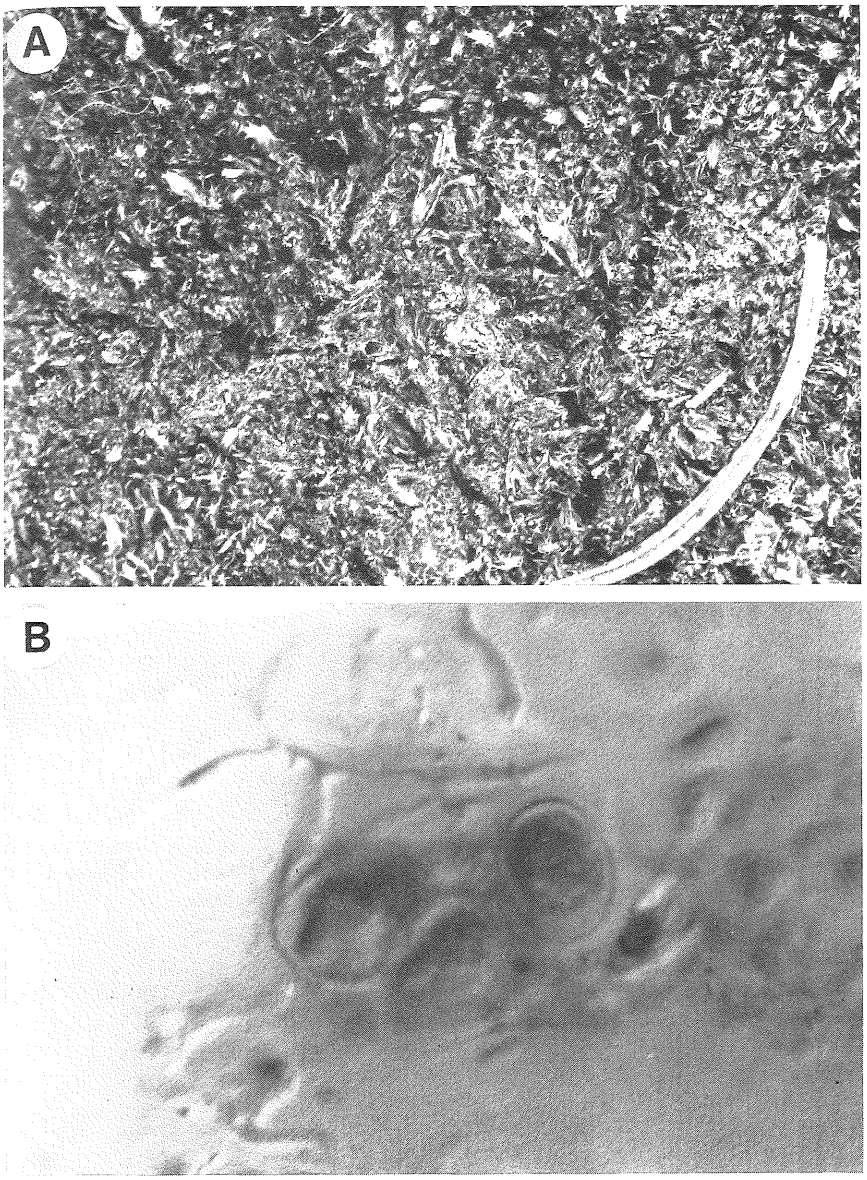


FIG. 5. *Velutipila poeltii* (IMI 309488). A, moss colony infested with chlorococcalean alga (? *Gyroeffyana humicola*) and *V. poeltii* (×2·5); B, algal cells and loosely ramifying fungal hyphae (×2200).

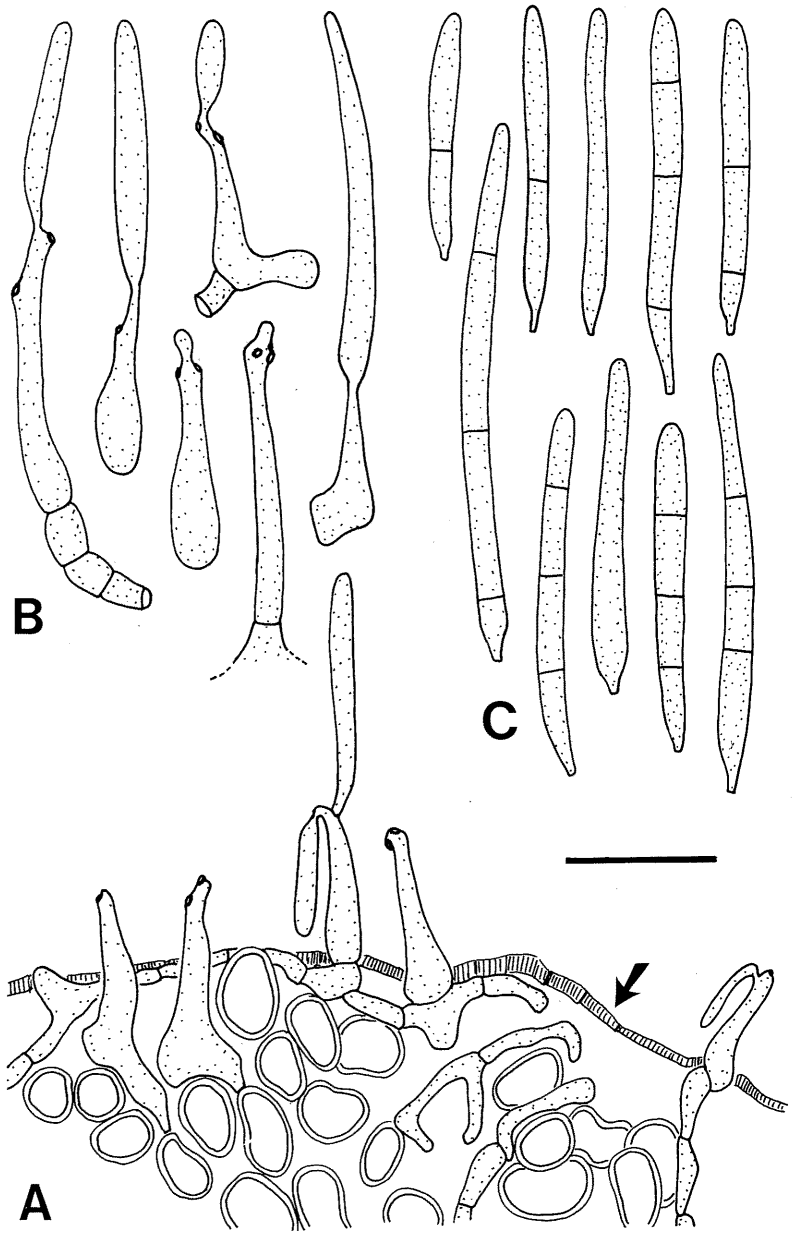
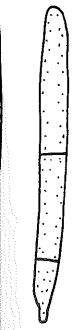
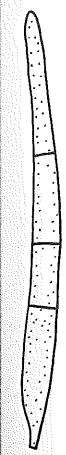


FIG. 6. *Velutipila poeltii* (IMI 309488). A, habit, showing algal cells and remnants of moss cuticle (arrow); B, conidiogenous cells; C, conidia. Scale = 10μm.

genus *Coccomyxa* Schmidle, rather than lichen-forming, as no morphologically distinguishable thallus was produced.

On Döbbeler's criteria, and the definition of Hawksworth (in press), *Velutipila poeltii* should be regarded as a specialized algal parasite rather than a lichen-forming fungus. No thallus structure comparable to that seen in other conidial lichenized fungi now being recognized (Hawksworth & Poelt, 1986) is developed. However, in view of the wide range of fungal-algal symbioses now known (Hawksworth, 1978, in press), it is to be expected that all cannot be neatly categorized in the absence of physiological, life-history, and ultrastructural investigations into the precise nature of the interactions between the bionts.







nants of moss

Acknowledgements

I am indebted to Dr D. J. Hill for the material on *Lemanea* and to Professor Dr J. Poelt for that described here as *Velutipila poeltii*. Dr D. John kindly determined the algae involved, and Mr A. C. Crundwell and Dr E. V. Watson the moss: Mrs C. Thatcher is thanked for microtome sections; Miss G. Godwin for help with the photography; and Mrs M. S. Rainbow for word processing.

References

BRIERLEY, W. B. (1913). The structure and life-history of Leptosphaeria lemaneae (Cohn). *Mem. Proc. Manchester lit. phil. Soc.* 57(8):1–21.

DEIGHTON, F. C. & PIROZYNSKI, K. A. (1972). Microfungi. V. More parasitic Hyphomycetes. *Mycol. Papers* 128:1–110.

DÖBBELER, P. (1984). Symbiosen zwischen Gallertalgen und Gallertpilzen der Gattung Epigloea (Ascomycetes). *Beih. Nova Hedwigia* 79:203–239.

FELDMANN, J. (1938). Le Blodgettia confervoides Harv. est-il un lichén? *Revue Bryol. Lichén.* 11:155–163.

HARVEY, W. H. (1858). Nereis Boreali-Americana: or, contributions to the history of the marine algae of North America. Part III.—Chlorospermeae. *Smithson. Contr. Knowl.* 10:1–119.

HAWKSWORTH, D. L. (1978). The taxonomy of lichen-forming fungi: reflections on some fundamental problems. In STREET, H. E. (ed.), *Essays in Plant Taxonomy*, 211–243. London & New York.

—— (in press). The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. *Bot. J. Linn. Soc.*

—— & POELT, J. (1986). Five additional genera of conidial lichen-forming fungi from Europe. *Plant Syst. Evol.* 154:195–211.

HUDSON, H. J. (1986). *Fungal Biology*. London.

INGOLD, C. T. (1955). Aquatic ascomycetes: further species from the English Lake District. *Trans. Br. Mycol. Soc.* 38:159–168.

KOHLMEYER, J. & KOHLMEYER, E. (1972). Is Ascophyllum nodosum lichenized? *Bot. Marina* 15:109–112.

—— & —— (1979). *Marine Mycology. The Higher Fungi*. New York, San Francisco & London.

LAW, R. & LEWIS, D. H. (1983). Biotic environments and the maintenance of sex—some evidence from mutualistic symbiosis. *Biol. J. Linn. Soc.* 20:249–276.

PATOUILLARD, N. (1908). Champignons nouveaux au peu connus. *Bull. Soc. Mycol. Fr.* 24:1–12.

PHILLIPS, W. & PLOWRIGHT, C. B. (1881). New and rare British fungi. *Grevillea* 10:65–74.

TSCHERMAK-WOESS, E. & POELT, J. (1976). Vezdaea, a peculiar lichen genus and its phycobiont. In BROWN, D. H., HAWKSWORTH, D. L. & BAILEY, R. H. (eds), *Lichenology: Progress and problems,* 89–145. London & New York.

WORONIN, M. (1870). Sphaeria lemaneae, Sordaria coprophila, fimeseda, Arthrobotrys oligospora. In DE BARY, A. & WORONIN, M. (eds), *Beiträge zur Morphologie und Physiologie der Pilze*. Vol. 1(3):1–36. Frankfurt.

WRIGHT, E. P. (1881). On Blodgettia confervoides of Harvey, forming a new genus and species of fungi. *Trans. R. Irish Acad.* 28:21–26.