First report of *Basidiolum fimbriatum* since 1861, with comments on its development, occurrence, distribution and relationship with other fungi

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An obscure parasitic fungus, *Basidiolum fimbriatum*, was found on *Amoebidium parasiticum* (*Amoebidiales*) associated with *Caenis* sp. (mayfly) nymphs, during a survey of gut fungi (*Trichomycetes*) from a small stream in northeastern Kansas, USA. The hindguts of the nymphs harboured a species of *Legeriomycetaceae* and *Paramoebidium* sp. This is the first report of the ectocommensal protozoan, *A. parasiticum*, associated with the gills of *Caenidae* (*Ephemeroptera*), and of *B. fimbriatum* in the 142 years since its original documentation from Wiesbaden, Germany. *B. fimbriatum* is recorded from two midwestern USA states (Kansas and Iowa) and the morphological and developmental features of the parasite on its host are compared with Cienkowski's original observations and interpretation. *B. fimbriatum* is characterized as a parasitic fungus possessing merosporangia that form on a simple pyriform thallus that penetrates and consumes its host via a haustorial network. The hypothesis that *B. fimbriatum* is most closely related to members of the order *Zoopagales sensu* Benjamin (1979) is proposed. The importance of future collections and molecular-based phylogenetic approaches to place this parasitic fungus within a current system of classification are highlighted.

INTRODUCTION

Basidiolum fimbriatum Cienkowski (1861) is one of the more obscure microscopic fungi. Hawksworth *et al.* (1995) included only the original citation for *B. fimbriatum* (Cienkowski 1861) and I believe that this is the first report of the fungus since that publication. At the time, Cienkowski (1861) was expanding on earlier reports by Lieberkühn (1856) and Schenk (1858) to detail further observations on the ontogeny of an enigmatic ectocommensal, associated with caddisfly (*Trichoptera*) and mosquito larvae as well as freshwater amphipods. He proposed the name *Amoebidium parasiticum* for the ectocommensal and illustrated it with a plate including 39 figures. However, 10 of the 39 figures also depicted a parasite on *A. parasiticum* which he named *B. fimbriatum* (Figs 14–20).

Amoebidium parasiticum has a known worldwide distribution associated with various aquatic Crustacea and Insecta (Lichtwardt 1986; http://ron.nhm.ukans. edu/~fungi). Attached with a secreted holdfast (Whisler & Fuller 1968), it forms an unbranched thallus and can produce sporangiospores or amoeboid cells from the entire protoplast that in turn may encyst and form cystospores. Two genera, *Amoebidium* and *Paramoebidium* (whose species are all endobionts in the guts of larval aquatic insects) comprise the *Amoebidiales*, one of four orders originally classified as *Trichomycetes*

(*Zygomycota*), more commonly known as gut fungi (Lichtwardt 1986). The inclusion of *Amoebidiales* within the *Trichomycetes* has been more a matter of convenience rather than an indication of any natural affinity. It is not uncommon for those studying gut fungi to encounter species of *Amoebidiales*, also associated with various arthropod hosts. Lichtwardt (1986) suggested that the *Amoebidiales* were not closely related to the other three orders of *Trichomycetes*, a notion which has been confirmed using sequence data to establish *A. parasiticum* as a protozoan (Benny & O'Donnell 2000, Ustinova, Krienitz & Huss 2000). Recent molecular based phylogenies place this species near the animal–fungal divergence (Mendoza, Taylor & Ajello 2002).

The taxonomic placement of the ectoparasite of *A. parasiticum*, *B. fimbriatum*, is enigmatic and remains an open question. Cienkowski (1861) called the ectoparasite *Basidiolum*, owing to the resemblance of the thallus to the basidium of higher fungi and used the epithet *fimbriatum*, because of its spore formation and appearance at maturity (bearing resemblance to tassels). Despite the relatively frequent observation of *A. parasiticum*, one of four species of the genus (Misra & Lichtwardt 2000), there have been no reports of *B. fimbriatum* since its original documentation from Wiesbaden, Germany. The intent of this report is to review and augment Cienkowski's observations of this ectoparasite, to record the known occurrences of

B. fimbriatum, and to comment on its possible taxonomic affinity with other fungi.

MATERIALS AND METHODS

Caenidae (*Ephemeroptera*) were included among an assortment of aquatic insect larvae collected by each of three undergraduate classes from Buck Creek, a small lotic system in Jefferson County, just north of Lawrence, Kansas (39° 06′ N, 95° 17.2′ W), 20–23 April 1998. Using a kick sampling technique, mayfly nymphs were dislodged from the stream bottom and collected with an aquatic sampling net. *Caenis* sp. nymphs, commonly found in slowly flowing, silted parts of the stream, were maintained in plastic collecting jars with minimal stream water at 4–10 °C for a few to several days after collection. Hindguts of the nymphs were removed with fine forceps and manipulated with dissecting pins before wet mounting to identify *Trichomycetes*. Gills were removed and mounted separately in water. Infested gills were examined at higher magnification (using phase and Nomarski interference contrast optics) and photographed (Kodak Ektachrome 320T film) before infiltrating the specimens with lactophenol cotton blue and sealing cover glasses with fingernail polish. An attempt was made to culture *Amoebidium* and its fungal parasite by placing infested gills on plates of dilute brain–heart infusion agar and tryptone-glucose-salts agar medium, each with a distilled water overlayer and antibiotic solution (Lichtwardt 1986). Subsequently, images of fixed material on semi-permanent slides were obtained using a Nikon Coolpix 950 digital camera. Preserved slides of specimens have been deposited at FH. The following is a list of slides (KS-) or Ektachromes (KU-) deposited with corresponding figure numbers: Figs 1–2 & 9, Slide KS-58-W4, Ektachromes KU-319-26, KU-319-27, KU-319-30; Figs 3, 8 & 11, KS-58-W6, KU-319-33, KU-319-34; KU-319-36; Fig. 4, KS-58-W10b), KU-320-3; Figs 5–6, KS-58-W6b), KU-320-7, KU-320-8; Fig. 7, KS-58-W6a), KU-320-4; Figs 10 & 12, KS-58-W10, KU-320-2, KU-320-1; Fig. 13, KS-58-W11b).

RESULTS

Caenid nymphs were selected for dissection to identify *Trichomycetes* from their hindguts because in several previous surveys, at this site, they had been shown repeatedly to harbour a species of *Legeriomycetaceae* (*Harpellales*). Eight of eleven nymphs dissected harboured non-sexual stages of a branched gut fungus and four of eleven also included *Paramoebidium* sp. The gut fungus will not be identified at this time because sexual stages necessary for proper identification have not been observed.

The operculate gills of these immature mayflies, appearing as two dorsal flaps on the abdomens of the nymphs, provide protection and permit water movement across the lamellate gills below. While the nymphs tended to be covered with silt, the gills were
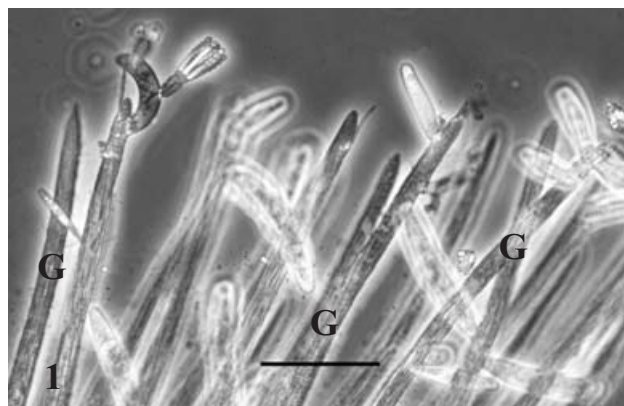
Fig. 1. Gill lamellae (G) of *Caenis* sp. with various developmental stages of *Amoebidium parasiticum* (refractive), one of which (upper left) is parasitized by a mature *Basidiolum fimbriatum*. Bar = 50 μm.

comparatively free of debris except that all eight of those examined externally were lightly to heavily infested with *A. parasiticum*. Five of the eight infested nymphs included *B. fimbriatum* parasitizing the ectocommensals (Fig. 1) and all developmental stages of the parasite were observed.

Cienkowski's (1861) original description is detailed and sufficient for species identification but is more concisely stated below, with terminology that reflects a contemporary understanding and interpretation of the morphology and ontogeny of the parasite.

**Basidiolum fimbriatum** Cienkowski, *Bot. Zeit.* **19:** 169 (1861).

Thallus pyriform to ovoid, to 10×20 μm, attached at narrowed base. Thallus sometimes thickened at base and refractive. *Spores* cuboidal to spherical, 3–4 μm diam, non-motile, released upon the deliquescence of the merosporangium. *Merosporangia* form on broad distal surface of the thallus, initially as 'knob-like' projections. Spores adhere to surface of host and enlarge to become a spore-producing thallus. *Haustorial penetration* of host initiated upon spore attachment, apparent with distortion of outer wall of host or slight swelling just beneath the penetrated thallus wall. Upon penetration and ramification, haustoria unevenly thickened, eventually consuming the contents of the host. *Sexual reproduction* unknown.

Known only as a parasite on *Amoebidium*.

Initially *B. fimbriatum* thalli were noted as projections on the surface of *Amoebidium*, often accompanied by a transparency of the parasitized specimens (using phase contrast optics with fresh material) (Figs 1–2). In mature stages of parasitism, spores were observed as chains on the distal surface of the thallus body (Figs 2–3). Sporangia developed from outgrowths (Figs 4, 7, 9–10) of the thallus proper or sporophore (i.e. the merosporangial type of development). Sporophores were occasionally curved at the base (Fig. 4). Non-motile spores were observed disarticulating from mature merosporangia (Figs 2–3) upon deliquescence of the
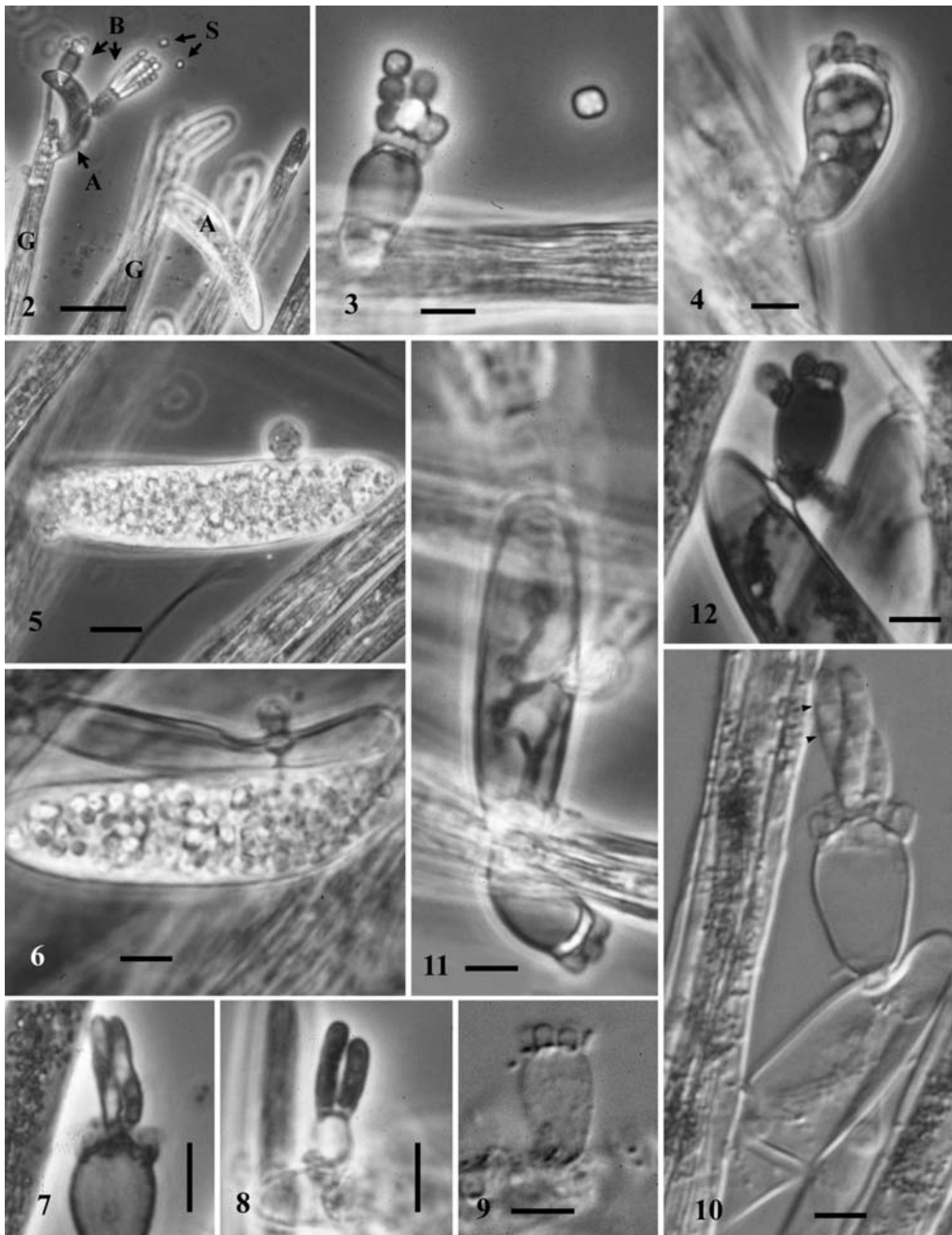
Figs 2–12. Phase contrast (2–8, 11, 12) and Nomarski (9, 10) microscopy of *Basidiolum fimbriatum* (B) parasitizing *Amoebidium parasiticum* (A) attached to the lamellae (G) of *Caenis* sp. nymphs. **Fig. 2.** Overview of infested gill with two thalli of *B. fimbriatum* parasitizing an *Amoebidium* thallus. Two spores (in focus) are drifting away from deliquescent merosporangia. **Fig. 3.** Mature merosporangia with disseminating spore possessing four refractive bodies. **Fig. 4.** Slightly bent thallus of *B. fimbriatum* attached to *A. parasiticum*. **Fig. 5.** Enlarged spore of *B. fimbriatum* attached to *A. parasiticum*. **Fig. 6.** Sporangiospore of *A. parasiticum*, showing haustorial penetration through detached sporangial wall of host. **Figs 7–8.** Immature *B. fimbriatum* merosporangia of similar size, borne on sporophores of different size. **Fig. 9.** Thallus showing outgrowths where merosporangia are formed. **Fig. 10.** Thallus with three, twisted merosporangia, undergoing spore division internally (arrowheads). Host wall penetration, indicated by wall distortion and basal swelling, with haustorial growth evident. **Fig. 11.** Three attached parasites (two in focus) and extensive haustorial ramification with swollen junctures giving knotted appearance. **Fig. 12.** Thickened refractive base of thallus with haustoria evident, extending from point of penetration of host. Bars: Fig. 2 = 25 μm, Figs 3–12 = 5 μm.
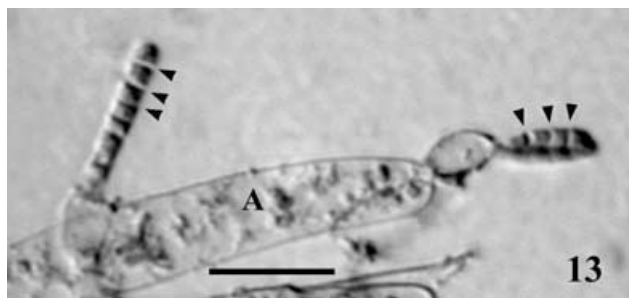
Fig. 13. Stained specimen, clearly indicating spore delimitation (arrowheads) of immature merosporangia in two thalli of *Basidiolum fimbriatum* attached to thallus of *Amoebidium parasiticum* (A). Bar = 25 μm.

sporangial wall, with as many as four distinct refractive inclusions (Fig. 3). Some spores were attached to otherwise apparently healthy thalli of *A. parasiticum* (Fig. 5). In some cases, penetration of the host wall occurred soon after spore attachment and prior to maturation of the parasitic thalli (Fig. 6). Intermediate stages exhibited sporangia with a distinct wall, typical of merosporangial development (Figs 7–8, 10). The sporophore of some specimens had merosporangia developing from outgrowths of the distal surface (Figs 7–8) with evidence of spore delimitation in some instances (Fig. 10, arrowheads). Advanced stages of development were observed with haustoria inside the evacuated thalli of the *A. parasiticum* (Figs 1–2, 10–12). With further development, haustoria were thickened, sometimes appearing unevenly swollen with ramification throughout the host (Figs 2, 10–12). Several specimens indicated an apparent adhesion to the host thallus (Figs 5, 12), host wall distortion (Figs 6, 10) and various stages of host penetration (Figs 2, 6, 10–12). After lactophenol cotton blue infiltration of immature merosporangia, lines of spore delimitation were clearly revealed (Fig. 13, arrowheads).

Culture attempts were unsuccessful. After several weeks on plates, microscopic examination of gills revealed spherical encysted amoebae of *A. parasiticum* with no indication of *B. fimbriatum* present.

DISCUSSION

Caenidae have been reported once as hosts of gut fungi. *Allantomyces caenidarum* M. C. Williams & Lichtw. 1993 and *Legeriomyces rarus* Lichtw. & M. C. Williams 1993 were reported in the hindguts of *Tasmanocoenis* sp. nymphs from Western Australia (Williams & Lichtwardt 1993). The branched species of *Harpellales* in *Caenidae* from the midwestern USA is *Legeriomyces*-like but I decline to name it because species identification would be premature without studying the sexual stages (White 1999). The *Legeriomyces*-like gut fungus occasionally attaches to *Paramoebidium* sp. thalli rather than to the gut lining, a feature that has not been noted with species of *Legeriomyces* previously, but is typical of *Simuliomyces microsporus* Lichtw. 1972 (Lichtwardt 1986). *Paramoebidium*, the other genus of *Amoebidiales*, differs from *Amoebidium* in that species

are restricted to the guts of various larval aquatic insects and lack the sporangiospore stage of *Amoebidium* (Lichtwardt 1986). *Paramoebidium* species are common inhabitants of mayfly nymph guts but the species diversity of both genera of *Amoebidiales* may be vastly underestimated because of limited morphological features available to differentiate them and the range of variation that is possible within any species or collection.

This is the first report of *A. parasiticum* on Caenid gills, yet another host among the many that have been reported (Lichtwardt 1986). The specimens discovered in northeastern Kansas have provided the first report of *B. fimbriatum* since Cienkowski's observations of it 142 years ago. However, I am aware of one other known occurrence of *B. fimbriatum*. The parasite was identified on *A. parasiticum* from a collection of daphnids and mosquito larvae collected on 26 July 1984, from a mud hole on a rutted road at the entrance to Milford Woods, on the southwest shore of Okoboji Lake, Dickinson County, northwest Iowa (43° 19.6′ N, 95° 11.8′ W) (Lichtwardt, unpubl.). It is reasonable to assume that such a disparate distribution and infrequent occurrence is a reflection of the very small size of the parasite and the few researchers who may have had the opportunity to encounter and recognize it. It is quite possible that the parasite occurs more commonly and is more widely dispersed than is currently known. Presumably, *Basidiolum fimbriatum* may parasitize *A. parasiticum* irrespective of the associated arthropod. *A. parasiticum* has been isolated in axenic culture previously (Whisler 1960, 1962, 1978, Lichtwardt 1986). Although attempts to isolate *Amoebidium* were unsuccessful, future isolation attempts are warranted because dual culture of *Basidiolum* with its *Amoebidium* host would make additional studies of this rare and obscure parasite possible.

My observations of *B. fimbriatum*, including attachment, penetration, thallus development and haustorial ramification resulting in death of *A. parasiticum*, support Cienkowski's observations. These photomicrographic images of *B. fimbriatum* are the only depictions of this fungus other than Cienkowski's original drawings. It is worthwhile to reiterate and discuss some of the key points and observations made in the original report. Owing to the obscurity of the parasitic fungus, some of Cienkowski's (1861) drawings of *B. fimbriatum* have been copied and rearranged as Figs 14–20. In the following synopsis, Cienkowski's descriptive assessment and terminology are consolidated with a modern interpretation (parenthetically) that has been used above.

Cienkowski (1861) recognized the parasite of *A. parasiticum* by the altered condition of the commensals on mosquito exuviae. The accuracy of the original observations and illustrations, obviously from detailed and careful examination of the specimens, deserve further comment. Some specimens of *A. parasiticum* bore pearshaped structures, with fine granularity, attached laterally or terminally (Figs 14–17). These structures had wart-like protuberances (Fig. 14a–c) on their distal surface lending some similarity to the basidium of
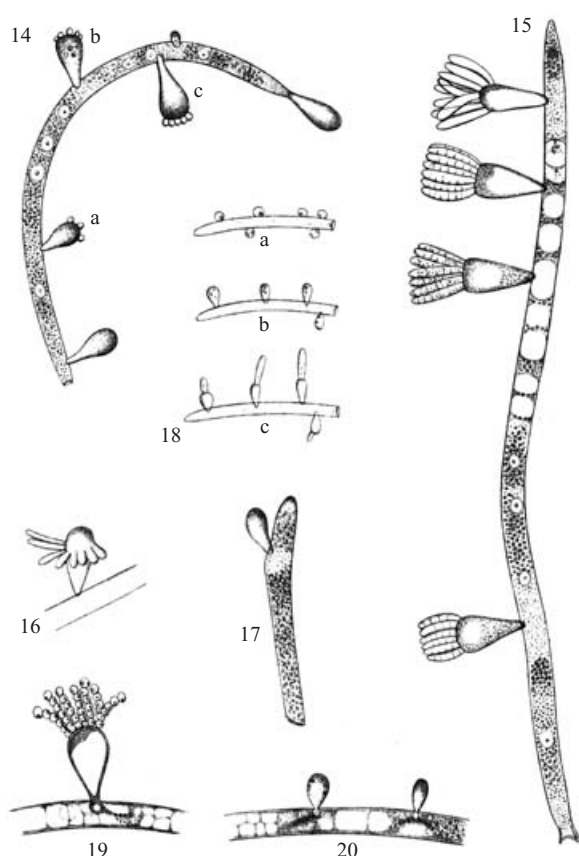
Figs 14–20. Structure and development of *Basidiolum fimbriatum* on thalli of *Amoebidium parasiticum*, copied and rearranged from Cienkowski's (1861) plate. **Fig. 14.** Pear-shaped thalli, some with protuberances just prior to sporulation (a–c), attached laterally and terminally. **Fig. 15.** Four laterally attached thalli with rod shaped structures (merosporangia) that have developed from protuberances. **Fig. 16.** Immature thallus with successive sporangial formation just below the vertex. **Fig. 17.** Single immature thallus causing host wall distortion at attachment site. **Fig. 18a–c.** Sequential series showing restricted growth form on immature host thalli. **Figs 19–20.** Attached thalli with ramifying haustoria emanating from small swelling inside the host. (No scale bars indicated on original; drawn at ×285.)

higher fungi. Straight to curved rod shaped merosporangia, arising from the wart-like protuberances (Fig. 15), were ultimately partitioned by lateral fission with a beaded appearance (Fig. 19). Swollen spores ultimately became a loose mass with no apparent motility, yet attached to thalli to continue the parasitic life cycle (Figs 14, 20). Cienkowski (1861) also noted that the spores had small 'dots' embedded in their interior.

Cienkowski (1861) observed, over several days, that thalli could undergo repeated sporulation. The first row of rods (merosporangia) attached slightly below the vertex (Fig. 16). Secondary merosporangia, thicker then their predecessors, formed toward the centre of the distal surface. All stages of development of *B. fimbriatum* were observed to be at random on *A. parasiticum* thalli of various sizes and maturity, including young thalli (Fig. 18) but were more commonly found on larger ones

(Figs 14–15, 17). Immature thalli, even with only one or two sporangia, underwent sporulation, ultimately with spores separating as spherical bodies (Fig. 18a–c).

Initially, Cienkowski was not certain whether the filamentous root was of parasitic origin or if it represented the condensed content of the *Amoebidium* (Figs 19–20). Uninterrupted examination of several attached spores provided conclusive evidence of the former. Several attached spores transformed after about twenty hours into the pyriform sporophore (Fig. 20). Within a few hours, rod-shaped sporangia developed and matured before disintegrating into pea-like spherical bodies (Fig. 19). Cienkowski was convinced of the parasitic nature of *B. fimbriatum* on *A. parasiticum* because it possessed a penetrating, root-like growth (i.e. haustorial) that was accompanied by loss of (healthy) host granularity, it often distorted the host thallus and no amoeboid cells were ever observed from infected thalli.

Cienkowski concluded that *Basidiolum* possessed a spore development that argued for its placement in the fungi, but that too little was known of its development to place it within the groups that were known at the time. The name *B. fimbriatum* was proposed on the basis of thallus shape and sporulation ontogeny, but the question of the natural affinity of this unusual parasite has remained unanswered to date. Therefore, I conclude with a morphologically based attempt to place *B. fimbriatum* in the realm of contemporary fungal systematics.

The spore forming structures of *B. fimbriatum*, merosporangia, are elongate endospore-forming structures, more or less cylindrical in multispored forms, with either an evanescent or persistent wall (Benny *et al*. 2001). According to Benny *et al*. (2001), merosporangia are formed in one family (*Syncephalastraceae*) of the *Mucorales* and in the *Dimargaritales*, *Kickxellales* and possibly the *Zoopagales*.

The *Syncephalastraceae* possess merosporangia but belong to a broader group (*Mucorales*) of facultative, non-haustorial parasites. The Dimargaritales are all haustorial parasites, but on other fungi, especially the *Mucorales*, and not protists. Further, they possess two-spored merosporangia or simple, branched sporiferous branchlets that arise from inflated or unmodified sporophore apices. The *Kickxellales* are characterized by unisporic sporangia that are usually released in a droplet of fluid but may be dry and possess spines and warts. Most Kickxellales are isolated from dung but may be obtained from soil as well. Therefore, I suggest that of all the merosporangiferous fungi, the *Zoopagales sensu* Benjamin (1979) includes members that are most similar to *B. fimbriatum*.

The *Zoopagales sensu* Benjamin (1979) are soil borne, obligate parasites of other fungi or small animals, including amoebae, with ectoparasites forming haustoria in the host. The thallus is a branched or unbranched inflated hyphal coil in the hosts and asexual reproduction is by multispored merosporangia or conidia (Benny *et al*. 2001). While these features have

been noted for *B. fimbriatum*, the precise placement among the five families (*Cochlonemataceae*, *Helicocephalidaceae*, *Piptocephalidaceae*, *Sigmoideomycetaceae* and *Zoopagaceae*) of *Zoopagales*, as presented in Benny *et al.* (2001), is difficult.

The *Cochlonemataceae* are parasites of amoebae, as well as nematodes and rotifers. Fertile hyphae or spores are found outside the host while the vegetative thallus may be completely internal. The *Zoopagaceae* include predaceous forms of these parasites. In *Helicocephalidaceae*, all species appear to be haustorial parasites of nematodes and their eggs. The *Sigmoidiomycetaceae* and *Piptocephalidaceae* are mycoparasites; the latter are all biotrophic, haustorial mycoparasites, mainly on *Mucorales*. Members of the *Piptocephalidaceae* have relatively fine somatic hyphae, a simple sporangiophore with the merosporangia (nearly all are multispored) borne on a terminal vesicle. *Syncephalis* and *Piptocephalis*, the most commonly recognized genera of the order, are relatively large and include a number of species. Both genera are culturable, although *Syncephalis* is more difficult, growing best on the original host. Additionally, *Syncephalis* includes smaller species, making them difficult to find and maintain (Benny *et al.* 2001).

Lichtwardt (1960, 1986) has noted the resemblance of *B. fimbriatum* to the merosporangia-bearing, terminal vesicle of a hypothetical sessile *Syncephalis*. Although I concur with this view, I decline at this time to place *Basidiolum* in the *Piptocephalidaceae*, despite that it may be the most appropriate of the five families. *Basidiolum* differs from all of the Piptocephalidaceae in that it is a protist parasite. While some members of the *Zoopagales* are known to parasitize amoebae, they differ morphologically. Finally, the absence of sexual production among the specimens of *Basidiolum* precludes any further speculation of possible fungal relationships. Therefore, based on habit and morphological criteria, I suggest that *B. fimbriatum* conforms with the description of the order *Zoopagales sensu* Benjamin (1979).

The exact placement of this parasitic fungus should be possible using molecular systematic techniques, especially as databases are expanding to include members of the *Zoopagales*, amongst the *Zygomycota* (Tanabe *et al.* 2000). Unfortunately, at the time of collection, too few specimens were available to preserve material for molecular analysis. If specimens of *B. fimbriatum* become available with future collections, DNA sequence data will test its hypothesized placement among the *Zoopagales sensu* Benjamin (1979). It is hoped that this report will help to stimulate the pursuit of this and other obscure fungi by those who are willing to seek them in the spirit of those who have already seen them.

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