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Review article

Trichomycetes – Fungi Associated with Arthropods: Review and World Literature

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Abstract

The class Trichomycetes (Zygomycota) is quite distinct, both morphologically and ecologically. Species of trichomycetes are intimately associated with arthropods – insects, millipedes and crustaceans. The class has four orders (Amoebidiales, Asellariales, Eccrinales, and Harpellales) and seven families. Currently 47 genera and 204 species of Trichomycetes are known world-wide, but many regions remain to be surveyed. Various aspects of trichomycete research such as taxonomy, ecology, host specificity, host-fungus relationships, and physiological studies are reviewed and discussed. Although these fungi are predominantly endobionts within the digestive tracts of adult or larval arthropods, species of *Amoebidium* are found attached externally to the host cuticle. These symbiotic fungi may be commensal or beneficial or deleterious, depending upon the species and other factors. However, the host-fungus relationships are not fully understood, though trichomycetes exhibit host specificity to varying degrees. Physiological investigations have been limited to nutritional and growth studies of some Harpellales. Unfortunately, only 17% of the known trichomycete genera and 11.6% of the total species have been cultured axenically. While Asellariales, Eccrinales, and Harpellales appear to be related phylogenetically, Amoebidiales do not appear to be related closely. Gaps in our knowledge about these fungi are identified and solutions to problems are suggested. Additionally, the world literature, some of which is scattered and obscure, has been consolidated.

Keywords: Arthropods, fungi, review, symbiosis, Trichomycetes, Zygomycota

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1. Introduction

Symbiotic relationships between fungi and plants have received considerably more attention than those involving fungi and animals. Symbioses between fungi and arthropods – the largest group of the animal kingdom – are understood mostly in terms of their parasitic relationships. However, the fungal class Trichomycetes (Zygomycota), constitutes an ecologically and morphologically distinct group of organisms that have varied relationships with their arthropod hosts. Known associations range from neutral or commensalistic to deleterious and possibly mutualistic in some cases. Species of Trichomycetes live obligately with arthropods, which include insects, millipedes, and various kinds of crustaceans. Except for *Amoebidium* spp., all trichomycetes thrive in the digestive tract, usually the hindgut, of their hosts. Although not much is known about the nutritional relationship with the host, it has been demonstrated in one trichomycete (*Smittium culisetae*) growing within mosquito larvae that the larvae survive through more instars than those without the fungus when they are under nutritional stress (Starr et al., 1979; Horn and Lichtwardt, 1981). Also, there is evidence that *S. morbosum* kills mosquito larvae (Sweeney, 1981a; Sato et al., 1989; López Lastra, 1990), and that *Harpella melusinae*, and some other genera of Harpellales, make adult blackflies (Simuliidae) infertile through the production of fungal cysts in their ovaries (Moss and Descals, 1986; Labeyrie et al., 1996).

Trichomycetes have been studied extensively in France by L. Léger, O. Duboscq, Odette Tuzet, and J.-F. Manier and their co-researchers. In the United States these fungi have been studied by R.W. Lichtwardt, his students, and a number of other investigators. Unfortunately, despite the known world-wide distribution of Trichomycetes (Fig. 1), these fungi have not been explored adequately in many regions (Hawksworth, 1997). Except for Hawaii (Lichtwardt, 1986), Costa Rica in Central America (Lichtwardt, 1994, 1997), and Queensland, Australia (Lichtwardt and Williams, 1990), the tropics remain largely unexplored. For example, from the South-east Asian region only *Amoebidium parasiticum* from Singapore (Johnson, 1963), and *A. parasiticum* and *Enterobryus* spp. from the Philippines are known (Reynold, 1967; Dogma, 1975). Similarly, from the Indian subcontinent only one trichomycete, *Enterobryus cingaloboli*, is reported from a millipede (Rajagopalan, 1967).

This neglect is due partly to the lack of training to embark on such inter-disciplinary research, which requires knowledge of both trichomycetes and their arthropod hosts. The neglect of tropical gut fungi also stems, in part, from the lack of available literature, which is quite scattered and often inaccessible

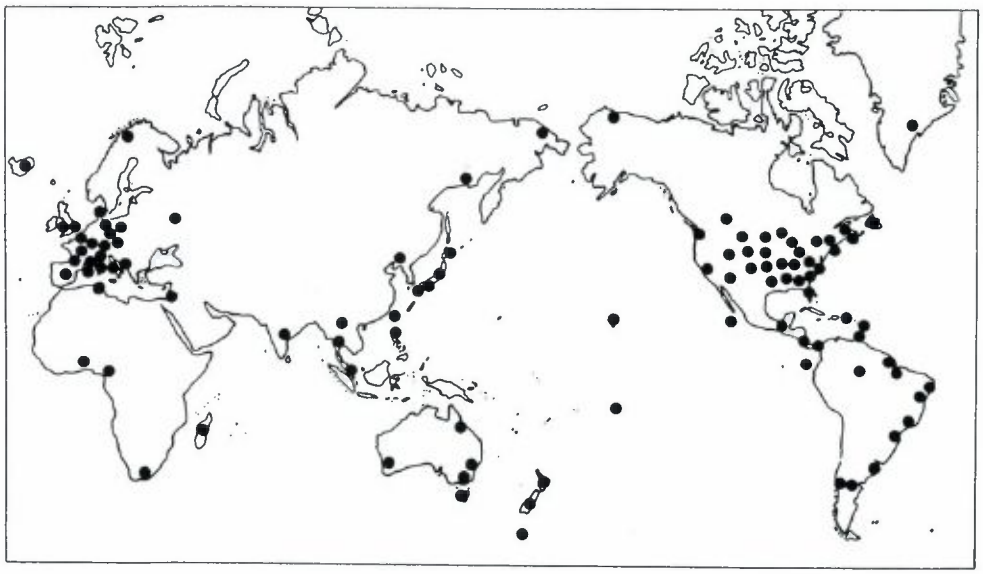


Figure 1. Known distribution of trichomycetes. Each dot shows the occurrence of trichomycetes in a state, region or country; most dots represent many collecting sites.

to many researchers. The studies of Lichtwardt (1994, 1997) in Costa Rica indicate that unexplored regions may have many new and interesting genera and species not found in temperate regions, and emphasize the need for "bioinventorying" of such regions. Such basic research on distribution of Trichomycetes is warranted and ultimately would augment our current understanding of their biogeography (Lichtwardt, 1995).

With these considerations in mind, the need for this review becomes evident. Published but scattered and sometimes obscure world literature on Trichomycetes has been brought together in this paper and the important aspects of research on Trichomycetes done so far are reviewed.

2. Brief Historical Background

Joseph Leidy (1849a, b; 1850a, b; 1853), an American naturalist, is credited for initiating the study of Trichomycetes. He found trichomycetes within the hindguts of some millipedes and a beetle, and described them under the generic name *Enterobrus* (= *Enterobryus*). However, he considered these gut dwellers to be colourless algae (Confervaceae).

Table 1. Classification and hosts of Trichomycetes

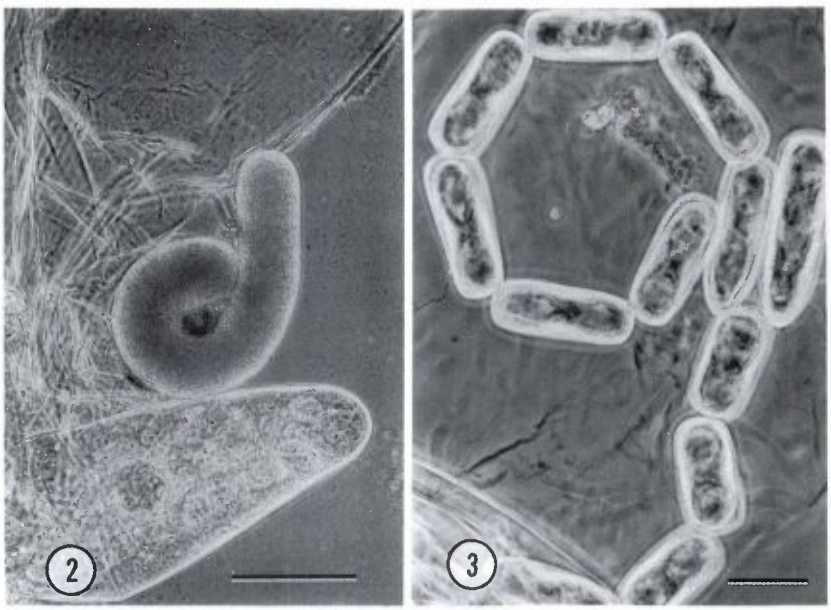
Amoebidiales	
Amoebidiaceae	
Amoebidium (4)	Freshwater small Crustacea and Insecta
Paramoebidium (6)	Larval Diptera: Simuliidae; Plecoptera, Ephemeroptera
Asellariales	
Asellariaceae	
Asellaria (6)	Freshwater, marine or terrestrial Isopoda
Orchesellaria (4)	Collembola
Eccrinales	
Eccrinaceae	
Alacrinella (2)	Isopoda: Limnoidae
Arundinula (6)	Decapoda: Astacidae, Galatheidae, Lithodidae, Paguridae
Astreptonema (5)	Amphipoda: Corophiidae, Talitridae, Gammaridae
Eccrinidus (1)	Diplopoda: Glomeridae
Eccrinoides (4)	Diplopoda: Glomeridae; Isopoda, Porcellionidae, Tylidae
Enterobryus (26)	Diplopoda: Odontopygidae, Xystodesmidae, Spirobolidae, Pachybolidae, Julidae, Polydesmidae, Platyrhacidae, Spirostreptidae, Paradoxosomatidae, Odontopygidae; Coleoptera, Passalidae, Hydrophilidae; Decapoda: Hippidae
Enteromyces (1)	Crustacea: Anomura and Brachyura
Enteropogon (1)	Crustacea: Anomura
Paramacrinella (1)	Amphipoda: Aoridae
Ramacrinella (1)	Amphipoda: Aoridae
Taeniella (1)	Crustacea: Anomura, Brachyura
Taeniellopsis (3)	Amphipoda: Talitridae
Palavasciaceae	
Palavascia (2)	Isopoda: Oniscidae
Parataeniellaceae	
Lajasiella (1)	Coleoptera: Scarabaeidae
Parataeniella (5)	Isopoda: Armadillidae, Trichoniscidae, Porcellionidae Armadillidiidae, Oniscidae
Harpellales	
Harpellaceae	
Carouxella (1)	Larval Diptera: Ceratopognidae
Harpella (4)	Larval Diptera: Simuliidae
Harpellomyces (1)	Larval Diptera: Thaumaleidae
Stachylina (19)	Larval Diptera: Chironomidae, Psychodidae
Legeriomycetaceae	
Allantomyces (1)	Larval Ephemeroptera: Caenidae
Austrosmittium (4)	Larval Diptera: Chironomidae
Bojamyces (1)	Larval Ephemeroptera: Leptophlebiidae
Capniomyces (1)	Larval Plecoptera: Capniidae
Caudomyces (1)	Larval Diptera: Tipulidae

Ejectosporus (1)	Larval Plecoptera: Capniidae
Furculomyces (2)	Larval Diptera: Chironomidae
Gauthieromyces (1)	Larval Ephemeroptera: Baetidae
Genistelloides (2)	Larval Plecoptera: Capniidae
Genistellospora (4)	Larval Diptera: Simuliidae
Glotzia (4)	Larval Ephemeroptera: Baetidae
Graminella (2)	Larval Ephemeroptera: Baetidae
Graminelloides (1)	Larval Diptera: Simuliidae
Lancisporomyces (1)	Larval Plecoptera: Nemouridae
Legeriomyces (3)	Larval Ephemeroptera: Baetidae, Ephemerellidae
Orphella (3)	Larval Plecoptera: Nemouridae
Pennella (7)	Larval Diptera: Simuliidae
Pteromaktron (1)	Larval Ephemeroptera: Baetidae
Simuliomyces (2)	Larval Diptera: Simuliidae; Plecoptera: Capniidae
Smittium (51)	Larval Diptera: Chironomidae, Culicidae, Simuliidae, Ceratopogonidae, Tipulidae, Psychodidae
Spartiella (2)	Larval Ephemeroptera: Baetidae
Stipella (1)	Larval Diptera: Simuliidae
Trichozygospora (1)	Larval Diptera: Chironomidae
Zygopolaris (2)	Larval Ephemeroptera: Heptaginiidae, Baetidae, and Ephemerellidae

The number in parentheses indicates the current number of species.

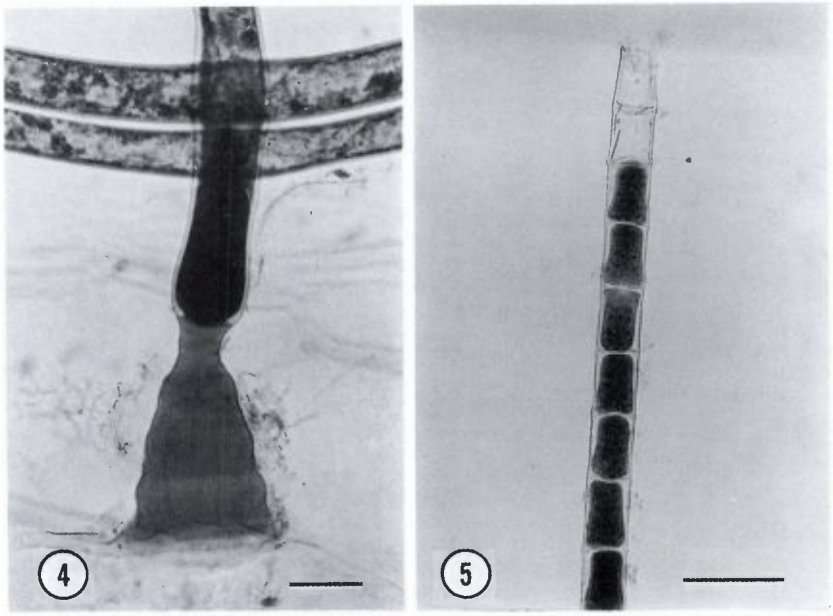
Robin (1853) described another species of *Enterobryus*. He thought that his *Enterobryus* and also those of Leidy belonged to the oömycete order Saprolegniales. A few years later, Lieberkühn (1856) and Schenk (1858) described an organism associated with the exoskeleton of aquatic arthropods which was later named *A. parasiticum* (Cienkowski, 1861). *Astreptonema*, another genus, was described by Hauptfleisch (1895) from the hindgut of an amphipod. He believed it to belong to the oömycete family Saprolegniaceae.

In the early part of the present century, the study of Trichomycetes gained momentum with the active research of two French protozoologists: L. Léger and O. Duboscq. Their work was compiled in a monograph in 1948 (Duboscq et al., 1948). They named these "hair-like" fungi Trichomycetes, and arranged them into two orders: Eccrinales and Amoebidiales. The only mycologist to study these organisms in the early years of the century was Roland Thaxter. He described *Enterobryus compressus* from a passalid beetle (Thaxter, 1920). The early part of the 20th century saw many new events such as the discovery of *Harpella melusinae* from blackfly (Simuliidae) larvae (Léger and Duboscq, 1929b), the first species of Harpellales; *Paramoebidium* in lotic populations of Simuliidae (Léger and Duboscq, 1929c); *Parataeniella* from the hindgut of the



Figs. 2–5. Trichomycetes representing three orders.
Figure 2. Thallus of *Paramoebidium curvum* (Amoebidiales) in the posterior end of the hindgut close to an anal papilla of a blackfly larva (Simuliidae). Such thalli produce swarms of amoebae at the time of host ecdysis. Scale bar = 100 µm.
Figure 3. *Asellaria ligiae* (Asellariales) showing arthrospores – asexual reproductive structures – within the hindgut of a marine isopod, *Ligia* sp. (Isopoda: Ligiidae). Scale bar = 25 µm.

terrestrial isopods, *Oniscus asellus* and *Tracheoniscus rathkii* (Poisson, 1929); *Asellaria* in the hindgut of *Asellus aquaticus* and *A. meridianus* (Poisson, 1932a) and the eccrinid genus *Palavascia* in the hindgut of an isopod, *Halophiloscia couchii* (Tuzet and Manier, 1947b). Thus, by 1947 representative members of all the currently recognized families were known. With the addition of new genera and species, 1920 and onward was the period when the study of Trichomycetes expanded, attracting many researchers, including mycologists, who published their work in areas such as ecology, nutrition, host-fungus relationships, host specificity, in addition to systematics and phylogeny (Lichtwardt, 1986). To date 47 genera and 204 valid species of trichomycetes are known. It is very likely that most species still remain undiscovered (Lichtwardt, 1986, 1997). A list of current genera, known number of species, and types of hosts that they inhabit is shown in Table 1. For more



Figs. 2–5. Trichomycetes representing three orders.

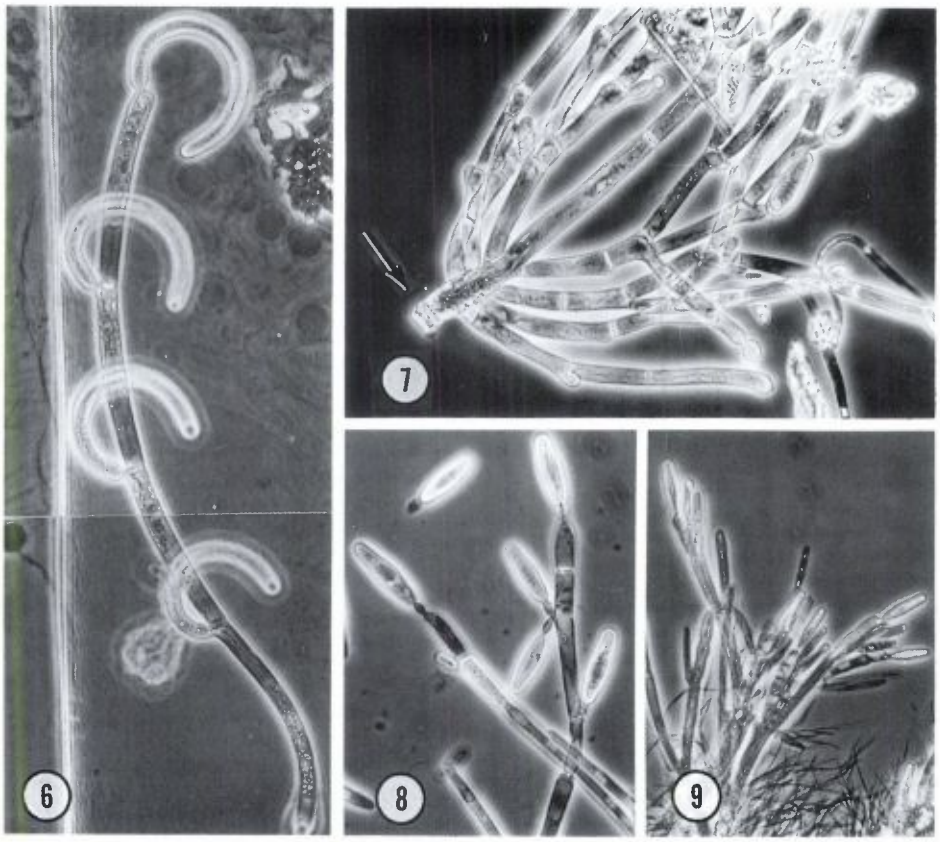
Figure 4. Large bell-shaped holdfast of *Enterobryus elegans* (Eccrinales), the first species of Trichomycetes described from the hindgut of a millipede (Diplopoda: Spirobolidae). Scale bar = 25 μm.

Figure 5. *Arundinula orconectis* (Eccrinales) from the foregut and of a freshwater crayfish, *Orconectis nais* (Decapoda: Astacidae); hyphal tip with sporangia, each containing a sporangiospore, except for the two terminal ones which have released their spores. Scale bar = 50 μm.

about the history of research on trichomycetes see Duboscq et al. (1948), Manier (1950, 1969b), Moss (1972), and Lichtwardt (1986).

3. Characteristics, Habit and Habitats

The thalli of trichomycetes, as the name suggests, sometimes look like "hair" within the digestive tract of their arthropod hosts. Predominantly, these fungi are found in the hindgut while some grow in the foregut (crustaceans) or in the midgut (peritrophic membrane) of Diptera larvae. Trichomycetes are frequently host specific and are obligately associated with the host. Their relationships, which is not well understood, may be



Figs. 6–11. Representative Harpellales from freshwater insect larvae.

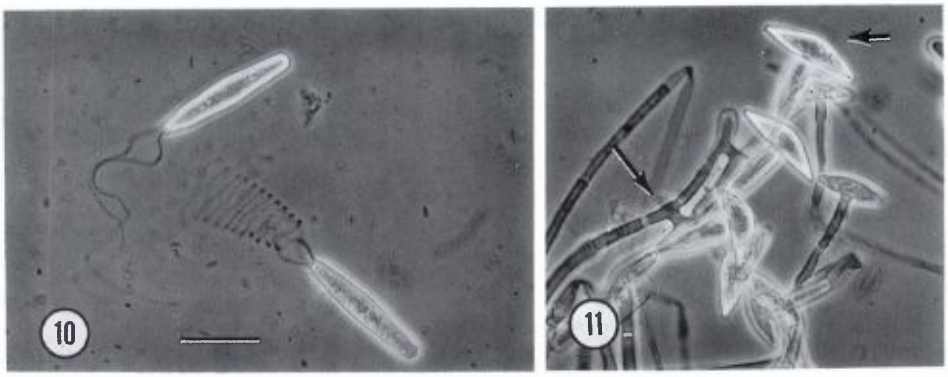
Figure 6. Curved trichospores of *Harpella meridianalis* attached to the peritrophic membrane of a blackfly larva.

Figure 7. *Genistellospora homothallica* with a holdfast (arrow) which was attached to the hindgut cuticle of blackfly larva.

Figure 8. Thallus and oval trichospores – asexual reproductive structures – of *Smittium culicis*, one of the two most common fungi that predominantly infest the hindguts of mosquito larva (Diptera: Culicidae); this was one of the first two trichomycetes to be cultured axenically.

Figure 9. Smittium culisetae, a common species infesting the hindgut of mosquito larvae; its growth and other physiological parameters have been extensively studied.

commensal, beneficial or deleterious depending upon the species and stage of development involved. Thalli may be single or in clusters, branched or unbranched, and septate or not, and have a holdfast (Figs. 4, 7). Trichomycetes



Figs. 6–11. Representative Harpellales from freshwater insect larvae.
Figure 10. Helically coiled and uncoiled trichospore appendages of *Genistelloides helicoides* infesting the hindgut of a stonefly (Plecoptera: Nemouridae).
Figure 11. *Simuliomyces spica* showing biconical zygospores (shorter arrow), which are sexual reproductive structures formed following conjugation of two cells (longer arrow); from the hindgut of a stonefly, *Allocapnia* sp. (Plecoptera: Capniidae). Scale bar = 25 μm for Figs. 6–11.

reproduce both sexually (infrequently) by means of zygospores (Fig. 11) and asexually (predominantly) through amoebae (Fig. 2), arthrospores (Fig. 3), cystospores, sporangiospores (Fig. 5), or trichospores (Figs. 6, 8–10).

Except for species of *Amoebidium*, trichomycetes are endobionts within the gut of terrestrial or aquatic (freshwater and marine) mandibulate arthropods. Carnivorous and predacious arthropods are not hosts to trichomycetes.

4. Collection, Isolation, Culture and Preservation

Trichomycetes are found by collecting arthropods from suitable aquatic and terrestrial habitats. In almost all instances the fungi cannot be seen until host digestive tracts are removed and opened. Insect larvae (such as blackflies, midges, mayflies, and stoneflies) infested with Harpellales (Table 1) are common in freshwater environments. In streams, some larval insect hosts prefer aerated microhabitats near riffles, while others may be under or on decomposed or decomposing vegetation (leaf-packs), living hydrophytes, pebbles, rocks, or various zones of sedimentation. Larvae collected from any of the above substrates can be placed in small jars with a little water and kept on ice for transport to the laboratory for dissection and study of their gut fungi.

The edges of waterfalls or seeping areas are also good sites for collecting some dipterans.

Still waters of lakes, ponds, or ditches (lentic aquatic environments) are ideal for larvae of midges and mosquitoes. From marine habitats hosts such as burrowing crabs and anomurids are normally found in the intertidal zone, and can be collected on the beaches or mudflats near the shore during low tide. Others live on rocky shores or in rock pools. Terrestrial arthropods – millipedes, beetles, isopods, and amphipods – can be collected from moist decomposing vegetation or logs.

Hosts from aquatic environments (freshwater) can be maintained for a few days or longer in a refrigerator with small amounts of water. However, overcrowding should be avoided. Hosts from marine habitats can be kept in seawater which should be aerated or periodically changed if kept for more than a day or two. Terrestrial arthropods can be kept with their moist substrates for longer periods of time. Hosts can be preserved in 70% ethanol for later identification or reference, but preserved specimens in most instances are not satisfactory for dissection. For details on dissection, refer to Lichtwardt (1986).

Of the four orders of the class Trichomycetes, only one species of Amoebidiales and a number of branched Harpellales have been cultured axenically. Whisler (1960) first cultured a trichomycete, *A. parasiticum*. Currently, only eight (17%) of the total genera (*Amoebidium*, *Austrosmittium*, *Capniomyces*, *Furculomyces*, *Genistelloides*, *Simuliomyces*, *Smittium* and *Trichozygospora*) and fewer than 12% of the recognized species have been brought into axenic culture, and most are maintained in the culture collection at The University of Kansas, Lawrence, KS, USA. These belong to the Amoebidiaceae and Legeriomycetaceae.

Cultures of these fungi can be grown in petri plates, slants, or broth. The most common media used are: tryptone glucose vitamin agar (TGv, Difco Tryptone is preferred) and 1/10th strength brain-heart infusion agar (1/10 BHIv). The formulae of these media can be found in Lichtwardt's (1986) monograph. In liquid media these fungi often grow better and produce more biomass in shaken cultures. Most cultured trichomycetes grow well at 20–24°C. Trichomycetes have been maintained with periodic transferring for many years on agar media overlayered with sterile distilled water and stored at 4°C, but cryopreservation in liquid nitrogen (–196°C) is preferred for long-term storage. Refrigerated cultures should be transferred every 2–4 months depending on the species. Some such cultures have been maintained up to 34 years without any apparent genetic changes (Lichtwardt, 1986, 1996; Grigg and Lichtwardt, 1996).

5. Physiological Investigations

Nutritional studies on *A. parasiticum* and *S. culisetae* have been done by Whisler (1962) and Williams and Lichtwardt (1972b), respectively. Addition of thiamine to tryptone-glucose salts medium increased the dry weight of *A. parasiticum*. Substitution of tryptone with methionine was not satisfactory. Glucose, mannose and fructose proved to be good sources of carbon, but *A. parasiticum* could not utilize nitrate. Similarly, for *S. culisetae* tryptone (2%), glucose (0.5%) and inorganic salts supported good growth in shake culture. Thiamine – even at low concentration (10 µg/l) – stimulated fungal growth. Glucose was found to be the best out of 18 carbon sources that were tried (Williams and Lichtwardt, 1972b). The majority of the culturable trichomycetes can be grown satisfactorily on a 1/10th dilution of Difco brain-heart infusion agar supplemented with thiamine and biotin (Lichtwardt, 1986).

Growth rate studies carried out for *S. culisetae* (Fig. 9) indicate that better growth was obtained in shake cultures than in stationary ones (Williams and Lichtwardt, 1972b; El-Buni and Lichtwardt, 1976a). Farr and Lichtwardt (1967) also have found maximum rates of growth at temperature ranging between 10°C and 32°C; but maximum dry weight occurred at 10°C. They also found *S. culisetae* to be quite tolerant of a wide range of hydrogen ion concentrations. Trichospore production in *S. mucronatum* doubled with the addition of sitosterol acetate and sitosterol in the medium, but ergosterol and cholesterol inhibited growth (El-Buni and Lichtwardt, 1976a). Mechanical shaking also enhanced sporulation in *S. culisetae* (El-Buni and Lichtwardt, 1976b). The individual lipid classes, phosphatides, and steroids have been quantitatively determined for *S. culisetae* (isolate HAW-13-2) by Patrick et al. (1973). Of the total lipids, which were 9.9% of the total mycelial weight, 76.3% were neutral while the rest (23.7%) were polar lipids. Others, namely triglycerides (26.6%), phosphatidyl choline (17.8%), steroids (12.9%), and free fatty acids (11.4%), were detected in descending percentages (Patrick et al., 1973). Starr et al. (1979) studied the sterols synthesized by 14 isolates of 4 species of *Smittium* (*S. culisetae, S. culicis, S. simulii,* and *S. mucronatum*) and 2 isolates of *A. parasiticum,* besides two fungi representing the outgroup Kickxellales: *Dipsacomyces acuminosporus* and *Linderina pennispora.* Their results indicate that while all species of *Smittium* produce desmosterol, neither *A. parasiticum* nor the two Kickxellales did so (Starr et al., 1979). Physiological studies done with *S. culisetae* by Horn (1990) further supported the concept that sporangiospore extrusion (see later) is pressure driven.

6. Host Specificity

Trichomycetes show host specificity, but to varying degrees. They may be species, genus or family specific depending on the fungus. Information about their full host range and specificity is limited because of limited collecting in some cases, and the inability to culture most trichomycetes for experimental work with other arthropods. *Asellaria armadillidii*, inhabiting the hindgut of *Armadillidium simoni*, has been found to cross-infest other isopods indicating that it is not strictly species specific (Manier, 1963a; Lichtwardt and Chen, 1964). Experiments to determine if normally uninfested *Aedes geniculatus* and *A. berlandi* could be infested with *S. culicis* (Fig. 8) indicated that these could be infested readily using the water where they thrive or other sources of water containing trichospores (Tuzet et al., 1961).

Coste-Mathiez (1970) observed that *S. mucronatum* from a chironomid host could infest a mosquito species, and *S. culicis* was transferrable from mosquitoes to chironomids, but development of the latter could not progress well in chironomids. Williams and Grigg (1990) working with various isolates of *Smittium* obtained from dipteran larvae, found that some *Smittium* isolates could infest "foreign" mosquitoes as well as blackfly larvae while others did not, and concluded that, some *Smittium* species tend to have a restricted host range while others may infest different insect host families. Horn (1989a–c, 1990) found that in *S. culisetae* and *S. culicis* extrusion (germination) of sporangiospores from the trichospores *in vitro*, is a process that involved two sequential treatments: phase I consisting of pH 10 in the presence of potassium and phase II, a lowering of alkalinity to pH 6–8. These stimuli mimic gut conditions in mosquito larvae and explain the host specificity of these fungi upon being ingested by mosquito larvae.

Moss (1972), experimenting with *Stachylina grandispora* and midge (Chironomidae) larvae combinations, found that the fungus had a wide host range except for the carnivorous genera of midges which this fungus could not infest. Although strictly carnivorous or predaceous arthropods are not known to be infested with trichomycetes, predacious *Culex halifaxii* mosquito larvae in one case became infested with *S. simulii* when allowed to consume infested nonpredaceous species of *Culex* in the laboratory (Lichtwardt, 1986).

Many field observations show infestation of certain trichomycete genera in one kind of host while other genera infest other hosts in the same habitat, thus indicating that host specificity does exist in nature.

7. Host-Fungus Relationships

Trichomycete research on host-fungus relationships has received minimal

attention for various reasons, most importantly because of the inability of the majority of these fungi to grow and reproduce *in vitro*. Only very few (11.6%) of these fungi have been cultured axenically so far. This kind of research, therefore, presents ample opportunities and challenges to biologists to culture them and to study their intriguing relationships with the host. Various relationships between the host and the fungus have been suggested on the basis of limited evidence, and have been considered to be commensalistic (ecto and endo), mutualistic, or parasitic. Generally, symbioses between fungi and animals have not received much attention. Cooke (1977), applying the broader sense of de Bary's 1877 concept of symbiosis, uses the term symbiosis to refer to "all associations where fungi come into contact with a living host from which they obtain, in a variety of ways, either major or minor metabolites or nutrients." Trichomycetes are obligate symbionts in nature having no known capacity for a free-living existence, other than as propagules. The classification of Cooke (1977), which is based on criteria of mutualism, neutralism and antagonism, combined with obligate or facultative dependency, describes six biological groups. Trichomycetes may exhibit either neutralism, mutualism or antagonism towards their host, but most species appear to belong to the neutral group – the 4th group of Cooke's classification. These obligate neutrals grow saprobically either on the integument or within the gut. And their association with the host appears to be permanent until the host molts and the fungi are shed with the molt. They utilize food material within the digestive tract of the host without exhibiting any sign of competition with the host. There is not much experimental proof to indicate whether arthropods need these fungi. However, Horn and Lichtwardt (1981) have demonstrated that when *S. culisetae* (Fig. 9) grows within a host (*Aedes aegypti*) more of the host's instars survive than those without the fungus in them, provided the larvae are deprived of certain essential nutrients. *Smittium* spp. produce desmosterol (Starr et al., 1979) and B-vitamins that appear to satisfy the needs of the larvae. These findings are suggestive of their mutualistic life if the host is nutritionally stressed. Such experiments require that cultures of fungi be available and that a host can be raised in the laboratory without microorganisms other than the fungi.

Sweeney (1981a) reported that *S. morbosum* killed 50–95% of the larvae of *Anopheles hilli* in laboratory cultures. Similar reports of mortality in laboratory-raised mosquito larvae were also published in Italy (Coluzzi, 1966) and Russia (Dubitskii, 1978). However, those investigators believed that the deaths were due to *S. culisetae* which, as reported later, resembles *S. morbosum*. The symptom (black spot in the abdomen) as reported by Dubitskii (1978) were also seen by Sweeney (1981a) which he believed to be caused by a melanization reaction around the fungal hyphae after the hyphae penetrated

the gut lining. Natural field infections by *S. morbosum* are known from Japan in *Aedes albopictus* and *Culex pipiens* (Sato et al., 1989) and in five species belonging to several genera of Culicidae from Argentina (López Lastra, 1990). Species of *Harpella* and some other genera of Harpellales have been known to make blackflies (Simuliidae) infertile occasionally by producing ovarian cysts that replace egg development (Yeboah et al., 1984; Moss and Descals, 1986; Lichtwardt, 1996; Labeyrie et al., 1996). These reports suggest that Harpellales may be parasitic at some developmental stages, but under conditions not presently understood.

Some species of Eccrinales that inhabit the gut of crabs and glomerid millipedes apparently are sensitive to the developmental stages of their host, and produce thick-walled resistant spores instead of the usual thin-walled spores just before the host undergoes ecdysis (Manier, 1969b; Hibbits, 1978). Species of *Paramoebidium* (Fig. 2), which live in the hindgut of mayflies, stoneflies and certain dipterans also form amoebae, cysts and cystospores upon injury of the host or when the larvae molt.

Thus, Trichomycetes have several types of relationships with their hosts. Which predominates may depend on the particular species of fungus and developmental stages of the fungus and the host. This field of inquiry is open to experimentation whenever cultured fungi can be used to infest/infect laboratory-raised arthropod hosts.

8. Ecology, Dispersal, and Distribution

The ecology of trichomycetes, which are obligate associates of their arthropod hosts, is determined largely by factors affecting their hosts. El-Sherif (1975), while investigating the changes in the level of infestation by two species of Harpellales (*Harpella melusinae* and *Stipella vigilans*) and a species of Amoebidiales (*Paramoebidium chattoni*) in larval blackfly populations (Simuliidae) in rivers and streams of North Wales and South East England, found that the level of infestation remained more or less unchanged over a year. However, this contrasts with the observations of Taylor et al. (1996) who found that the level of infestation of *S. ornatum* (Simuliidae) by *H. melusinae* in a stream in Hampshire varied greatly (twenty-fold) over a short period of time (nine days) and concluded that there was no simple relationship between fungal infestation and the measured factors – host density, stream temperature, and suspended solids. Distribution of *Amoebidium* and *Smittium* species in mosquito larvae at thirty six sites spread over six county areas on the Platte River floodplain of Central Nebraska, USA, has been studied by Grigg (1988) and Grigg and Williams (1989). Their results

indicate that the percentage of trichomycete infestation remained similar from year to year. According to them, host continuity is not necessary for trichomycete infestation. Lichtwardt and Williams (1988b) also have studied distribution and species diversity in two Rocky Mountain streams. They found that, while some gut fungi were distributed widely, others were localized in their distribution; neither was there a general change in fungal species diversity over time nor at sites. Occurrence and abundance of eccrinaceous fungi in fourteen species of brachyuran crabs from Tampa Bay, Florida, USA, were studied by Mattson (1988). He found fungi in six species of crabs studied, but in varying percentages. He also observed that crabs with fungi were either herbivorous and/or detritivorous. Despite the various studies cited above, ecological aspects of trichomycetes need additional attention.

The dispersal and geographic distribution of Trichomycetes is limited by the dispersal or occurrence of their hosts within and among different geographic regions of the world. Members of Eccrinales and Asellariales could disperse widely because of the ability of their adult hosts to migrate or disperse, particularly in marine habitats. The possibility that some arthropods along with their gut fungi have been dispersed through human activities cannot be ruled out (Lichtwardt, 1986, 1996).

Harpellales are more or less restricted in their ability to disperse because they occur in non-flying larval stages of arthropods. However, their dispersal through ovarian cysts in a few species of insects belonging to simuliids, chironomids and ephemeropterans has been suggested, but not yet demonstrated (Undeen and Nolan, 1977; Yeboah et al., 1984; Moss, 1986; Moss and Descals, 1986; Labeyrie et al., 1996; Lichtwardt, 1996). That birds or other animals may disperse phoretically some of these fungi remains a possibility.

Knowledge of the full geographic distribution of trichomycetes is limited (Fig. 1). However, they are known from all geographic areas where their hosts and habitats have been searched for by competent researchers (Lichtwardt, 1996). Moreover, a few fungi encountered in temperate regions of the world also occur in tropical parts. All indications are that trichomycetes are widely distributed, but additional studies are needed to substantiate the extent of the distribution of individual species and to discover new taxa.

9. Systematics, Phylogeny and Other Studies

The class Trichomycetes belongs to the kingdom Fungi and the phylum Zygomycota. As presently constituted the class is artificial. It has four orders: Amoebidiales, Asellariales, Eccrinales, and Harpellales, and seven families consisting of 47 known genera and currently 204 species. The order

Amoebidiales, however, is not closely related to other orders of the class. Indeed, it is believed that the species of the order are not even fungi. This is described below.

As has been indicated, earlier studies of trichomycetes were largely the province of protozoologists. More recently mycologists, invertebrate pathologists, and some other biologists have contributed to the study of this group of fungi, but both their numbers and location in different parts of the world are still relatively few. There are a limited number of trichomycetes in culture and hence their systematic studies have been advanced largely through the dissection of hosts collected in the field.

To identify trichomycetes, investigators can refer to publications that have appeared since the monograph of Lichtwardt (1986). These include Lichtwardt, 1994, 1997; Lichtwardt and Arenas, 1996; Lichtwardt and Williams, 1990, 1992a,b,c,d; Lichtwardt et al., 1987, 1991a,b, 1997; Longcore, 1989; Van Dover and Lichtwardt, 1986; Williams and Lichtwardt, 1987a,b, 1990, 1993.

Relationships among the orders and families of Trichomycetes were suggested by Lichtwardt (1986), as shown in Fig. 12. There is evidence that Kickxellales (Zygomycota) and Harpellales share a common ancestry. They have some serological affinity (Sangar et al., 1972; Peterson and Lichtwardt, 1987), both have an unusual biumbonate septal structure (Moss and Young, 1978), and produce monosporous sporangia in basipetal series. They also share molecular similarities in their rDNA sequences (O'Donnell and Cigelnik, 1994). The Asellariales and Eccrinales may be derived from the Harpellales, based upon structural similarities, but molecular data are not yet available because no species in these two orders has been cultured *in vitro*. Amoebidiales, as stated above and as shown in Fig. 12, may not be monophyletically related to the three orders of "true" Trichomycetes, even though they infest some of the same hosts and show some morphological parallelisms with those orders. This presumed lack of affinity is substantiated by serological (Sangar et al., 1972; Peterson and Lichtwardt, 1987) and rDNA data (O'Donnell and Cigelnik, 1994 and unpublished). If these relationships prove to be correct, then the class Trichomycetes, as currently constituted, is an artificial class, and the term "trichomycetes" is one of convenience, just as is the category "fungi."

While studying the fine structure of zygospores of Harpellales, Moss and Lichtwardt (1977) observed four nuclei in the mature reproductive complex of *H. melusinae*: one nucleus each in the zygospore, zygosporophore, and the two conjugants. This led them to hypothesize, "that these four nuclei are derived from a meiotic division of the diploid nucleus within the fused conjugants and that the zygospore never contains the zygotic nucleus." Recent isozyme pattern studies for culturable trichomycetes also suggest the haploid nature of these

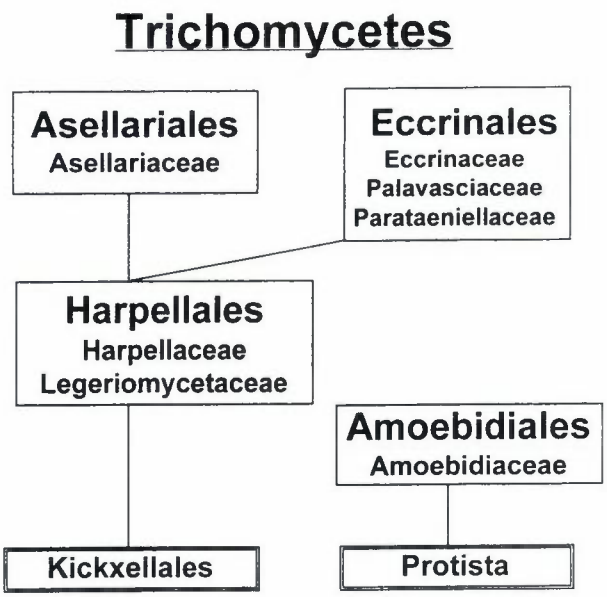


Figure 12. Hypothesized relationships of orders of Trichomycetes; Amoebidiales are not closely related to the other three orders.

fungi (Grigg, 1994; Grigg and Lichtwardt, 1996). Thus, haploidy in the somatic cells of trichomycetes conforms to most other fungi.

Moss (1972, 1974, 1976) observed mitotic nuclear division in the generative cell of *Stachylina grandispora* and found that after the division, one nucleus remains in the generative cell while the other migrates to the developing trichospore before the formation of a septum. Eccrinales have also been studied cytologically by Lichtwardt (1954a).

The ultrastructure of vegetative hyphae, trichospores and their development, appendages and their ontogeny, and the extrusion of trichospores have been studied in some Harpellales. Those studied include *S. culisetae, S. culicis, S. morbosum, H. melusinae, H. leptosa, Genistellospora homothallica, Trichozygospora chironomidarum, Zygopolaris ephemeridarum,* and *Stachylina grandispora* (Farr, 1965; Farr and Lichtwardt, 1967; Horn, 1989c, 1990; Reichle and Lichtwardt, 1972; Moss, 1972, 1975, 1976; Manier, 1973a, Preisner, 1973; Moss and Lichtwardt, 1976, 1977, 1980; Sato et al., 1989, Sato and Aoki, 1989; Sato, 1992, 1993). The unique development of the trichospores and their appendages in Harpellales has been reported by Moss and Lichtwardt (1976). Their study indicated that the trichospores are dehiscent, monosporous sporangia with the appendages contiguous with the sporangial

wall and produced outside of the plasmalemma of the generative cell. While studying the ultrastructural changes in trichospores of *S. culisetae* and *S. culicis* during in vitro sporangiospore extrusion ("germination") and holdfast formation, Horn (1989c) found no ultrastructural changes at Phase I (pH 10) during the process of extrusion (see previous discussion). Moss (1975) has also studied the ultrastructure of the septal apparatus of *Astreptonema gammari* (Eccrinales) and *Orchesellaria mauguioi* (Asellariales). Also, *Paramoebidium* (Amoebidiales) has been studied ultramicroscopically by Dang and Lichtwardt (1979). They witnessed polyhedral viruslike particles in the cytoplasm.

10. Future Research Needs

Future research on Trichomycetes can best be managed for more productive and fruitful discoveries using inter-and multidisciplinary approaches. A group of mycologists and entomologists is needed basically to study the fungal and host systematics and their ecology and to prepare a world-wide inventory of the group. The known trichomycetes are probably only a fraction of the actual extant taxa (Lichtwardt, 1986). In addition to studies on the host-fungus relationships, and their biogeography, there is need to develop methods for axenic culture of many other genera and species and to explore their intricate physiological and ecological requirements. Cytological investigations on these are very limited and worthy of pursuit. The phylogeny of this group would be better understood by additionally studying their isozyme patterns and DNA sequences utilizing modern molecular techniques and tools, especially PCR for unculturable species. Enzymatic and molecular data will also supplement and clarify the existing morphologically based taxonomic system.

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