

Review

A Review of Ectoparasitic Fungi Associated With Termites

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Abstract

Termites and ectoparasitic fungi have been at odds for millions of years. Surprisingly, fungi rarely kill their host and termites are continuously parasitized, albeit at low rates. ‘Termitophilous’ fungi have succeeded in the difficult task of infiltrating the ecological fortress of social immunity that is the termite colony. Here we review 34 definitive ectoparasitic fungal species from nine genera specialized to infest the cuticle of 50 + termite species. In general, reports of fungal ectoparasites on termites are underestimated and the actual prevalence of infestation is likely much greater in nature. In this review, we synthesize >120 yr of reports and studies on ectoparasitic fungi and their termite hosts to present an update to where our knowledge rests and where the proceeding steps should be focused. In reviewing this material, we aim to unite knowledge from two disciplines, entomology and mycology, creating a literary source useful for entomologists and mycologists alike. We provide a comprehensive summary of all fungal genera, illustrations showing morphological distinctions and development on the termite host, a glossary of mycological terminology, and an updated chart of the biogeography of these groups. Additionally, we provide a phylogenetic summary of parasite lineages and their known hosts as well as the first review of molecular evidence obtained from these fungal species.

Key words: social insect, ectoparasite, entomopathogenic, mycoparasite, species diversity

Ectoparasitic fungi are an intriguing and diverse group of organisms often adapted to live amongst Earth’s most diverse creatures, insects. As the name suggests, ectoparasitic fungi exploit the external surface of their insect hosts; but their co-evolution and species interactions have only recently been studied intensively, with mycologists and entomologists seeking to learn more about their associations (Vega and Blackwell 2005).

Some of the most unique associations occur between fungi and termites, which are among the oldest living eusocial organisms. Termites comprise 3,100+ species and are spread geographically across the globe (Krishna et al. 2013). Eusociality has rarely evolved in nature, and in ants and termites it is the key to their ecological dominance (Wilson and Hölldobler 2005). Termites’ proximity to soil and social living conditions increase the risk of being exposed to various microorganisms, including fungi (Sands 1969, Blackwell and Rossi 1986, Rosengaus et al. 2003, Hughes et al. 2008, Guswenrivo et al. 2017). For over a century, the termite cuticle has been noted as a surface commonly exploited by ectoparasitic fungi; they have the potential to impede host activity, induce behavioral deficiencies, or even cause disease and host death (Weir and Blackwell

2005, Guswenrivo et al. 2017). Not all relationships between termites and fungi are parasitic; Macrotermitinae termites cultivate the Basidiomycete fungi, *Termitomyces*, to be used as a food source (Batra and Batra 1979, Tayasu et al. 2000, Mueller and Gerardo 2002). Another striking instance of a termite-fungi symbiosis is exhibited by the termite-ball fungus (*Fibularhizoctonia* spp.), which mimics termite eggs to exploit resources available within the nest (Matsuura et al. 2000). This relationship is considered somewhat parasitic; however, it can provide important benefits to its host. Some termite workers intentionally forage for termite ball fungus for their own gain, utilizing its hyphae as a food source and its cellulases to aid in the breakdown of plant material (Ye et al. 2019).

Despite variation in the fungi that infest termites, one commonality the ectoparasitic fungi described in this review share is that they are largely restricted to termites as their primary obligate host. Chouvenc et al. (2011) reviewed all pathogens of termites to assess their use as a means of biocontrol and concluded that 1) fungal ectoparasites are likely a poor choice because they do not directly harm their host (Gouger and Kimbrough 1969, Blackwell and Kimbrough 1976b, Blackwell and Rossi 1986), 2) field result efficacy of entomopathogenic

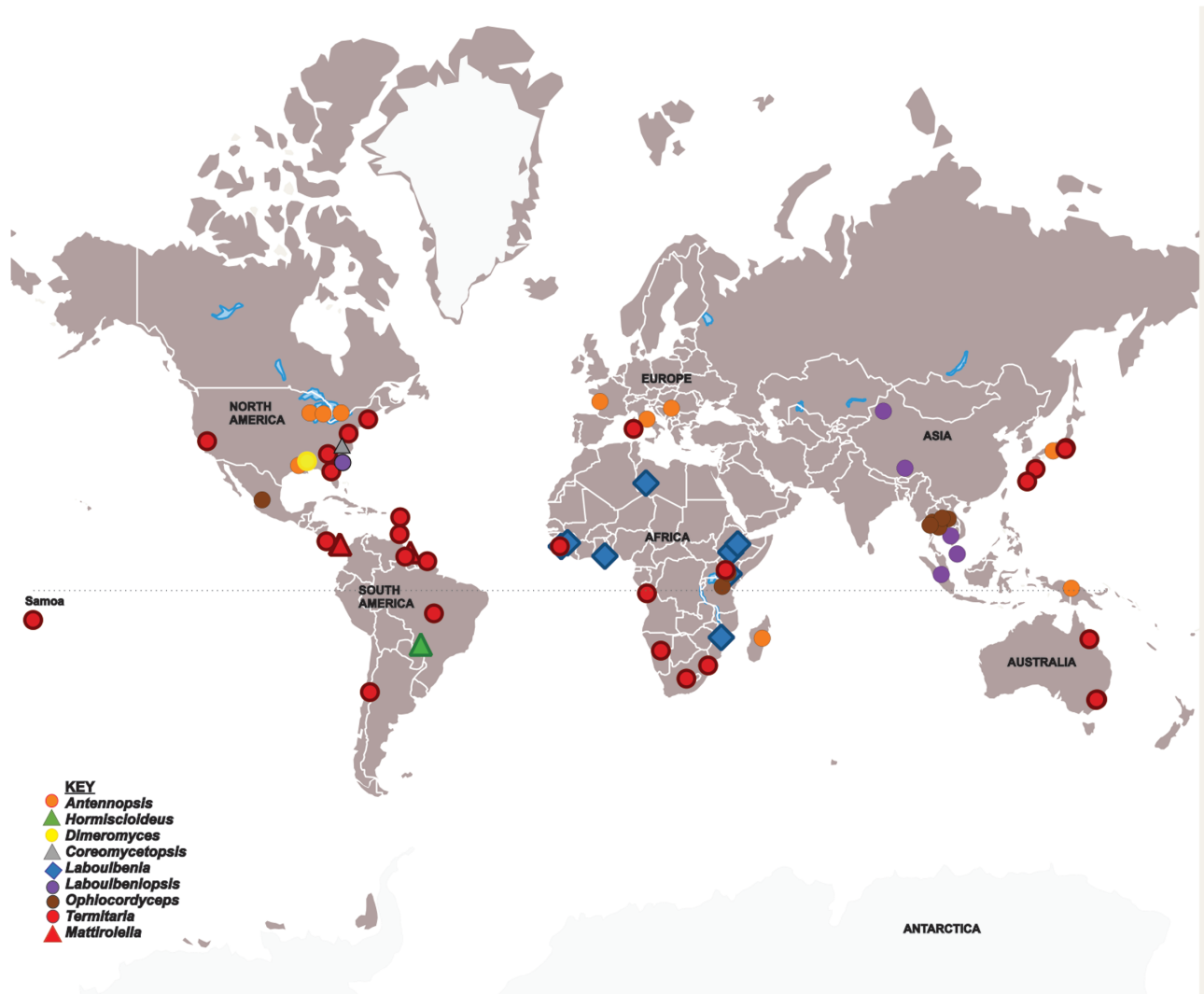


Fig. 1. Map shows known geographic locations of ectoparasitic fungal genera reported on termites. Detailed locality information used to build map included in Supp Table 1 (online only).

fungi is not properly evaluated (Culliney and Grace 2000, Rath 2000), and 3) laboratory experiment protocols are too basic to be conclusive (Delate et al. 1995, Wang and Powell 2004, Chouvenec et al. 2008).

Most ectoparasitic fungal genera are reported to be geographically restricted, although some appear to be distributed worldwide (Fig. 1, Supp Table 1 [online only]) (Blackwell and Kimbrough 1978, Blackwell and Rossi 1986). To date, records of ectoparasitic fungi infesting termites have been largely limited to isolated reports of new fungal species, new morphological discoveries, or geographic range expansions (Fig. 2). Modern work synthesizing the pathogenic relationships between fungal parasite and termite host are lacking, as no such report of progress has been provided in nearly 35 yr. In 1986, Blackwell and Rossi synthesized all known records of fungal ectoparasite and termite host biogeographical ranges and provided a checklist of 20 valid species and nine genera. Since this time, 15 new species have been described, several preexisting species synonymized, new host associations and taxonomic affinities have been identified (Table 1), and molecular evidence obtained (Table 2). Additionally, the status of the commonly observed genus *Amphoromorpha* has since been under debate; in 1989, Blackwell and Malloch provided morphological evidence that observations of this fungi are likely a secondary capillaconidial form of the sac-like fungi *Basidiobolus* (Blackwell and

Malloch 1989, Blackwell et al. 2020). *Basidiobolus* fungi are not considered to be obligate ectoparasites on termites (Vega and Blackwell 2005), therefore are not included in this review. Much of this review consists of a comprehensive breakdown of each of the fungal-host associations, focusing on the presentation, individual and colony rate of infestation, morphological diagnosis, and detailed drawings and descriptions of their general life cycle. This is followed by an overview of the phylogenetic lineages of the parasite with their known hosts (Fig. 3), molecular progress made on the fungal parasites, and suggested future directions. As one goal of this review is to provide a resource for mycologists and entomologists, we include a short glossary to define discipline-specific terminology and jargon useful when detailing parasite-host relationships (Supp Table 2 [online only]).

Overview of Fungal Genera

Phylum Ascomycota

- Class Sordariomycete
- Order *Incertae sedis*
 - Antennopsis
- Class Laboulbeniomyces

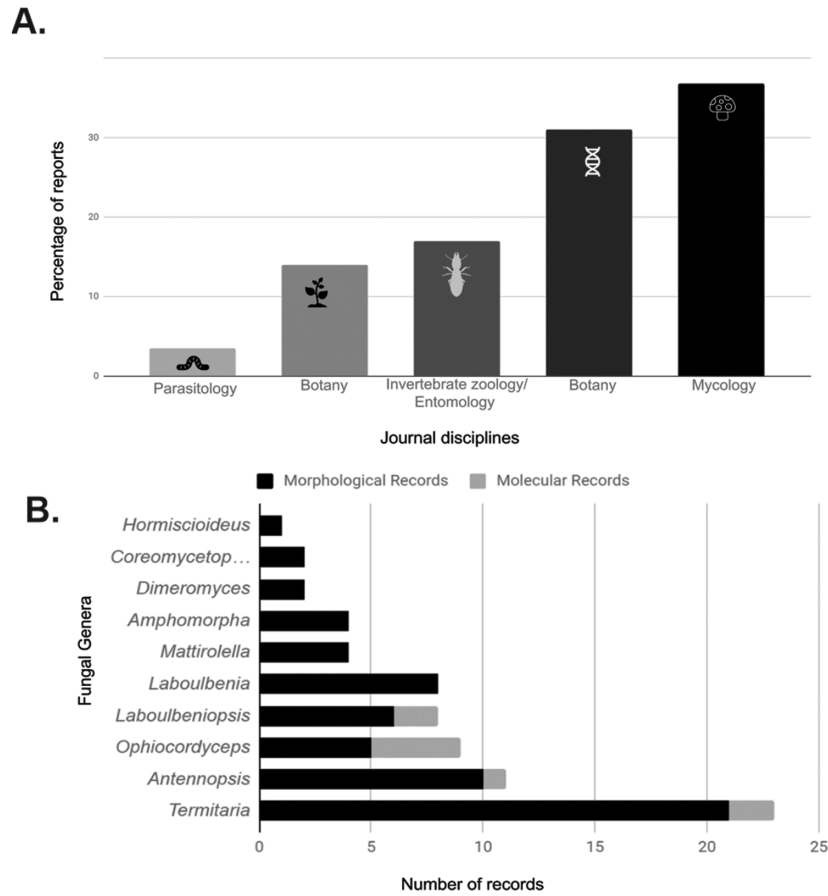


Fig. 2. Charts summarizing >120+ yr of literary records on ectoparasitic fungi. (A) percentage of reports published in journals of various disciplines. (B) Morphological vs. molecular records for each fungal group.

Order *Incertae sedis*
 Laboulbeniopsis
 Hormiscioideus
 Order Laboulbeniales
 Family Laboulbeniaceae
 Coreomycetopsis
 Dimeromyces
 Laboulbenia
 Order Hypocreales
 Family Ophiocordycipitaceae
 Ophiocordyceps
 Order Ophiostomatales
 Family Kathistaceae
 Class Hyphomycetes
 Order *Incertae sedis*
 Mattirolella
 Termitaria

The Ectoparasite-Host Relationship

Past studies have used a variety of terms to describe the number of individuals 'infected' within a colony, and how many thalli are found on each individual. To summarize their observations most consistently and accurately, we use the following terms to describe ectoparasite-host relationships. The word 'infested' best describes termites that exhibit ectoparasitic fungal growths on their outer body surface, a condition referred to as ectoparasitosis. Most ectoparasitic fungal infestations on termites cause very low, indirect harm to their host. For

this reason, the terms 'entomopathogenic' and 'infection' will only be used in cases where disease or mortality occurs to the host as a direct result of ectoparasitosis. We use the term 'incidence of infestation per colony' to describe the number or percentage of individuals each ectoparasitic fungus infests within an observed colony, and 'incidence of infestation per individual' in place of the term 'infection strength' used by Guswenrivo et al. in 2017 to describe the numbers of thalli per individual termite. Termites exhibit distinct castes which can be susceptible to fungal ectoparasites at different incidence. Seasonality, a change in physiologic status or in the occurrence of an infection (or infestation) that conforms to seasonal patterns (CDC 2014), is another important factor to consider when describing the relationship between fungal parasite and termite host.

Antennopsis

Perhaps the most common and specialized ectoparasitic fungi found on termites belong to the genus *Antennopsis* (Guswenrivo et al. 2017). This genus, which is comprised of three species, *Antennopsis gallica* (Heim and Buchli, Hyphomycetes: Gloeohaustoriales) (Heim and Buchli 1951), *Antennopsis gayi* (Buchli, Hyphomycetes: Gloeohaustoriales) (Buchli 1966), and *Antennopsis grassei* (Buchli, Hyphomycetes: Gloeohaustoriales) (Buchli 1960b), was erected in 1951 by Heim who proposed its placement as a new order Gloeohaustoriales within the Class: Hyphomycete. Placement of the *Antennopsis* into commonly accepted fungal taxonomic groupings (Tubaki 1963) is considered challenging (Gouger and Kimbrough 1969) and its original designation continues to be used

Table 1. Status of ectoparasitic taxa (2020)

Taxon name	Taxonomy	Mycobank	Year of effective publication
<i>Antennopsis gallica</i>	Fungi, Dikarya, Ascomycota, Antennopsis	292533	Heim and Buchli 1951
<i>Antennopsis gayi</i>	Fungi, Dikarya, Ascomycota, Antennopsis	282985	Buchli 1966
<i>Antennopsis grassei</i>	Fungi, Dikarya, Ascomycota, Antennopsis	326248	Buchli 1960
<i>Dimeromyces isopteris</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales Dimeromyces	582818	Kimbrough et al. 1972
<i>Dimeromyces majewskii</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Dimeromyces	313123	W. Rossi and Ces. Rossi 1977
<i>Hormiscioideus filamentosus</i>	Fungi, Dikarya, Ascomycota	11437	Blackwell and Rossi 1978
<i>Laboulbenia felicias-caprae</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniomycetes, Laboulbeniomycetidae, Laboulbeniales, Laboulbeniaceae, Laboulbenia	316124	Rossi 1974
<i>Laboulbenia hagenii</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	636147	Thaxter 1895
<i>Laboulbenia buccalis</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	826854	W. Rossi and Leonardi 2018
<i>Laboulbenia geminata</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	332776	Buchli 1966
<i>Laboulbenia brignoli</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	103486	W. Rossi and M. Blackwell 1986
<i>Laboulbenia ghanaensis</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	103489	W. Rossi and M. Blackwell 1986
<i>Laboulbenia antemmalis</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniales, Laboulbenia	826834	W. Rossi and Leonardi 2018
<i>Laboulbeniopsis termitarius</i>	Fungi, Dikarya, Ascomycetes, Laboulbeniopsis	237417	Thaxter 1920
<i>Coreomycetopsis oedipus</i>	Fungi, Dikarya, Ascomycota, Pezizomycotina, Laboulbeniomycetes, Laboulbeniomycetidae, Laboulbeniales, Coreomycetopsis	192090	Thaxter 1920
<i>Termitaria coronata</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	249949	Thaxter 1920
<i>Termitaria longiphialidis</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	111059	Kimbrough and Lenz 1982
<i>Termitaria macrospora</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	111060	Kimbrough and Lenz 1982
<i>Termitaria rhombicarpa</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	111061	Kimbrough and Lenz 1982
<i>Termitaria snyderi</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	250364	Thaxter 1920
<i>Termitaria thaxteri</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Termitaria	280162	Reichensperger 1923
<i>Mattirorella crustosa</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Mattirorella	317420	S. R. Khan and Kimbrough 1974a
<i>Mattirorella silvestrii</i>	Fungi, Ascomycota, Pezizomycotina, Ophiostomatales, Kathistaceae, Mattirorella	317421	S. Colla 1929
<i>Ophiocordyceps koningsbergi</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	504292	Penzig and Saccardo 1904,
<i>Ophiocordyceps bispora</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	504232	Stifler 1941
<i>Ophiocordyceps octospora</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	504315	Blackwell and Gilbertson 1981
<i>Ophiocordyceps termitiphila</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	831296	Tasanathai et al. 2019
<i>Ophiocordyceps communis</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	311805	Kobayasi and Shimizu 1978
<i>Ophiocordyceps asiatica</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	504216	Sung et al. 2007
<i>Ophiocordyceps brunneirubra</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	831297	Tasanathai et al. 2019
<i>Ophiocordyceps kkokpasiensis</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	831289	Tasanathai et al. 2019
<i>Ophiocordyceps mosingtoensis</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	831290	Tasanathai et al. 2019
<i>O. pseudocommunis</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	831291	Tasanathai et al. 2019
<i>O. pseudorhizoidea</i>	Fungi, Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Ophiocordyceps	830982	Tasanathai et al. 2019

Chart shows current accepted nomenclature, synonyms, and molecular progress of each fungal group.

Table 2. Chart shows current progress on molecular work for all known fungi that exclusively infest termites

Taxon name	Accession #	Gene regions sequenced	Sequence contribution
<i>Antennopsis gallica</i>	Not available	18S	Guswenrivo et al. 2017
<i>Laboulbemiopsis termitarius</i>	18S-MF785100.1, AY212810.1	18S	Guswenrivo et al. 2017, Henk et al. 2003
<i>Termitaria snyderi</i>	18S-AY212812, AH013151.2, TUB-AY278207.1, AY278206.1, AY212812.1	18S-classified, unclassified-18S	Henk et al. 2003, Hojo et al. 2002
<i>Ophiocordyceps bisporea</i>	genome-GCA_900080695.1	partial draft genome (6,359,382bp)	Conlon et al. 2017
<i>Ophiocordyceps communis</i>	18S-GU723768.1, TEF-MK284268.1, MK284267.1, MK284266.1, GU797125.1, RPB2-MK214095.1, MK214096.1, MK214097.1, MK214109.1, MK214110.1, MK214111.1	18S, ITS1, 5.8S, ITS2, 28S, TEF, RPB2	Tasanathai et al. 2019
<i>Ophiocordyceps asiatica</i>	RPB1-MK214106.1, MK214105.1, RPB2-MK214092.1, MK214091.1, TEF-MK284263.1,	RPB1, RPB2, TEF	Tasanathai et al. 2019
<i>Ophiocordyceps abrunneirubra</i>	RPB1-MK751467.1, MK751465.1, MK751466.1, RPB2-MK751468.1, MK214103.1, MK214102.1	RPB1, RPB2	Tasanathai et al. 2019
<i>Ophiocordyceps khokpasiensis</i>	TEF-MK284271.1, MK284269.1, MK284270.1, RPB2-MK214098.1, RPB1-MK214112.1, MK214113.1, MK214114.1,	RPB1, RPB2, TEF	Tasanathai et al. 2019
<i>Ophiocordyceps mosingoensis</i>	RPB1-MK214116.1, MK214115.1, RPB2-MK214100.1, MK214099.1, TEF-MK284273.1, MK284272.1	RPB1, RPB2, TEF	Tasanathai et al. 2019
<i>Ophiocordyceps pseudocommunis</i>	RPB1-MK214117.1, RPB2-MK214101.1, TEF-MK284274.1	RPB1, RPB2, TEF	Tasanathai et al. 2019
<i>Ophiocordyceps pseudorbizoidea</i>	RPB1-MK751469.1, MK214104.1, RPB2-MK214090.1, MK214089.1, TEF-MK284262.1, MK284261.1	RPB1, RPB2, TEF	Tasanathai et al. 2019

in morphological studies (Heim and Buchli 1951, Buchli 1960, Buchli 1966, Gouger and Kimbrough 1969, Rossi and Cesari-Rossi 1977, Blackwell and Rossi 1986, Myles 1998). Recent molecular data (18S rRNA gene sequences) generated from *A. gallica* have suggested placement in Class: Sordariomycetes, despite exhibiting markedly different morphology and life history strategies from other fungi in this group (Guswenrivo et al. 2018). *Antennopsis* fungi are extremely widespread from tropical to temperate regions where they infest termites from the following families: Kalotermitidae, Rhinotermitidae, and Termitidae (Blackwell and Rossi 1986). Its most current geographic distribution is shown in Fig. 1; *Antennopsis* has been reported on nearly every continent apart from Australia (Heim 1951, Buchli 1960, Buchli 1966, Gouger and Kimbrough 1969, Blackwell 1980, Blackwell and Rossi 1986, Myles et al. 1998).

Fungal Distribution on the Host Body

All three species of *Antennopsis* appear to be specific to termites and are distributed on all regions of the host body (Table 3). Buchli (1960b) discovered *A. grassei* in Madagascar infesting all body regions and castes (including larvae and eggs) of the following termite species: *Neotermes amplus* (Sjostedt, Blattodea: Kalotermitidae), *Neotermes desneuxi* (Sjostedt, Blattodea: Kalotermitidae), and *Glyptotermes longiceps* (Paulian, Blattodea: Kalotermitidae). *Antennopsis gayi*, from New Guinea (Buchli 1966), infested the setae and spines of *Coptotermes elisae* (Desneux, Blattodea: Rhinotermitidae) and *Coptotermes obiratus* (Hill, Blattodea: Rhinotermitidae). Additional observations have been made of both fungal species occurring on termites in Madagascar, South America, Africa, and Asia (Blackwell and Rossi 1986, Guswenrivo et al. 2017). Most information regarding *Antennopsis* infestation of termites is based on reports of the commonly documented species *A. gallica*. *Antennopsis gallica* is most frequently found on the head, thoracic plates, tergites, abdomen, and legs of its hosts (Heim and Buchli 1951, Gouger and Kimbrough 1969). A termite survey in Florida revealed incidence of *A. gallica* infestation in which thalli of various developmental stages were found on *Reticulitermes virginicus* (Banks, Blattodea: Rhinotermitidae) and *Reticulitermes flavipes* (Kollar, Blattodea: Rhinotermitidae) hosts (Gouger and Kimbrough 1969). In 1998, Myles et al. counted 3,404 fungal thalli distributed in the following body locations and frequencies: head region (18.6%), the thorax (34.6%), and the abdomen (46.8%). The level of infestation was heaviest on terminal castes comprising soldiers and reproductives that cease molting, a mechanism that sheds fungal thalli. Larger body regions supported proportionately larger numbers of fungal thalli as a function of their relative surface area.

Transmission

Transmission is suspected to occur from direct contact with contaminated individuals or galleries (Heim and Buchli 1951, Buchli 1966), adhere via mucilaginous secretions and a cellular holdfast, and spread to new colonies from swarming reproductives. This theory is in debate, Gouger and Kimbrough (1969) found no evidence of the fungus in galleries and most conidial heads were not adhesive or sticky despite observations of conidia adhering to hairs and cuticles of several termites. Myles et al. (1998) believe its small size (>100 cells in length) and the elevated position of the conidial heads are important factors in the transmission of this fungus; *Antennopsis* thalli extend just above the level of termite setae, where they are believed to be at an optimal height for conidial dissemination and inter-termite body contact while still being close enough the cuticular surface to be removed by

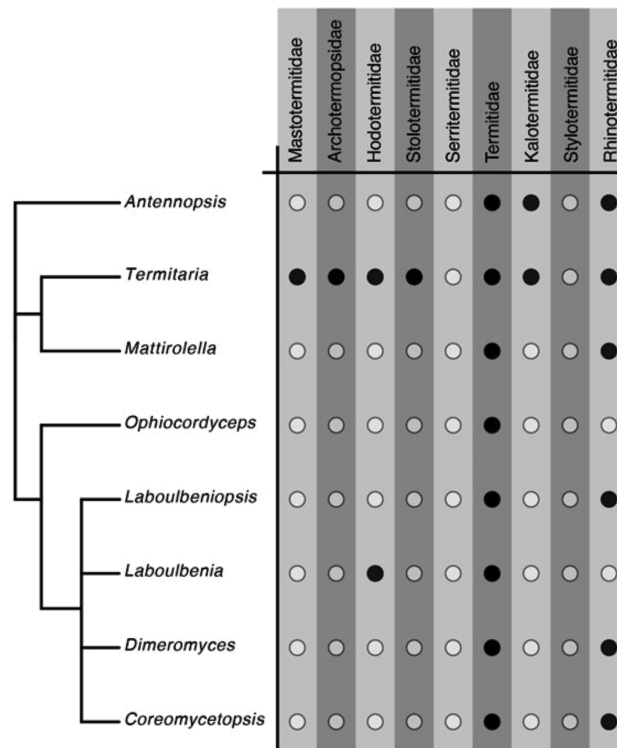


Fig. 3. Phylogenetic distribution of known fungal-host associations. Phylogenetic tree based on NCBI taxonomy as of September 2020, accessed through phyloT v2. While some taxa (i.e., *Antennopsis* and *Laboulbeniopsis*) have not been placed at the family or ordinal level, we included these as *Incertae sedis* within a supported higher clade by collapsing nodes into polytomies. Filled in circles indicate a known relationship between a member of a termite and fungus taxon.

termite grooming by mouthparts. To determine the accurate transmission mechanisms of *Antennopsis*, it must be induced to grow on artificial media where host and parasite can be observed in a controlled environment (Kimbrough and Gouger 1969).

Incidence of Infestation per Individual and Colony

Nymphoids and soldier castes of *R. flavipes* are typically most heavily infested by *A. gallica* and workers are least infested (Buchli 1952, Myles et al. 1998); the reason behind lower incidence in workers is potentially linked to frequent grooming, but also likely due to increased molting frequency observed in this caste (Heim and Buchli 1951, Buchli 1952, Buchli 1966, Myles 1998). Guswenrivo et al. (2017) found conflicting results in which workers were more infested (17.8–25%) than soldier castes (0–10% infestation rate) in 3 colonies of *Reticulitermes speratus* (Kolbe, Blattodea: Rhinotermitidae). It is suspected that the worker-specific behaviors such as grooming, which typically serves as an anti-fungal defense strategy, can facilitate fungal spore transmission (Guswenrivo et al. 2017). In 1977, Rossi and Rossi reported a 21–23% infestation incidence to be the maximum infestation incidence for a single mound (Rossi and Rossi 1977a) and in Gouger and Kimbrough (1969) study, colonies of *Reticulitermes virginicus* and *R. flavipes* (Gouger and Kimbrough 1969) were 'slightly infested' by *A. gallica*, with only 5–10 fungal thalli per insect. In large colonies, *Antennopsis* was commonly reported at a range of 1–35 thalli/individual (Gouger and Kimbrough 1969, Kimbrough and Gouger 1970, Blackwell and Kimbrough 1978, Blackwell 1980, Myles et al. 1998); however, small founding colonies exhibit much higher rates of infestation. Myles et al. 1998 observed extreme variation in incidence of infestation per individual; some *R. flavipes* individuals were infested with a single thallus, while nearly one-third were carrying 100+ thalli. Previously, the highest observed number of thalli on a single termite was 150 (Blackwell and Kimbrough 1976b); however, higher numbers (479 thalli) have since been observed (Myles

et al. 1998). *Antennopsis* infestation exhibits seasonality; therefore, infestation incidence vary considerably depending upon the season. For instance, Buchli (1952) described winter as being the season with the highest incidence of infestation, perhaps due to lowered rates of termite activity and molting; seasonal variation will likely differ with latitude; however, more work must be done.

Impact on Host

The mortality rate of termites infested by *Antennopsis* in large well-established colonies is low; under these conditions no differences have been observed in social behavior, size, color, turgidity, or bodily damage for infested individuals (Kimbrough and Gouger 1969, Myles 1998, Guswenrivo et al. 2017). In Buchli (1960a), 100 % colony foundation success was observed for non-infested termites, whereas 0% of infected colony founder couples were successful ($n = 20$). Likewise, in small, founding colonies of *R. lucifigus* (Rossi, Blattodea: Rhinotermitidae) infested with *A. gallica*, mortality rate was found at rates as high as 70%–75% of colony members (Heim and Buchli 1951, Buchli 1960a, Buchli 1966). The increased impact *Antennopsis* has on small colonies compared to large colonies ($n = 200+$) is likely a result of factors related to the biology of both the parasite and the host. In large established colonies, fungi remain latent and grow slowly, often going undetected by its host. The fungus is kept in check when the termite molts its exoskeleton and sheds traces of fungal forms; the remaining terminal caste members (no longer molt), tolerate the remaining fungi without any discomfort (Buchli 1960). When imaginal swarming termites are infested with *Antennopsis*, prior to colony foundation, they typically perish within 12 mo after the first conidiophores appear (Buchli 1960a, Buchli 1966). Young colonies of wood-inhabiting species infested by *Antennopsis* are restricted to small wooden chambers until the colony expands its nest to galleries within surrounding soil (Buchli 1966). The nest of established colonies consists of a vast network of chambers; this increase in space

allows increased movement within the nest in which the fungus rarely comes into contact with termites (Buchli 1966).

Antennopsis does not penetrate the host body upon attachment and decline in health of host populations occurs indirectly; at high population sizes conidiophores produce a glue that affects termite movement and feeding, which causes disruption of the molting process leading to injury (Heim and Buchli 1951; Buchli 1952, 1960a,b; Buchli 1966). The absence of haustorium suggests it does not absorb nutrients from its host cytoplasm, but instead inhabits and obtains nutrients from the hosts' 'social skin' a term proposed to describe the collective cuticular surfaces of social insects that serve as a nutrient rich niche-space for fungi (Myles et al. 1998). Because it interferes with swarming success and infests eggs, *Antennopsis* presents a potential opportunity to be used as a microbial control agent for termites that form small, confined colonies, such as those in the families Rhinotermitidae and Kalotermitidae, but likely not soil-dwelling termites (Termitidae) (Buchli 1960a, Buchli 1966; Guswenrivo et al. 2017). To best understand this fungus and its potential in this capacity, we need more data and must further investigate its behavioral effects on termites (Guswenrivo et al. 2017).

Identification

Antennopsis fungi are composed of a basal multicellular holdfast surrounded by a thick brown outer membrane, a stalk-like conidiophore that is brown at the base and hyaline at the head, with a conidiferous head at the terminal end (Buchli 1960a). Similar ectoparasites, *Coreomyces* and *Laboulbeniopsis*, can be readily distinguished by a holdfast composed of single-celled initials (Thaxter 1920). The three species of *Antennopsis* are distinguished primarily by the appearance of their conidiferous heads. Further diagnostic details are presented for each species below.

General Lifecycle

Antennopsis infestation is initiated when a conidial spore is transmitted via direct physical contact between host nestmates (potentially via wood galleries) and adheres to their cuticle via mucilaginous secretions (Buchli 1952, Buchli 1960a, Gouger and Kimbrough 1969) (Fig. 4). A basal cellular holdfast develops and divides to produce three (*A. grassei*) or four cells (*A. gallica*, *A. gayi*), then lateral and central septa form, and wall pigmentation occurs (Buchli 1952, Buchli 1966, Gouger and Kimbrough 1969). The conidial spore germinates within 8 days (Buchli 1960a) and protrudes from the dorsal wall of holdfast cells at various rates. Within 20 days (Buchli 1960a) the hyaline septate conidiophores become pigmented and constricted 15–20 μm from the base (Gouger and Kimbrough 1969). Conidiophores grow and extend from a single central cell (*A. gayi*), two central cells (*A. gallica*) or two apical cells (*A. grassei*) until they are at an optimal height for conidia dissemination (app.100–200 μm ; Gouger and Kimbrough 1969). They terminate in single (*A. gallica*, *A. grassei*) or double conidial heads (*A. gayi*), which disintegrate to release ellipsoid conidia covered in mucilaginous secretions, apex first, followed by successional conidia (Gouger and Kimbrough 1969).

Laboulbeniopsis

Background

Laboulbeniopsis termitarius (Thaxter: Ascomycetes) was initially described as a species of *Thaxteriola* in 1920, when Thaxter discovered sexual ascospores (formed via spontaneous spore formation and development within an ascus) and young thalli on the cuticle of termites (Kimbrough and Gouger 1969, Blackwell and Kimbrough 1976b). It was 'rediscovered' via light microscopy in 1970 by

Kimbrough and Gouger, and Blackwell and Kimbrough (1976a,b), who provided morphological data and a full account of its development using SEM showing it is an Ascomycote fungi (Henk et al. 2003). Similarly, to *Antennopsis*, which exhibits a wide geographic distribution, *Laboulbeniopsis* has been reported on Rhinotermitidae and Termitidae hosts in North, Central, and South America as well as in Africa, Asia and Europe (Thaxter 1920, Kimbrough and Gouger 1970, Blackwell and Kimbrough 1976a, Rossi and Rossi 1977b, Blackwell 1980, Blackwell and Rossi 1986; Fig. 1, Table 1).

Fungal Distribution on the Host Body

Past surveys have shown that this fungus is not restricted to a certain location on its host (Table 3). Blackwell (1980) observed *L. termitarius* thalli on the legs, mouthparts, and antennae of *R. flavipes* and Gouger and Kimbrough (1969) found it on all parts of the body with highest prevalence on the abdomen, antennae, and tarsi. Some individuals exhibited high numbers of thalli (30–35 thalli) and the following fungal distribution on the host body observed: 4–5 on antennae, often on antennal tips, 6–10 on legs often on tarsi, 3–4 on abdomen often on ventral side, with occasional thalli found elsewhere, including on the stalks of mature fungi (Kimbrough and Gouger 1970). Guswenrivo et al. (2018) observed the most infested body part of *R. speratus* to be the antennae, followed by the abdomen, leg, head, and thorax. There is not enough information to conclude that presence on the host body varies between species, we suspect this variation reflects observations within a limited number of studies.

Transmission

Termites likely expose each other to ectoparasitic fungi when they contact appendages infested with arched thalli that produce clumps of adhesive spores in an asynchronous fashion (Kimbrough and Gouger 1970). Seasonal differences did not typically cause significant differences in infestation rate (Guswenrivo et al. 2018) but the number of thalli per termite individual was lower during times when the host termite was most active and fungal removal behaviors were elevated. The host, *R. speratus*, has the highest activity at 25–30°C and activity decreases over 30°C (Kambara et al. 2017), therefore at 25–30°C grooming activities with nestmates would be on the rise and useful as an antifungal defense (Boucias et al. 1996, Shimizu and Yamaji 2003, Yanagawa and Shimizu 2005, Guswenrivo et al. 2018).

Incidence of Infestation per Individual and Colony

Infestation incidence was surveyed in laboratory settings and determined to be >20% in most studies (Kimbrough and Gouger 1970, Blackwell 1980, Henk et al. 2003). Rossi and Cesari-Rossi (1977) found it to be an extremely common parasite of *R. lucifigus* in Rome with infestation incidence of 70% in a single mound; infested individuals typically carried <10 thalli per individual. Incidence rates of *L. termitarius* in colonies of *R. flavipes* and *R. virginicus* termites varied in different studies (Kimbrough and Gouger 1970, Blackwell 1980). In 1980 Blackwell observed that 91% of *Reticulitermes* colonies collected in Georgia were infested with *L. termitarius*, and the number of individuals affected within a colony was 25–53%. These numbers were higher than those observed in a study of *R. flavipes* in Baton Rouge, Louisiana, in which observed infestation rates were much lower (20%) (Henk et al. 2003). In 2018, Guswenrivo et al. investigated infestation incidence using molecular techniques and visual observations of Japanese *R. speratus* termites. They first used nested PCR to determine a more accurate estimate of how many thalli could be found per individual, a measure they also refer to as 'infection strength'. A low infection strength was three thalli per termite

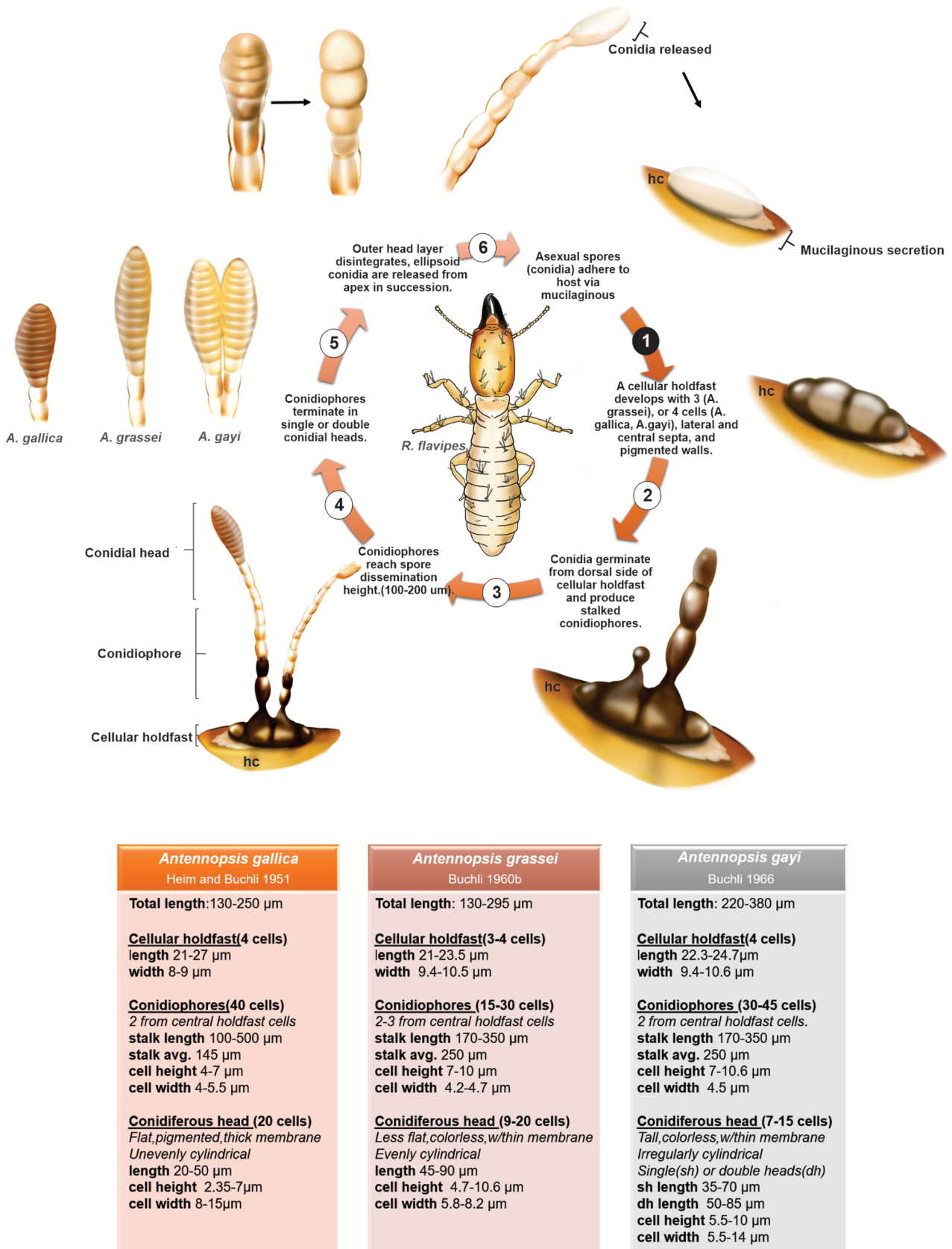


Fig. 4. General life cycle of *Antennopsis*. General life cycle (asexual) of *Antennopsis gallica* (Heim and Buchli 1951), with diagnostics and variations shown for *A. gayi* (Buchli 1966) and *A. grassei* (Buchli 1960b). General morphology and development *Antennopsis* as it is described in Gouger and Kimbrough 1969. Visual references used to create illustrations included in figure (Gouger and Kimbrough 1969, Buchli 1960a, Buchli 1952).

Table 3. Fungal distribution

Fungal distribution on host body	Head capsule	Mouthparts	Antennae	Thorax	Abdomen	Legs	Wings
<i>L. brignolii</i>	✓	✓	✓	✓	✓	✓	
<i>L. ghanaensis</i>	✓				✓		
<i>L. hagenii</i>	✓				✓		
<i>L. felicis-caprae</i>	✓	✓	✓	✓	✓	✓	
<i>L. antennalis</i>			✓				
<i>L. bucallis</i>		✓				✓	✓
<i>D. isopterus</i>	✓	✓	✓	✓	✓	✓	
<i>D. majewskii</i>	✓						
<i>O. bispora</i>				✓	✓	✓	
<i>O. octospora</i>						✓	
<i>O. asiatica</i>				✓			
<i>O. brunneirubra</i>	✓			✓			
<i>O. khokpasiensis</i>				✓			
<i>O. mosingtoensis</i>				✓			
<i>O. pseudocommunis</i>				✓			
<i>O. pseudorhizoidea</i>				✓			
<i>O. termiticola</i>				✓			
<i>C. oedipus</i>			✓				✓
<i>L. termitarius</i>	✓	✓	✓	✓	✓	✓	✓
<i>H. filamentosus</i>	✓	✓	✓	✓	✓	✓	✓
<i>A. gallica</i>	✓	✓	✓	✓	✓	✓	✓
<i>A. grassei</i>	✓	✓	✓	✓	✓	✓	✓
<i>A. gayi</i>							
<i>T. snyderi</i>	✓	✓	✓	✓	✓	✓	✓
<i>T. coronata</i>	✓	✓	✓	✓	✓	✓	✓
<i>T. macrospora</i>				✓	✓	✓	
<i>T. rhombicarpa</i>	✓	✓	✓	✓	✓	✓	✓
<i>T. longiphialidis</i>	✓	✓	✓	✓	✓	✓	✓
<i>M. silvestri</i>	✓	✓	✓	✓	✓	✓	✓
<i>M. crustosa</i>	✓	✓	✓	✓	✓	✓	✓

Not listed Rare Present Common

Chart lists known distribution of ectoparasitic fungal thalli on termite host body by species.

(9.1%) although presence of a single thallus per individual was considered to be common (Guswenrivo et al. 2018). They found three to eighteen termite workers in 500 individuals were infested across the eight colonies investigated (none were soldiers). Within colonies the incidence rate was determined by Kimbrough and Gouger (1970) to be less than 40% of colonies examined; however, incidence within individuals was determined to range widely from 10 to 90% of individuals infested with at least a single thallus.

Impact on Host

Much like other species of Laboulbeniales, *L. termitarius* has no direct pathological effect on its termite host (Kimbrough and Gouger 1970). It is possible that in large numbers movement is hindered; however, further evidence or claims of harm to the host has not been documented.

Identification

Although they superficially resemble male members of the dioecious *Laboulbenia* species, the two-phased process of spore maturation and germination distinguishes *Laboulbeniopsis* and *Coreomycepsis* (Kimbrough and Gouger 1970). The monotypic genus *Laboulbeniopsis* is morphologically distinguished by its small shape and three main body structures: a brown foot cell that is black

at the attachment point, a two-celled hyaline stalk, and a pale brown terminal sporangium (Thaxter 1920, Kimbrough and Gouger 1969, Blackwell and Kimbrough 1976a, Henk et al. 2003). The lower stalk cell is almost twice as long as the upper stalk cell and is continuous throughout the thallus via simple pores and a specialized pore between the stalk and foot cell (Blackwell and Kimbrough 1976a). Blackwell and Kimbrough (1978) cite the following similarities to other fungi from the order: *Laboulbeniales* have an entomogenous habit, simultaneous spore formation, the presence of secretory vesicles, and effervescent asci. *Laboulbeniopsis*, however, differs in its lack of haustoria, a uniascal thallus. Additionally, the formation of a hyaline thallus from a globose pigmented unicellular spore is distinct (Blackwell and Kimbrough 1976a).

General Life Cycle

The lifecycle of this fungus has been well-described by several authors and clarifications made as scientific technologies have progressed (Fig. 5). In 1970, Kimbrough and Gouger detailed the complete lifecycle and development of *L. termitarius* and described a two-phased process of spore maturation and germination. In the apex of the ascus, free-cell formation of spores is initiated, and they continue development near the stalk cell region (Kimbrough and Gouger 1970). Residual cytoplasm is present at all times, and hyaline spores are liberated

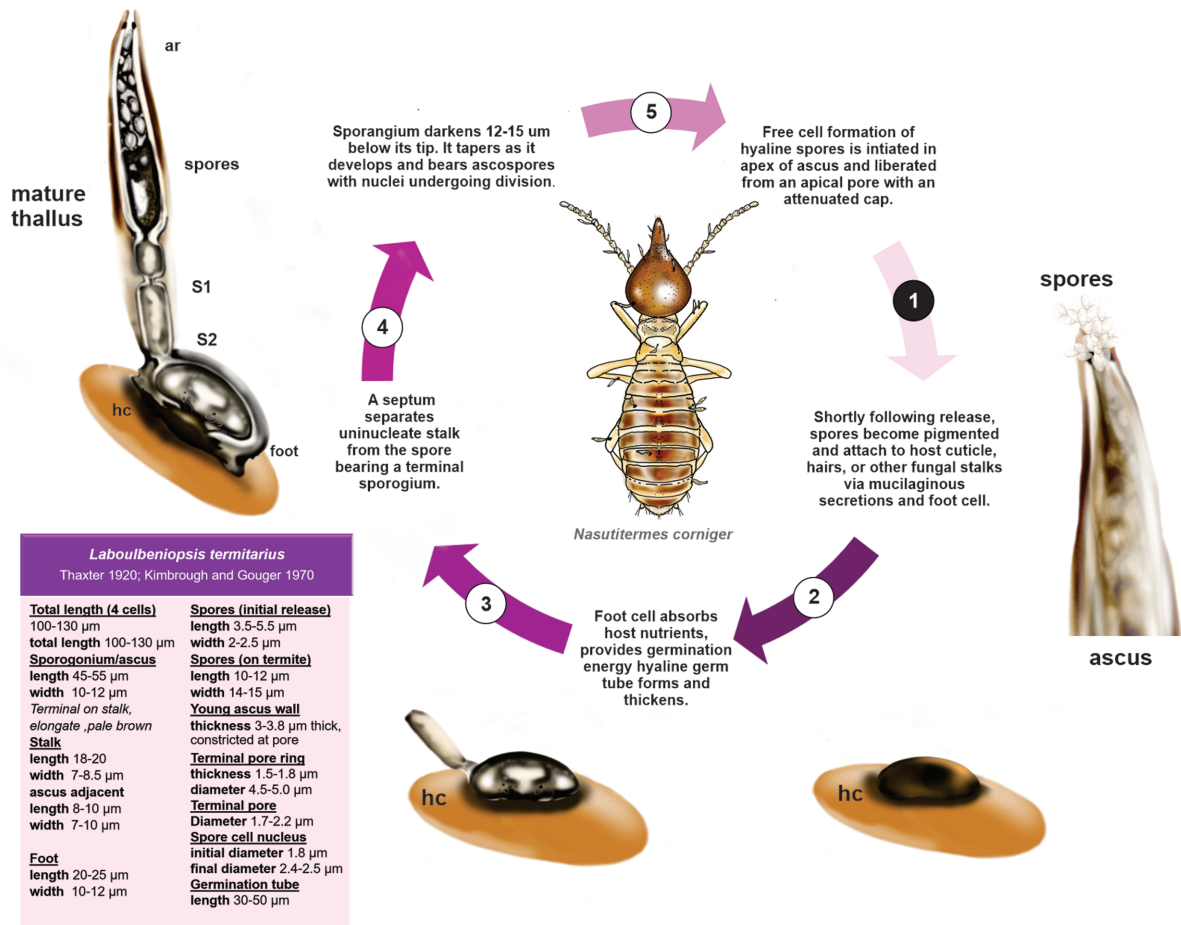


Fig. 5. General life cycle of *Laboulbeniopsis termitarius*. Diagnostic morphology and development of *Laboulbeniopsis termitarius* as it is described in (Blackwell and Kimbrough 1976a and Kimbrough and Gouger 1970). Visual references used for illustrations included in figure—micrographs—Blackwell and Kimbrough 1976a). ar=apical ring, hc=host cuticle.

individually via an apical pore that constricts their shape as they are liberated (Kimbrough and Gouger 1970). Shortly following release, the spores become pigmented and attach to the termite host cuticle, hairs, or mature *Laboulbeniopsis* thalli via an elliptically shaped foot cell surrounded by a thin mucilaginous secretion and a dark void pad (Kimbrough and Gouger 1970, Blackwell and Kimbrough 1976a). At either end of the foot cell, a dense area ring consists of empty canals, and no penetration or damage to the cuticle occurs (Blackwell and Kimbrough 1976a). Although all other *Laboulbeniales* use haustoria to absorb nutrients from the host and nourish the growing thallus (Benjamin 1971) it is believed the foot cell has absorptive properties and the continuity of the cytoplasm through the septal pores allows transfer of nutrients to occur upward through the thallus (Blackwell and Kimbrough 1976a). Each uninucleated spore swells and thickens at the inner wall layer (Kimbrough and Gouger 1970). In their observations, it could not be determined if pigmented spores were the products of fusion (evidenced by nuclear growth prior to germination) or enlargement of a single spore. Germination of the stalk occurs via formation of hyaline germ tubes that become progressively thick-walled, elongated and broad (Kimbrough and Gouger 1970). The stalk consists of two cylindrical cells, a cell adjoining the foot cell, and a shorter cell adjoining the sporogonium (Thaxter 1920). A septum separates the uninucleate stalk from a terminal spore-bearing structure, the sporangium (Kimbrough and Gouger 1970, Blackwell and Kimbrough 1978). As the sporangium matures, it becomes tapered

and bears sexual ascospores (Kimbrough and Gouger 1970, Blackwell and Kimbrough 1976a). The sporangium wall is constricted near its pore and pigments become intensified at 12–15 μm below the tip leaving a long attenuated cap which opens upon spore liberation (Kimbrough and Gouger 1970). Development of spores into a four-celled thallus is believed to be very short-lived (Kimbrough and Gouger 1970, Blackwell and Kimbrough 1976b).

Hormiscioideus

Background

In 1978, Blackwell and Kimbrough described the fungus *Hormiscioideus filamentosus* (Blackwell and Kimbrough, Ascomycota), a member of a monotypic genus from a single Brazilian termite collection. This species is morphologically like other small filamentous fungi found on arthropods and was found on *Armitermes neotenicus* (Holmgren, Blattodea: Termitidae) (Termitidae) from Mato Grosso, Brazil (Blackwell and Kimbrough 1978; Fig. 2). Due to its simplicity, it is difficult to assess the relationship of other fungi using morphology; however, it has been referred to as a Hyphomycete fungus (Wijayawardene 2012), perhaps due to its presence of hyphae (Sutton 2014). No molecular sequences are available for this fungus and although a large quantity of material was collected at the time, there has been only one study of this filamentous termite ectoparasite to date.

Fungal Distribution on the Host Body

This fungus is found on all parts of the body and extremities of its host (*A. neotenicus*) and has been documented on all termite castes, including young alates, nasute soldiers, and workers (Blackwell and Kimbrough 1978) (Table 3).

Incidence of Infestation per Individual and Colony

Of the 36 colonies of various termite species collected from northern Brazil, *H. filamentosus* was found in only one colony where 60% of individuals were reported to be infested (1–25 thalli per individual; Blackwell and Kimbrough 1978). No information has been provided for potential routes of transmission.

Impact on Host

This termite attaches to the host via haustoria; however, its impact is known. Based on its low prevalence in colonies and on individuals its impact on the hosts' survival is suspected to be low. Laboratory studies and ultrastructural work is needed to determine the extent of what harm, if any, it poses to its host.

Identification

Hormiscioideus is defined as having simple or branched filaments coming up from a thick cellular base, reproducing via filament fragmentation with internal proliferation, and connecting to the insect cuticle via small haustorial connections (Blackwell and Kimbrough 1978). *H. filamentosus* exhibits a range of 1–10 of these cellular filaments attached to a thick-walled, yellow-brown cellular base that matures to form a crust or pulvinate structure, and tapers at the top. Although other fungi reproduce by filament fragmentation and

internal proliferation, *H. filamentosus* is unique in its wide cell shape, coloration, and tapering filaments (Blackwell and Kimbrough 1978). For instance, a similar fungus *Chantransiopsis* produces conidia and exhibits a black foot, whereas *H. filamentosus* has a light base and no spores (Thaxter 1914, Blackwell and Kimbrough 1978). Although it shares traits possibly influenced by convergence due to a shared environment, it can be distinguished from other termite ectoparasites by its basal cell and filament arrangements as well as its mode of reproduction, as stated previously (Blackwell and Kimbrough 1978).

General Lifecycle

The development of *Hormiscioideus* fungus is simple, much like its morphology (Fig. 6). First, filaments arise from a base of thickened cells and haustorial connections attach the fungus to the insect cuticle. Simple or branched filament cells are produced, often growing twice as long as wide with a brown cellular base (Blackwell and Kimbrough 1978). The filaments continue to grow and at maturity, the base appears to be a flat cellular crust or a pulvinate structure. Reproduction occurs via irregular fragmentation and internal proliferation thus continuing the infestation.

Coreomycetopsis

Background

The monotypic genus *Coreomycetopsis* was first described on *Nasutitermes corniger* (Motschulsky, Blattodea: Termitidae) by Thaxter in 1920 and consists of superposed cells, a basal foot cell attached to the host, and a terminal sporogonium cell. *Coreomycetopsis oedipus* (Thaxter, Laboulbeniomycetidae: Laboulbeniales) is a

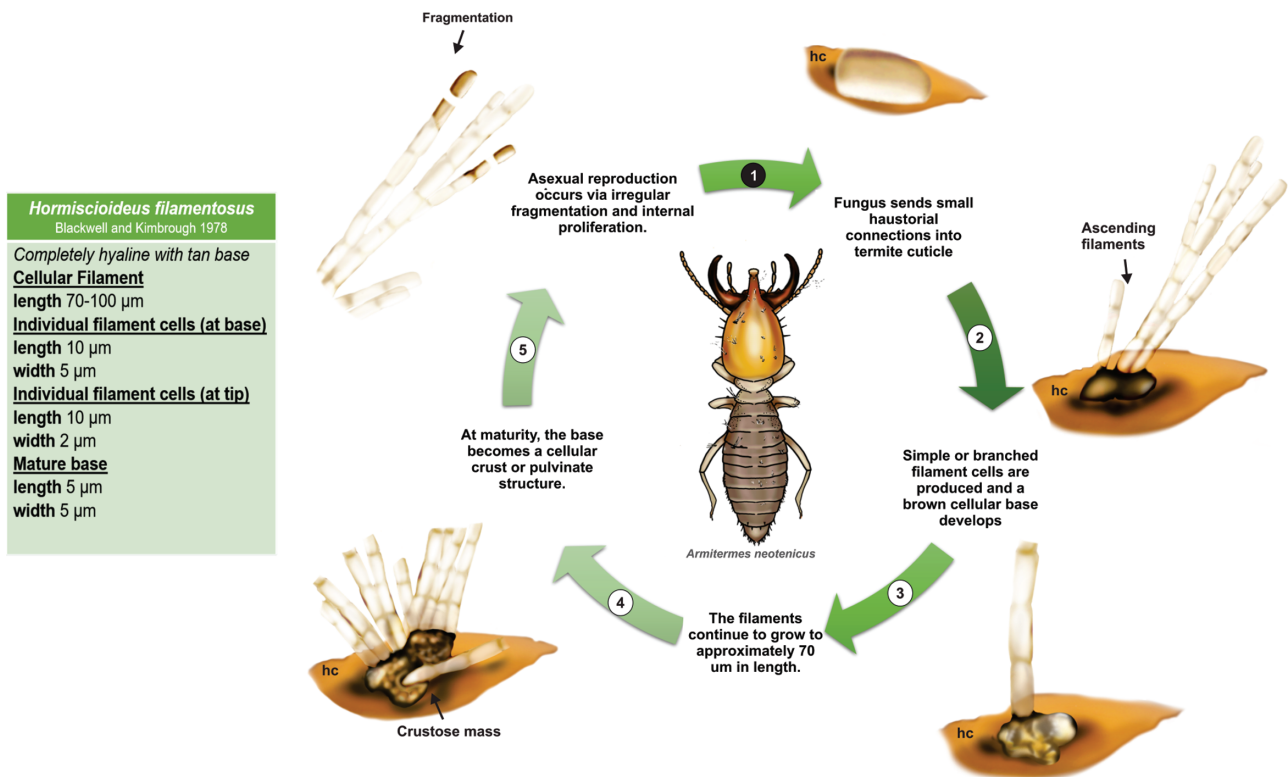


Fig. 6. General Summary of *Hormiscioideus filamentosus*. General life cycle (asexual) of *Hormiscioideus filamentosus*. Morphology and development of *H. filamentosus* as it is described in Blackwell and Kimbrough (1978). Visual references used to create illustrations included in figure from micrographs in Blackwell and Kimbrough (1978). Reproductive stage via fragmentation and internal filament proliferation (arrow). hc=host cuticle.

morphologically complex fungus found on Rhinotermitidae and Termitidae hosts and is restricted to geographic locations in the New World (Thaxter 1920, Blackwell et al. 1986). It is typically found in association with the fungus *L. termitarius* (Blackwell and Kimbrough 1976a, b), which presents a similar foot structure, however, differs drastically in its distinct spore-production process. In Blackwell and Kimbrough (1976a, b), it was observed on *R. virginicus*, and it was confirmed that *C. oedipus* develops from phialoconidia, whereas *L. termitarius* develops from ascospores.

Fungal Distribution on the Host Body

C. oedipus, initially found by Thaxter (1920) in Grenada, has been documented on the tips of the legs of *Eutermes morio* (*N. corniger*). Its thalli position is influenced by the protection afforded by the insect surface structure, and it is commonly found beneath 'claws' and rarely on antennae (Thaxter 1920, Blackwell and Kimbrough 1976b).

Transmission

Termites likely become infested by spores in their gallery or by infested termite interactions (Blackwell and Kimbrough 1976a, b). It is believed that in natural settings spring rains would promote its growth, therefore seasonality may play a role in its life cycle (Blackwell and Kimbrough 1976b).

Incidence of Infestation per Individual and Colony

When observed in laboratory settings, 98% of the termite colony was infested with this fragile fungus. Individual infestation rate of this fungus was typically low, however up to 12 thalli were found on a single termite leg (Blackwell and Kimbrough 1976b). No further information is provided regarding incidence of infestation for this species.

Impact on Host

Nutrient absorption occurs via a foot pad. Because invasive haustoria or penetration peg structures do not form, harm to the host, i.e., decrease in survival, is thought to be unlikely (Blackwell and Kimbrough 1976b). No further information is provided regarding harm to the host.

Identification

C. oedipus is composed of a bent fungal axis (10–15 superposed cells), a basal foot cell and a terminal sporogonium cell. The color of *C. oedipus* ranges from faint yellow to hyaline, making it hard to detect despite being larger in size than most *Laboulbeniales* (Thaxter 1920). The phialospores are long, oval, hyaline and pointed at the base while the sporogonium is straight, symmetrical, and broader than the stalk (Thaxter 1920). Its close association with *L. termitarius* on the termite host, as well as its ultrastructurally identical foot cell with complex secretory canals and secreted adhesive pads are so similar some have suggested these fungi are closely related (Blackwell et al. 2003; Blackwell et al. 1986; Blackwell 1994; Blackwell and Kimbrough 1976a, b). It is distinguished from similar appearing fungi such as *Coreomyces* and *L. termitarius* by its reproductive agent; *C. oedipus* produces phialospores in a sporogonium instead of ascospores in an ascus (Blackwell et al. 1986, Thaxter 1920).

General Lifecycle

Termites likely become infested by spores in their gallery or by interactions with infested termites (Blackwell and Kimbrough 1976a, b) (Fig. 7). The sixth or seventh axis cell from the apex is proliferous and divides to form a central sub-pyiform cell and lateral cells that

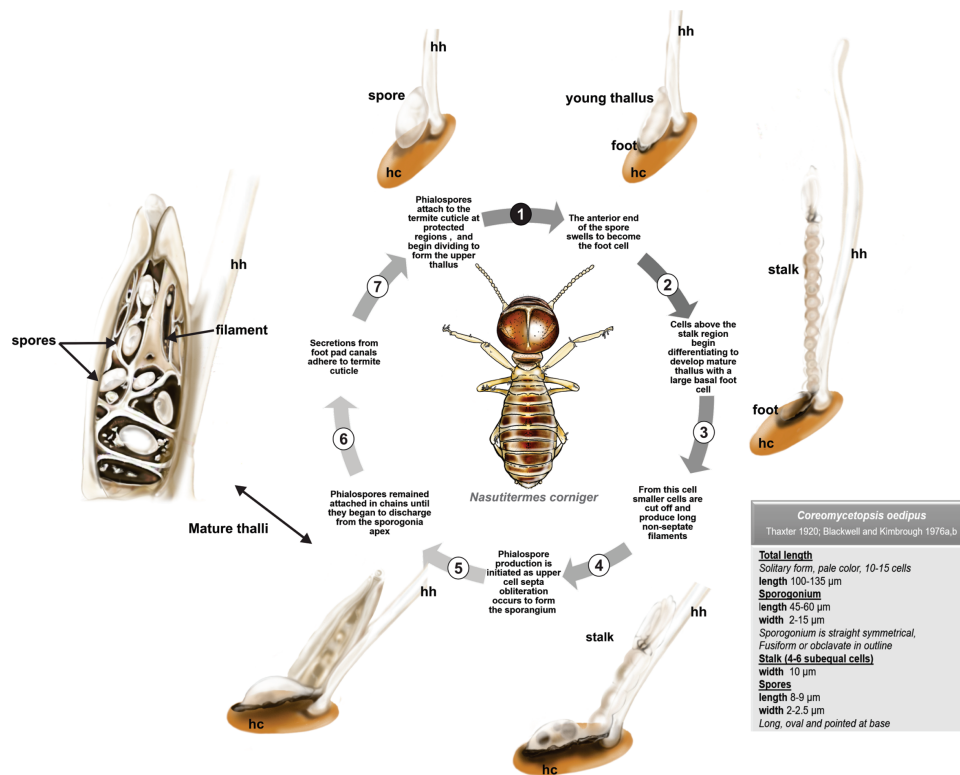


Fig. 7. General life cycle of *Coreomycetopsis oedipus*. Diagnostic morphology and development of *Coreomycetopsis* as it is described in Thaxter (1920) and Blackwell and Kimbrough (1976). Visual references used to create illustrations included in figure- micrographs (Blackwell and Kimbrough 1976). hc = host cuticle, hh = host hair.

grow upward (Thaxter 1920). As new sporophores grow upward, successive septa are destroyed or absorbed and terminally simple hyaline spores are cut off and set free in the sporogonium then discharged through a terminal perforation (Thaxter 1920; Blackwell and Kimbrough 1976a, b).

Dimeromyces

Background

The genus *Dimeromyces* infests an array of arthropods, ranging from mites to beetles (Dogonniuck et al. 2019), however, only two out of 109 *Dimeromyces* species have been found on termites (Kimbrough et al. 1972, Rossi and Cesari-Rossi 1977). Kimbrough et al. (1972) first described *Dimeromyces isopterus* (Kimbrough, Laboulbeniales) on *R. flavipes* termites in Florida. In 1977, Rossi and Cesari-Rossi described a second species, *Dimeromyces majewskii* (Rossi and Cesari-Rossi, Laboulbeniales), ectoparasitizing *Alyscotermes kilimandjaricus* (Sjostedt, Blattodea: Termitidae) Sjöst in Kenya. Ectoparasitic fungi are typically host-specific; however, *D. isopterus* also may infest its termitophile co-inhabitants; it has been found infesting co-inhabitants including a beetle (*Pasimachus depressus* (Lecount, Coleoptera: Carabidae)) and a mite (unpublished data discussed in Blackwell and Kimbrough 1978). It is currently only known from Rhinotermitidae and Termitidae hosts from North America and Africa. Aside from a brief species validation report (Kimbrough 1986), only two papers have been published since the genus was first described in 1972, so we consider the available distribution data to likely be underestimates.

Fungal Distribution on the Host Body

D. isopterus was observed in Gainesville, Florida where it was distributed across all body parts of *R. flavipes*, most commonly on the head and abdomen (Kimbrough et al. 1972) (Table 3). No caste preference has been described for this genus, however *D. majewskii* parasitizes the heads of a soldierless termite species (*A. kilimandjaricus*; Rossi and Cesari-Rossi 1977). Further details on transmission, infestation rate in colonies/populations, and its impact to hosts are not documented in any works of this fungus on termites to date.

Incidence of Infestation per Individual and Colony

The mechanism for transmission for *Dimeromyces* species associated with termites has not been determined. Overall, infestation rate is low within a colony, and usually less than 10 thalli occur, of approximately the same stage, in individuals infested with *D. isopterus*. Interestingly, Blackwell and Kimbrough 1978 note that *D. isopterus* was not restricted to termite hosts; it was observed to infest mites (unidentified species) and beetles (*Trichopsenius depressus*) known to actively groom *R. flavipes* and occupy the same nest space (unpublished data discussed in Blackwell and Kimbrough 1978). It is not known the rate at which the termitophiles were infested; however, this occurrence does suggest that either *D. isopterus* is closely related to nontermite *Dimeromyces* forms, or these similarities are simply a result of convergence due to selection for similar habitats (Blackwell and Kimbrough 1978).

Impact on Host

The impact that *Dimeromyces* parasites have on their termite hosts has not been determined; however, due to its low presence in colonies and on individuals it is suspected to be low and not have a large effect on their survival rate.

Identification

Dimeromyces fungi are dioecious, therefore male and female thalli are present, often growing next to each other. The general structure of the female thallus is a foot cell, receptacle, unbranched perithecia and asci with ascospores, while males exhibit a primary appendage, receptacle, and antheridia (Kimbrough et al. 1972). The developmental stages of the perithecium are considered to be similar to those found in fungi that do not infest termites: *Stimatomyces baeri* (Karst., Laboulbeniales: Laboulbeniaceae), *Laboulbenia flagellata* (Peyr., Laboulbeniomycetidae: Laboulbeniales), and *Peyritschella gaminata* (Thaxter, Laboulbeniomycetidae: Laboulbeniales) (Thaxter, 1986). *D. majewskii* is typically larger than *D. isopterus* aside from the perithecia size, which is larger in the latter. *D. majewskii* is completely hyaline with a pigmented foot, and male individuals are composed of an elongate receptacle (4 cells), a single antheridium, and an appendix (Rossi and Cesari-Rossi 1977). The second and third receptacle cells are flat and give rise to a small round cell and the antheridium is carried by the fourth cell. Female receptacles are formed by five cells separated by oblique septa, and are comprised of a single perithecium (originating from fourth cell), primary and a secondary appendage (Rossi and Cesari-Rossi 1977). In both species that parasitize termites, the female thallus is considerably larger than the male (Kimbrough et al. 1972, Rossi and Cesari-Rossi 1977). *D. isopterus* exhibits a four-celled receptacle, five-celled, unbranched appendages terminating in a mucoid cell and collarette, and one to three perithecia with trichogynes bearing four asci and hyaline ascospores. The male thallus comprises a four to five celled primary appendage and a two to three celled receptacle that divides to form a single antheridium bearing two to four antheridial cells (Kimbrough et al. 1972).

General Lifecycle

Dimeromyces infestation is initiated when paired ascospores land on the host cuticle and germinate (Fig. 8). In 1972, the development of *D. isopterus* was examined by Kimbrough et al. They determined that three to four superposed cells comprising the female thalli produce a primary appendage from their terminal spore segment, and the perithecium initially elongates to form a trichogyne, sexual apparatus, and perithecia with a crosswall (Kimbrough et al. 1972). Males are produced alongside the female, and lack perithecia, instead producing antheridia. The males develop a stalk cell, two basal support cells, and superposed cells that divide obliquely to form two to four antheridia that form speratio in their beaks; cross-septa form at 12 μm from the antheridial initial (Kimbrough et al. 1972). For both sexes, the spore tips (apices) break, exposing a flared terminal cell and a thick inner wall covered in mucilaginous secretions within the primary appendages.

Laboulbenia

Background

Within the order Laboulbeniales, which has over 2,000 known species and 133 genera (Lee et al. 2011), exists the genus *Laboulbenia* (600+species). These fungi most commonly infests beetle, but in 1895, Roland Thaxter documented *L. hagenii* (Thaxter, Laboulbeniomycetidae: Laboulbeniales) on *Macrotermes bellicosus* (Smithean, Blattodea: Termitidae) termites in the East African country of Mozambique and in 1986, *Laboulbenia ghanaensis* (Rossi and Blackwell, Laboulbeniomycetidae: Laboulbeniales) was described infesting termites as well. Since then, five additional species have been described that are associated with termites: *L. brignolii* (Rossi and Blackwell, Laboulbeniomycetidae: Laboulbeniales)

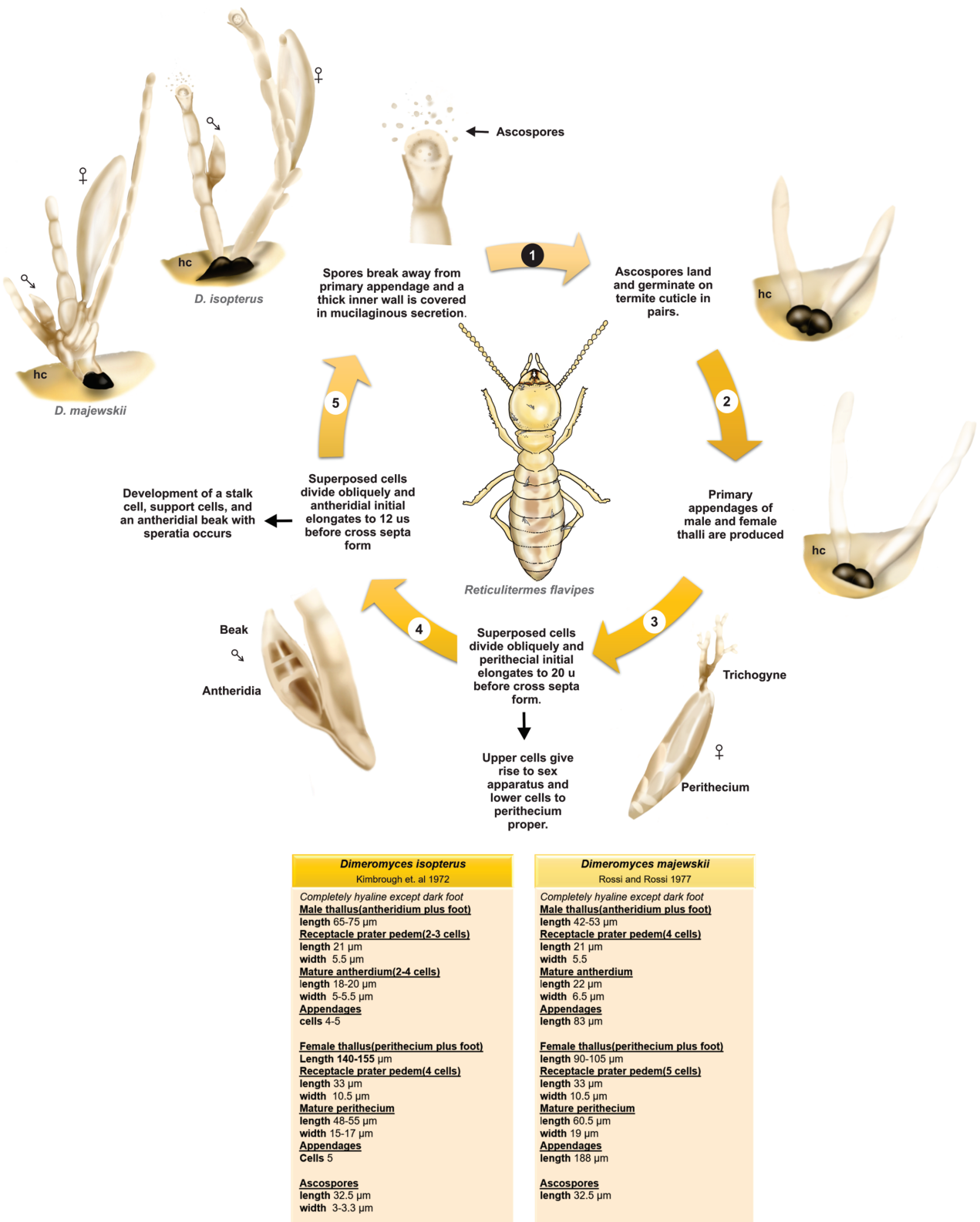


Fig. 8. General Summary of *Dimeromyces*. General life cycle (sexual) of *Dimeromyces isopterus* (Kimbrough et al. 1972), with variations shown for *Dimeromyces majewskii* (Rossi and Cesari-Rossi 1977). Visual references for illustrations modified and included in figure-line drawing from Rossi and Cesari Rossi 1977 (*D. majewskii*) and line drawing and micrographs (Kimbrough et al. 1972 *D. isopterus*). hc = host cuticle.

W. Rossi and Blackwell, *Laboulbenia felicit-caprae* (Rossi, Laboulbeniomycetidae: Laboulbeniales) W. Rossi, *Laboulbenia geminata* (Buchli, Laboulbeniomycetidae: Laboulbeniales) Buchli ex

W. Rossi and Blackwell, *Laboulbenia buccalis* (Rossi and Leonardi, Laboulbeniomycetidae: Laboulbeniales) Rossi and Leonardi and *Laboulbenia antemnalis* (Leonardi and Rossi, Laboulbeniomycetidae:

Laboulbeniales) Leonardi and Rossi (Leonardi and Rossi 2018). *Laboulbenia* infests termites from the families Termitidae and Hodotermitidae and is restricted to termite hosts from Africa (Buchli 1966, Rossi 1974, Thaxter 1895, Rossi and Blackwell 1986, Rossi and Leonardi 2018). All species in the genus *Laboulbenia* are dioecious with the exception of a few ground beetle parasites where no male structure (antheridium) has been found (Rossi and Leonardi 2018). The general body plan of the genus *Laboulbenia* is as follows: foot cell (haustorium), male appendage bearing antheridia, female appendage bearing perithecium and trichogyne (Buchli 1966).

Fungal Distribution on the Host Body

Laboulbenia has been documented on all regions of the termite body; however, it is most abundantly described on the head, labial palps, and antennae (Rossi 1974, Blackwell and Rossi 1986). In 1895, Thaxter documented the first case of fungal parasites on termites when he described *L. hagenii* associated with worker larvae of *M. bellicosus*; however, he does not note the fungal distribution on the host body. Fungal distribution on the host appears to vary between *Laboulbenia* species; *L. brignolii* was reported on the head of a single worker from *Macrotermes herus* (Sjöstedt, Blattodea, Termitidae), although very few thalli were reported and were mostly broken (Rossi and Blackwell 1986). In the same study, *L. ghanaensis* thalli were abundantly found on the head, and occasionally on the abdomen of several soldiers and workers of *Amitermes evuncifer* (Silvestri, Blattodea: Termitidae) (Rossi and Blackwell 1986). *L. felicitis-caprae* has been reported on various body regions of *Anacanthotermes ochraceus* (Burmeister, Blattodea: Hodotermitidae), with the highest abundances on the head, labial palps, and antennae (Rossi 1974) and *L. geminata* is found on *Odontotermes badius* (Sjöstedt, Blattodea: Termitidae), however the caste and body region are not noted (Buchli 1966). As the name suggests, *L. antennalis* are typically found on the antennae of their host, *M. bellicosus* (Rossi and Leonardi 2018) and they infest relatively few termites within a colony (1–2 pairs of thalli per antennae) (Rossi and Leonardi 2018). Another species described by Rossi and Leonardi in 2018, *L. buccalis*, was discovered on most termites collected, and the number of thalli per termites was high. It is documented on the mouthparts of workers, soldiers, and nymphs of *A. evuncifer* with few exceptions (Rossi and Leonardi 2018) except in one instance where it was found on the tibia of soldiers (Rossi and Leonardi 2018).

Transmission

Laboulbenia's sticky spores can be transmitted only by direct contact between insects or substrates (De Kesel 1995a,b; Riddick and Schaefer 2005). Some insect hosts spread spores during courtship rituals, however the blind sterile worker castes likely spread spores via social behavior. Some of these behaviors such as antennal interactions (antennation) and mouth-feeding (trophallaxis) have led to *Laboulbenia* infestations on other insect hosts, including flea beetles (Try et al. 2017, Rossi and Leonardi 2018) and flies (Rossi and Ponziani 2008). Rossi and Leonardi 2018 suspect that transmission to new host colonies for *Laboulbenia* on termites occurs through infested sexual alates after they discovered *L. buccalis* thalli under the wing pads of *A. evuncifer*.

Incidence of Infestation per Individual and Colony

The number of fungal thalli per termite, and individuals infested per colony are not well-documented for species of *Laboulbenia* associated with termites. The only documentation of incidence is as follows; *L. antennalis* infestation rate is very low within a colony, and was observed to cause only in one or two pairs of thalli on each

antennae whereas *L. buccalis* infested its hosts more heavily (Rossi and Leonardi 2018).

Impact on Host

This fungus is suspected to have a low impact on the survival of its host; however, no further information is provided in reports of *Laboulbenia* on termites.

Identification

Laboulbenia is dioecious and similar in body plan to *Dimeromyces* fungi, comprised of a male appendage with antheridia and a female thallus (five cells) with perithecium and inner appendage (Buchli 1966, Rossi and Leonardi 2018) (Fig. 9). *L. hagenii* is most readily diagnosed by its small size, brown coloration, and slightly tapering perithecium (Thaxter 1895). It typically has eight appendages that arise from two basal cells (inner and outer) followed by a square cell with four short rigid hyaline branches with blunt tips that never extend beyond the perithecium (Thaxter 1895). *L. felicitis-caprae* appears similar to *L. hagenii* in its small size and perithecium shape, but instead has a squat receptacle shape, as well as antheridial and paraphysal apparatus (Rossi 1974). It bears two outward-facing antheridia on rectangular cells and its perithecium is strongly pigmented at its pre-apical region with hyaline ostiolar lips (Rossi 1974). *L. buccalis* is diagnosed by a grayish-brown female thallus (cells III and IV) slightly hunched perithecium, downturned apex with large round unequal lips, simple and elongate hyaline outer appendages (Rossi and Leonardi 2018). *L. geminata* develops as a 'twin fungus' on its host *Odontotermes badius*, and although no morphological measurements could be confirmed for this group, it is distinct from *L. hagenii* in that it has double ascospores, and the antheridium develops as the base of a long appendage (Buchli 1966, Rossi and Blackwell 1986). *Laboulbenia brignolii* exhibits a short, stout receptacle nearly hyaline, and a unique assemblage of cells, most broader than they are wide, a triangular cell above a pentagonal basal cell (Rossi and Blackwell 1986). This fungus also exhibits a light-brown perithecium with an outwardly pointed apex and subequal, rounded hyaline lips (Rossi and Blackwell 1986). It too grows in pairs, but only one individual has a single perithecium that survives to maturity and is thicker in appearance (Rossi and Blackwell 1986). This same phenomenon is seen in *L. ghanaensis*, in which one perithecium survives while both antheridia survive to a functional stage (Rossi and Blackwell 1986). The fungal growth observed for *L. ghanaensis* is the smallest of all *Laboulbenia* species associated with termites. *Laboulbenia* exhibits hyaline appendages and grayish-brown sexual organs (Rossi and Blackwell 1986). Cell shapes are diagnostic; the basal cell is the most narrow, cell V is very small and wedge-shaped, an extremely small basal cell comprising the inner appendage and a suprabasal cell is separated from cell III from a short horizontal septum (Rossi and Blackwell 1986). The male appendage bears one antheridium and the perithecium is one-half free, and tapers towards the stout truncate apex where it exhibits hyaline round ostiolar lips (Rossi and Blackwell 1986). It can be readily distinguished from *L. felicitis-caprae*, which exhibits paired antheridia as opposed to single antheridia, a stout basal cell of outer appendage, and a darker perithecium apex (Rossi and Blackwell 1986). The basal cell I of the female thallus in *L. antennalis* is hyaline and long, while the second cell is pale reddish brown, distinctly longer than the basal cell, and the stalk cells are completely free from the reddish-brown perithecium. The appendage is elongate, and

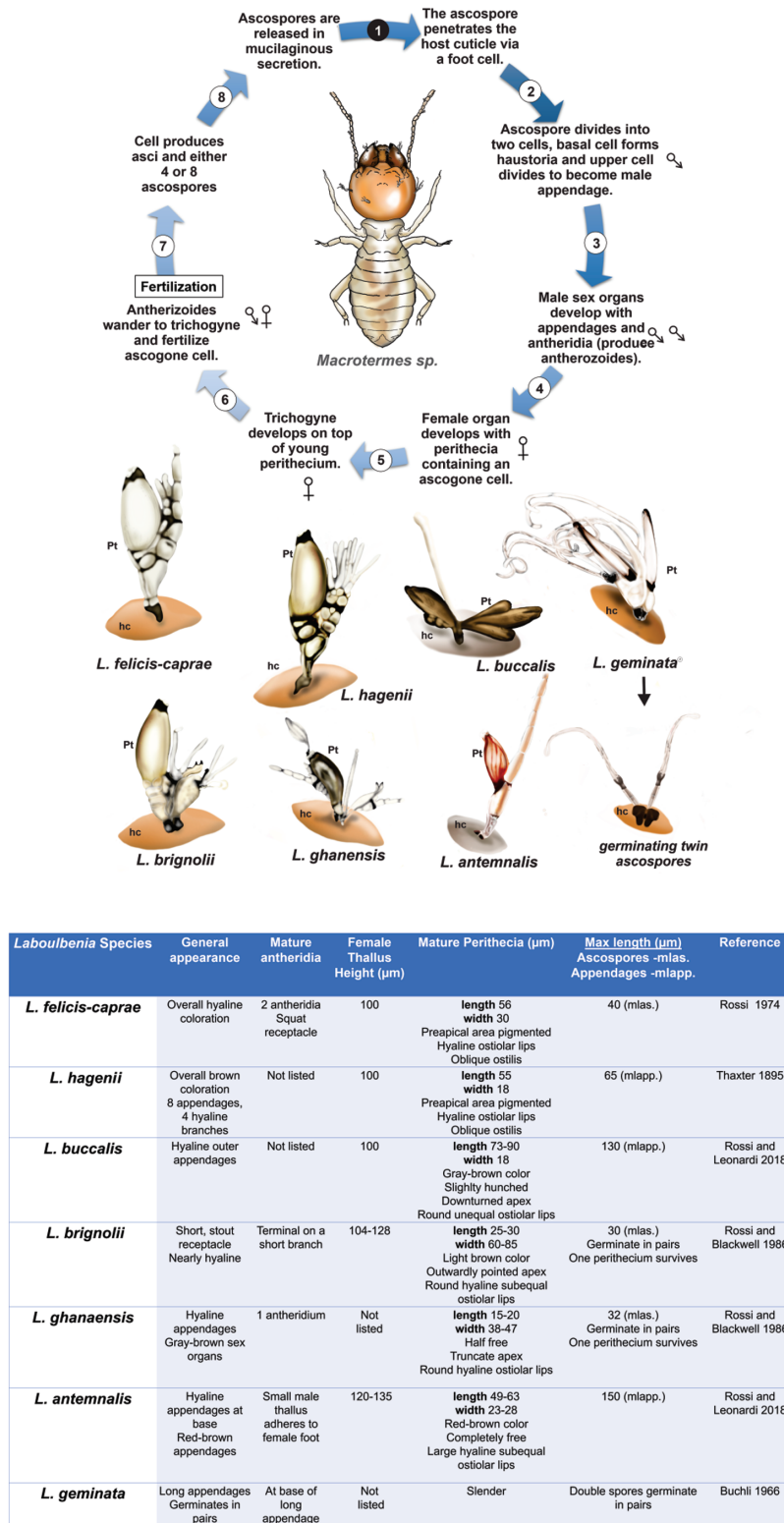


Fig. 9. General life cycle of *Laboulbenia*. Diagnostic morphology and development of *Laboulbenia* as it is described in references. References for color illustrations included in figure- line drawing from *L. hagenii* (Buchli 1966), line drawing from *L. geminata* (Buchli 1966), micrographs for *L. buccalis* and *L. antennalis* (Rossi and Leonardi 2018), *L. felcis-caprae* (Rossi 1974), *L. brignolii* (Rossi and Blackwell 1986), *L. ghanensis* (Rossi and Blackwell 1986).

the perithecium tapers towards the tip with a flat apex, large hyaline subequal lips and a blackened inner side. The male thallus comprises a linear series of cells which in its early stages acts as a phialide (comparable to *Termitaria*), which elongates and breaks. The only comparable species to the *L. antennalis*

in the genus is *L. endogea* (Picard, Laboulbeniomycetidae: Laboulbeniales) Picard which infests Scartinae beetles (Rossi and Santamria 2008, Rossi and Leonardi 2018) and exhibits a female thallus bearing an undivided stalk-cell of the appendage (Rossi and Leonardi 2018).

General Life Cycle

Ascospores surrounded in a sticky mucus are released and attach to the host cuticle where they divide into two cells (Fig. 9). The pointed dark basal cell forms the haustoria which is responsible for absorption of nutrients from the insect body while the upper cell swells and divides successively to become the primary, secondary and tertiary male appendages with antheridia on top; the size and number of appendages is species dependent (Buchli 1966). The female perithecium forms via lateral cell division, a trichogyne forms at the apex, and a peripheral cell envelops the central ascogonic cell (Buchli 1966). Following ascogonic cell fertilization, the trichogyne disappears, the ascogone divides, and the perithecium becomes dark and sacciform. The fungus attaches to the host cuticle at various places via a foot cell and the cells comprising the parasites body give rise to male sexual appendages carrying antheridia, which produce many antherozoids that exit via an apical orifice. The antherozoids move through the trichogyne of the female organ (perithecium) to the ascogone cell, where sexual fertilization occurs. Following ascogone formation, either four or eight ascospores are produced and develop for the extent of the parasites' lifetime.

Ophiocordyceps

Background

This genus *Ophiocordyceps* was first erected in 1931 (Petch) to describe a new fungus ectoparasitic on beetles, ants, and cockroaches that produces clavate asci and long multiseptate whole spores (Tasanathai et al. 2019). *Ophiocordyceps* is a unique organism, well-known for its zombifying behavioral effects on ants (Andersen and Hughes 2012; de Bekker et al. 2014; Mongkolsamrit et al. 2012). Although behavioral manipulation has not been observed in infested termites, it does appear to hijack a preexisting behavior in this group: the excavation of a nuptial chamber during colony foundation. Of the >235 ectoparasitic species (Spatafora et al. 2015, Khonsanit et al. 2018, Luangsaard et al. 2005), >10 have been documented to infect termites. They include *Ophiocordyceps bispora* (Stiffler, Hypocreales: Ophiocordycipitaceae), *O. konigsbergeri* (Penz & Sacc., Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps termitophila* (Kobayasi & Shimizu, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps octospora* (Blackwell and Gilbertson, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps asiatica* (Tasanathai, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps brunneirubra* (Tasanathai, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps khokpasiensis* (Tasanathai, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps mosingoensis* (Tasanathai, Hypocreales: Ophiocordycipitaceae), *Ophiocordyceps pseudocommunis* (Tasanathai, Hypocreales: Ophiocordycipitaceae) *Ophiocordyceps pseudorbizoidea* (Tasanathai, Hypocreales: Ophiocordycipitaceae) and *Ophiocordyceps termiticola* (Tasanathai, Hypocreales: Ophiocordycipitaceae) (Tasanathai et al. 2019). This genus targets subterranean termites (Termitidae; *Macrotermes*) and can be found in Africa, North America, and most frequently Asia (Kobayasi 1941; Stiffler et al. 1941; Kobayasi and Shimizu 1978; Blackwell and Gilbertson 1981, 1984; Suh et al. 1998; Sung et al. 2007; Tasanathai et al. 2019).

Fungal Distribution on the Host Body

Ophiocordyceps has been reported on multiple castes, but is most often documented on winged reproductives (Table 3). Tasanathai et al. (2019) provide detailed images and descriptions of seven new species parasitizing founder king and queen reproductives (Macrotermitinae subfamily). The stroma was observed to extend above the soil (Fig. 10a). With the exception of *O. brunneirubra*, which germinates from between the prothorax and head, *O. asiatica*, *O. khokpasiensis*,

O. mosingoensis, *O. pseudocommunis*, *O. pseudorbizoidea*, and *O. termiticola* were found between the prothorax and mesothorax of founding reproductives (Tasanathai et al. 2019). *Ophiocordyceps bispora* has been reported on the host thorax (Conlon et al. 2017), leg (Blackwell and Gilbertson 1981), and abdomen (Suh et al. 1998) of reproductives (alates) and workers (Ochiel et al. 1996, Suh et al. 1998, Conlon et al. 2017). *O. termitophila* was found on the abdomen and thorax of founding termites in Japan (Kobayasi and Shimizu 1978), and *O. octospora* has been discovered on the leg of unspecified castes of *Tenuirostritermes tenurotermes* (Desneux, Blattodea: Rhinotermitidae) (Blackwell and Gilbertson 1981).

Impact on Host

The number of *Ophiocordyceps* is most significant when only a few individuals survive to start a new colony, and infection quickly follows ascospore contamination (Tasanathai et al. 2019). *Ophiocordyceps* are minor pathogens of termites during unfavorable parasite conditions (Ochiel et al. 1997), but mortality has been reported to be high when conditions are favorable, such as during short rainy periods (Blackwell and Gilbertson 1984). Ochiel (1997) observed 20 termites gathered under a rock that had died *en mass* and Blackwell and Gilbertson (1984) observed high mortality of termites introduced to soil contaminated with *O. bispora*. *Ophiocordyceps* species are presumed to kill its host when hyphae enter the cuticle, mycelium fills the interior, and/or stroma emerges host and into the soil (Tasanathai et al. 2019). This was observed for *O. octospora* where mycelium completely filled the interior of the termite so that only the resistant cuticle remained. Hyphae emerged through breaks in the cuticle and in some cases through pores in the cuticle and outer cuticle damage was also observed (Blackwell and Gilbertson 1981).

Incidence of Infestation per Individual and Colony

The infestation incidence of *Ophiocordyceps* on individual termites is typically very low, perhaps due to its lethality under optimal conditions. In colonies of *O. bispora* and *O. octospora*, infected individuals typically carry one to seven stroma per individual ($n = 20$, $n = 19$ respectively; Blackwell and Gilbertson 1981). Tasanathai et al. (2019) did not note the number of stroma per individual; however, they did note that two individuals were infected in the process of colony foundation. *O. communis* typically infests 2, rarely 3 adult termites that become surrounded by mycelium. *O. asiatica*, *O. brunneirubra*, *O. khokpasiensis*, *O. mosingoensis*, *O. pseudocommunis*, *O. pseudorbizoidea*, and *O. termiticola* were documented infesting 1–2 members of a founding termite pair (Tasanathai et al. 2019).

Transmission

For *Ophiocordyceps* associated with termites in Thailand, it was reported that infection came on fast via ascospore infectiousness that seems to target subterranean termites (Tasanathai et al. 2019). Experiments under laboratory conditions used to test pathogenicity of *O. bispora* have given variable results; conidia from in vitro cultures and sprayed directly onto termites had little effect, but when termites interacted with soil contaminated with ascospores and fungal fragments, they were infected in high levels (Ochiel et al. 1997). Until the infection unit and mode for ascospore germination has been determined, this fungus cannot be used as a microbiological control agent.

Identification

Ophiocordyceps exhibits both a sexual (teleomorph) and an asexual form (anamorph) (Fig. 10 a,b). The sexual form consists of perithecia

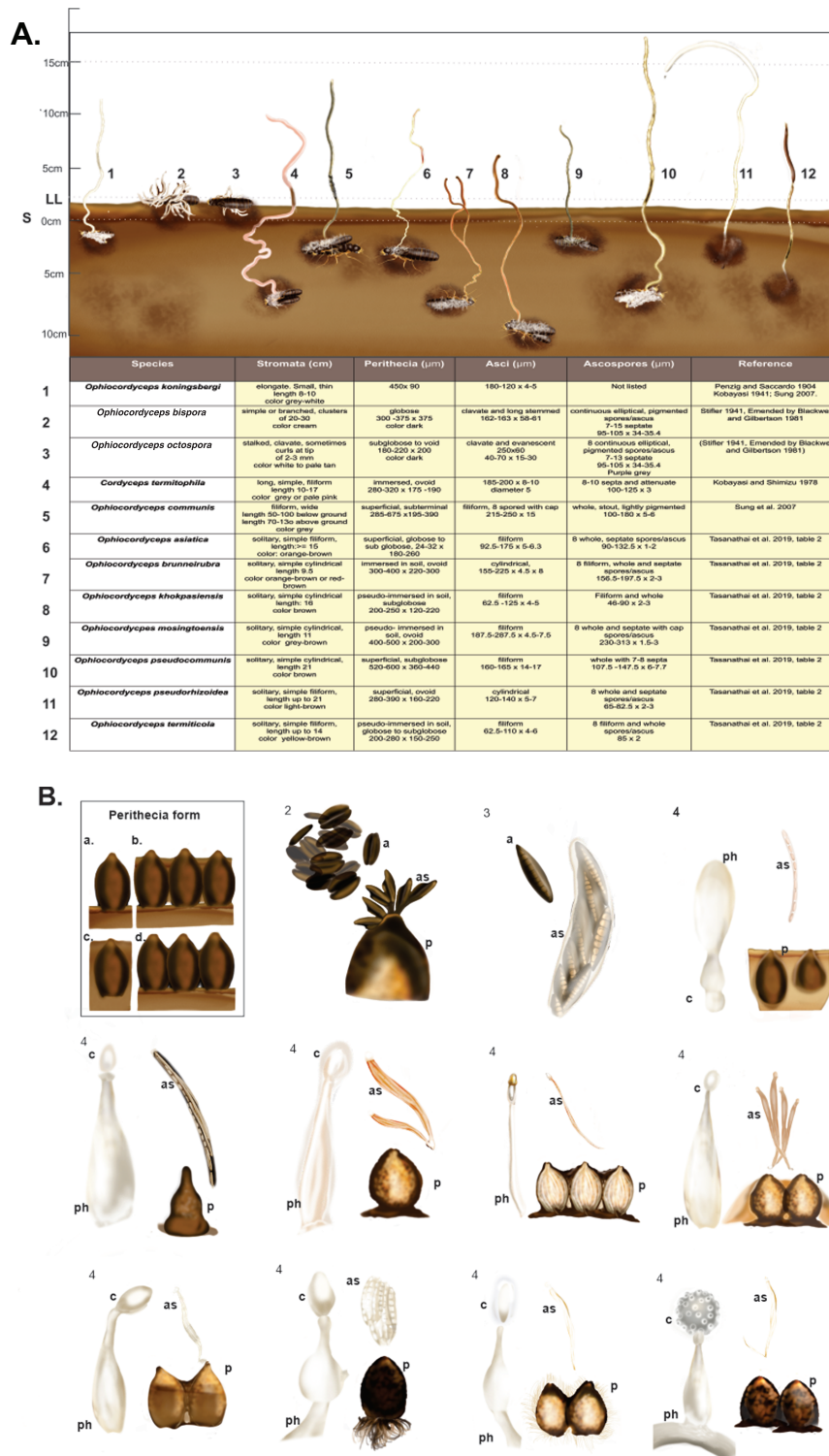


Fig. 10. General Life Cycle of *Ophiocordyceps*. (A) Diagnostic morphology and environmental presentation of host as it is described in references included in table. Stromata extend above the soil horizon as described in literature and mummified subterranean termites remain buried. Visual references for micrographs used to create illustrations are provided in diagnostic table. (B) The perithecial form/disposition illustration on the upper left corner of diagnostic figure boxes is modified from Kobayasu 1941. a = ordinal superficial, b = pseudo-immersed perithecia, c = compact perithecia, d = ordinal immersed perithecia. Numbers 2–12 correspond with taxa listed on chart. A = ascospore, p = perithecia, as = ascus, ph = phialide, c = conidia.

that produce multiseptate ascospores within their asci while the asexual form (anamorph) consists of specialized phialides that produce asexual conidiospores. In Fig. 9, we provide diagnostic illustrations and a comprehensive table incorporating all major diagnostic features to demonstrate key morphological variation exhibited

across these fungi (Blackwell and Gilbertson 1981, Kobayasi 1941, Stifler 1941, Kobayasi and Shimizu 1978, Sung 2007, Tasanathai et al. 2019). *Ophiocordyceps* species from Asia typically exhibit long fibrous stromata that extend above the soil and house perithecia (Kobayasi 1941; Kobmoo et al. 2012, 2015; Luangsaard et al.

2005; Tسانathai et al. 2019). *O. asiatica* is readily distinguished by its dark brown stroma and a small superficially grown perithecium while *O. brunneirubra* exhibits a reddish-brown stroma and a hyaline anamorph exhibiting golden capped conidia (Tسانathai et al. 2019). *O. khokpasiensis* barely emerges from the soil and produces pseudo-immersed perithecia and *O. mosingoensis* produces a more robust stroma compared to *O. khokpasiensis* and *O. termiticola* (Tسانathai et al. 2019). As the names suggest, *O. pseudocommunis* bears similarity to *O. communis*, and *O. pseudorbizoidea* appears similar to *O. rbizoidea* (a fungus found on beetles; Tسانathai et al. 2019). *O. rbizoidea*, a fungi found on beetles has longer and wider asci and ascospores than those of *O. pseudorbizoidea*, while in *O. communis* (Sung et al. 2007) and *O. pseudocommunis*, the ascospores are longer (Tسانathai et al. 2019). *O. bispora* and *O. octospora* vary considerably in appearance from the species from Asia listed above. Stromata of *O. bispora*, discovered in 1941 in Africa (Stifler) occur in clusters of 20–30 instead of a single or branched strand. As the name suggests each ascus bears two ascospores, which differs from a *O. octospora* (Blackwell and Gilbertson 1981), which is distinguished by its smaller spore size, lighter colored spores, and the production of eight spores within an ascus.

Termitariales

Termitaria and Mattirolella

Background

The genus *Termitaria* was erected in 1920 to describe two new species of asexual ascomycote fungi (Thaxter 1920), growing exclusively on the exoskeleton of termites. In 1982, Kimbrough and Lenz described three new species of *Termitaria* on the cuticle of Australian termites and designed a key to all known *Termitaria* species. Members of this genus are perhaps the most conspicuous of the ectoparasitic termite fungi and present as various lesions that include the following forms: disciform (circular), ellipsoid, elongate, rhomboid, star-shaped, and beaked (Fig. 11). Internally, these lesions are very rigidly organized into layers. The basal pseudo-cellular layer is composed of parallel sporogenous elements vertically arising to form an even hymenial surface separated into an endogenous upper layer filled with hyaline spores, which are discharged through a terminal perforation (Thaxter 1920). The fungal lesions are referred to as a ‘sporocarp’ or ‘sporodochium’. They consist of tight or loose columns of phialides with conidia produced endogenously in basipetal succession into collarettes at a spore-producing region known as the conidiogenous (spore-producing) locus (Khan and Aldrich 1973, Khan and Kimbrough 1974b). A similar genus, *Mattirolella* was discovered by Colla 1929 and contains two species; *Mattirolella crustosa* (Khan and Kimbrough, Termitariales: Kathistaceae) and *Mattirolella silvestri* (Colla, Termitariales: Kathistaceae) (Colla 1929, Khan and Kimbrough 1974a, Kimbrough and Thorne 1982). They are distinct in their arrangement of sterile hypha, and an epihymenium forming often a pycnidium and ostiole.

Due to highly similar morphology, sporodochia and haustorial development, and the presence of Phialoconidia, two genera, *Termitaria* and *Mattirolella* were placed into a new form-order known as the Termitariales (Khan and Kimbrough 1974a, Kimbrough and Lenz 1982). Since 1920, ten species of fungi from Termitariales have been documented infesting termite exoskeletons, eight of which have been formally described: *M. silvestri*, *M. crustosa*, *Termitaria snyderi* (Thaxter, Termitariales: Kathistaceae), *Termitaria coronata* (Thaxter, Termitariales: Kathistaceae), *T. thaxteri*, *Termitaria longiphialidis* (Kimbrough and Lenz, Termitariales:

Kathistaceae), *Termitaria macrospora* (Kimbrough and Lenz, Termitariales: Kathistaceae), and *Termitaria rhombicarpa* (Kimbrough and Lenz Termitariales: Kathistaceae) (Kimbrough and Lenz 1982). Two species currently remain ambiguous in their designation, due to a lack of synapomorphies provided by their authors. Reichenasperger (1923) proposed the name *T. thaxteri* for a species found on three isolates of Brazilian termites and Pickens (1952) mentions another species, *T. pacedensis*, but insufficient details make it difficult to evaluate the species.

Fungal Distribution on the Host Body

Termitaria sporodochia develop on various regions of their host, including regions of the legs, antennae, and abdominal cuticle, with no immediately obvious pattern to the infestation (Table 3). The most commonly reported species, *T. snyderi*, has been described on all body parts of soldier and worker termites (Buchli 1966), and is ellipsoid to circular in shape (Thaxter 1920, Khan and Aldrich 1974, Khan and Kimbrough 1974b, Kimbrough and Lenz 1982). It is most observed on the abdomen, thorax, head and legs of its host, but is also documented to encircle entire antenna in its younger stages (Thaxter 1920, Reichenasperger 1923, Feytaud and Dieuzeide 1927, Tate 1927, Khan and Kimbrough 1974a, Blackwell et al. 2003). *Termitaria coronata* has been reported to form dark echinulate sporodochia on soldier and worker termites of *Nasutitermes costalis* (Holmgren, Blattodea: Termitidae), *Nasutitermes guayanae* (Holmgren, Blattodea: Termitidae), *Nasutitermes luzonicus* (Oshima, Blattodea: Termitidae), *Nasutitermes exitosus* (Hill, Blattodea: Termitidae), *Nasutitermes surinamensis* (Holmgren, Blattodea: Termitidae), and *Nasutitermes longipennis* (Hill, Blattodea: Termitidae) (Thaxter 1920, Tate 1927, Colla 1929, Kimbrough and Lenz 1982, Ensaf et al. 2006). It has been reported on the tibia, abdomen, thorax, head and legs of its host (Thaxter 1920, Kimbrough and Lenz 1982). In *N. longipennis* colonies with high ratios of workers to soldiers, soldiers were still the most highly infested caste. Of the Australian species, *T. macrospora* was found on the thorax or abdomen of older worker hosts (*Mastotermes darwiniensis* (Froggatt, Blattodea: Mastotermitidae)) and is ellipsoid or circular in shape. *T. rhombicarpa* is circular or rhomboid in shape and has been found on the thorax, abdomen, and leg segments of larger workers and nymphal stages of its host (*Porotermes adamsoni* (Froggatt, Blattodea: Stolotermitidae)) and is distributed as follows; dorsal abdomen (16–21.3%), antennae (14.7–37.7%), and legs (19.7%–22.0%) (Kimbrough and Lenz 1982, Lenz and Kimbrough 1982). Over a 1-yr period, Lenz and Kimbrough (1982) observed 2,800 individuals and determined that *T. longiphialidis* infested termite castes in the following percentages; 80% workers, 64% soldiers, and 68% nymphs (Kimbrough and Lenz 1982). Workers and nymphs showed circular lesions on all regions of the body whereas soldiers were only infested on antennae and legs; fungal lesions were distributed as follows; dorsal abdomen (16–21.3%), antennae (14.7–37.7%), and legs (19.7–22.0%) (Lenz and Kimbrough 1982). *M. crustosa* was distributed on *N. ephratae* and *N. corniger*; on *N. corniger* it was distributed on soldiers and workers in the following distribution; lower abdomen (65%), legs (20%), and upper abdomen (15%) (Kimbrough and Thorne 1982). Soldiers are the most highly infested caste, despite making up only 17% of the termite colonies observed (Thorne and Kimbrough 1982). *M. silvestri* infests all castes of host species, the abdomen, thorax, head, antenna, and maxillary palpi (Colla 1929, Barbosa 2015).

Transmission

Following observations of conidia in the gut contents of termite hosts, it was suggested that *Termitaria* infestation was initiated upon ingestion of spores (Ensaf et al. 2006); however, it is likely their

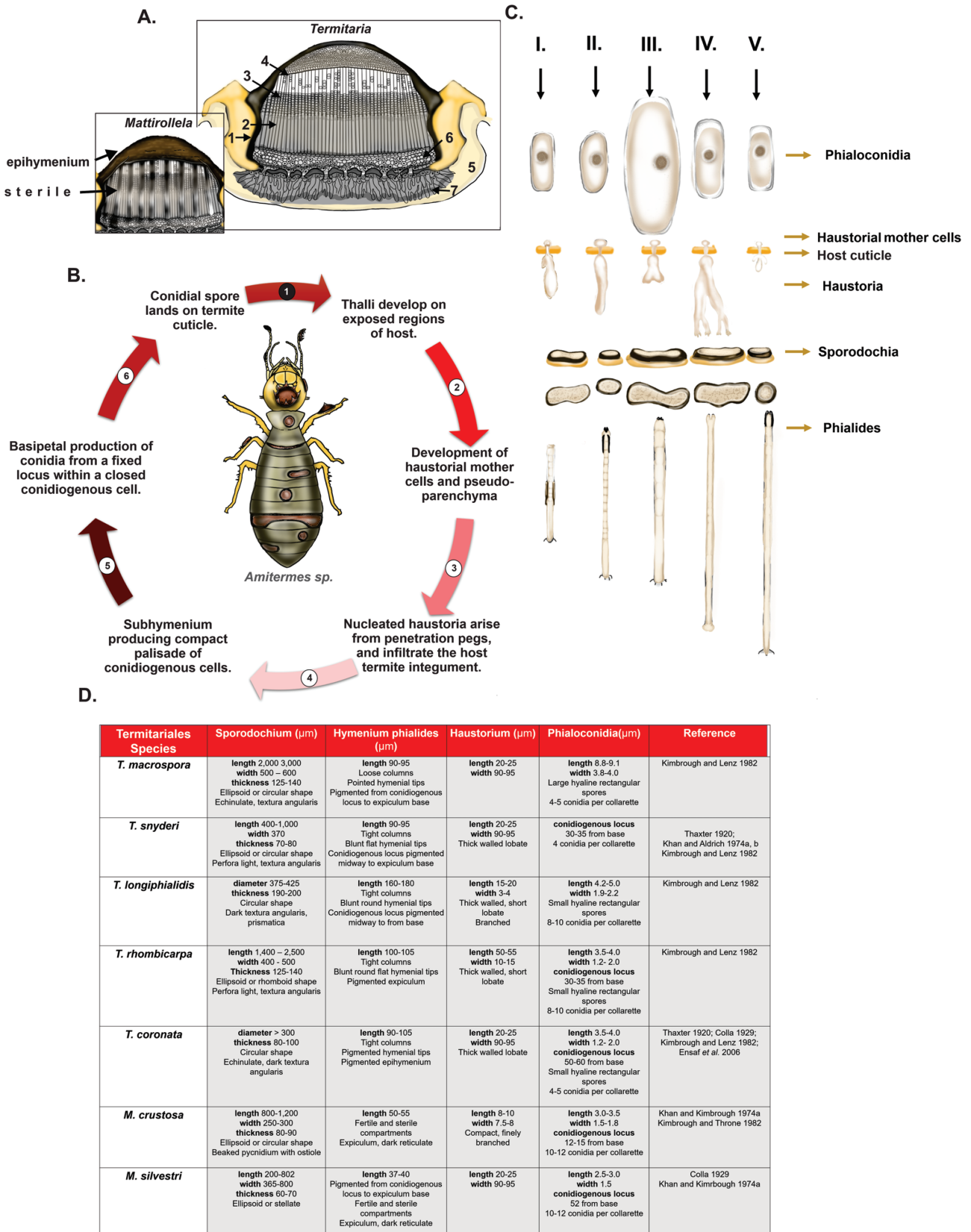


Fig. 11. General life cycle of *Termitaria* and *Mattirolella*. (A) General Morphology of *Termitaria*. 1-epiculum, 2-phialides, 3-collarete, 4-conidia, 5-insect cuticle, 6-haustorial mother cells, 7-haustoria. *Mattirolella* differs in phialide structure; alternating sterile phialides. (B) General life cycle of *Termitaria snyderi*, very similar to all species within genus *Termitaria* and *Mattirolella* (Khan and Aldrich 1975; Khan and Kimbrough 1974a). (C) Comparative morphology of 5 *Termitaria* species, redrawn from Lenz and Kimbrough 1982. I-*T. snyderi*, II-*T. coronata*, III-*T. macrospora*, IV-*T. rhombicarpa*, V-*T. longiphialidis*.

findings coincide with previous explanations. Maekawa et al. (2005) discovered asexual conidia in the gut of non-infested *Reticulitermes* workers and considered this to be evidence that they may remove *Termitaria* from their body surfaces via social grooming interactions. They suggest another possible mechanism for infestation; spores enter through hosts through wounds or places where the cuticle is thinnest or trachea openings (Ensaf et al. 2006). The mode of transmission for these fungi cannot be clarified without laboratory cultivation and observation. Termite molting and colony activities may reduce the rates of reinfestation, fungal maturation, and spore dissemination between *Termitariales* fungi and host (Thorne and Kimbrough 1982). An intriguing theory for transmission of *M. crustosa* was proposed by Kimbrough and Thorne (1982). They raise questions regarding the striking similarity in resemblance of the pointed *Mattirolella* sporodochia and the pointed heads of the nasute termite soldiers they infest. It is proposed that termites interact with the sporodochia, mistaking them for nestmates, thereby enhancing spore dissemination (Kimbrough and Thorne 1982).

Incidence of Infestation per Individual and Colony

Low infestation incidences were observed for both genera; termites infested with *Termitaria* typically exhibit 1 lesion and termites infested with *Mattirolella* typically exhibit 5 lesions (Barbosa 2015). In the host species, *T. snyderi*, approximately 10% of each colony was infested (Thaxter 1920, Reichensperger 1923, Feytaud and Dieuzaide 1927, Tate 1927, Buchli 1966, Khan and Kimbrough 1974a, Blackwell 1980, Blackwell et al. 2003). Termites infested with *T. coronata* tolerate infestation with little harm if the proportion of thalli on their body remains below 20% (Ensaf et al. 2006) and the incidence of infestation within a colony is typically between 0.95 and 4.6% (Ensaf et al. 2006). Lenz and Kimbrough (1982) report the following colony infestation rates for *Termitaria* species discovered in Australia; *T. macrospora* (0–10%), *T. rhombicarpa* (0.05–7.1%), *T. longiphialidis* (5.8–6.6%). *T. rhombicarpa* infestation was observed at higher percentages for soldiers and larger workers, likely because young termites are groomed more frequently; therefore, fungal sporodochia are more frequently removed (Lenz and Kimbrough 1982). *T. longiphialidis* infestation was observed in the following caste percentages; workers (80%), soldiers (64%), and nymphs (68%) (Lenz and Kimbrough 1982).

M. crustosa incidence was reported at a rate of 2–4.4%, and individual termites with 2–3 sporodochia (Colla 1929, Kimbrough and Thorne 1982, Thorne and Kimbrough 1982). *M. silvestri* was found to infest colonies at a rate of 19.47% in a single colony and individual termites with 1–5 sporodochia (Barbosa 2015). *M. crustosa* infests soldiers at considerably high rates, often between 85 and 95% of all infested individuals (Thorne and Kimbrough 1982). *M. silvestrii* also infest soldiers at high rates (47.36%) (Barbosa 2015).

Impact on Host

Despite the presence of hyper-trophoid cells existing below the exoskeleton, these genera are not believed to kill their host directly (Thaxter 1920, Kimbrough and Lenz 1982); however, they have been found to negatively affect survivorship in older individuals and swelling has been observed in surrounding tissues. The sporodochia do not seem to disturb the host; however, infested sites range from hypertrophied to slight malformation and can reduce agility dependent upon location. (Thaxter 1920, Reichensperger 1923, Feytaud 1927, Tate 1927, Buchli 1966, Khan and Kimbrough 1974b, Blackwell 1980, Blackwell et al. 2003). *Termitaria* tends to indirectly cause reduced survivorship to termites (Colla 1929, Khan and Kimbrough 1974b, Lenz and Kimbrough 1982). For instance,

T. macrospora infestation resulted in decreased vigor, molting success, and agility of its hosts (McMahan and Watson 1977, Kimbrough and Lenz 1982, Lenz and Kimbrough 1982). *T. rhombicarpa* infestation resulted in malformation of body parts are lower wood consumption rates, thus decreasing survival of affected individuals (Lenz and Kimbrough 1982).

Much like *Termitaria* fungi, *Mattirolella* haustoria penetrate and hypertrophy the epidermal cells of its hosts (Colla 1929, Khan and Kimbrough 1974a). Sporodochia on large body regions, such as the head, abdomen, and thorax inflict little morphological effect on the host, however legs and antennae exhibit considerable malformation. (Reichensperger 1923, Colla 1929, Khan and Kimbrough 1974b). Infested termites died more rapidly than non-infested individuals and a link between molting and survivorship has been considered (Thorne and Kimbrough 1982). Additionally, size variation has been observed; colony members infested with *M. silvestri* are smaller than noninfested members (Barbosa 2015).

Identification

Termitariales fungi are identified by spore number, size, and shape, conidiogenesis zone location, haustorial morphology, dimensions of the thallus, and pigmentation (Thaxter 1920, Reichensperger 1923, Feytaud 1927, Kimbrough and Lenz 1982). *T. rhombicarpa* can be distinguished by the rhomboid shaped sporodochium it forms on the host as opposed to the elliptical/circular lesions typically formed by other *Termitaria*. As its name suggests *T. macrospora* produces 4–5 massive spores per collarette (dimensions: 3.8 × 9.1 μm). Another Australian species, *T. longiphialidis*, is best identified by having the longest phialides of any *Termitaria* species (length: 160–180 vs 110–115 μm). *T. coronata* can be distinguished from all *Termitaria* species, in the appearance of its sporodochium, with its echinulate surface and the high position of its conidiogenous locus (diameter: 50–60 vs 20–25 μm). *Mattirolella* species form an epihymenium over the phialidial hymenium, which alternates between sterile and fertile columns, making it clearly distinct from all *Termitaria* species.

General Life Cycle

Termitaria has only been observed to have an asexual life cycle (Fig. 11). Asexual conidia germinate and form a thallus on the surface of the termite exoskeleton on an exposed body part, including the head, legs, antennae and abdomen thallus consists of a basal layer of cells, some or all of which may be haustorial mothercells (Khan and Aldrich 1975). Each of the dark, thick-walled haustorial mother cells of the pseudoparenchymatous crust possesses a pale circular area at the base, actually an opening in the cell wall through which penetration pegs exit the cell to enter the host exoskeleton. From the penetration points pegs the walled, nucleated haustoria penetrate through the exoskeleton to the basement membrane of the termite integument (Khan and Aldrich 1975). They send haustoria, root-like protrusions that infiltrate structures to absorb water or nutrients, into the host cuticle but are considered ectoparasites because they do not enter the abdominal cavity (Thaxter 1920, Kimbrough and Lenz 1982). Another notable feature of *Termitaria* infestation is the presence of a dark, lichenoid well-defined rim (expiculum) along the periphery of each lesion. Throughout each mature lesion are hundreds of asexual spores referred to as ‘conidia’ although they are absent from the expiculum. Above the basal layer, the cells of the sub-hymenium give rise to a compact palisade of conidiogenous cells that are enclosed by a border of dark-walled cells forming a sporodochium (Khan and Kimbrough 1974a). Khan and Aldrich (1973) reported basipetal production of conidia from a fixed locus

within a closed conidiogenous cell; conidium release occurred upon synchronous rupture of the conidiogenous cell apices.

Discussion

Modern Molecular Advances

Recent advances in our current understanding of the relationships between fungus and host are owed to new molecular insights. Prior to 1998, no sequences had been produced for any ectoparasitic termite fungi. There is only a small number of fungal species parasitizing termites, and for just one-third ($n = 12$) of species are molecular sequences published. Thus far, the following taxa have been sequenced for the ribosomal gene 18S: *A. gallica*, *L. termitarius*, and *T. snyderi* (Hojo et al. 2002, Blackwell et al. 2003, Guswenrivo et al. 2017). With these data, the inferred phylogeny confirmed relationships suggested by morphology. Evidence of genetic structure across geographic ranges was suggested for these taxa. Guswenrivo et al. (2018; using a nested PCR to sequence 18S), developed a fast efficient protocol to detect fungal infestation on *R. speratus* infested with *L. termitarius* and *A. gallica*. Briefly, the protocol involves sequencing present fungal species in small titers to get a better understanding of their dynamics in host populations. Blackwell et al. (2003) found a 34-bp insertion or deletion of bases (indel) when comparing their sequences to those of Guswenrivo et al. (2018), likely due to the fact that samples were from a different collection site (i.e., geographic range variations likely exist as samples were from Kyoto, Japan and Louisiana, United States). Attempts to extract and amplify DNA from *C. oedipus* were unsuccessful (Blackwell et al. 2003) perhaps due to its scarcity; as is the case for most other ectoparasitic fungi on termite, it has yet to be successfully cultured under lab conditions and more samples are required from the field for successful amplification (Guswenrivo et al. 2018). Hojo et al. (2001) sequenced three types of unclassified *Termitaria* (Black-type, White-type and Intermediate-type) and inferred a genus host phylogeny suggesting parallel cladogenesis between termite and host; aside from an instance where Black-type may have shifted between *Hodotermopsis japonica* (Holmgren, Blattodea: Termopsidae) and *R. speratus* hosts (Hojo et al. 2001). Henk et al. (2003) further inferred phylogenetic relationships (parsimony and maximum likelihood methods) between *Termitaria* and other morphologically distinct Ascomycetes (*Kathistes* sp.) based on the ssuRNA gene and B-tubulin gene. This emphasizes the importance of including DNA sequences from a variety of Ascomycetes when comparing entomophagous fungi. The majority of molecular evidence to date from ectoparasitic termite fungi comes from the genus *Ophiocordyceps*. In 2017, Conlon et al. sequenced the first draft genome of a termite fungal pathogen. Their work on *O. bispora*, a parasite found on fungus-farming termites (Macrotermitinae), provides important comparative phylogenetic information and confirms a teleomorph-anamorph relationship between *O. bispora*'s *Hirsutella thompsonii*. In 1998, Su et al. provided ribosomal DNA evidence (28S and 18S) to validate that the genus *Cordycepioideus* belongs in the group Clavicipitaceae and is not within the Hypocrealean group where it had been placed originally. The most comprehensive sampling to date was carried out in 2019; 7 out of 12 *Ophiocordyceps* spp. currently known to be associated with termites were described and sequenced (Tasanathai et al. 2019). They obtained 96 new sequences (18S, ITS1, 5.8S, ITS2, 28S, TEF, and RPB2) from 20 specimens, providing complete records of 7 new *Ophiocordyceps* species from Thailand alone. All GenBank accession numbers and sequenced genes are included in Table 1. The small size of ectoparasitic termite fungi has caused difficulty in DNA extraction and amplification (Weir and Blackwell 2001) thus future works where multiple fungal samples are pooled may improve successful amplification.

Future Directions

Nearly 35 yr ago, Blackwell and Rossi (1986) extensively analyzed the biogeographical patterns of termite ectoparasites exhibited across these unique associations. Since this time, collection efforts for the fungi (and the termite) have been limited or nonexistent (*Hormiscioideus*, *Dimeromyces*, and *Coreomycetopsis*). This leaves us still with many questions that can only be answered with increased taxon sampling, molecular sequencing, and biological studies. For example, how can we determine if ectoparasitic termite fungi are truly restricted by their host or geographic range, or if they are instead restricted by our current knowledge? Additionally, molecular evidence provided for *Ophiocordyceps* on termites has shed light on how prevalent cryptic speciation and species complexes are within these groups, thus making molecular work vital to move the field forward (Tasanathai et al. 2019). Although these mysterious mycological agents are even smaller than the insects that they live amongst, revealing the extent of the relationships between fungus and termite host is a unique opportunity to learn more about the biology of both groups.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

Supplemental table 1. Detailed locality information used to build map included in supplemental table 1. Most localities in literature were vague and did not include specific gps coordinates. Nearest cities, national parks, and central point coordinates of available locality records were used in these cases.

Supplemental table 2. Glossary for mycological terminology used throughout this manuscript.

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