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Review Article

Ecto- and Endoparasitic Fungi on Ants from the Holarctic Region

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The ant-specific fungi *Aegeritella, Laboulbenia, Rickia, Hormiscium,* and *Myrmicinosporidium* in the Holarctic region—nine species—are reviewed. Present knowledge is highly biased geographically, as shows the single record for Holarctic Asia, and this is to solve. The phylogenetic position of *Aegeritella, Hormiscium*, and *Myrmicinosporidium* is unknown. Hosts seem to be also skewed phylogenetically although this may be a true pattern.

1. Introduction

Extensive, massive mycoses are an extremely rare instance in ants [1] and involve individuals, rather than whole colonies. A fortiori, documented population level attacks are practically nonexistent. A case concerning *Tetramorium caespitum* [2, 3] seems to be an isolate within ant literature. Here we deal with ecto- and endoparasitic fungi, and we limit our survey to those that are ant specific. We differentiate parasitic fungi, that are not deadly to ants, and pathogenic fungi, which kill the host. Thus, generalist entomopathogenic fungi like *Beauveria* and *Metarhizium* or ant specifics like *Pandora myrmecophaga* (Figure 1) or *Telohannia solenopsae* are not included. Recent revisions of entomopathogens are those from Roy et al. [4], Kleespies et al. [5], Oi and Pereira [6] and, centred in social insects, in the seminal book by Schmid-Hempel [7]. We aim to review the knowledge of taxonomic and geographic distribution and, whenever possible, natural history and/or ecology of selected groups of fungi. The Holarctic is understood as comprising the nontropical parts of Europe and Asia, Africa north of the Sahara, and North America south to the Mexican desert region.

The fungi considered in this paper show a gradient of negative effects on the host. From a seemingly near absolute absence of any measurable—or measured—effect in some cases (*Aegeritella*, *Hormiscium,* and *Laboulbenia camponoti*), to a mild effect in other Laboulbeniales (reduced immunological response in *L. formicarum*; S. Cremer pers. comm.), or a possible strong negative effect in *Myrmicinosporidium*). This effect may concern exclusively infested individual ants (*Myrmicinosporidium*) although in some cases, because of the fungus life cycle and the social nature of ants, with many physical contacts between colony members outside of the nest and in the nest galleries, this may be multiplied and traduced directly to the colony level (Laboulbeniales, or *Aegeritella*). This general absence of strong negative effects indicates probably a very old interaction with ants.

An unfortunate circumstance is the completely unknown phylogenetic position of some of those specific ant fungi, and this is calling for a dedicated, focused study, using molecular techniques. We stress the necessity of enhanced attention from the part of myrmecologists and mycologists towards this interesting group of ectoparasitic fungi. Just remembering their existence, and with a little care and open mind, many more instances of Laboulbeniales, *Aegeritella*, *Myrmicinosporidium*, and pathogenic fungi on ants should surface in ample areas within the Holarctic region.

2. Material and Methods

Apart from our current files, we did a search in the ant data base FORMIS (version 2011) [9]. Search terms are as follow: ectoparasitic, endoparasitic, fungus, fungi, Laboulbeniales, *Laboulbenia, Rickia, Aegeritella, Myrmicinosporidium*, and filtered out a posteriori by geographical region

Figure 1: *Pandora myrmecophaga* having killed a worker *Formica rufa*, from The Netherlands, showing the characteristic attachment to the distal part of a grass leave caused by the summit disease [after [8]; Photo by H. Niesen; with permission).

(Holarctic). Within each fungus species, we give the country, ant species attacked, and reference. Taxonomical scheme and terminology follow Index Fungorum [10] (http://www.indexfungorum.org/).

3. Results

3.1. Ectoparasitic Fungi on Ants

3.1.1. Aegeritella Bałazy & J. Wiśn. Anamorphic Pezizomycotina. Those fungi were first noted by Wiśniewski in 1967 [11] although its fungal nature was not proven then. The fungi grow over the cuticle like dark protuberances (= bulbils). On a first sight, they look like dirt, and its form is usually a dome, rounded in perimeter, and up to 400 μm diameter (Figure 2). The number of bulbils may be from a single one to several hundreds. The distribution of bulbils on the body of ants is heterogeneous, being more abundant at the rear part [12–14]. The total number of bulbils is inversely related to ant size, with bigger ants having less bulbils than smaller ants [14]. Bulbils have been detected in workers and queens.

The ant-fungus relationship has not been properly ascertained although a reduced life duration or activity level has been suggested [15, 16]. In a similar vein, Bałazy et al. [17] note some workers with hundreds of bulbils, having immobilized bucal palps, all covered by hyphae. Nothing is known of the dynamics of infestation or transmission mechanisms of those enigmatic fungi, not even its phylogenetic position within the realm of Fungi.

(1) *Aegeritella superficialis* Bałazy & J. Wiś. 1974.

Europe

Czech Republic: *Formica sanguinea* Latreille, *Formica rufa* L., *Formica polyctena* Förster, *Formica pratensis* Retzius, *Formica truncorum* Fabricius, *Formica lugubris* Zetterstedt, *Formica exsecta* Nylander [18, 19].

Germany: *Formica polyctena* Förster [16].

Italy: *Formica lugubris* Zetterstedt [20].

Poland: *Formica polyctena* Förster, *Formica rufa* L., *Formica pratensis* Retzius; *Formica truncorum* Fabricius, *Formica fusca* L. [21–24]; *Formica sanguinea* Latreille [25].

Rumania: *Formica rufa* group [26].

Spain: *Formica decipiens* Bondroit [12].

Switzerland: *Formica rufa* L., *Formica polyctena* Förster, *Formica lugubris* Zetterstedt, *Formica sanguinea* Latreille [15].

(2) *Aegeritella tuberculata* Bałazy & J. Wiś. 1983.

Europe

Czech Republic: *Lasius distinguendus* Emery, *Lasius nitidigaster* Seifert (as *Lasius rabaudi*), *Lasius umbratus* (Nylander) [19].

Poland: *Lasius flavus* (Fabricius), *Formica fusca* L. [27].

Spain: *Lasius umbratus* (Nylander), *Lasius distinguendus* (Emery) [28], *Lasius umbratus* ([29], as *L. distinguendus*); *Formica pressilabris* Nylander [12]; *Formica rufa* L., *Formica rufibarbis* Fabr. [14]. Canary islands: Tenerife, *Lasius grandis* Forel [13].

North America

USA, Alaska: *Lasius pallitarsis* (Provancher) ([30], as *Lasius sitkaensis*).

(3) *Aegeritella roussillonensis* Bałazy, Lenoir & J. Wiś. 1986.

France. On *Cataglyphis cursor* (Fonscolombe) [17].

(4) *Aegeritella maroccana* Bałazy, Espad. & J. Wiś. 1990.

Morocco. On *Aphaenogaster baronii* Cagniant [31].

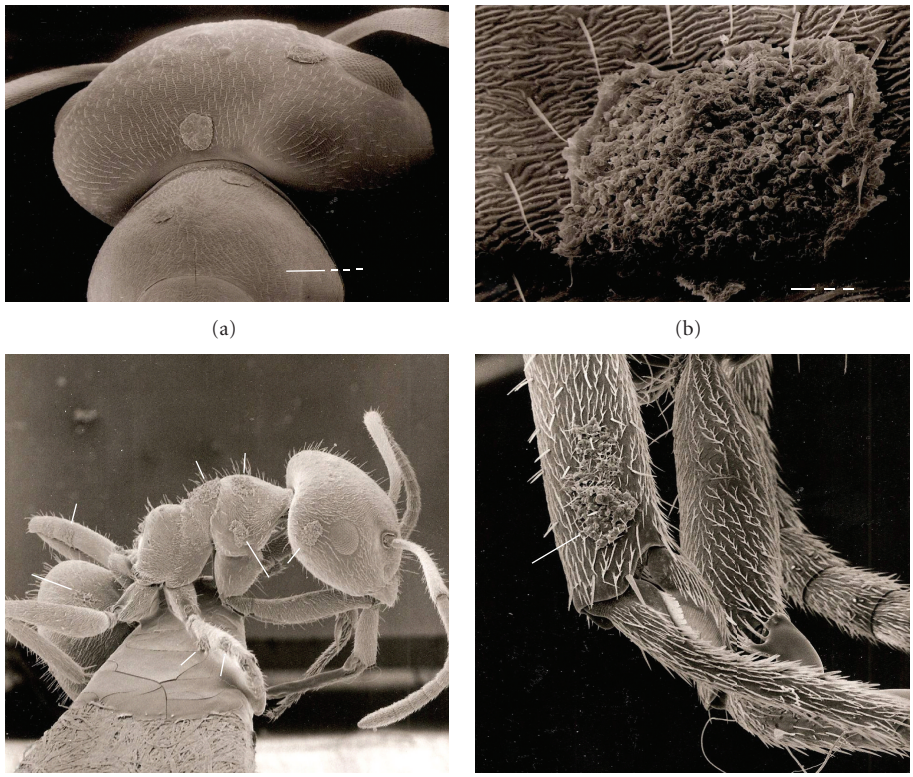
(5) An unidentified *Aegeritella* was noted on two workers

Polyergus breviceps Emery from Arizona [30].

3.1.2. Hormiscium Kunze, Incertae Sedis Pezizomycotina

(1) *Hormiscium myrmecophilum* Thaxter, 1914.

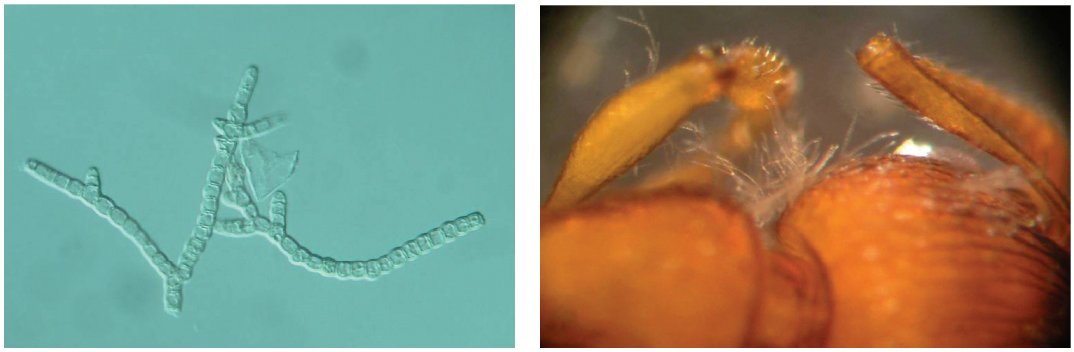
The species was described from an Amazonian *Pseudomyrmex* and remained elusive since its original description until it was found in Europe eighty years later. The filamentous, somewhat dichotomic thallus is undifferentiated and grows directly out of different parts of the ant body, without any apparent attaching structure. Mycelia have a maximum length of 163 μm and constant width of 10 μm. (Figure 3). Spores are unknown.



(a) (b)

(c) (d)

Figure 2: (a) *Aegeritella tuberculata* on *Formica pressilabris* (Spain). Two bulbils are in the pronotum, one at the back of head, (b) closeup of a bulbil; (c) *A. tuberculata* on *Lasius grandis* from Tenerife, Canary Islands; white arrows indicate bulbils; (d) closeup of bulbils in the first leg.



(a) (b)

Figure 3: *Hormiscium myrmecophilum*. (a) hyphae on *Myrmica* sp.; (b) worker *Myrmica sabuleti* with hyphae on the head and lateral pronotum.

Europe

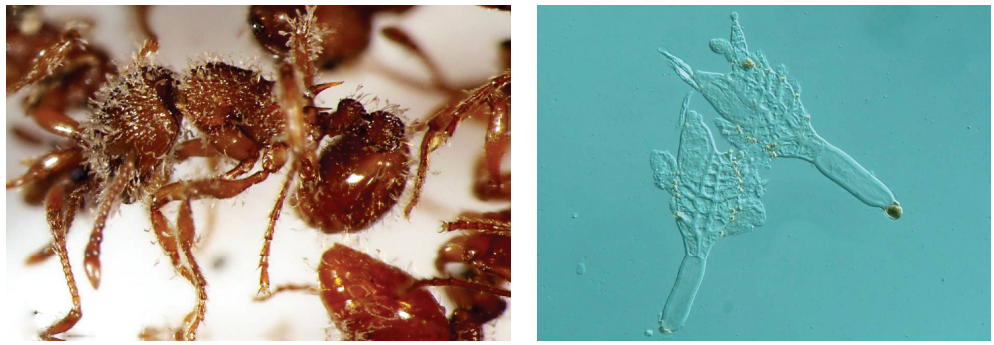
Portugal. On *Myrmica* sp. [32].

Spain. On *Myrmica sabuleti* Meinert (present paper).

3.1.3. Laboulbeniales (Ascomycota). Laboulbeniales are unusual among fungi because of their limited thallus with determinate growth. They are obligate external parasites of arthropods, especially insects. One key peculiarity is the ability to grow on their hosts without inflicting any noticeable injury. Ten orders of insects, in addition with millipedes and acari, may be affected although 80% of some 2000 species are recorded from beetles [33]. Only six are known to date infesting ants from the Holarctic region, and all castes are known to be susceptible to infestation.

(1) *Rickia wasmannii* Cavara, 1899.

The species is extremely characteristic in its microscopic morphological aspect (Figure 4) and is limited to several



(a) (b)

Figure 4: (a) *Rickia wasmannii* on *Myrmica scabrinodis* from Slovakia. Each "spatulate hair" is a thallus of *Rickia*. Photo by P. Bezděčka; with permission; (b) two mature thalli. Spores are oozing out of the perithecium on the specimen from the right.

species of *Myrmica*. Infested ants may harbour from a few thalli to several hundred thalli all over the body. Heavy infestations are visible to the naked eye and give a greyish shade, a pulverulent image to living individuals. Worker and queens may be infested.

Europe

Austria: *Myrmica rubra* (L.) [34].

Bulgaria: *Myrmica scabrinodis* Nylander [35].

Czech Republic: *Myrmica slovaca* Sadil, *Myrmica scabrinodis* Nylander [36].

France*: Myrmica scabrinodis* (Nylander) [37].

Germany: *Myrmica rubra* (L.) [38].

Hungary: *Myrmica slovaca* Sadil (as *M. salina*), *M. scabrinodis* Nylander, *M. specioides* Nylander, *M. vandeli* Bondroit [39].

Italy: *Myrmica scabrinodis* Nylander [40].

Luxembourg: *Myrmica rubra* L. [41].

Rumania: *Myrmica scabrinodis* Nylander [39].

Slovakia: *Myrmica scabrinodis* Nylander [42].

Slovenia: *Myrmica sabuleti* [41].

Spain: *Myrmica specioides* Bondroit [28, 43]; *Myrmica spinosior* Bondroit ([43], as *M. sabuleti*).

Switzerland: *Myrmica rubra* (L.) ([44], as *M. laevinodis*).

United Kingdom: *Myrmica sabuleti* Meinert [45, 46].

(2) *Rickia* sp.1.

Greece: On *Messor* (unpublished observation: description is pending).

(3) *Laboulbenia camponoti* S. W. T. Batra 1963.

Under the binocular, the thallus looks like a distorted ant hair (Figure 5) and is found all over the body, albeit more abundant in dorsal surfaces and external surface of legs. Density is much lower than in other ant-specific Laboulbeniales. In the Holarctic, it has been detected exclusively in *Camponotus* species, all six from the subgenus *Tanaemyrmex*.

Asia

Turkey: *Camponotus baldaccii* Emery [47].

Europe

Bulgaria: *Camponotus aethiops* (Latreille), *Camponotus universitatis* Forel, *Camponotus* sp. (as *C. pilicornis*) [35].

Spain: *Camponotus pilicornis* (Roger) [48]; *Camponotus sylvaticus* (Olivier) [49].

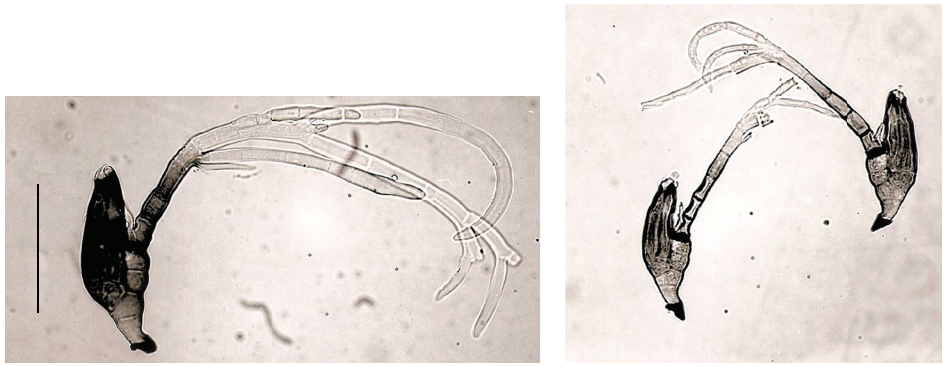
(4) *Laboulbenia formicarum* Thaxt, 1902.

This is one of the smallest Laboulbeniales (up to 0.3 mm total length). Thalli can be extremely abundant on infested workers (Figure 6), which go foraging seemingly unaffected amid noninfested workers.

North America

Canada: *Lasius alienus* (Förster) [50].

USA: *Formica argentea* Wheeler [51]; *Formica aserva* Forel ([52], as *F. subnuda*); *Formica curiosa* Creighton ([53], as *F. parcipappa*); *Formica incerta* Buren [51]; *Formica lasioides* Emery [54]; *Formica montana* Wheeler ([54], as *F. neocinerea*); *Formica neogagates* Viereck [51, 55]; *Formica pallidefulva* Latreille ([54], as *F. nitidiventris*; [56], as *F. schaufussi*); *Formica puberula* Emery [52]; *Formica subintegra* Wheler [54]; *Formica subpolita* Mayr ([52], as *F. camponoticeps*); *Formica subsericea* Say [54]; *Formica vinculans* Wheeler [54]; *Lasius alienus* (Förster) ([55, 57], as *L. americanus*); *Lasius murphyi* Forel [58]; *Lasius neoniger* Emery [51, 59]; *Lasius pallitarsis* (Provancher) ([30], as *L. sitkaensis*); *Myrmecocystus mimicus* Wheeler [60]; *Polyergus breviceps* Emery [54]; *Polyergus lucidus* Mayr [54]; *Prenolepis impairs* (Say) [54].



(a) (b)

Figure 5: *Laboulbenia camponoti* from *Camponotus sylvaticus* (Spain); line: 1 mm. (a) A mature specimen; (b) two immature specimens.

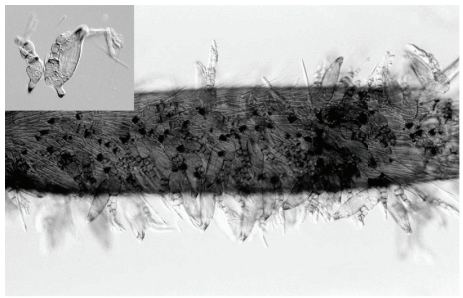


Figure 6: *Laboulbenia formicarum* on *Lasius grandis*. Worker tibia, showing full-grown thalli and dark spots which indicate attachment point of spores (more than 50 in the viewed side). Inset: one mature (right) and immature (left) specimens of *Laboulbenia formicarum*.

Europe

France: *Lasius neglectus* Van Loon, Boomsma & Andrásfalvy [61].

Portugal (Madeira): *Lasius grandis* Forel [62].

Spain: *Lasius neglectus* Van Loon, Boomsma & Andrásfalvy [63].

3.2. Endoparasitic Fungi on Ants

3.2.1. Incertae Sedis

Myrmicinosporidium durum Hölldobler 1933. Those fungi were first noted by Hölldobler [64, 65] although they were formally described later, in 1933 [66]. Its phylogenetic position is still unknown, and their true fungal nature has been only proved recently [67]. Infested ants are usually well detected because the darker spores are visible through the integument (Figure 7); spores number may be very low, but usually they reach more than one hundred in a single ant. The caveat here is that the fungus may be much difficult to detect in ants having fuscous or black colouration. As a consequence, host range is probably biased. The usual aspect of concave spores, with a bow-like depression, is an artefact of fixation in alcohol [68].

Although the infested workers are almost certainly killed by the fungus when spores begin producing hyphae, life span seems not to be curtailed [67]. Infested workers seem scarcely affected in its normal behaviour [67, 69], and infested queens may participate in swarming flights [69] and show normal fertility [68]. Males have been found infected too [70]. Life cycle and mode on infestation are unknown although reports of *Myrmicinosporidium* from callow workers in *Pogonomyrmex badius* indicate that the infection is carried over from immature stages [71]. It is perhaps significant that the majority of diseased ants were collected in late summer and fall. After hibernation, those infected workers die [69]. Its geographical distribution is ample as is also the range of hosts.

Europe

Austria: *Plagiolepis vindobonensis* Lomnicki [67].

Croatia: *Temnothorax recedens* (Nylander), *Temnothorax affinis* (Mayr), *Temnothorax unifasciatus* (Latreille), *Plagiolepis pygmaea* (Latreille) [67].

France: *Solenopsis fugax* (Latreille), *Pheidole pallidula* (Nylander) [72]; *Temnothorax unifasciatus* (Latreille), *Temnothorax recedens* (Nylander) [68].

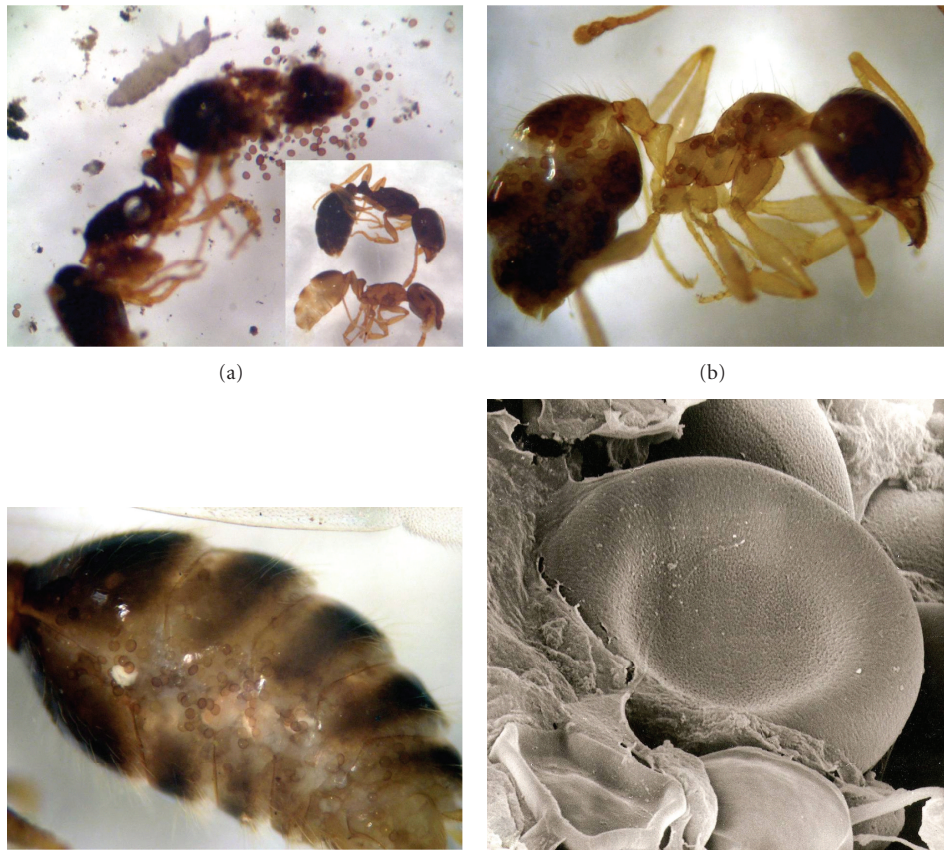
Germany: *Solenopsis fugax* (Latreille) [64, 65]), *Temnothorax tuberum* (Fabricius) [66].

Hungary: *Solenopsis fugax* (Latreille), *Tetramorium caespitum* (L.), *Plagiolepis taurica* Santschi [73].

Italy: *Temnothorax unifasciatus* (Latreille) [67, 69], *Temnothorax albipennis* (Curtis) [67], *Temnothorax angustulus* (Nylander) [67], *Temnothorax exilis* (Emery) [67], *Temnothorax nylanderi* (Forster) [67], *Chalepoxenus muellerianus* (Finzi) [67].

Spain: *Pheidole pallidula* (Nylander), *Solenopsis* sp., *Strongylognathus caeciliae* Forel, *Tetramorium semilaeve* (André), *Plagiolepis pygmaea* (Latreille) [70], *Temnothorax lichtensteini* (Bondroit), *Temnothorax racovitzai* (Bondroit) [72].

Switzerland: *Solenopsis fugax* (Latreille) [68].



(a) (b) (c) (d)

Figure 7: (a) *Myrmicinosporidium* mature spores inside workers *Tetramorium semilaeve* (inset: darker, infested worker, and normally coloured worker); (b) *Pheidole pallidula* with many spores on thorax, coxae, and gaster; (c) gaster of a male *Pheidole pallidula* with spores; (d) SEM image of a spore, showing the artifactual characteristic doughnout shaped form resulting from the alcohol fixation.

North America

USA: *Pogonomyrmex barbatus* (F. Smith) [67]; *Solenopsis carolinensis* Forel, *Solenopsis invicta* Buren, *Pheidole tysoni* Forel, *Pheidole bicarinata* Mayr, *Pyramica membranifera* (Emery), *Pogonomyrmex badius* (Latreille) [67]; *Nylanderia vividula* (Nylander) ([67], as *Paratrechina vividula*).

3.2.2. Dubious Cases. Across literature, two cases have been described but not identified. Although unproven, those are highly likely to belong in *Aegeritella* because of the macroscopic description given.

Bequaert ([56], page 74) wrote "*A number of so-called "imperfect fungi"—incompletely developed, conidia-bearing or sterile stages of various Ascomycetes—have been recorded from ants. A nest of* Formica rufa *Linné, at Potsdam, Germany, was heavily infested with fungous growths, about the size of a pinhead and attached mainly to the thorax, more rarely to other parts of the body. The ants were apparently but little hampered by their parasites. From cultures obtained with these fungi, Bischoff concluded that thy belonged to several species, among them a* Mucor, *a* Penicillium *and a yeast. Thaxter also found in the vicinity of Cambridge, Mass., a fungus forming blackish incrustations on various parts of ants and giving rise to a few short, colorless, erect branches; the exact nature of this plant has not been determined, nor is the name of its host mentioned.*"

Donisthorpe ([74], page 235 and Figure 86) commenting on *Lasius umbratus* var. *mixto-umbratus* Forel, [now *Lasius (Chthonolasius)* unrecognisable species] noted "*On August 11th, 1912, when at Weybridge in company with Professor Wheeler, we found two colonies of this variety, very many of the ants of both being infested with a curious dark brown warty growth in patches on parts of the body and legs—this Wheeler thought might be a fungus which was unknown to him. I kept a number of these ants in captivity, and added uninfected workers of* umbrata *from other localities; the growth however did not increase nor spread to the new ants, but rather seemed to decrease. I sent some of the infested ants alive and others in spirit, to Dr. Baylis Elliot, and she considered the patches were colonies of unicellular organisms growing on the outside of the ants; eventually she came to the conclusion that they were not fungoid growths, but probably colonies of an alga.*" Thus, albeit without a named host, *Aegeritella* is probably present too in the United Kingdom. A search with Donisthorpe's collection and/or in the vicinities of Weybridge could confirm this.

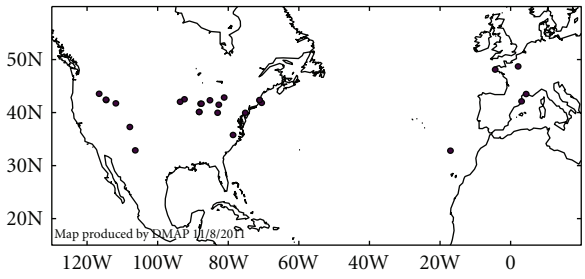


Figure 8: Distribution of *Laboulbenia formicarum*. North American records date from 1902 to 1979 and belong in 24 ant host species of five genera. European records date from 2003 to 2011 and imply two host species of *Lasius*.

4. Discussion

4.1. On Fungus Taxonomy. Laboulbeniales are taxonomically and nomenclaturally stable. There seems to be no major problem in morphological identification of the species involved. Perhaps, only, it would be worth examining the possibility of several species within *Laboulbenia formicarum* since its hosts belong in five genera, from three tribes—Formicini, Lasiini, and Plagiolepidini—in Formicinae.

Aegeritella is an especially difficult situation. Apart from its doubtful position within Fungi, bulbils are usually not in a perfect fruiting condition, and microscopic preparations are not easy to do since the bulbils are tightly attached to the ant's surface, anchored by the pubescence and hairs of the ant. The two most abundant species (*A. superficialis, A. tuberculata*) are well differentiated by the presence of hyphal elements in *A. superficialis* and by its absence in *A. tuberculata* [17].

Myrmicinosporidium is also an unsolved problem. All records but one are based simply on the presence of spores, which have a strikingly similar appearance across the two continents. Although they seem to be close to Chytridiomycetes [67], it remains to be studied where do those fungi belong within the phylogeny, and also the conspecificity of all so-called *M. durum* records. A similar situation is that of *Hormiscium*, from which only hyphae are known.

4.2. Host Phylogeny. A minimum of 13 subfamilies of ants are found in the Holarctic region. Only two (Myrmicinae and Formicinae) are noted with ecto- or endoparasitic fungi. Why should the distribution be so biased? If this is not a sampling artefact, it is noteworthy that the two subfamilies appear close together in the last comprehensive ant phylogenies [75, 76], thus indicating perhaps an ancestral susceptibility for both subfamilies.

Aegeritella is found on *Formica* and *Lasius*. *Laboulbenia* species infest exclusively ants from the subfamily Formicinae and *Rickia* infests Myrmicinae. This host specificity is not rare with Laboulbeniales [33]. Inasmuch *L. formicarum* is hosted by 24 ant species that belong in three tribes (Formicini, Lasiini, and Plagiolepidini), this calls for a dedicated evaluation (molecular and morphological) of the cospecificity of all populations of *L. formicarum*.

Myrmicinosporidium may be found in both ant subfamilies although the majority of cases belong in the Myrmicinae. We may speculate if the generic name is entirely appropriate or there is a detection bias of unknown origin towards Myrmicinae. Infested species belong in six tribes in Myrmicinae (Dacetini, Formicoxenini, Myrmicini, Pheidolini, Solenopsidini, and Tetramoriini), and one tribe in Formicinae (Plagiolepidini), widely scattered within ant phylogeny ([75], Figure 1; [76], Figure 1). Specificity is evidently not to uncritically assume in this fungus.

4.3. Geographical Distribution and Host Number. Knowledge is absolutely fragmentary and skewed. Asia in special, with a single record of ecto- and endoparasitic fungi, is a promising region to explore. The genus *Myrmica* with its many species should be searched for *Rickia*, and the genera *Formica* and *Lasius* for *Aegeritella*. Within Europe, countries such as Ireland, Belgium, The Netherlands, Denmark, Poland, or Portugal are obvious candidates for *Rickia*. The northernmost locale for *Rickia* seems to be Denbies Hillside, at 51°14′N [45]. Some cases, such as *Laboulbenia formicarum* (Figure 8) or *Myrmicinosporidium durum* (Figure 9) agree with the usual worldwide or wide-ranging specific distribution of fungi although others are only known from its original description, from a single locality (*Aegeritella maroccana, Aegeritella roussillonensis*).

With host number, the situation seems to be dichotomous. Some fungi are known from a range of hosts: *A. superficialis* 9 hosts, *A. tuberculata* 10, *L. formicarum* 24, *L. camponoti* 7, *R. wasmannii* 8, and *Myrmicinosporidium* 27, while other fungi are known from single hosts, in parallel with geographical range, likely reflecting a sampling artefact. Horizontal transmission to slave-making ants is possible, as attested by *Aegeritella* [30] and *Laboulbenia formicarum* [54] on *Polyergus*, and by *Myrmicinosporidium* in *Chalepoxenus* [67] and *Strongylognathus* [70].

In the USA, three species (*Pheidole,* and 2 *Solenopsis*) from a single farm in Houston Co., Alabama [71] were noted as infested with *Myrmicinoporidium*. In southern Hungary, three genera (*Plagiolepis, Solenopsis,* and *Tetramorium*) [73] were noted as hosts in a single locality. A similar situation is that of an organic citrus field in Spain [70], in which up to four different genera (*Pheidole, Plagiolepis, Tetramorium,* and *Solenopsis*) have been detected as hosts during several years, their nests being at distances of 5–20 m. The disease may qualify as chronic in the three localities. In this last locality, *Aegeritella* on *Formica rufibarbis* and *Laboulbenia camponoti* on *Camponotus aethiops, C. pilicornis,* and *C. sylvaticus* exist too. The single circumstance we can suggest for this "abnormal" abundance of parasitic fungi in this last site is the intensity—monthly samples—and duration—since 2002 and ongoing—of ecological studies with abundant insect collection. This is suggestive of a general low-prevalence but ample geographic distribution. Thus, we cannot but expect a growth of information if proper attention is directed to those ecto- and endoparasitic fungi of ants. Myrmecologists, please, be aware!

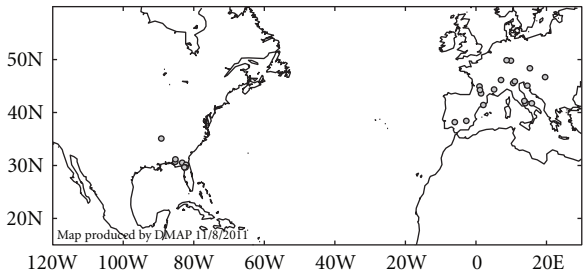


Figure 9: Distribution of *Myrmicinosporidium* sp. Eight ant host species are known from USA, and 19 from Europe.

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