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An Overview of Arthropod-Associated Fungi from Argentina and Brazil

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Abstract Arthropod pests in forest and agricultural systems are affected by many pathogenic organisms. Among them, entomopathogenic fungi are the one most common control agents that regulate their populations. This review compiles the information available from Argentina and Brazil about the entomopathogenic fungi occurring in agricultural and natural environments. The scientific names of the fungi are listed according to the latest phylogenetically based classification of fungi. We present an updated list of arthropod-pathogenic fungi occurring in 15 of the 23 provinces of Argentina and 20 of the 27 states of Brazil based on published literature and our personal observations. The list includes a total of 114 fungal species from 53 genera: of Blastocladiomycetes (2 genera), Entomophthorales (8 genera), Harpellales (13 genera), and a diverse assortment of ascomycetes (primarily from Hypocreales) in 22 anamorphic and 5 teleomorphic genera. In the both countries, molecular studies on arthropod-pathogenic fungi are still in their early stages and have focused primarily on intraspecific variability and adequate generic assignment. This listing seeks to encourage more active collection and characterization of these fungi by both traditional and molecular approaches from the obviously rich but underexplored flora of fungi affecting arthropods throughout this large region of South America.

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Introduction

Like virtually all other organisms, arthropods are susceptible to microbial infections. These disease-causing microbes may cause significant mortality that can under appropriate conditions substantially control or even decimate arthropod populations and may do so before host populations reach economic threshold levels [1]. Fungal pathogens of arthropods tend to be more commonly observed, more numerous and taxonomically diverse, more prevalent, and better documented than the viruses, bacteria, and protozoa affecting these invertebrates. Despite the importance of entomopathogenic fungi, there has been little attempt to synthesize an overview of the flora of these

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microbes in South America. The combined land areas of Argentina and Brazil comprise nearly 63% of the South American continent and a much larger proportion of the area east of the Andes. While this overview of fungal entomopathogens from the provinces of Argentina and states of Brazil is not completely representative of all of South America, the findings compiled here are the most inclusive and current listing of fungi affecting arthropods for this region. The literature on these fungi is obviously scattered among many local, national, and international publications in a number of languages, and this is the first attempt to review and to synthesize the knowledge of these fungi from natural and agricultural environments in this part of the world. We have included only naturally occurring pathogens collected from insects in the field or that might have spontaneously affect caged populations of insect pests. Fungi that might have been introduced intentionally from other parts of the world as microbial biocontrol agents and fungus associations with susceptible hosts determined experimentally through laboratory studies are not considered here and are excluded from consideration.

It is hoped that this effort will provide a useful reference to these fungi and it will both assist and stimulate further exploration in these countries and, indeed, throughout South America to expand our knowledge about the flora of fungal entomopathogens, and to facilitate the recognition and description of what we expect to be many new taxa of fungi from arthropods in this part of the world where the microbial biodiversity is so obviously rich but underexplored.

The updated fungal taxonomies used here incorporate the recently published phylogenetic classification of fungi produced by an ambitious international effort among mycologists to determine phylogenetic relationships among an unprecedently large and representative sampling of fungi from every major group based on phylogenetic analyses of multiple gene sequences [2]. This initial analysis was followed by a formal taxonomic reclassification of the fungi [3] to reflect these newly determined relationships. The fungi affecting arthropods are very taxonomically diverse, and this new reclassification of all fungi strongly affects the taxonomies of some of the most important groups of fungi attacking terrestrial arthropods. This overview compiles most of existing literature about the mycobiota of these fungi and their hosts for most of the South American continent, but it also seeks to encourage the widespread adoption of the newest (and, in truth, the most useful) classifications of these fungi.

The floristic data compiled here synthesize references in which the fungi were identified by only traditional morphologic criteria; these obviously include the earliest and, in some instances, the most tentative or speculative identifications of these fungi from this part of the world, although many of the fungi mentioned here were also described from these countries and for which the identifications are definitive. The appropriate rise of molecular (genomically based) approaches for fungal identifications has already dramatically affected fungal classifications based as seen from the phylogenetic overview of all major fungal groups [2] and the resultant reclassification reflecting these findings [3].

Many major genera of fungi affecting arthropods are also now undergoing molecular reclassifications that are substantially refining the classifications of their species and of our understandings of their biology while tending to increase the total number of taxa included in them. The major molecular revisions of conidial entomopathogens began with the reclassifications of *Verticillium* section *Prostrata* [4–6] and *Paecilomyces* section *Isarioidea* [7, 8]. These approaches have been expanded with the addition of still more genes for the ongoing reclassifications of species within *Beauveria* ([9], SA Rehner, JM Sung and RA Humber, unpubl.) and *Metarhizium* [10, 11].

Diverse molecular taxonomic studies in Argentina and Brazil have contributed to the growing global effort: ITS 18SrDNA sequences were used to distinguish a new species of mite-pathogenic Entomophthorales, *Neozygites tanajoae* Delalibera, Humber & Hajek, from the more widely known *N. floridana* (Weiser & Muma) Remaud. & Keller [12]. Studies using repetitive DNA sequences—BOX repetitive elements, repetitive extragenic palindromic (REP), and enterobacterial repetitive intergenic consensus (ERIC) elements—have characterized the genotypes of the chalkbrood fungus, *Ascosphaera apis* (Maassen ex Claussen) Olive & Spiltoir, from Argentina and Chile [13]. Studies have sought to characterize intraspecific genetic variability using RAPD, AFLP, and telomeric probes with *Metarhizium acridum* (Driver & Milner) Bischoff, Rehner & Humber [14, treated as *M. flavoviride* W. Gams & Rozsypal], *Nomuraea rileyi* (Farlow) Samson [1, 15], *Isaria fumosorosea* Wize [16], and *Beauveria bassiana* (Bals.) Vuill. [17]. More recently, the ability to distinguish species of *Isaria* and *Paecilomyces* by internal transcribed spacer (ITS1 and ITS2) sequences was confirmed [18]. Also, mitochondrial rDNA sequences to characterize species from clavicipitoid conidial entomopathogens [19] generated patterns of relationships nearly congruent with those found using several nuclear genes by Sung et al. [20] for their phylogenetic revision of the very important hypocrealean ascomycete family Clavicipitaceae *sensu lato*.

Materials and Methods

The bibliography cited here was compiled primarily from searches for the scientific names of fungal genera and families and of major host species in major online bibliographic databases: Web of Science (Thompson ISI), CABI Silver Platter abstracts, ScienceDirect (www.info.sciencedirect.com), PubMed (www.ncbi.nlm.nih.gov/), Google Scholar (www.scholar.com), and CAPES portal (http://www.periodicos.capes.gov.br). Additionally, cited publications were carefully examined to assure that supplementary information unregistered in electronic databases was also captured here. Most of the cultures and herbarium specimens associated with the most recent fungal collections are deposited in the collections in Centro de Estudios Parasitológicos de Vectores (CEPAVE; La Plata, Buenos Aires, Argentina), Embrapa Genetic Resources and Biotechnology (Cenargen; Brasília, DF, Brazil), Embrapa Soybean (Londrina, PR, Brazil), and in the USDA-ARS Collection of Entomopathogenic Fungal Cultures (ARSEF; Ithaca, NY, USA). Some records reported here provide previously unpublished information of natural infections in Argentina or Brazil and are noted by the observing author's initials (DSG, CLL or RAH).

Results

Phylogenetically based reclassification of fungi

The new phylogenetic interpretation of fungi moves far beyond accepting that the Oomycota, biflagellate watermolds that were formerly regarded as fungi belong in the huge kingdom variously called either Straminipila or Chromista; this new grouping includes all organisms with a tinsel-type flagellum decorated with hair-like mastigonemes and that has a completely different mode of action than mastigoneme-free whiplash flagella or cilia. The posteriorly uniflagellate chytrid fungi, however, continue to be recognized as true fungi but have been split among three phyla, the Chytridiomycota and Blastocladiomycota, and the (often polyflagellate) rumen 'chytrids' in Neocallimastigomycota [3].

The phylogenetic reclassification of fungi [2, 3] confirmed that the phylum/division Zygomycota as long recognized by mycologists is polyphyletic and was deconstructed by Hibbett et al. [3] into one phylum—Glomeromycota (comprising only the arbuscular mycorrhizal fungi)—and four other groups recognized for now as subphyla not yet placed into any new, appropriate phyla. Insect-associated fungi are prominent in at least two of these zygomycetous subphyla: Entomophthoromycotina (with the sole order Entomophthorales) and Kickxellomycotina (which includes the Harpellales, the order comprising the majority of endo and ectocommensal fungi previously classified in the now-abandoned class Trichomycetes).

Watermold and zygomycete entomopathogens

Entomogenous (straminipilan) oomycetes from the order Saprolegniales [now in the class Peronosporomycetes] group in Argentina and Brazil include *Leptolegnia chapmanii* Seymour, a virulent and specific pathogen of aedine and culicine mosquitoes such as *Aedes albifasciatus* (Theobald), *A. aegypti*, and *Culex dolosus* and *Cx. pipiens* [21–24]. *Saprolegnia ferax* (Gruith.) Nees has been recorded from *Culex dolosus*, *C. maxi* Dyar, and *Cx. pipiens* Wied. in Buenos Aires province [25].

Insect-pathogenic chytrid fungi (with posteriorly uniflagellate zoospores) are now classified primarily in the order Blastocladiales in the newly recognized phylum Blastocladiomycota. The major Argentine and Brazilian representatives are *Coelomomyces* species affecting various species of *Culex* in Argentina [26, 27] but the much rarer *Coelomycidium simulii* Debaisieux is also known from four Argentinean provinces as a larval pathogen of various black fly species (Diptera: Simuliidae) [28].

The Entomophthorales from Argentina and Brazil are not so well known as entomopathogenic ascomycetes and their conidial states, but the observed diversity and geographical dispersion of entomophthoraleans in both countries suggests that these fungi to be more widespread and taxonomically diverse than has yet been appreciated. *Conidiobolus* species (Ancylistaceae) include *C. coronatus* (Cost.) Batko are known from *Delphacodes kuscheli* Fennah and *D. haywardii* Muir (Hemiptera: Delphacidae) in northern Argentina and central Brazil [29, 30]; *C. obscurus* (Hall & Dunn) Remaud. & Keller is known from the aphids *Myzus* sp., *Nasonovia ribisnigri* (Mosley) and *Brevicoryne brassicae* L. in Buenos Aires province [31]; and unidentified *Conidiobolus* species are known from psychodid flies and cicadellid hemipterans in the Brazilian states of Bahia and Mato Grosso [32–34]. The wholly entomopathogenic family Entomophthoraceae is known from sites throughout Brazil and, to a lesser extent, Argentina. Several entomophthoraceous species, especially ones that are common and globally distributed, cause significant disease outbreaks among susceptible hosts: *Zoophthora radicans* (Brefeld) Batko from a number of aphids—*Myzus persicae* (Sulzer), *Acyrthosiphon pisum* (Harris), *Macrosiphum euphorbiae* (Thomas), *N. ribisnigri*, *Brevicoryne brassicae* L., and *Capitophorus elaeagni* (del Guercio)—as well as other hemipterans from the Cicadellidae (*Empoasca kraemeri* Ross & Moore and *Empoasca* sp.) and Psyllidae (e.g., *Gyropsylla spegazziniana* (Lizer)) from Buenos Aires and Corrientes provinces and the states of Goiás, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul [31, 33, 35, 36, 37, 38]. *Pandora neoaphidis* (Remaud. & Hennebert) Humber affects aphids such as *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (L.), *N. ribisnigri* in Buenos Aires and Santa Fe provinces and Paraná state [31, 36]. *Pandora gammae* (Weiser) Humber is an important pathogen common on two Plusiinae species, *Pseudoplusia. includens* (Walker) and *Rachiplusia nu* (Guenée), and in Argentina and Brazil is spread over a wide region [39, 40]. A closely related fungus, from the genus *Furia* has been reported on Plusiinae in Rio Grande do sul [41]. *Batkoa apiculata* (Thaxter) Humber is frequently reported in Brazil (Bahía, Goiás, São Paulo, and Paraná) from hosts such as *Lagria villosa* Fabr. (Coleoptera: Lagriidae) and nematoceran flies [34, 42] but most often from Hemiptera such as *Mahanarva fimbriolata* (Stål; Cercopidae) and unidentified Cicadellidae [32, 33, 43]. A similar fungus, *Batkoa dysderci* (Viégas) Humber, from a *Dysdercus* sp. (Hemiptera: Pyrrocoridae) from São Paulo state has not been recovered since its original description in 1939 [44]. The globally widespread *Entomophaga aulicae* and *Entomophaga grylli* species complexes from Lepidoptera—from *P. sequax* in Paraná [36]—and Acrididae (Orthoptera)—from *Dichroplus elongatus* Giglio-Tos., *D. pratensis* Bruner, *D. punctulatus* (Thunb.), *Baeacris punctulatus* (Thunb.) in Paraná [36, 45] and Bahía on *Rhammatocerus brasiliensis* Bruner, *R. bruneri* Giglio-Tos., *Abacris dilecta* Walker, *A. flavolineata* de Geer, and other unidentified acridids [34], respectively, are both present and potentially much more widely distributed in both countries than currently known.

Other less common entomophthoraceous species from Argentina and Brazil include the *Entomophthora muscae* species complex from muscid flies in Bahía [34] as well as *Entomophthora ferdinandii* Keller from *Musca domestica* in chicken houses in Buenos Aires province [46]. The aphid-specific pathogen *Entomophthora planchoniana* Cornu is known from Buenos Aires province from *Myzus persicae*, *Aphis fabae* Scop., *A. gossypii* Glover, *Capitophorus elaeagni, Macrosiphum euphorbiae*, and *N. ribisnigri* [31]. Unidentified or undescribed *Entomophaga* species from Cicadellidae (Hemiptera, including *Empoasca kraemeri*) in Goiás [33] and *Entomophaga tipulae* (Fres.) Humber from unidentified species of Tipulidae and *Anopheles* (Diptera: Culicidae) [34]. *Pandora nouryi* (Remaud. & Hennebert) Humber was found on *Heterocaecilius* (Psocoptera: Pseudocaeciliidae) in Buenos Aires province [47]. Otherwise unidentified *Zoophthora* species have been collected in from Paraná and São Paulo states [36] from Noctuidae (Lepidoptera)—*Anticarsia gemmatalis* Hübner, *Pseudoplusia includens*, *Rachiplusia nu*, *Pseudaletia sequax* Franclemont—as well as from *Nabis capsiformis* Germar (Heteroptera: Nabidae) and from the aphid *Capitophorus elaeagni* in Buenos Aires province [31].

Species of *Neozygites* (Entomophthorales: Neozygitaceae) are known globally from hemipterans (mostly aphids or scale insects in the superfamily Coccoidea) or from mites. Argentine and Brazilian collections of *Neozygites* fit this pattern but with most collections being from mites in the states of Bahía, Pernambuco, Piauí, São Paulo and Paraná: *N. tanajoae* Delalibera, Humber & Hajek is a highly specific pathogen of cassava green mite, *Mononychellus tanajoa* (Bondar) [12, 48, 49] in Bahía state. Other unidentified *Neozygites* collections from tetranychid mites—*Tetranychus urticae* Koch, *T. evansi* Baker & Pritchard, *T. ludeni* Zacher, and *Mononychellus planki* (McGregor)—are known from Pernambuco, Paraná, and São Paulo states and Buenos Aires province [36, 49–52]. A series of unidentified mite-pathogenic Entomophthorales found as resting spores (but that probably are attributable to *Neozygites*) are known from *Asca* sp. (Ascidae), Phytoseiidae (*Amblyseius igarassuensis* Gondim Jr. & Moraes and Stigmaeidae (*Agistemus* sp.) [51]. The known *Neozygites* pathogens from hemipterans are *N. fresenii* (Nowak.) Remaud. & Keller from aphids in Buenos Aires province—*A. fabae*, *B. brassicae*, and *M. persicae* [31, 53]—and *N. fumosa* (Speare) Remaud. & Keller from *Phenacoccus herreri* Cox & Williams (Pseudococcidae) from Bahía state [54].

The study of endocommensal trichomycetous fungi in South America has been primarily in Argentina where a relatively rich and well-dispersed flora of these fungi has been found mostly thanks to work by or in collaboration with RW Lichtwardt (University of Kansas). The Trichomycetes is no longer recognized as a class, but the most common species (including all of Argentinean and Brazilian collections) are from the order Harpellales and are now classified in the phylogenetically unassigned subphylum Kickxellomycotina. The Harpellales known to date from Argentina (Buenos Aires, Chubut, Jujuy, Misiones, Neuquén, Salta, and Tierra del Fuego provinces) from diverse black fly (Simuliidae) species of *Simulium*, *Cnesia*, and *Gigantodax* include *Genistellospora homothallica* Lichtw. and *Harpella meridianalis* Lichtw. & Arenas, *H. tica* Lichtw., *Pennella montana* Lichtw., *P. simulii* Williams & Lichtw., *Simuliomyces microsporus* Lichtw., *Smittium imitatum* Lichtw & Areans, and *S. simulii* Lichtw. [55–57]. Brazilian collections of infested Simuliidae (all from Amazonas) include the fungi *Genistellospora tropicalis* Ríos-Velásquez, Alencar, Lichtw. & Hamada, *Harpella amazonica* Ríos-Velásquez, Lichtw. Hamada & Alencar, and unidentified (possibly new) *Harpella* sp., *Smittium aciculare* Lichtw., and *S. brasiliense* Ríos-Velásquez, Lichtw., Hamada & Alencar [58]. Larval midges (Diptera: Chironomidae) from the genera *Chironomus*, *Cricotopus*, *Paraheptagyia*, *Syncrictopus*, *Tienemaniella,* and other unidentified midges were found to contain *Smittium cellaspora* Williams, *Sm. cylindrosporum* Lichtw. & Arenas, *Sm. esteparum* Ferrington, Lichtw. & López Lastra, *Sm. megazygopsorum* Manier & Coste, *Sm. tronadorium* Ferrington, Lichtw. & López Lastra, *Sm. urbanum* López Lastra, Mazzucchelli & Lichtw., *Stachylinoides arctata* Ferrington, Lichtw. & López Lastra, *Stachylina grandispora* Lichtw., *St. jujyensis* Mazzucchelli, López Lastra & Lichtw., *St. minima* Williams & Lichtw., *St. platensis* López Lastra, Lichtw. & Ferrington, as well as *Stachylinoides arctata* Ferrington, Lichtw. & López Lastra in the Argentinean provinces of Buenos Aires, Chubut, Jujuy, Neuquén, Río Negro, Tierra del Fuego, and Tucumán [55–57]; a Brazilian (Amazonas) *Crictopus* sp. contained thalli of *Stachylina paucispora* Lichtw. [58]. Larvae of Culicidae (Diptera) representing *Aedes crinifer* (Theobald), *Ae. serratus* (Theobald), *Culex dolosus*, *Cx. maxi* Dyar, *Psorophora ferox* von Humboldt, and other unidentified mosquitoes were found in Buenos Aires province and Amazonas state affected by *Smittium culisetae* Lichtw., *Sm. culicis* Manier, and *Sm. morbosum* Sweeney var. *rioplatensis* López Lastra [58–60]. *Carrouxella coemeteriensis* Lichtw., López Lastra & Ferrington was found from *Dasyhelea necrophila* Spinelli & Rodríguez (Diptera: Ceratopogonidae) in Buenos Aires province [55], and an unidentified larva of Ephemeroptera from Tierra del Fuego was affected by a *Glotzia* sp. [57].

Coleopterans can also bear infestations of Harpellales: In Río Negro (AR) *Coleopteromyces amnicus* Ferrington, Lichtw. & López Lastra occurred in a larval Scyrtidae [55], and in Amazonas (BR), unidentified larvae of Passalidae may be hosts of *Leidyiomyces attenuatus* (Leidy) Lichtw., White, Cafaro & Misra or *Passalomyces compressus* (Thaxt.) Lichtw., White, Cafaro & Misra [57].

Ascomycete and conidial entomopathogens

Most ascomycete pathogens of insects or other arthropod hosts are found in the conidial (anamorphic) rather than sexual (teleomorphic) states and are recorded in the literature under the names of these conidial states; the sexual states of the majority of these fungi are rare or remain wholly unknown. Among the insect-associated ascomycete fungi, uncertainties remain about the extent to which species in ubiquitous genera such as *Cladosporium*, *Aspergillus*, *Penicillium*, and *Fusarium* are pathogenic to arthropods or might be opportunistic secondary pathogens or saprobes that colonize available cadavers.

Few ascomycete yeasts from the subkingdom Saccharomycotina (which includes brewer's yeast) are known from arthropods and whether such yeasts or yeast-like fungi are pathogenic for any arthropods from which they may be collected is an open question. Nonetheless, *Geotrichum candidum* Link (Saccharomycetales: Endomycetaceae) is reported from mosquitoes—*Psorophora ferox*, *Culex pipiens*, and *Cx. renatoi* Lane & Ramalho—in Buenos Aires province [27].

Filamentous ascomycetes from the Dothideomycetes (subkingdom Pezizomycotina) associated with insects are reported so far from Brazil but not Argentina include *Cladosporium cladosporioides* (Fres.) de Vries (order Dothideales) from *Euphalerus clitoriae* Burckhardt & Guajará (Hemiptera: Psyllidae) in Pernambuco [61], *Cl. herbarum* (Pers.) Link from *Aphis gossypii* in Rio de Janeiro [33], and a *Cladosporium* species from mites—*Mononychellus tanajoa* (Bondar; Tetranychidae) and *Retracus johnstoni* Keifer (Phytoptidae)—in Maranhão, Pernambuco, and Bahía states [51; DSG and RAH, unpublished]. *Myriangium duriaei* (Mont. & Berk.) Tuck (Dothideomycetes: Myriangiales) appears to be obligatorily associated with scale insects and is known from *Cornuaspis beckii* (Newstead), *Insulaspis gloveri* (Packard), *Pinnaspis aspidistrae* (Signoret), *Parlatoria pergandii* Comstock, *P. ziziphus* (Lucas), and *Unaspis citri* (Comstock) from Tucumán (BR) and Rio Grande do Sul and São Paulo states [62–65]. Much of the (now rather old) global literature on *Myriangium* species fails to note their associations with the scale hosts below and incorporated into the ascomata of these fungi so much as with the plant species on which these fungus/scale insect combinations occur.

Chalkbrood diseases of bees caused by *Ascosphaera* species occur in most regions of the world. *A. apis*—the only South American chalkbrood fungus known to date—is reported Buenos Aires province and Rio Grande do Sul state from *Apis mellifera* L. (Hymenoptera: Apidae) [13, 66]. *Ascosphaera* and related species of the family Ascosphaeraceae are now classified in the Eurotiomycetes (all of which have completely closed fruiting bodies) in the order Onygenales; the order Ascosphaerales is no longer accepted. Arguably, the best known and most ubiquitous fungi from Eurotiomycetes are the conidial states in the family Trichocomaceae in *Aspergillus* and *Penicillium*; while it is not surprising that some species from these genera are reported from insects from Argentina and Brazil, their pathogenicities for arthropod hosts remain unconfirmed. *Aspergillus clavatus* Desm. has been reported from *Myzus persicae* (Aphididae) from Paraná [33], *A. flavus* Link from *Aleuas lineatus* (Orthoptera: Acrididae) in Argentina [67] and *Musca domestica* in Rio de Janeiro [68], and *A. parasiticus* Speare from *Piezodorus guildinii* Westw. (Hemiptera: Pentatomidae] and *Spodoptera frugiperda* (JE Smith; Lepidoptera: Noctuidae) in Buenos Aires province [67, 69] and from *P. guildinii* and *Dichelops melacanthus* (Hemiptera: Pentatomidae) from São Paulo and Paraná states [69, 70; DSG, unpubl.]. A *Penicillium* sp. is from *Orthezia praelonga* (Hemiptera: Ortheziidae) in Espirito Santo state [33] and *P. corylophilum* Dierckx from *Musca domestica* in Rio de Janeiro [68]; any claim for the pathogenicity of any *Penicillium* species against any arthropod host should be considered as dubious and needing careful experimental confirmation.

We do not try here to discuss the class Laboulbeniomycetes from Argentina and Brazil because of these fungi are both extraordinary diverse and taxonomically complex despite their presence as (only rarely harmful) ectoparasites on arthropod hosts. Knowledge of these tiny but elaborately constructed fungi rests substantially on the many publications of Roland Thaxter (in the USA) and Carlos Spegazzini (especially from Argentinean collections) that classified these fungi in many more than 100 genera and hundreds of species. The most comprehensive treatments of South American Laboulbeniales are those by Spegazzini [71].

The perithecial ascomycetes (class Sordariomycetes) and their conidial (anamorphic) states from the order Hypocreales include some of the most important and widespread pathogens of insects and other arthropods and occur in several families of the Hypocreales. Relatively few hypocrealean entomopathogens belong to the family Nectriaceae, but those that do include *Fusarium coccophilum* (Desm.) Wollenw. & Reink. (the conidial state of *Cosmospora [=Nectria] flammea*) from *Parlatoria ziziphus* (Hemiptera: Diaspididae) from São Paulo state [63] and *Fusarium oxysporum* Schltdl. from mosquitoes (*Culex* sp. and *P. ferox*) in

Buenos Aires province [27], and also a fungus with tetraradiate conidia, *Tetracrium coccicola* van Höhnel from diaspidid scale insects—*Aonidiella aurantii* (Maskell), *Insulaspis gloverii* Packard, *Parlatoria pergandei* Comstock, *P. ziziphus*, *Uniaspis citri* (Comstock)—from Tucumán province and São Paulo state [62, 63]. Another conidial entomopathogen in the Nectriaceae, *Tubercularia coccicola* J.A. Stev., is known from the diaspidid scale insects *A. aurantii* and *U. citri* from Tucumán province [62]. *Clonostachys rosea* (Link: Fries) Schroers, Seifer & W. Gams (=*Gliocladium roseum*; family Bionectriaceae) is an uncommon pathogen known from cicadellid hemipterans such as *Oncometopia tucumana* Schröder and *Sonesimia grossa* Signoret from Tucumán and Entre Ríos provinces, respectively [72].

The perithecial (teleomorphic) and conidial (anamorphic) fungi from the very speciose family Clavicipitaceae—and the families Cordycipitaceae and Ophiocordycipitaceae recently segregated from Clavicipitaceae [20]—comprise the most diverse and important group of fungal entomopathogens. Most insect-associated hypocrealean sexual states were originally described as *Cordyceps* species but the phylogenetic reclassification of Clavicipitaceae redistributed hundreds species among *Cordyceps* (strict sense) in the Cordycipitaceae, *Ophiocordyceps* and *Elaphocordyceps* (whose species are mostly mycoparasitic) in the Ophiocordycipitaceae, and *Metacordyceps* in the Clavicipitaceae [20].

Argentinean and Brazilian collections of entomopathogens remaining in the Clavicipitaceae in its newly restricted strict sense are fungi in well known genera: *Aschersonia.* cf. *goldiana* Sacc. & Ellis from *Bemisia tabaci* (Genn.) biotype B from São Paulo and Goiás states ([73]; DSG, unpublished) and an *Aschersonia* sp. from *Dialeurodes citri* (Ashmead) from Paraná state [33]—as well as a *Hypocrella* sp. from Goiás state [42] that often appears together with its conidial *Aschersonia* state; *Metarhizium anisopliae* (Metschn.) Sorokin in the broad sense [11] occurs commonly on a wide range of hosts from Coleoptera, Diptera, Hemiptera, Lepidoptera, and Orthoptera from throughout Argentina and Brazil [74–76], but the identifications of all *M. anisopliae* need to be reconfirmed (or changed) according to the newly expanded and molecularly based taxonomy of this complex [11]. *Metarhizium acridum* (Driver & Milner) JF Bisch., Rehner & Humber has been found from *Schistocerca pallens* (Thunberg; Orthoptera: Acrididae) from Rio Grande do Norte and Bahía states ([77, 78]; SEM Sánchez and RAH, unpublished) and is probably the genotypically correct identification for most *Metarhizium* collections from grasshoppers. *N. rileyi* is a very common and widespread pathogen of lepidopterans mostly in Noctuidae—*A. gemmatalis*, *Ps. includens*, *R. nu*, *Alabama argillacea* (Hübner), *S. frugiperda, P. sequax, Trichoplusia ni* (Hübner)—but also *Spilosoma virginica* (F.; Arctiidae) and *Chlosyne lacinia saundersii* Doubleday & Hewitson (Nymphalidae) in Argentina (Buenos Aires, Córdoba, Salta, Santa Fé and Tucumán provinces) and Brazil (Bahía, Goiás, Mato Grosso do Sul, Paraná. Rio Grande do Sul, and São Paulo states) [36, 79–82]. Except for the *Hypocrella* teleomorphs of *Aschersonia* species, no teleomorphs for *Metarhizium* or *Nomuraea* species have been recorded from anywhere in South or North America (RAH, unpublished). An isolated case of another Hypocreales, *Evlachovaea* sp. has been reported on *Triatoma sordida* (Stål) in the state of Goiás [83].

Entomopathogens from the new family Ophiocordycipitaceae in these countries include a substantial diversity of *Hirsutella* species: *H. citriformis* Speare from *Ectopsocus californicus* (Banks) Psocoptera: Ectopsocidae) from Buenos Aires [47]; the mononematous *H. guyana* Minter & Brady from *Empoasca kraemeri* (Hemiptera: Cicadellidae) from Ceará and Rio Grande do Norte [33]; *H. saussurei* Cooke ex Speare from adult wasps (Hymenoptera: Vespidae; DSG, unpublished) from Tucumán; *H. strigosa* Petch from *Doru lineare* (Eschscholtz; Dermaptera: Forficulidae) from Buenos Aires [47]; *H. subramanianii* Samson & Evans from *Pachycondylia* sp. (Hymenoptera: Formicidae: Ponerinae) from Pará [84]; *H. thompsonii* Fisher from Eriophyiidae (Acari) in *Calacarus heveae* Feres, *Epitrimerus goniathrix* Micos & Flechtmann, and *Dichopelmus notus* Keifer from Corrientes province and Mato Grosso and São Paulo states ([51, 85], DSG, unpublished) as well as *Phyllocoptruta oleivora* (Ashmead) from Tucumán and São Paulo [86, 87]; *H. versicolor* Petch from an Membracidae (Hemiptera) in Pará and Rondônia states [33]; and *Hirsutella verticillioides* Charles is known from *Leptopharsa heveae* (Drake & Poor; Hemiptera: Tingidae) from Pará [88, 89]. Other unidentified *Hirsutella* species are recorded to attack mites (Acari)—*Tarsonemus* sp (Tarsonemidae), *Propius syagris* Gondim Jr, Flechtmann & Moraes

(Eriophyiidae) and *Notostrix attenuata* Gondim Jr, Flechtmann & Moraes—from São Paulo [51] and from Ceará, Pernambuco and Rio de Janeiro states [33, 51] from the mites *Amrineus cocofolius* Flechtmann, *N. attenuata* and *Propilus syagris* (Eriophyidae), *Retracus johnstoni* (Phytoptidae), and *Tarsonemus* sp. (Tarsonemidae) as well as from a leafhopper, *Empoasca kraemeri* (Hemiptera: Cicadellidae). *Paecilomyces lilacinus* (Thom) Samson is known from *Triatoma infestans* (Klug; Hemiptera: Reduviidae), *Deois flavopicta* (Hemiptera: Cercopidae), and from *Chlosyne lacinia saundersi* (Lepidoptera: Nymphalidae), *Cerotoma* sp. (Coleoptera: Chrysomelidae) and *Lagria villosa* (Coleoptera: Lagriidae) from Santiago del Estero province and Goiás, Paraná, and Rio de Janeiro states [33, 90]; *P. lilacinus*, which is confirmed to belong in Ophiocordycipitaceae [8], remains for now taxonomically 'homeless' since it is excluded phylogenetically from both *Paecilomyces* (now restricted to Eurotiomycetes) and *Isaria* (all of whose species are in Cordycipitaceae) following the phylogenetically based dissolution and reclassification of *Paecilomyces* section *Isarioidea* [8]. Another conidial entomopathogen now classified in Ophiocordycipitaceae is *Tolypocladium cylindrosporum* W. Gams from the Argentinean Antarctic [91] by baiting soil samples even though this species is known elsewhere from infected insect hosts.

Teleomorphic species originally classified in *Cordyceps* but now transferred to *Ophiocordyceps* include *O. amazonica* (Henn.) GH Sung, JM Sung, Hywel-Jones & Spatafora from *Locusta* (Orthopterra: Acrididae) from an unspecified Brazilian site [92], *O. australis* (Speg.) GH Sung, JM Sung, Hywel-Jones & Spatafora from *Pachycondyla striata* Fr. Smith (Formicidae: Ponerinae) from Brazil [93], *O. dipterigena* (Berk. & Broome) GH Sung, JM Sung, Hywel-Jones & Spatafora from unidentified muscoid flies in Tucumán and Rio Grande do Sul [62, 94], *O. myrmecophila* (Ces.) GH Sung, JM Sung, Hywel-Jones & Spatafora from various Brazilian coleopterans and hymenopterans [93], *O. sobolifera* (Hill ex Watson) GH Sung, JM Sung, Hywel-Jones & Spatafora from *Proarna bergi* (Distant; Homoptera: Cicadidae) from Jujuy province [95], and *O. unilateralis* (Tulasne & C. Tulasne) Petch from *Campanotus femoratus* F. and *Atta cephalotes* L. (Hymenoptera: Formicidae) from Misiones province and Amazonas state [93, 96, 97].

It may be fair to suggest that the majority of teleomorphic and anamorphic entomopathogens in the Hypocreales are now classified in the family Cordycipitaceae, whose type genus is the newly restricted *Cordyceps*. The most common entomopathogen from this family, however, is *B. bassiana*. in the broad sense (known globally from more than 700 hosts from Coleoptera, Hemiptera, Lepidoptera, and other orders of insects) occurs throughout Argentina and Brazil on a large and diverse spectrum of hosts [33, 76, 82, 98–101]; *B. amorpha* (v. Höhnel) Samson & Evans was redescribed from coleopterans collected in Pará [102], and *B. brongniartii* (Sacc.) Petch is known from diverse hosts throughout Argentina [98]. *Gibellula* species are pathogenic to spiders worldwide but *G. brunnea* Samson & Evans is known from Pará [103], *G. mainsii* Samson & Evans from Rondônia [103], and *G. pulchra* Cavara from *Helvibis longicaudata* (Araneae: Theridiidae) from São Paulo [104]. The important *Isaria* species from these countries include both *I. amoenerosea* P Hennings and *I. farinosa* (Holmsk.) Fr. from *Lagria villosa* F. (Coleoptera: Lagriidae) from São Paulo and Paraná states [36] and Alagoas state [33], respectively; *I. fumosorosea* Wize is known from *Bemisia tabaci* (Gennadius), *B. tabaci* biotype B (Hemiptera: Aleyrodidae), *Oliarus* sp. (Hemiptera: Cixiidae), and *Spaethiella* sp. (Coleoptera: Chrysomelidae) from Buenos Aires and Corrientes provinces, and Amazonas and Paraná states [16, 33, 105, 106]; *I. javanica* (Frieder. & Bally) Samson & Hywel-Jones from *Trialeurodes vaporariorum* (Westwood; Hemiptera: Aleyrodidae) from Buenos Aires [106]; and *I. tenuipes* Peck from *Anticarsia gemmatalis, Pseudoplusia includens* and other Noctuidae from Mato Grosso and Paraná states [33, 36]. The fungus formerly known as *Verticillium lecanii* (Zimmerm.) Viégas has been reclassified phylogenetically in *Lecanicillium* and recognized as a species complex, each of whose three component species is present in Argentina and Brazil: *L. lecanii* (Zimmerm.) Zare & W. Gams, the type species of the genus, is known from *B. tabaci* biotype B and *T. vaporariorum* among the whiteflies (Aleyrodidae), from the aphids (Aphididae) *Aphis fabae*, *Cinara atlantica* Wilson, *C. pinivora* Wilson, *Schizaphis graminum* (Rondani), *Toxoptera citridicus*, from the scale insects *Pulvinaria flavescens* Brethes (Coccidae) and *Icerya purchasii* Maskell (Margarodidae) [62, 106–110].

Lecanicillium longisporum (Petch) Zare & W. Gams and *L. muscarium* (Petch) Zare & W. Gams, both of which are segregates in the *V. lecanii* species complex [111], are known from *T. vaporariorum* and (for *L. muscarium*) also from *Delphacodes kuschelii* Fennah (Hemiptera: Delphacidae), respectively [76, 106]. *Cordyceps singeri* Mains is known from spiders in Tucumán [112], and *Cordyceps tuberculata* (Lebert) Maire affects Orthoptera and Lepidoptera from Brazil [93].

Several other entomopathogens from Argentina and Brazil are known to belong in Clavicipitaceae in the broad sense but cannot yet be re-assigned under the revised 3-family taxonomy [20]. Among these fungi are *Acremonium roseum* (Oudemans) W. Gams from Plusiinae (Lepidoptera: Noctuidae) from northeastern Brazil [33], an *Acremonium* sp. from *Leptopharsa heveae* (Hemiptera: Tingidae) from the Distrito Federal and Mato Grosso in Brazil [33], *Cordyceps ignota* March. from spiders (Theraphosidae) in Argentina [112, 113], *Cordyceps martialis* Speg. (cited as *C. submilitaris* Henn.) from Misiones province [97], and *Cordyceps cicadae* (Miq.) from Argentinean cicada nymphs [93]. *Sporothrix insectorum* de Hoog & Evans (Sordariomycetes: Ophiostomatales: Ophiostomataceae) is formally reported in Brazil from *Leptopharsa heveae* (Hemiptera: Tingidae) from Amazonas [114] and has been widely studied by a number of laboratories. A degree of controversy remains, however, about the correct identification of the various isolates in Brazil that have been identified as *S. insectorum*. It appears that at least some of these isolates may be more accurately identified as *Lecanicillium aphanocladii* Zare & W. Gams or as *Aphanocladium album* (Preuss) W. Gams. *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. (whose anamorph is a *Glomerella* species) is another anamorph in Ophiostomatales that was reported from *Orthezia praelonga* (Hemiptera: Ortheziidae) in Rio de Janeiro state [33]. As with some other fungi best known as being phytophagous, the nutritional relationship of *Colletotrichum* species with any insect hosts must be treated as doubtful and needing to be confirmed.

Basidiomycete entomopathogens

The only basidiomycete fungi with any clear and consistent relationship with arthropod hosts other than for the dispersal of spores on the cuticles of living hosts are the unusual zoophilic rust fungi of the order Septobasidiales (Pucciniomycetes), and primarily, the many species of *Septobasidium* that parasitize coccid scale insects. The taxonomy of these fungi is complex is known almost wholly from a famous 1938 monograph by Couch [115] that listed the presence in Brazil of some 30 *Septobasidium* species. As with the ectoparasitic ascomycetes of the Laboulbeniales, it is neither easy nor necessary to list these Brazilian *Septobasidium* collections here; a list of these Brazilian *Septobasidium* spp. was published in Brazil in 1939 [116]. Argentinean collections of *Septobasidium* were not mentioned by Couch [115] but the genus is known from Córdoba [117] and elsewhere in Argentina [118, 119]. *Johncouchia mangiferae* Hughes & Cavalcanti was described from throughout Pernambuco state as the anamorph of *Septobasidium pilosum* Boed. & Steinm. [120]; such an anamorph is notable since few basidiomycetes are reported to have separately named conidial states.

Discussion

This overview notes the presence of more than 114 species of fungi from some 53 genera and nearly all major groupings of fungi in Argentina and Brazil. Blastocladiomycetes (posteriorly uniflagellate fungi formerly included among the Chytridiomycota) included species of *Coelomomyces, Coelomycidium*. Fungi of the Entomophthorales included species of *Batkoa, Conidiobolus, Entomophaga, Entomophthora, Furia, Neozygites*, *Pandora, Zoophthora*. Trichomycetous fungi in the Harpellales (an order now classified in the subphylum Kickxellomycotina) included representatives from *Carouxella, Coleopteromyces, Genistellospora, Glotzia, Harpella*, *Pennella, Plecopteromyces, Simuliomyces, Smittium*, *Stachylina, Stachylinoides*; the genera of the Eccrinales (*Leidyiomyces, Passalomyces*) and Amoebidiales (which are not yet known from Argentina and Brazil) have recently be determined not to be true fungi but were transferred to the protistan class Mesomycetozoea [121]. It is not surprising that there is a relatively small diversity of lower fungi (the watermolds, Entomophthorales and trichomycetous fungi) known from these countries since they require more specialized knowledge and collecting techniques to detect. The ascomycetous entomopathogens from these countries are usually more prominently visible and are certainly easier to isolate in cultures in a laboratory. As is also to be expected, these ascomycetes are usually found in the field (and are most easily maintained in vitro) in their conidial states. The main conidial ascomycetous genera included here include *Aspergillus, Aphanocladium, Aschersonia, Beauveria, Cladosporium, Clonostachys, Evlachovaea, Fusarium, Geotrichum, Gibellula, Hirsutella, Isaria, Lecanicillium, Metarhizium, Nomuraea, Paecilomyces, Tetracrium*. The sexual ascomycete genera reported here include species *Myriangium*, *Ascosphaera*, *Cordyceps*, and the recently segregated *Ophiocordyceps.*

Many fungi may be found occasionally on one or a few invertebrate hosts and is true of most of the species noted here. Some of these fungi, however, are pathogens that can become established and spread easily among their susceptible hosts, thereby causing widespread epizootic disease outbreaks. Fungi with the greatest known epizootic potential in Argentina and Brazil include conidial fungi (in alphabetical order) such as *Aschersonia* cf. *goldiana* on *Bemisia tabaci* [73]; *Metarhizium anisopliae* on spittlebugs; *N. rileyi* on caterpillars (especially on *Anticarsia gemmatalis*, *Pseudoplusia includens* [79], *Alabama argillacea* [80], and *Spilosoma virginica* (DSG, unpubl.), and *Trichoplusia ni*); *Hirsutella thompsonii* on *Phyllocoptruta oleivora* [86]; *Lecanicillium lecanii* on *Cinara atlantica* and *Coccus viridis* [122, 123]; *L. lecanii* and *Isaria fumosorosea* on *B. tabaci* [107]; *Isaria amoenorosea* on *Lagria villosa*; and *Isaria tenuipes* on *A. gemmatalis* and *P. includens* [Sosa-Gómez unpub.]. Entomophthoralean fungi known to produce epizootics include *Neozygites tanajoae* on *Mononychellus tanajoa* and a *Neozygites* sp. on *Mononychellus planki*, *Tetranychus urticae* and *T. ludeni* [50, 124]; *Batkoa apiculata* on spittlebugs, *L. villosa*, and small flies; *Entomophaga* cf. *grylli* on *Baeacris punctulatus*; *Entomophaga aulicae* on *Pseudaletia sequax*; *Pandora neoaphidis* on several species of aphids; *Pandora gammae* on *P. includens*; *Entomophthora ferdinandii* on *Musca domestica* [46]; and *Zoophthora* spp. on *P. includens* and *Gyropsylla spegazziniana* ([35]; DSG, unpub.).

Most of the fungi discussed here affect insects but a few are mite or spider pathogens such as *Hirsutella thompsonii* on *Dichopelmus notus* Keifer, a pest of Paraguay tea, and *Neozygites* sp. on Tetranychidae mite populations on soybeans, and *Neozygites tanajoae* described from cassava green mites. Most of the arthropod hosts are agricultural pests or vectors of significant human diseases. Among the arthropod-pathogenic species included here, only *Conidiobolus coronatus* and *Paecilomyces lilacinus* are also known as mycotic agents able to cause significant human or veterinary diseases; the globally distributed and common *C. coronatus* has been reported repeatedly from northern and northeastern regions of Brazil (states of Maranhão, Pará and Mato Grosso) [125, 126]. Even though these two species have proven records as mycotic agents in vertebrates, such mycoses are rare in comparison with the overall distribution and incidence of the causative fungi. Among all other entomopathogenic fungi, there is a lower risk of safety toward humans and other vertebrates although the allergenicity of their conidia (especially for the *Beauveria* and *Metarhizium* species) may be an issue for workers in facilities producing and formulating them for biocontrol applications [127].

The nutritional association between a fungus and a cadaver of an invertebrate may range from that of a primary pathogen that infects and kills to a saprobe colonizing an available food source whose death was unrelated to the fungus growing on it, and that association may be difficult to interpret correctly. Most fungi noted here are indisputably primary pathogens of their hosts, but we have tried to note when the fungus/host association may be more benign. The trichomycetous fungi of Harpellales are usually commensal or mutualistic, for example, and only rarely appear to be clearly deleterious to their hosts. The unique relationship with *Septobasidium* species and the scale insects they affect more closely resembles helotism in which the fungus protects and husbands while still exploiting some individuals in the host populations of its scale insect ‘helots’ or ‘serfs’ [115]. The true relationships between species of *Cladosporium* and other conidial ascomycete genera often associated with cadavers of mites, psyllids, and aphids need to be explored further; bioassays and histopathological studies could confirm whether such fungi are primary infective agents of their hosts [128] or might be secondary or facultative pathogens attacking insects only if they are already weakened by other pathogens or parasites or that colonize cadavers as saprobes. *Cladosporium* species are nearly ubiquitous on leaf surfaces and may grow so rapidly over the cadavers of aphids that may be killed by, for example, entomophthoralean pathogens that the presence of the real pathogen is obscured unless the cadaver and/or the surface of the plant around the cadaver are examined carefully.

The distributions of all species reported here can only reflect the collecting activities of individual specialists rather than the real distributions of places where these fungi may occur without their having been collected or formally reported. The flora of fungi associated with arthropods in these two countries comprising most of the South American continent is much larger than is yet known, especially because of since these two countries include habitats ranging from the Argentinean Antarctic and Tierra del Fuego to the equatorial tropics and Amazon River basin, and from the Atlantic coast onto the slopes of the Andes Mountains. The roster of insect-associated fungi from this region will expand with further collecting activities, but it will also grow as the molecularly based taxonomic revisions that segregate new taxa from existing species and genera are applied to fungi already maintained in culture collections and laboratories. The biodiversity of Brazil is widely understood to be among the richest on earth, but the microbial biodiversity of both Brazil and Argentina remains very poorly explored in comparison with that of these countries' plants and animals. We hope that this overview of a very specialized set of fungi will encourage further exploration throughout South America for fungi that may have unrecognized potential as biocontrol agents or as sources of compounds with unique properties that could be useful in agricultural settings or even in medical or veterinary contexts.

Apart from any consideration of their biodiversity and systematics, the natural environmental roles of entomopathogenic fungi must not be forgotten: They exert key roles as natural mortality factors reducing populations of insect pests. These organisms are as susceptible to losses from their natural habitats due to environmental changes or the losses or alterations of their habitats as any plants or animals that have already gained world attention as their natural populations decline or become extinct. Integrated pest management programs should consider the positive benefits of expanding the uses of modifying our agricultural and other practices to use environmentally benign agrochemicals—and, indeed, the adoption of more microbially based pest control strategies—to avoid the unintentional elimination of beneficial fungi or other biological control organisms that can cause 'rebound' resurgences of pest populations freed from such natural control agents.

The entomopathogenic fungi in this part of the world deserve to be both isolated in culture and preserved for incorporation in future research programs. The richer the germplasm resources of these fungi are, the greater will be the abilities of science to find improved biocontrol agents, to explore the unique capabilities of these fungi to produce biologically active compounds with many possible uses, and also to support the broader effort to catalog, and to understand the diversity and interactions of organisms occurring in natural environments.

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