Diversity of spider families parasitized by fungal pathogens: a global review

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Abstract. In this paper the findings of a global literature and social media survey of spider mycoses are presented. Our survey revealed that spider mycoses occur in the geographic belt between latitude 78° N and 52° S, and that more than 40 out of the known 132 spider families (>30%) are attacked by fungal pathogens. Jumping spiders (Salticidae), cellar spiders (Pholcidae), and sheet web spiders (Linyphiidae) are the families most frequently reported to be attacked by fungal pathogens (combined >40% of all reported cases). Ninety-two percent of the infections of spiders can be attributed to pathogens in the order Hypocreales / phylum Ascomycota (i.e., almost exclusively families Cordycipitaceae and Ophiocordycipitaceae). Within the Hypocreales, the anamorph genus *Gibellula* is an historically species-rich and widespread genus of specific spider-pathogenic fungi. For ≈70 species of spider-pathogenic fungi their hosts could be identified at least to family level. The data presented here reaffirms the findings of previous studies that spider-pathogenic fungi are most common and widespread in tropical and subtropical forested areas, with free-living cursorial hunters (especially Salticidae) being most frequently infected. Free-living cursorial hunters (especially Salticidae) and subterranean cellar spiders (Pholcidae) are the most frequently fungus-infected spiders in North America, whereas web-weavers (especially Linyphiidae and Pholcidae) are the most common spider hosts in Europe. Our survey implies that spider-pathogenic fungi are an important mortality factor of spiders which has hitherto been underestimated.

Keywords: Araneae; Cordycipitaceae; Ophiocordycipitaceae; *Gibellula*; mortality factor; spider mycoses; hosts

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1. INTRODUCTION

Fungal pathogens are undoubtedly an important source of mortality for a large number of arthropod groups. Insects alone are attacked by >700 species of entomopathogenic fungi (Hajek & St. Leger 1994; Consolo et al. 2003) and accordingly, these fungi have been extensively studied. By way of contrast, spider-pathogenic fungi have attracted less scientific interest. They have been almost neglected as spider enemies by arachnologists. This is evident from the fact that in most books on spider biology, fungal pathogens were not mentioned in chapters dealing with the spiders' natural enemies (see Gertsch 1979; Nentwig 1987a; Wise 1993; Foelix 2011; Bradley 2013).

Although a larger number of papers on the taxonomy of spider-pathogenic fungi exist, most of these studies are of limited value for the arachnologist because the authors of such studies invariably referred to the spider hosts as "unknown spider". The lack of knowledge of the identity of spider hosts can be explained 1) by the fact that almost all of these past studies on spider-pathogenic fungi were conducted by mycologists with little interest or expert knowledge regarding the identification of spiders, 2) by the poor interdisciplinary collaboration between mycologists and arachnologists, and 3) by the extreme difficulty to reliably identify parasitized spiders whose identifying features are often completely overgrown by the pathogen (Evans 2013; Durkin et al. 2021; Mendes-Pereira et al. 2022).

Evans (2013) stated with regard to the topic spider-pathogenic fungi "This has been a somewhat neglected topic: typically, a no-man's land between mycologists and arachnologists". In the current review we try to close the gap between mycology and arachnology – thereby pursuing a mycological-arachnological interdisciplinary approach by looking at spider-pathogenic fungi from an arachnological point of view (Fig. 1). It is hoped that this review will generate interest among arachnologists in the topic spider-pathogenic fungi and that it will inspire them to start exploring the still unresolved problems on this topic

in the future. Aside from that, we hope that it will also benefit mycologists by broadening their horizons in terms of spider host–fungal pathogen relationships. Historically the mycological literature has lumped all arachnids in with Insecta when dealing with invertebrate-pathogenic fungi. Where there have been distinctions this has been between mites and 'spiders'. In the mycological literature 'spiders' has also included the opilionids. In this review we do not treat the mites or opilionids and consider only the families within the order Araneae.

2. METHODS

2.1 Data collection. – We searched published reports on fungal pathogens in the Web of Science, Scopus, Google Search, Google Scholar, Google Books, Google Pictures, ProQuest Dissertations and Theses, as well as USDA-ARS Collection of Entomopathogenic Fungal Cultures – Catalog of Strains following the same search method as Nyffeler et al. (2022). Additionally, we made a library search of books and scientific journals not included in the electronic databases. Social media sites (e.g., BugGuide, What's That Bug, iNaturalist, Facebook, Flickr, Getty Images, Reddit, Yahoo, and YouTube) were also searched for information on spider-pathogenic fungi. Our survey resulted in a total of 484 records of entomogenous fungi growing on spiders, 90% of which could be identified, while 10% remained unidentified (Table S1, Supplemental Materials). In 375 cases (roughly 77%) the spider host could be determined at least to family level (Fig. 1), whereas in 109 cases (23%) the spider hosts remained unidentified (Table S1, Supplemental Materials).

With regard to the cases with identified spider host, information on the place of discovery of the fungus-infected spider was available in 331 cases (Table S1, Supplemental Materials), and these data were used for the statistical comparison of the dominant fungus-infected spider families in different major geographic regions (see Fig. 7). Records referring to the Russian Federation (see Humber 2014) were listed under Europe in all cases.

2.2 Taxonomic comments. – We have the following comments regarding the taxonomy of fungi and spiders, respectively.

2.2.1 Anamorph / teleomorph concept in mycology: Fungi in the phyla Ascomycota and Basidiomycota usually have two different reproductive stages: an asexual stage (= anamorph) and a sexual stage (= teleomorph) (Hodge 2003). The anamorph and teleomorph reproductive stages of a particular fungus were historically recognized as distinct species, although they may be genetically identical. Sometimes only one of the two reproductive stages of a fungal pathogen is known. With the advent of molecular phylogenetics the links between anamorph and teleomorph species is now becoming clear. As a result, the last 10+ years has seen a move towards the One Fungus One Name concept. This is a dynamic concept that is beyond the scope of this review to fully detail.

2.2.2 Identification of unidentified fungi: Some photographs depicting unidentified fungi were identified to the lowest taxon possible. In the case of subterranean fungus-infected pholcids from Europe and North America it must be said that they all looked very much alike (Fig. 2A–E). Mycosed pholcids are conspicuous by white, fluffy spheres surrounding the spider body and each of the leg joints (Eiseman et al. 2010; Martynenko et al. 2012). The resemblance in appearance of the mycosed pholcids (Fig. 2A–E) indicates that they were all attacked by a group of related fungal pathogens. This is confirmed by the observation that fungi from only one family (i.e., Cordycipitaceae) were isolated from dead subterranean pholcids (see Cokendolpher 1993; Keller 2007; Eiseman et al. 2010; Martynenko et al. 2012; Jent 2013; Humber 2014; Kathie T. Hodge; pers. comm.) which led us to assume that they are exclusively attacked by fungi from this family – at least in Europe and North America. Consequently, fungi on subterranean dead pholcids were consistently assigned by us to the family Cordycipitaceae, as far as fungi from Europe and North America were concerned.

2.2.3 Identification of spiders: Some photographs depicting unidentified fungi were identified to the lowest taxon possible on our behalf by the following spider taxonomists: Anyphaenidae (R. Bennett, A. Dippenaar, C. Haddad, M. Ramirez, L. Sousa Carvalho, D. Ubick, A. Zamani), Cheiracanthiidae (R. Raven), Ctenidae (H. Höfer), Philodromidae (B. Cutler), Salticidae (B. Cutler, G.B. Edwards, D. Hill), Theraphosidae (R. West), Thomisidae (B. Cutler), Trachelidae (T. Bauer, C. Haddad, Y. Marusik, M. Ramirez, and A. Zamani), Uloboridae (A. Brescovit), and further taxonomic advice (D. Logunov).

2.2.4 Further taxonomic comments: Nomenclature of spider taxa was based on the World Spider Catalog 2023 except for the nephilids. Contrary to the World Spider Catalog 2023 we placed the genus *Trichonephila* Dahl, 1911 in the family Nephilidae (sensu Kuntner et al. 2019). *Argyroneta aquatica* (Clerck, 1757) previously placed in the family Cybaeidae is now placed in Dictynidae (World Spider Catalog 2023).

Several authors reported the Corinnidae among the spider families known to be infected by fungal pathogens (Costa 2014; Shrestha et al. 2019; Arruda 2020; Kuephadungphan et al. 2022). All these reports can be traced back to Costa (2014), who mentioned a fungus-infected spider from the genus *Trachelas* Koch, 1872 and who erroneously placed this genus in the family Corinnidae. But according to the World Spider Catalog 2023, the genus *Trachelas* belongs to the family Trachelidae. Thus, the example of a fungus-infected corinnid previously quoted in the literature by the above authors was incorrect. However, a corinnid spider parasitized by a fungus from the genus *Gibellula* has most recently been discovered in the Brazilian Atlantic forest (Mendes-Pereira et al. 2022). Furthermore, a dead corinnid spider with fungus hyphae growing on its body was found encased in a Baltic amber sample (Wunderlich 2004).

A second incorrect statement refers to the spider family Ctenizidae. Originally the Ctenizidae was a large family made up of 135 species placed in 9 genera all of which

construct burrows in the ground sealed by a trapdoor made of soil, saliva, and silk (i.e., trapdoor spiders; see Gertsch 1979; World Spider Catalog 2018a / Version 18.5). In July 2018, many species previously placed in the Ctenizidae were transferred to other families (i.e., Actinopodidae, Antrodiaetidae, Cyrtaucheniidae, Dipluridae, Euctenizidae, Halonoproctidae, Idiopidae, Microstigmatidae, and Nemesiidae; see World Spider Catalog 2018b / Version 19.0). Accordingly, the family Ctenizidae was reduced from 135 species (in 9 genera) to 53 species (in 2 genera) (see World Spider Catalog 2018a). Today, the revised family Ctenizidae is made up of only 5 species placed in the genera *Cteniza* Latreille, 1829 and *Cyrtocarenum* Ausserer, 1871, all of which occur in the European Mediterranean region (see World Spider Catalog 2023). In the Mycology literature we find many reports from Asia and South America of fungus-infected "trapdoor spiders" which were referred to as Ctenizidae (see Yakushiji & Kumazawa 1930; Petch 1937, 1939; Kobayasi 1941; Mains 1954; Haupt 2002; Evans 2013; Hughes, et al. 2016; Shrestha et al. 2019). However, according to today's concept of spider taxonomy these species are no longer ctenizids, but belong to other families instead (e.g., the Asian trapdoor spider genus *Latouchia* Pocock, 1901 has been transferred to the family Halonoproctidae; see World Spider Catalog 2023). Nevertheless, white/light spots or patches have been observed on adult spiders in the genera *Cteniza* and *Cyrtocarenum* indicating that fungus-infections can occur in spiders of the family Ctenizidae in Europe (Arthur Decae, pers. comm.).

A further incorrect statement refers to the spider *Stenoterommata platensis* Holmberg, 1881 which was cited by Shrestha et al. (2019) as belonging to the family Nemesiidae. In reality this spider is placed in the family Pycnothelidae according to the World Spider Catalog 2023. However, during our literature survey we found another record for a spider from the family Nemesiidae that apparently had been infected by a fungus (see Isaia & Decae 2012).

2.2.5. Predation strategies of the documented spider families: Information on the predation strategies of the documented spider families (Appendix 2) was taken from Nentwig (1987b). Additionally, information for Arkyidae is based on http://www.arachne.org.au/01_cms/details.asp?ID=2384 Accessed 27 October 2022.

2.3 Statistical methods. – To test whether the percentages of fungus-infected spiders of a particular spider group differed statistically significantly between two continents, a chi-square calculator test (without Yates's correction) was performed using MedCalc statistical software (https://www.medcalc.org/calc/comparison_of_proportions.php).

3. RESULTS

3.1 Which fungi are engaged in the parasitization of spiders? – In Tables 1–2 the entomogenous fungal taxa associated with spider hosts tracked down during our survey are listed. Appendix 1 includes roughly 70 different pathogenic fungal taxa with known spider host identity; for the sake of completeness, a larger number of described fungal taxa with unidentified spider hosts have been included in the list. Based on the > 400 records of identified fungi examined in this study it can be concluded that about 90% of them clearly classify as spider pathogens, while the remaining 10% are either facultative pathogens, non-pathogens, or fungi whose trophic status is ambiguous (Table 1). The sexual stage (anamorph) prevails, comprising roughly 2/3 of all identified fungal species (Appendix 1).

Spider-pathogenic fungi belong for the most part to the phylum Ascomycota, with the order Hypocreales highly prevailing (Table 1; Figs. 2–6). The order Hypocreales was represented by the families Bionectriaceae, Clavicipitaceae, Cordycipitaceae, Nectriaceae, and Ophiocordycipitaceae (Table 1). Hypocreales are classified as pathogenic with the exception of one species in the family Nectriaceae whose status is ambiguous.

Based on our survey, Cordycipitaceae was the most prominent spider-pathogenic fungal family, accountable for ≈3/4 of all recorded spider infections (Table 1). Within the Cordycipitaceae, the genus *Gibellula* (including its teleomorph form *Torrubiella*) is a particularly species-rich and widespread group of specific spider-pathogenic fungi (see Chen et al. 2021; Mendes-Pereira et al. 2023). Up to the present, 40–50 *Gibellula* spp. have been listed in the global fungal databases "Index Fungorum" and "MycoBank", some of which, however, have been declared to be synonyms (see Shrestha et al. 2019). In our review we list 33 species of *Gibellula* and 29 species of *Torrubiella* as spider pathogens (Appendix 1). So far, spiders from >20 families have been observed to be infected by pathogens from the genus *Gibellula* (Appendix 2). Fungi in the genera *Acrodontium, Clathroconium, Paecilomyces,* and *Verticillium* are also considered to be spider pathogens (Table 1; see Edwards 1980; Evans & Samson 1987; Luangsa-ard et al. 2005; Evans 2013).

For the remaining fungal taxa (i.e., *Apiotrichum*, *Aspergillus, Basidiobolus*, *Cladosporium, Conidiobolus, Filobasidiella, Mucor, Penicillium,* etc.) their status as pathogen or saprobe is often still controversial or undefined (see Table 1; Malloch et al. 1978; Greif & Currah 2007; Yoder 2009; Evans 2013; Bibbs et al. 2013; Heneberg & Rezac 2013; Henriksen et al. 2017; Shrestha et al. 2019). Noordam et al. (1998) comment on such cases "*their biology remains unknown; possibly they are essentially saprophytes, with a facultative parasitism on litter-inhabiting invertebrates*". In line with this, Evans (2013) termed fungi of the genera *Conidiobolus* and *Mucor* associated with spider hosts as "opportunistic pathogens" (= "facultative pathogens" sensu Noordam et al. 1998). The category of unclassified fungi includes also fungal hyphae attached to extinct dead spiders found as inclusions in Baltic amber, although there is a strong suspicion that in such cases the fungi in question are most often saprobes (Wunderlich 2004). One of the fungi, growing on an extinct spider, has been identified to be *Arachnomycelium filiforme* (see Wunderlich 2004).

3.2 What infection mechanisms are used by spider-pathogenic fungi? – The infection mechanism differs between araneomorph above-ground spiders (Figs. 3–5) and mygalomorph ground-burrowing spiders (Fig. 6). The infection mechanism of anamorph subterranean spiders (Fig. 2A–E) is similar to that of araneomorph above-ground spiders.

3.2.1 Infection mechanism in araneomorph above-ground spiders: Above-ground spider hosts were commonly found on elevated sites attached to the underside of leaves (Fig. 2F), where temperature and humidity conditions are optimal for fungal growth (Humber & Rombach 1987; Sanchez-Pena 1990; Samson & Evans 1992; Hywel-Jones 1996; Tzean et al. 1997; Andersen et al. 2009; Brescovit et al. 2019; Kuephadungphan et al. 2019, 2022; Mongkolsamrit et al. 2022). Discharged from the spider cadavers the spores disperse rapidly over a wide area potentially infecting many spiders perched on lower leaves. Once the spores adhere to a spider's cuticle, they germinate, and germ tubes penetrate the exoskeleton, intruding into the spider's body cavity (Kuephadungphan et al. 2022). The fungus can make use of openings or weak spots in the exoskeleton (i.e., mouth, anus, lung stigma, genital opening, intersegmental membranes at the leg joints, or directly through the thin abdominal cuticle) as entry points for the infection (see Yoder 2009; Martynenko et al. 2012; Kuephadungphan et al. 2022). [In medium- to larger-sized araneomorphs the abdomen appears to be the body part most vulnerable during the premature stages of a fungal infection (Figs. 3–5), whereas in small-sized araneomorphs fungal infections were most commonly first visible on the legs (Bishop 1990; Noordam et al. 1998).] We know from insect model systems that the pathogen penetrates the cuticle using lipases, proteases and chitinases (Nigel Hywel-Jones, unpubl. data). The mechanisms used by pathogenic fungi to infect insects and araneomorph spiders apparently are very similar (also see Brescovit 2019; Kuephadungphan et al. 2022). Once in the hemolymph the fungus then develops as a yeast phase. It gets its nutrients from the hemolymph and in the case of insects also from fat bodies that the host

relies on for nutrient storage. Death is associated with the yeast phase filling up the **hemolymph** depriving the host of nutrients and oxygen. It is only after the host dies that the fungus converts back to a mycelial form and invades the muscle tissue of the cephalothorax, legs etc. This is why the external fungus first appears from the abdomen or occasionally the leg joints. It has been hypothesized that – once the fungus invaded the brain – the spider's behavior is manipulated ("zombie spiders") causing it to climb the plant to an elevated site where it will die on a leaf underside (Fig. 2F; Shrestha et al. 2017; Arruda 2020; Arruda et al. 2021; Kuephadungphan et al. 2022; Saltamachia 2022). Much of our perception of spider behavioral manipulation has been inferred from extensive research done on fungus-infected ants. The approach of comparing fungus-infected ants and spiders with each other is reasonable since it appears that the two arthropod groups show the same type of altered host behavior (see Samson et al. 1988; Andersen et al. 2009; de Bekker et al. 2014; Loreto & Hughes 2019). After the death of the spider the fruiting bodies burst out the cadaver (Brescovit 2019). The behavior of pursuing elevated sites on the underside of leaves for spore release can be seen as an adaptation to optimize the fungal reproductive success (Fig. 2F; Jensen et al. 2001; Andersen et al. 2009; Hughes et al. 2016).

3.2.2 Infection mechanism in mygalomorph ground-burrowing spiders: Belowground spider hosts are for the most part trapdoor spiders from various families, although other types of mygalomorphs get infected by the same group of fungi (Fig. 6). Fungal pathogens engaged in the infection of ground-burrowing spiders are several species in the teleomorph genus *Cordyceps sensu lato* (Fig. 6), on the one hand, and the anamorph *Purpureocillium atypicola*, on the other hand. Reports on mycosed trapdoor spiders originate predominantly from South America and Asia (Mains 1954; Kobayasi & Shimizu 1977; Coyle et al. 1990; Haupt 2002; Evans 2013; Hughes et al. 2016; Chirivi et al. 2017).

The infection of spiders by the teleomorph *Cordyceps* unfolds as follows: sexual propagules (ascospores) adhere to the spider's cuticle, whereupon germ tubes are formed that penetrate the cuticle and enter the body cavity similar to the way described for anamorph spiders in subsection 3.2.1. Again, yeast-like hyphal bodies develop in the hemolymph and reproduce, gradually replacing the host tissue which ultimately leads to the spider's death. The fruit-body (stroma), up to 10 cm in length, emerges from the spider cadaver, grows along the burrow, and pushes through the trapdoor to facilitate the aerial dispersal of the ascospores (Figs. 6B–D; Kobayasi & Shimizu 1977; Evans 2013; Hughes et al. 2016; Chirivi et al. 2017).

The infection of spiders by the anamorph *Purpureocillium atypicola* plays out similar to that of *Cordyceps*, except that in this latter case fungal reproduction takes place by means of asexual spores (conidia) produced at the upper end of the fruit body (synnema; Fig. 6A). As in the previous example, the conidia are dispersed aerially (Coyle et al. 1990; Haupt 2002).

Evans (2013) noted that in the case of trapdoor spiders the question, how the aerially dispersed spores (ascospores and conidia) reach their target (i.e., the spider cuticle), remains an unresolved mystery given that trapdoor spiders live in their burrows beneath the soil surface with little exposure to airborne spores. But the hidden, sedentary life only applies to the female trapdoor spiders, whereas the males likely come into contact with airborne spores while wandering around on the soil surface in search of female burrows during the mating season (see Schwendinger 1991; Bond & Stockman 2008). [It must be added that male and female spiders alike get infected by fungal pathogens (Noordam et al. 1998; Gonzaga et al. 2006; Brescovit et al. 2019)]. This suggests possible male-to-female transmission of fungal pathogens during the mating process. The possibility of spider-to-spider transmission of fungal pathogens had already been suggested by Henschel (1998). Alternatively, there is a possibility that in some trapdoor spiders known to disperse as tiny juveniles by ballooning (see Coyle et al. 1985; Buzatto et al. 2021) those could get exposed to fungal spores after

leaving the mother's burrows similar to the situation observed in immature araneomorphs (see Bishop 1990a). For comparison, in cicadas another arthropod group parsitized by fungi from the genus *Cordyceps*, which develop in burrows up to two meters deep, the infection is also picked up by the immature stage before burrowing into the soil (Nigel Hywel-Jones, pers. obs.).

3.3 Diversity of spider families parasitized by pathogenic fungi. – Our survey revealed that **more than 40** out of the currently accepted 132 spider families **(>30%)** contain species which get attacked by fungal pathogens (Fig.1; Table 2; Appendix 2). The majority (88%) of the reported fungus-infected spiders belong to the suborder Araneomorphae (Figs. 2–5). The list of araneomorph families known to be fungus-infected under natural conditions includes the Agelenidae, Amaurobiidae, Anyphaenidae, Araneidae, Arkyidae, Cheiracanthiidae, Clubionidae, Corinnidae, Ctenidae, Cybaeidae, Deinopidae, Desidae, Dysderidae, Eresidae, Hahniidae, Hersiliidae, Hypochilidae, Lamponidae, Linyphiidae, Liocranidae, Lycosidae, Nephilidae, Oonopidae, Oxyopidae, Philodromidae, Pholcidae, Pisauridae, Salticidae, Sicariidae, Sparassidae, Tetragnathidae, Theridiidae, Thomisidae, Trachelidae, Trechaleidae, Uloboridae, and Zodariidae (Fig. 1; Table 2).

Only 12% of the documented spider mycoses are attributed to the suborders Mygalomorphae/Mesothelae (Fig. 1; Table 2). The list of fungus-infected mygalomorph/mesothel families includes the Actinopodidae, Atracidae, Atypidae, Barychelidae, Ctenizidae, Dipluridae, Euchtenizidae, Halonoproctidae, Heptathelidae, Idiopidae, Nemesiidae, Porrhothelidae, Pycnothelidae, and Theraphosidae (Fig. 1; Table 2).

Apart from these naturally occurring fungal infections, laboratory infections by fungi have been reported for the following spider families: Antrodiaetidae, Dictynidae, and Ischnothelidae (Fig.1; Table 2). It can be expected that these latter spider families are parasitized by fungi under natural conditions as well. Furthermore, it is worth mentioning that

fungal hyphae attached to spider cadavers encased in samples of Baltic amber were reported in the literature, whereby this refers to the spider families Anapidae, Corinnidae, Gnaphosidae? and Synotaxidae (Wunderlich 2004). Although the fossil species of "amber spiders" in question are considered to be extinct (Wunderlich 2004), the four families, to which they belong, are still extant today (see World Spider Catalog 2023).

Jumping spiders (Salticidae), cellar spiders (Pholcidae), and sheet-web spiders (Linyphiidae) are the spider families most frequently reported to be infected by fungal pathogens, these three families combined being accountable for >40% of all documented spider mycoses (Fig. 1). Each of these families is typically associated with a particular environment. Salticids (Figs. 4A–D) were the dominant fungus-infected above-ground spiders of the tropics/subtropics and of North America (Evans & Samson 1987), whereas linyphiids (Fig. 3) prevailed among the fungus-infected above-ground spiders in Europe (Bristowe 1948, 1958; Duffey 1997; Noordam et al. 1998; Meyling et al. 2011). Fungus-infected pholcids (Figs. 2A–E) are very common in subterranean spaces such as basements, caves and tunnels in Europe and North America (Martynenko et al. 2012; Bradley 2013).

3.4 Geographic differences in the percent composition of dominant spider families parasitized by pathogenic fungi. – Fungal infections of spiders have been observed in the geographic belt between latitude 78° N and 52° S (Bristowe 1948; O'Donnell et al. 1977). That is, on all continents except Antarctica, and with spider mycoses occurring in very different climate regions. Spider-pathogenic fungi have excellent long-distance dispersal capabilities taking advantage of their spider hosts' powerful means of dispersal (Bishop 1990a). On board of parasitized immature spiders such fungi can theoretically "balloon" over distances of 100 –200 kilometres (see Decae 1987; Bishop 1990a). There seems to be an exception to this in the case of fungus-infected subterranean pholcids (*Pholcus* spp.) in Europe and North America; subterranean species from this particular family – such as the

common species *Pholcus phalangioides* (Fuesslin, 1775) – apparently do not disperse via ballooning (Schäfer et al. 2001; Simonneau et al. 2016). The inability of certain pholcids to balloon could be interpreted as an adaptation to these spiders' specific living conditions in caves, basements and tunnels, and seems to be limited to subterranean members from this family. In Fig. 7 the parasitization of spiders by pathogenic fungi in different geographic regions is compared.

Fig. 7 shows that intercontinental differences in the frequency with which different fungus-infected spider groups were reported exist. The following points are notable:

1) Salticidae is overall the above-ground spider family most frequently reported as hosts of fungal pathogens in the Tropics/Subtropics and North America (Fig. 7). The distinctive shape of the cephalothorax makes these spiders identifiable even when completely covered by mycelium. The percentage of fungus-infected salticids in the Tropics/Subtropics does not differ statistically significantly from that in North America (23% vs. 25%; Chi-square test, $\chi^2 = 0.046$, $df = 1$, $P > 0.05$). The predominance of the salticids among the fungus-infected spiders may be explained by the fact that salticids 1) are among the most common spiders in warmer areas, thus, making available a huge number of potential hosts for fungal attacks (Nelson et al. 2004), and 2) that these spiders are highly exposed to the attacks by airborne fungal spores while searching the plant surface for prey or potential mates during the daylight hours (Evans & Samson 1987). Average annual temperatures in the cold/temperate zones of Europe are significantly lower compared to North America and the Tropics/Subtropics which explains why salticids as thermophilic animals are less common in Europe (see Nyffeler & Sunderland 2003). The much lower availability of salticids as potential hosts for pathogenic fungi might explain why this spider family is apparently less targeted by fungi in this part of the globe. So far published reports of fungus-infected salticids from Europe are lacking (Fig. 7).

2) Linyphiidae are one of the most frequently reported spider groups parasitized by fungal pathogens in Europe but not in the Tropics/Subtropics and North America (Fig. 7). The percentage of linyphiids infected by fungi in Europe is statistically significantly higher than that in the Tropics/Subtropics (28% vs. 2%; Chi-square test, $\chi^2 = 39.247$, $df = 1$, $P < 0.0001$) or in North America (28% vs. 3%; Chi-square test, $\chi^2 = 17.274$, $df = 1$, $P < 0.0001$). This can be explained by the fact that linyphiids, which are well-adapted to moderate and colder climates, are the most common and widespread above-ground spiders across large parts of Europe (Bristowe 1958; Nyffeler & Sunderland 2003). As opposed to this, only relatively few reports on fungus-infected linyphiids are known from the Tropics/Subtropics and North America, two geographic regions where linyphiids are less common (Nyffeler & Sunderland 2003).

3) Pholcidae are among the spider groups most frequently reported to be attacked by fungal pathogens in North America and Europe (Fig. 7). The percentage of fungus-infected pholcids in North America does not differ statistically significantly from that in Europe (32% vs. 34%; Chi-square test, $\chi^2 = 0.083$, $df = 1$, $P > 0.05$). These are spiders with a subterranean life style which inhabit caves, tunnels, and basements in buildings (Yoder et al. 2009; Martynenko et al. 2012; McNeil 2012; Humber et al. 2014; Dubiel 2015; Kubátová 2017; CABI 2022). Such subterranean spaces maintain a microclimate characterized by high humidity (98–100% RH) and moderate temperatures which are optimal for fungal growth (see Yoder 2009; Martynenko et al. 2012). The spiders most frequently reported in this context are cellar spiders in the genus *Pholcus* Walckenaer, 1805 (i.e., *Pholcus phalangioides*) (Fig. 2A–E; Keller 2007; Martynenko et al. 2012; Jent 2013; Humber et al. 2014). In North America and Europe, fungi isolated from mycosed pholcids belonged exclusively to the family Cordycipitaceae (Appendix 1–2). The following fungi were isolated from subterranean pholcids: the anamorphs *Beauveria alba* [= *Engyodontium album*], *Engyodontium aranearum*,

Engyodontium rectidentatum, and *Lecanicillium tenuipes*, as well as the teleomorph *Torrubiella pulvinata* (Cokendolpher 1993; Keller 2007; Eiseman et al. 2010; Martynenko et al. 2012; Jent 2013; Humber et al. 2014; Dubiel 2015; Kubátová 2017; Kathie T. Hodge, pers. comm.). There are few reports of fungal infections on subterranean spiders from tropical/subtropical regions. In a cave in Cuba a pholcid in the genus *Modisimus* Simon, 1893 was infected by a *Mucor* sp. (Mucoraceae; Mercado et al. 1988). The percentage of pholcids infected by fungi in the Tropics/Subtropics is statistically significantly lower than that in North America (3% vs. 32%; Chi-square test, $\chi^2 = 41.459$, $df = 1$, $P < 0.0001$) or Europe (3% vs. 34%; Chi-square test, $\chi^2 = 48.085$, $df = 1$, $P < 0.0001$). We cannot rule out that the low percentage of pholcids in the Tropics/Subtropics is biased in the sense that fungus-infected pholcids from tropical/subtropical subterranean basements and caves may have been less frequently investigated so far. In Brazil, plant-dwelling pholcids in the genus *Metagonia* Simon, 1893 infected by *Gibellula* sp. have been reported (Fig. 2F; Costa 2014).

4) Another notable point to mention is that in the Tropics/Subtropics both araneomorph and mygalomorph spiders are routinely attacked by fungal pathogens, whereas reports of fungus-infected mygalomorphs from Europe and North America are very scarce (≤ 5% of all reports; Fig. 7). For example, in Southwestern Europe only one mycosed trapdoor spider per ≈60–70 burrows was found (Vera Opatova, pers. comm.). The percentage of mygalomorphs infected by fungi in the Tropics/Subtropics is statistically significantly higher than that in North America (19% vs. < 2%; Chi-square test, $\chi^2 = 12.289$, $df = 1$, $P < 0.01$) or Europe (19% vs. 6%; Chi-square test, $\chi^2 = 7.415$, $df = 1$, $P < 0.01$). Most reports of fungal attacks on mygalomorphs refer to trapdoor spiders in the families Actinopodidae, Barychelidae, Halonoproctidae, and Idiopidae (Coyle et al. 1990; Schwendinger 1996; Haupt 2002; Chirivi et al. 2017; Pérez-Miles & Perafan 2017; and others).

3.5 Are spider-pathogenic fungi host-specific? – The host specificity of spider-pathogenic fungi varies considerably between the different pathogen species. Evans (2013) suggested that many spider-pathogenic fungi are highly specific and "that this specificity must operate at the exoskeleton level". Some fungal pathogens are host specific to the extent that they have been found so far from only one single spider host (Kuephadungphan et al. 2022). Spider-pathogenic fungi of this type include *Gibellula bang-bangus*, *Gibellula brevistipitata*, *Gibellula cebrennini*, *Gibellula dimorpha*, *Gibellula fusiformispora*, *Gibellula longicaudata*, *Gibellula longispora*, *Gibellula nigelii*, *Gibellula parvula, Gibellula pilosa, Gibellula pigmentosinum, Gibellula scorpioides, Gibellula solita, Gibellula unica, Jenniferia cinerea, Jenniferia griseocinerea, Jenniferia thomisidarum*, and others (see CABI 2022; Kuephadungphan et al. 2022; Mongkolsamrit et al. 2022). Thus, based on current knowledge these fungi appear to have a very narrow host range. However, due to the fact that such assessments are often based on a very low number of observations, it can not be ruled out that in some of these cases a broader host range will come to light in the future, once a larger number of host records will have been made available.

Others are spider-specific fungal pathogens with a wide host range across many spider families. *Purpureocillium atypicola* is perhaps the most prominent example of a spider-specific fungal pathogen with a wide host range. Spiders from ten families could be infected with *Purpureocillium atypicola* under laboratory conditions (Greenstone et al. 1987). The fact that this fungus is utilizing a wide range of hosts under laboratory conditions has been verified by our survey according to which spiders from 16 families are infected by *Purpureocillium atypicola* under natural conditions (Appendix 2). Other examples of fungi which infect a range of hosts from different spider families are *Gibellula leiopus* and *Gibellula pulchra*, two species with a broad geographic distribution (Samson & Evans 1973; Strongman 1991; Bałazy 1970; Kubátová 2004; Selçuk et al. 2004; Zare & Zanganeh 2008;

Dubiel 2015; Savić et al. 2016; Shrestha et al. 2019). Based on our survey these two very common fungal pathogens utilize seven different spider families as hosts in the case of *Gibellula leiopus* and eight families in the case of *Gibellula pulchra* (Appendix 2). It seems that exclusively araneomorph spiders are attacked by *Gibellula* spp. (Shrestha et al. 2019; Kuephadungphan et al. 2022). By way of contrast, mygalomorph spiders, whose body is covered with a strong exoskeletal cuticle, apparently remain unaffected from the attacks by *Gibellula* spp. fungi (Shrestha et al. 2019). Nevertheless, attacks by fungi from the genus *Gibellula* are apparently not strictly limited to araneomorph spiders, because Brazilian researchers recently reported on a harvestman of the family Stygnidae being infected by a *Gibellula* sp. (Villanueva-Bonilla et al. 2021).

Apart from these spider-specific fungal pathogens, there are other pathogens with lower host specificity, which infect spiders and other arthropods alike. An example of a fungal taxon with an extremely wide host range is *Beauveria bassiana* known to attack over 700 species in 15 insect orders in addition to spiders and mites (Sosnowska et al. 2004; Cummings 2009; Meyling et al. 2011).

4. DISCUSSION

4.1 How many species of spider-pathogenic fungi exist worldwide? – Fungi in general and spider-pathogenic fungi in particular remained understudied (Boomsma et al. 2014). Only about 5% of all extant fungal species have been described so far (see Hawksworth & Rossman 1997; Bhalerao et al. 2019). If this figure is used to estimate by extrapolation the number of still undiscovered spider-pathogenic fungi, then it follows that >1,000 unnamed species might exist. If we are only talking about the genus *Gibellula*, it was suggested that this genus alone probably contains hundreds of unnamed species (Harry Evans, pers. comm.). In fact, new species of spider-pathogenic fungi are being discovered all the time (e.g., Han et. al. 2013; Shrestha et al. 2019; Chen et al. 2017, 2018, 2021, 2022a,b; CABI 2022;

Kuephadungphan et al. 2022; Mendes-Pereira et al. 2022; Mongkolsamrit et al. 2022; Tan et al. 2022; Zhou et al. 2022; Nigel Hywel-Jones, pers. obs.).

Furthermore, because the biology of a large number of fungal species is still unexplored, their status as pathogen or saprobe is currently unknown or controversial (see Noordam et al. 1998; Evans 2013). So it could be that some species currently classified as saprobes are in fact facultative pathogens which would further increase the true number of existing species of spider-pathogenic fungi.

4.2 Low-investment vs. high-investment reproductive strategy in hypocrealean fungi. – A comparison between fungus-infected above-ground spiders (araneomorphs) with fungus-infected ground-burrowers (mygalomorphs) shows that the fungi attacking these two types of spiders differ in their reproductive patterns in terms of energy expenditure which can be explained as follows: The majority of fungus-infected above-ground spiders are small-sized often measuring only ≈1–5 mm in body length (Mains 1939; Bristowe 1948, 1958; Bishop 1990a,b; Noordam et al. 1998; Meyling et al. 2011; Brescovit et al. 2019). Spiders of that size have a body mass of ≈1–5 mg according to Nyffeler & Sunderland (2003). For comparison, the ground-burrowing trapdoor and purse-web spiders are much larger (≈10–35 mm body length) (Coyle et al. 1990; Bellmann 1997; Ono 2001; Ríoríos-Tamayo & Goloboff 2018) with a body mass of ≈500–2500 mg per spider (Anderson 1987; Bradley 1996; Hardy 2018). Ground-burrowing theraphosids can reach a body mass of up to 30,000 mg (Baerg 1963). The amount of energy which can be extracted by a fungal parasite from a large burrowing spider host is roughly 100–10,000 times larger than that extracted from a small above-ground host. Thus, fungi parasitizing above-ground spiders (araneomorphs) exhibit a low-investment reproductive strategy as opposed to the fungi found on the ground-burrowers (mygalomorphs). The fungi parasitizing ground-burrowers invest a much higher amount of energy into their reproductive effort (also see Evans & Samson 1987). Subterreanean pholcids

such as *Pholcus phalangioides* are also relatively small araneomorphs, with a body mass of ≈10–30 mg (Schmitz 2015). The fungi which attack pholcids (i.e., *Beauveria alba*, *Engyodontium aranearum*, and *Torrubiella pulvinata*) also exhibit a low-investment reproductive strategy (Fig. 2A–E).

The low-investment strategy of the fungi parasitizing small above-ground spiders – such as *Gibellula* spp. works in such a way that a spider is manipulated to climb a plant, whereupon spores are released from tiny fruit bodies growing on the meanwhile dead spider body (Fig. 2F). This procedure requires little energy – taking into account that small spiders are excellent climbers which due to their low body mass have to exert little resistance against the force of gravity and that little energy needs to be invested to produce the tiny fruit bodies.

For the ground-burrowing spiders the situation is completely different. Fungi parasitizing this type of spiders – usually found in the genera *Cordyceps* and *Purpureocillium* – die in their underground burrows and then use phototrophic fruit bodies to push above ground (Fig. 6A–D; Cummings 2009; Hughes et al. 2016; Rowley et al. 2022). These types of fungi must produce stout, fleshy fruit bodies strong enough to push through the earth (i.e., theraphosids) or to open trapdoors (i.e., trapdoor spiders) and which are long enough to emerge several cm above the ground surface to facilitate aerial dispersal of the released spores (Fig. 6 A–E). The production of such stout fruiting bodies is costly in energy. Only heavy built spider hosts – usually mygalomorphs – provide a sufficiently large amount of energy to facilitate the costly production of this type of reproductive structure (Fig. 6E).

4.3 In which habitats do spider mycoses occur most frequently? – High rates of fungus infection were documented for above-ground spiders in tropical/subtropical forested areas (including national parks and wildlife sanctuaries) in Brazil, China, Ghana, Indonesia, and Thailand (Tables 3–4; Nentwig 1985; Evans & Samson 1987; Humber & Rombach 1987; Samson & Evans 1974, 1982, 1992; Rong & Botha 1993; Tzean et al. 1997; Selçuk et al.

2004; Aung et al. 2006; Shrestha et al. 2019; Kuephadungphan et al. 2019, 2022; Mongkolsamrit et al. 2022). As Aung et al. (2008) point out, fungal pathogens show their highest dominance in humid tropical forests. Cacao farms in Ecuador and Ghana are further tropical habitats in which high rates of fungus infection were observed (Table 3–4). Evans & Samson 1987). Citrus, coffee, guava, rice, and sugar-cane plantations are other tropical/subtropical habitats in which spider-pathogenic fungi were found (Table 3). According to several field assessments, infection rates by hypocrealean fungi of ≈10–35% were observed for tropical spider populations, although there were also exceptions to this with infection levels of ≤ 1% (Table 4).

The reports of fungus-infected above-ground spiders in North America refer in particular to temperate forests. Fairly high infection rates were observed in the mountainous area of western North Carolina and eastern Tennessee (Mains 1939; Bishop 1990a). Mains (1939) found ≈70 small spiders parasitized by *Cordyceps thaxteri* at one location. In Bishop's (1990a) study from Tennessee, 5–20% of immature spiders (i.e., Araneidae, Linyphiidae, Salticidae, and Thomisidae) collected from a forest-meteorology tower were infected by hyphomycete fungi, with a maximum infection rate occurring in autumn (Table 4). High infection rates of pholcid populations by hyphomycete fungi were observed in basements of old houses and in caves at various locations in USA (Eiseman et al. 2010; Jent 2013; Humber et al. 2014; Kathie T. Hodge; pers. comm.). Still another notable point to mention is that about half a dozen cases of fungal-infected trachelids (e.g., *Trachelas tranquillus* (Hentz, 1847)) were reported from North America (Table 2; Appendix 2). The fungal pathogens attacking *Trachelas* spiders were usually *Gibellula* spp. (Appendix 2). *Trachelas* often hides very deep in cracks of dead wood which seems to favor fungal infestation (Tobias Bauer, pers. comm.).

The reports from Europe refer to temperate forests, tree-covered dunes, meadows, vegetable fields, fens, and swampy areas as regards above-ground spiders (Table 3). The majority of European above-ground spider hosts infected by hyphomycete fungi were small sheet-weavers (Bristowe 1958; Duffey 1997; Noordam et al. 1998; Meyling et al. 2011). The fungal pathogens engaged in these infections belonged to the genera *Gibellula* and *Torrubiella* (Bristowe 1958; Duffey 1997) or remained unidentified (Noordam et al. 1998). High infection rates of spider populations by fungi occurred in particular in damp places such as swampy areas in eastern England (Ellis 1956; Bristowe 1958; Duffey 1997). High infection rates of 20–85% have been reported for European above-ground spider populations dominated by sheet-weavers (Table 4).

As in North America, in European subterranean spaces a high percentage of pholcids are infected by hyphomycete fungi (Keller 2007; Martynenko et al. 2012). Martynenko et al. (2012) reported that the infection rates of *Pholcus* populations due to *Beauveria alba* in tunnel systems in the Ukraine was ≈70–75% (Table 4). These tunnels, characterized by high relative humidity, are optimal habitats for spiders to be infected by fungal pathogens.

Fungal infestations of spiders occur even in the cold, Arctic climate of the Island of Jan Mayen, Norway (70°59′N / 8°32′W) where huge numbers of small linyphids were killed by a hyphomycete in the genus *Cordyceps* not further identified (Bristowe (1948, 1958). Bristowe (1958) noted *"….when I visited the arctic island of Jan Mayen in 1921, I noticed thousands of the dead bodies of each of the four species comprising its spider fauna. They were covered with a white fungus identified as* Cordyceps*… …Now I believe it kills the spiders and is almost the only enemy these spiders have in this cold damp island."* The only spider-pathogenic species in the genus *Cordyceps* so far known from outside of the tropics/subtropics apparently is *Cordyceps thaxteri* (see Mains1939; Savić et al. 2016). In

non-mycological literature of that time the name 'Cordyceps' was often used to generally describe any fungus infecting an insect or, in this case, a spider.

4.4 Possible ecological implications of spider mycoses for the spiders. – In the tropics/subtropics and in North America/Europe, above-ground spiders exhibit important ecosystem services by exerting top-down control of herbivorous insects including numerous crop and forest pests (Nyffeler & Sunderland 2003; Nyffeler & Birkhofer 2017). Samson & Evans (1973) suggested that heavy infestation of above-ground spider populations by hypocrealean pathogens might interfere with the natural suppression of herbivorous insects. Heavy hypocrealean infestation of spiders was reported especially from humid forested areas, sugar-cane and cacao plantations in tropical/subtropical regions, on the one hand, and from forested and swampy areas in temperate climates, on the other hand (Williams 1921; Mains 1939; Bristowe 1958; Samson & Evans 1973; Bishop 1990a; Duffey 1997; Meyling et al. 2011). As pointed out by Samson & Evans (1973) much more data on variables such as infection rates, spider densities, and prey densities must be acquired before final conclusions on potentially disruptive effects of fungal pathogens on spider herbivore suppression can be drawn.

Fungal pathogens such as *Purpureocillium atypicola* and some *Cordyceps* spp. (Fig. 6) may play a significant role in the regulation of mygalomorph spider populations in tropical/subtropical regions (Coyle et al. 1990; Schwendinger 1996; Haupt 2002). Mygalomorph spiders, for their part, serve as food for the larvae of spider-hunting wasps (Pompilidae). In turn, the adults of such wasps act as pollinators of a variety of different plants (Ollerton et al. 2003; Johnson 2005; Shuttleworth & Johnson 2006, 2009, 2012; Phillips et al. 2021). Whether locally heavy fungal infestation of mygalomorph spider populations indirectly affects the pollination success of spider hunting wasp-pollinated plants remains to be explored.

What about the spiders dwelling in subterranean spaces? Such spiders (represented for the most part by pholcids) feed extensively on disease-carrying mosquitoes (Strickman et al. 1998; Martynenko et al. 2012). It is safe to assume that fungal pathogens heavily impact the abundances of subterranean pholcids in Europe and North America (Martynenko et al. 2012). Whether this has noticeable adverse effects to human health by disrupting the natural suppression of disease-carrying mosquitoes still needs to be investigated. Be that as it may, pholcids are definitely prominent members of subterranean food webs (Souza-Silva et al. 2011) and the fact that they are attacked so heavily by fungal pathogens is of ecological significance.

Finally, we would like to add that fungi may have an adverse effect on spider survival in still another way. The fact is that airborne fungal spores from many different fungal families (e.g., Botryosphaeriaceae, Davidiellaceae, Helotiaceae, Massarinaceae, Microascaceae, Nectriaceae, Phragmidiaceae, Pleosporaceae, Trichocomaceae, Trichosphaeriaceae, and Venturiaceae) are blown by wind into the webs of orb-weaving spiders (Smith & Mommsen 1984; Nyffeler et al. 2016, 2023). The trapped spores are ingested by the spiders along with silk material during the recycling process of old webs prior to the construction of new webs, and the consumption of spores may have a detrimental effect on spider survival because of the presence of noxious secondary compounds in the spores (see Smith & Mommsen 1984; Nyffeler et al. 2023).

5. CONCLUDING REMARKS

Our review reveals that spiders from at least 40 families are parasitized by fungal pathogens. This is a much higher number of fungus-infected spider families compared to the < 10–20 families reported from previous reviews (see Evans 2013; Costa 2014; Humber et al. 2014; Shrestha et al. 2019; Durkin et al. 2021; Kuephadungphan et al. 2022). The fact that 1) such a high number of spider taxa are parasitized by pathogenic fungi, and that 2) such a high

number of spider-specific fungal pathogens have evolved (>80 different spider-pathogenic fungi being described, with probably hundreds of unnamed species still to be discovered (see Shrestha et al. 2019; Harry Evans, pers. comm.)) leads to the conclusion that pathogenic fungi are among the spiders' major natural enemies. This conclusion is supported by the widespread occurrence of spider-pathogenic fungi in diverse habitat types over a large area of the globe (from latitude 78° N to 52° S). Our conclusion that fungal infection is an important mortality factor for spiders is at odds with the way spider-pathogenic fungi have previously been covered in most text books on spider biology (see above). With this paper we wish to raise awareness among arachnologists, mycologists, and ecologists that many ecologically significant trophic links between spider-pathogenic fungi and their spider hosts exist and that it would be worthwhile for them to pursue future arachnological-mycological interdisciplinary research in this very fascinating, yet unexplored frontier between arachnology and mycology.

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Table 1. – Taxonomical classification of spider-pathogenic fungi and other spider-associated fungi. Numbers in the table based on Table S1 (Supplemental Materials). Type of infection: P = Pathogen; FP = Facultative pathogen (sensu Evans 2013); S = Saprobe. – Fourty-eight records in which the fungi could not be identified were not included in this compilation. *After revision some pathogenic species in the genus *Verticillium* were transferred to *Lecanicillium* in the family Cordycipitaceae (see Evans 2013).

PHYLUM / Class	**Order**	**Family**	**Genus / Type of Infection**	**No. of cases in each family**
PHYLUM: ASCOMYCOTA				
Class: Sordariomycetes	Hypocreales	Cordycipitaceae	*Akanthomyces* / P *Beauveria* / P *Cordyceps* / P *Engyodontium* / P *Gibellula* / P *Granulomanus* / P *Hevansia* / P *Isaria* / P *Jenniferia* / P *Lecanicillium* / P *Polystromomyces* / P *Pseudogibellula* / P *Torrubiella* / P	320 (74.2%)
		Ophiocordycipitaceae	*Hirsutella* / P *Hymenostilbe* / P *Ophiocordyceps* / P *Purpureocillium* / P *Tolypocladium* / P	73 (16.9)
		Clavicipitaceae	*Metarhizium* / P *Neoaraneomyces* / P *Pseudometarhizium* / P	4 (0.9%)
		Bionectriaceae	*Clonostachys* / P	1 (0.2%)
		Nectriaceae	*Aphanocladium* / ?	1 (0.2%)
		Unidentified	Unidentified / P	6 (1.4%)
Class: Eurotiomycetes	Eurotiales	Trichocomaceae	*Aspergillus* / S ? *Paecilomyces* / P *Penicillium* / S ?	6 (1.4%)
Class: Ascomycetes	Incertae sedis	Incertae sedis	*Acrodontium* / P *Clathroconium* / P	4 (0.9%)
Class: Incertae sedis	?	Plectosphaerellaceae*	*Verticillium** / P	3 (0.7%)
Class: Dothideomyces	Capnodiales	Davidiellaceae	*Cladosporium* / S ?	1 (0.2%
PHYLUM: BASIDIOMYCOTA				
Class: Tremellomycetes	Trichosporonales	Trichosporonaceae	*Apiotrichum* / S ?	2 (0.5%)
	Tremellales	Tremellaceae	*Filobasidiella* / S ?	1 (0.2%)
PHYLUM: ENTOMOPHTHOROMYCOTA				

Class: Entomophthoro-mycetes	Entomophthorales	Ancylistaceae	*Conidiobolus* / FP	2 (0.2%)
		Basidiobolaceae	*Basidiobolus* / S ?	1 (0.2%)
PHYLUM: MUCOROMYCOTA				
Class: Incertae sedis	Mucorales	Mucoraceae	*Mucor* / FP	6 (1.4%)
Total identified fungi				431 (100%)

Table 2. – Diversity of spider families parasitized by fungal pathogens. Types of fungi: ● = Hypocreales; (●?) = possibly Hypocreales ⌂ = Deuteromycetes; ◊ = Entomophthorales; ○ = Eurotiales; □ = Mucorales; † = Trichosporonales; Δ = Unknown fungi; ○ = Hyperparasite overgrowing a Hypocreales.

#	Spider family	Tropics/Sub-tropics (Africa, Asia, Neotropics, Oceania)	North America	Europe	Extinct (inclusions in Baltic amber)	Laboratory
01	ACTINOPODIDAE	●				
02	AGELENIDAE			●		
03	AMAUROBIIDAE	Δ		●○		
04	ANAPIDAE				Δ	
05	ANTRODIAETIDAE					●
06	ANYPHAENIDAE	●	Δ			●
07	ARANEIDAE	●	●			●
08	ARKYIDAE	●				
09	ATRACIDAE	●				
10	ATYPIDAE	●		†		
11	BARYCHELIDAE	●				
12	CHEIRACANTHIIDAE	Δ●				
12	CLUBIONIDAE	●		●		
14	CORINNIDAE	●			Δ	
15	CTENIDAE	●				
16	CTENIZIDAE			Δ		
17	CYBAEIDAE		Δ			
18	DEINOPIDAE	●				
19	DESIDAE	●○				
20	DICTYNIDAE					Δ
21	DIPLURIDAE	⌂				
22	DYSDERIDAE		(●?)			
23	ERESIDAE	Δ				
24	EUCTENIZIDAE		○			
25	GNAPHOSIDAE?				Δ	
26	HAHNIIDAE		Δ	●		
27	HALONOPROCTIDAE	●				
28	HEPTATHELIDAE	●				
29	HERSILIIDAE	●				
30	HYPOCHILIDAE		●			

31	**IDIOPIDAE**	●				
32	**ISCHNOTHELIDAE**					□
33	**LAMPONIDAE**	●				
34	**LINYPHIIDAE**	●	●	●		●
35	**LIOCRANIDAE**	○				
36	**LYCOSIDAE**	●	●	●		
37	**NEMESIIDAE**			Δ		
38	**NEPHILIDAE**	●	●			
39	**OONOPIDAE**	◊				
40	**OXYOPIDAE**	●	●			
41	**PHILODROMIDAE**	●	Δ			
42	**PHOLCIDAE**	●	●	●		●
43	**PISAURIDAE**	●				
44	**PORRHOTHELIDAE**	Δ				
45	**PYCNOTHELIDAE**	●				
46	**SALTICIDAE**	●	●			
47	**SICARIIDAE**	Δ				●
48	**SPARASSIDAE**	●				
49	**SYNOTAXIDAE**				Δ	
50	**TETRAGNATHIDAE**	●	●	●		
51	**THERAPHOSIDAE**	●				●
52	**THERIDIIDAE**	●	□	●		●
53	**THOMISIDAE**	●	●	●		●
54	**TRACHELIDAE**	●	●			
55	**TRECHALEIDAE**	●Δ				□
56	**ULOBORIDAE**	●				
57	**ZODARIIDAE**	●				

Table 3. – Diversity of habitat types from which spider mycoses had been reported (based on literature).

Habitat type	**Tropics / Subtropics**	**North America**	**Europe**	**Source**
Tropical & subtropical forests (including National Parks and Wildlife Sanctuaries)	●			Samson & Evans 1973; Evans 1974; Nentwig 1985a; Selçuk et al. 2004; Brescovit et al. 2019; Arruda 2020; Saltamachia 2022; Zhou et al. 2022
Atlantic forest	●			Gonzaga et al. 2006; Costa 2014; Mendes-Pereira et al. 2022
Southern deciduous forest		●		Bishop 1990a
Temperate forests		●	●	Mains 1939; Bałazy 1970; Kubátová 2004; Tkaczuk et al. 2011
Nature Parks, Wildlife Preserves		●		https://bugguide.net/node/view/492026/bgimage; https://bugguide.net/node/view/1079720/bgimage
Cacao plantation	●			Samson & Evans 1973; Evans & Samson 1987
Citrus plantation	●	●		Muma 1975; Sanchez-Pena 1990
Coffee plantation	●			Wolcott 1948
Guava plantation	●			Johnston 1915
Rice plantation	●			Heinrichs 1994; Hywel-Jones 1996
Sugar-cane plantation	●			Williams 1921; Evans & Samson 1987
Vegetable field	●		●	Meyling et al. 2011; Chen et al. 2017
Meadows			●	Ellis 1956; Sosnowska et al. 2004
Rush communities (Juncaceae)			●	Sosnowska et al. 2004
Fallows covered by *Festuca pratensis*			●	Ryszkowski & Wicherek 1997
Ravine bank	●			Coyle et al. 1990
Subterranean caves	●	●	●	Mercado et al. 1988; Yoder et al. 2009
Subterranean tunnels			●	Martynenko et al. 2012
Subterranean basements		●	●	Humber 2014; CABI 2022
Gardens	●			Kobayasi 1941
Roadside	●			Kobayasi 1941
Fens and swampy areas			●	Bristowe 1948, 1958; Ellis 1956; McLean 1993; Duffey 1997
Filterbed			●	Duffey 1997
Tree-covered dunes			●	Noordam et al. 1998
Arctic island, between stones			●	Bristowe 1948, 1958
Aquatic environments – Diving bell spider *Argyroneta aquatica*			●	Noordam et al. 1998

Table 4. – Infection rate of spider populations (in %) caused by fungal pathogens based on literature data. N/A = information not available.

Infected spider taxon	Fungal pathogen	Habitat type	Infection rate (%)	Reference
TROPICS / SUBTROPICS				
Actinopus sp. (Actinopidae)	*Purpureocillium atypicola*	Ravine bank – Argentina	34.0 [*n* = 50]	Coyle et al. 1990
Latouchia sp. (Halonoproctidae)	*Purpureocillium atypicola*	N/A – Japan	18.2 [*n* = 22]	Haupt 2002
Prothemenops siamensis Schwendinger, 1991 (Idiopidae)	*Purpureocillium atypicola*	N/A – Thailand	High infectation rate	Schwendinger 1996
Helvibis longicauda Keyserling, 1891 (Theridiidae)	*Gibellula pulchra*	Atlantic Forest – Brazil	♂♂ =19.4 [*n* = 36], ♀♀ = 9.4 [*n* = 149], Overall = 11.6 [*n* = 185]	Gonzaga et al. 2006; Cardoso et al. 2018
Macrophyes pacoti Brescovit, Oliveira, J. C. M. S. M. Sobczak & J. B. Sobczak, 2019 (Anyphaenidae)	*Gibellula* sp.	Tropical forest – Brazil	27.2 [*n* = 2,565]	Arruda 2020
Jumping spiders (Salticidae) and others	*Gibellula* spp. + others	Tropical forests and cacao farms – Ghana	80 spiders killed by fungi in a cacao farm and 120 spiders in a tropical forest	Samson & Evans 1973; Evans 1974; Evans & Samson 1987
Orb-weaving spiders (Araneidae, Nephilidae)	*Purpureocillium atypicola*	Tropical forest – Panama	≤ 1.0 [*n* >1800]	Nentwig 1985a,b
Atypena formosana (Oi, 1977) (Linyphiidae)	*Gibellula leiopus / Gibellula pulchra*	Rice fields – Philippines	1.0 [*n* = N/A]	Heinrichs 1994
TEMPERATE CLIMATE				
Ballooning spiders (Araneidae, Linyphiidae, Salticidae, Thomisidae)	*Gibellula* sp. or *Torrubiella* sp.	Southern deciduous forest –USA, Tennessee	5.0–20.0 [*n* ≈ 700]	Bishop 1990a,b
Small unidentified spiders on leaves	*Cordyceps thaxteri*	Temperate forest – USA, North Carolina	≈70 spiders killed by the fungus in one spot	Mains 1939
Centromerus sylvaticus (Blackwall, 1841) (Linyphiidae)	Unidentified	Dune habitat – Netherlands	20.0–50.0 [*n* = 2,615]	Noordam et al. 1998
Sheet-web spiders (Linyphiidae)	*Gibellula* spp.	Agricultural fields – Denmark	50.0–85.0 [*n* = 40]	Meyling et al. 2011
Sheet-web spiders (Hahniidae, Linyphiidae)	*Gibellula aranearum / Torrubiella albolanata*	Fens and swampy areas – England	Countless spiders killed by fungi	Bristowe 1958; Duffey 1997
Unidentified spiders	*Gibellula pulchra*	Fallows covered by Festuca pratensis – France	>70.0 [*n* = High]	Ryszkowski & Wicherek 1997.
Pholcus sp. (Pholcidae)	*Beauveria alba*	Subterranean tunnels, Ukraine	70.0–75.0 [*n* = High]	Martynenko et al. 2012
ARCTIC CLIMATE				
Sheet-web spiders (Linyphiidae)	*Cordyceps* sp.	Arctic Island – Norway	Thousands of spiders killed by the fungus	Bristowe 1948, 1958

Appendix 1 . – Fungal pathogens infecting different groups of spider hosts (references in Supplemental Materials). *Africa, Asia, Central & South America, Oceania. – Taxonomic specification: *Cordyceps* sp. 1 relates to Barychelidae and Idiopidae; *Cordyceps* sp. 2 relates to Atracidae; Cordyceps sp. 3 relates to Linyphiidae. – Type of infection: P = Pathogen; FP = Facultative pathogen; S = Saprobe; U = Unknown type of infection. – Reproductive stage: A = Anamorph; T = Teleomorph. – Host association: ● = identified host; × = unidentified host.

Fungal taxon	Type of infection	Reproductive stage	Above-ground spiders – Tropics / Subtropics*	Above-ground-spiders – North America	Above-ground spiders – Europe	Ground-burrowing spiders – Tropics / Subtropics*	Spiders in subterranean spaces
HYPOCREALES							
Bionectriaceae							
Clonostachys aranearum	P	A	×				
Clavicipitaceae							
Metarhizium anisopliae	P	A			×		
Metarhizium brunneum	P	A			×		
Neoaraneomyces araneicola	P	?	●				
Pseudometarhizium araneogenum	P	?	●				
Cordycipitaceae							
Akanthomyces aranearum	P	A	●		●		
Akanthomyces araneogenum	P	A	●				
Akanthomyces coccidioperitheciatus	P	A	×				
Akanthomyces kanyawimiae	P	A	×				
Akanthomyces koratensis	P	A	●				
Akanthomyces lecanii	P	A	×				
Akanthomyces neoaraneogenum	P	A	×				
Akanthomyces ryukyuensis	P	A	×				
Akanthomyces sulphureus	P	A	×				
Akanthomyces thailandicus	P	A	×				
Akanthomyces waltergamsii	P	A	×				
Beauveria alba	P	A	●				●
Beauveria araneola	P	A	×				
Beauveria bassiana	P	A		●	●	●	
Beauveria brongniartii	P	A				●	
Beauveria sp.	P	A	●				
Beauveria spp.	P	A					●

Beauveria (or Entomophthora)	P	?		●			
Cordyceps arachnogena	P	T	×?				
Cordyceps araneae	P	T	×?				
Cordyceps caloceroides	P	T				●	
Cordyceps cylindrica	P	T				●	
Cordyceps grenadensis	P	T	×?				
Cordyceps ignota	P	T				●	
Cordyceps kuiburiensis	P	T	×?				
Cordyceps nidus	P	T				●	
Cordyceps ogurasanensis	P	T	×?				
Cordyceps pseudonelumboides	P	T	×?				
Cordyceps singeri	P	T				×	
Cordyceps thaxteri	P	T	×	●	●		
Copdyceps sp. 1	P	T		?		●	
Cordyceps sp. 2	P	T				●	
Cordyceps sp. 3	P	T			●		
Engyodontium aranearum	P	A					●
Engyodontium rectidentatum	P	A			●		●
Engyodontium sp.	P	A	●				
Engyodontium or Lecanicillium	P	A	●				
Gibellula alata	P	A	×				
Gibellula aranearum	P	A	●		●		
Gibellula aurea	P	A	●				
Gibellula bang-bangus	P	A					●
Gibellula brevistipitata	P	A	●				
Gibellula brunnea	P	A	●				
Gibellula cebrennini	P	A	●				
Gibellula clavata	P	A	●				
Gibellula clavifera	P	A	●				
Gibellula clavispora	P	A	×				
Gibellula clavulifera	P	A	×				
Gibellula clavulifera var. Alba	P	A	●				
Gibellula curvispora	P	A	×				
Gibellula dabieshanensis	P	A	×				

Gibellula dimorpha	P	A	●		
Gibellula fusiformispora	P	A	●		
Gibellula gamsii	P	A	×		
Gibellula leiopus	P	A	●	●	●
Gibellula longicaudata	P	A	●		
Gibellula longispora	P	A	●		
Gibellula mainsii	P	A	●		
Gibellula mirabilis	P	A	●		
Gibellula nigelii	P	A	●		
Gibellula parvula	P	A	●		
Gibellula penicillioides	P	A	×		
Gibellula pilosa	P	A	●		
Gibellula pigmentosinum	P	A	●		
Gibellula pulchra	P	A	●	●	●
Gibellula scorpioides	P	A	●		
Gibellula shennongjiaensis	P	A	×		
Gibellula solita	P	A	●		
Gibellula trimorpha	P	A	●		
Gibellula unica	P	A	●		
Gibellula or Torrubiella	P	?		●	
Granulomanus sp.	P	A	●		
Hevansia arachnophila	P	A	×		
Hevansia* c.f. *aranearum	P	A		●	
Hevansia cinerea	P	A	×		
Hevansia koratensis	P	A	●		
Hevansia longispora	P	A	×		
Hevansia minuta	P	A	●		
Hevansia nelumboides	P	A	×		
Hevansia novoguineensis	P	A	●		
Hevansia ovalongata	P	A	×		
Hevansia websteri	P	A	×		
Hevansia sp.	P	A	●	●	
Isaria farinosa	P	A	×	×	
Isaria tenuipes	P	A			×
Jenniferia cinerea	P	?	●		

Jenniferia griseocinerea	P	?	●				
Jenniferia thomisidarum	P	?	●				
Lecanicillium aphanocladii	P	A	●			●	
Lecanicillium aranearum	P	A	×				
Lecanicillium araneicola	P	A	×				
Lecanicillium araneogenum	P	A	●				
Lecanicillium huhutii	P	A	×				
Lecanicillium lecanii	P	A	×				
Lecanicillium muscarium	P	A			×		
Lecanicillium tenuipes	P	A		×	×		●
Polystromomyces araneae	P	?	×				
Pseudogibellula formicarum	P	A	×				
Pseudogibellula sp.	P	A	●				
Torrubiella alboglobosa	P	T	×				
Torrubiella albolanata	P	T	×		●		
Torrubiella arachnophila	P	T	×				●
Torrubiella aranicida	P	T	×		●		
Torrubiella aurantia	P	T	×				
Torrubiella corniformis	P	T	×				
Torrubiella ellipsoidea	P	T	×				
Torrubiella falklandica	P	T	×				
Torrubiella farinacea	P	T	×				
Torrubiella flavoviridis	P	T	×				
Torrubiella formosana	P	T	×				
Torrubiella globosoides	P	T	×				
Torrubiella gonylepticida	P	T	×				
Torrubiella inegoensis	P	T	×				
Torrubiella leiopus	P	T	×				●
Torrubiella longissima	P	T	×				
Torrubiella mammillata	P	T	×				
Torrubiella minuta	P	T	×				
Torrubiella miyagiana	P	T	×				
Torrubiella neofusiformis	P	T	●				
Torrubiella oblonga	P	T	×				

Torrubiella ooaniensis	P	T	×				
Torrubiella pallida	P	T	×				
Torrubiella plana	P	T	×				
Torrubiella pulvinata	P	T	×				●
Torrubiella ratticaudata	P	T	●				
Torrubiella rokkiana	P	T	×				
Torrubiella rosea	P	T	×				
Torrubiella ryogamimontana	P	T	×				
Nectriaceae							
Aphanocladium album	?	A	×				
Ophiocordycipitaceae							
Hirsutella darwinii	P	A	×				
Hymenostilbe verrucosa	P	A		×			
Hymenostilbe **sp.**	P	A	●				
Ophiocordyceps arachneicola	P	T	●				
Ophiocordyceps aranearum	P	T	×		×		
Ophiocordyceps caloceroides	P	T	×			●	
Ophiocordyceps engleriana	P	T	×				
Ophiocordyceps ghanensis	P	T	×				
Ophiocordyceps mrciensis	P	T	×				
Ophiocordyceps spiculata	P	T	×				
Ophiocordyceps verrucosa	P	T	×				
Purpureocillium atypicola	P	A	●	●		●	
Tolypocladium cylindrosporum	P	A			×		
CAPNODIALES							
Davidiellaceae							
Cladosporium cladosporioides	S?	A		×			
Cladosporium **spp.**	S?	A					●
ENTOMOPHTHORALES							
Ancylistaceae							
Conidiobolus coronatus	FP	A	×	×			
Conidiobolus sp.	FP	A			●		
Basidiobolaceae							
Basidiobolus sp.	S?	?	●				
EUROTIALES							
Trichocomaceae							
Aspergillus baeticus	S ?	A					●

Aspergillus niger	S ?	A				●	
Aspergillus tennesseensis,	S ?	A					●
Aspergillus sp.	S ?	A	●		●		
Paecilomyces spp.	P	A	×	×			●
Penicillium tealii	S ?	A	×				
Penicillium vulpinum	S ?	A					●
Penicillium spp.	S ?	A					●
MUCORALES							
Mucoraceae							
Mucor fragilis	FP	A		●			
Mucor sp.	FP	A					●
Sporodiniella umbellata	?	?		●			
TRICHOSPORONALES							
Trichosporonaceae							
Apiotrichum dulcitum	S ?	A			●		
Apiotrichum porosum	S ?	A			●		
Tremellaceae							
Filobasidiella arachnophila	S ?	T		●			
INCERTAE SEDIS							
Incertae Sedis							
Acrodontium crateriforme	P	A		●			
Clathroconium arachnicola	P	A	×				
Clathroconium sp.	P	A					●
Plectosphaerellaceae							
Verticillium lecanii	P	A		×			
Vericillium sp.	P	A	●				

Appendix 2. – Spiders from various taxa infected by fungal pathogens (based on literature and social media data). *Indicates fungal hyphae on dead spiders encased in samples of Baltic amber. **Indicates fungal infections under laboratory conditions; all other spider taxa were observed to be infected in the field.

#	Spider family / genus	Predation strategy	Fungal pathogen	Reference
1	**ACTINOPODIDAE**			
	Actinopus	Trapdoor	*Purpureocillium atypicola*	Coyle et al. 1990
2	**AGELENIDAE**			
	Coelotes; Tegenaria?; Urocoras	Web	*Gibellula leiopus; Gibellula pulchra*	Santamaria & Girbal 1996; Dubiel 2015; Savić et al. 2016
3	**AMAUROBIIDAE**			
	Amaurobius	Web	*Gibellula* sp. possibly overgrown with a hyperparasite; N/A	Internet source 1; Kim 2009
4	**ANAPIDAE***			
	Palaeomysmena	Web?	Fungal hyphae in Baltic amber	Wunderlich 2004
5	**ANTRODIAETIDAE****			
	Atypoides	Trapdoor	*Beauveria brongniartii*	Vincent 1986, 1993; Dubois et al. 2008
6	**ANYPHAENIDAE**			
	Iguarima;Lupettiana; Macrophyes	Hunt	*Gibellula leiopus; Gibellula aurea; Gibelluls* spp. *Hevansia sp.*	Muma 1975; Costa 2014; Brescovit et al. 2019; Arruda 2020; Arruda et al. 2021; Mendes-Pereira et al. 2022; Internet source 3
7	**ARANEIDAE**			
	Araneus; Argiope; Eriophora; Eustela; Micrathena	Web	*Akanthomyces; Gibellula* spp.; *Neoaraneomyces; Purpureocillium atypicola; Pseudometarhizium*	Nentwig 1985; Costa 2014; Chen et al. 2017, 2018; Durkin et al. 2021
8	**ARKYIDAE**			
	Arkys	Hunt	*Gibellula* sp.	Internet source 2
9	**ATRACIDAE**			
	Atrax	Web	*Cordyceps*	Anonymous 2009a
10	**ATYPIDAE**			
	Atypus	Purse web	*Purpureocillium atypicola; Apiotrichum* spp.	Yasuda 1915; Heneberg & Rezac 2013
11	**BARYCHELIDAE**			

	Strophaeus, Idiophthalma	Trapdoor	*Cordyceps* sp.	Pérez-Miles & Perafan 2017; Fernando Pérez-Miles, pers. comm.
12	**CHEIRACANTHIIDAE**			
	Cheiracanthium spp.	Hunt	*Gibellula* sp.; N/A	Steven Axford (photo); Charles Haddad, pers. comm.
13	**CLUBIONIDAE**			
	Clubiona	Hunt	*Akanthomyces aranearum; Gibellula leiopus; Gibellula pulchra; Gibellula* spp.; *Verticillium* sp.	Leatherdale 1970; Austin 1984; van Vreden & Ahmadzabidi 1986. McLean 1993; Bellmann 1997; Barrion 2001; van Helsdingen 2007
14	**CORINNIDAE**			
	Protoorthobula, N/A	Hunt	Fungal hyphae in Baltic amber; *Gibellula aurea*	Wunderlich 2004; Mendes-Pereira et al. 2022
15	**CTENIDAE**			
	N/A	Hunt	*Gibellula* sp., N/A	Internet source 4; Hubert Höfer, pers. comm.
16	**CTENIZIDAE**			
	Cteniza, Cyrtocarenum	Trapdoor	N/A	Arthur Decae, pers. comm.
17	**CYBAEIDAE**			
	N/A	Web	N/A	https://www.inaturalist.org/observations/89047072
18	**DEINOPIDAE**			
	N/A	Web	*Gibellula fusiformispora*	Kuephadungphan et al. 2020, 2022
19	**DESIDAE**			
	Cambridgea	Hunt	Most likely a hyperparasite of a *Gibellula* sp.	Internet source 5
20	**DICTYNIDAE****			
	Argyroneta	Web	N/A	Noordam et al. 1998
21	**DIPLURIDAE**			
	Linothele	Web	Deuteromycetes	Paz 1993
22	**DYSDERIDAE**			
	Dysdera	Hunt	Hypocreales ?	Internet source 6
23	**ERESIDAE**			
	Stegodyphus	Web	N/A	Henschel 1998
24	**EUCTENIZIDAE**			
	Myrmekiaphila	Trapdoor	N/A (probably a hyperparasite)	Internet source 7

25	**GNAPHOSIDAE?***			
	N/A	Hunt	Fungal hyphae in Baltic amber	Wunderlich 2004
26	**HAHNIIDAE**			
	Antistea, Cicurina	Web	*Torrubiella albolanata;* either Eurotiomycetes or *Fungi Imperfecti*	Bristowe 1958; Cokendolpher 2004
27	**HALONOPROCTIDAE**			
	Latouchia; N/A	Trapdoor	*Cordyceps cylindrica; Purpureocillium atypicola*	Kawamura 1929; Petch 1939; Kobayasi 1941; Mains 1954; Kobayasi & Shimizu 1977; Haupt 2002
28	**HEPTATHELIDAE**			
	Heptathela	Trapdoor	*Purpureocillium atypicola*	Yokoyama & Hashiya, 1994; Yokoyama & Ichikawa 1984
29	**HERSILIIDAE**			
	N/A	Hunt	*Gibellula pulchra; Gibellula* spp.	Nigel Hywel-Jones (unpubl. data); Internet source 8 + 9
30	**HYPOCHILIDAE**			
	Hypochilus	Web	*Hevansia* cf. *aranearum*	Internet source 10
31	**IDIOPIDAE**			
	Arbanitis; *Idiops; Prothemenops;* N/A	Trapdoor	*Cordyceps nidus; Cordyceps* sp.; *Purpureocillium atypicola*	Orchard 1996; Schwendinger 1996; Schwendinger & Hongpadharakiree 2014; Castillo et al. 2015; Chirivi et al. 2017; Pérez-Miles & Perafan 2017; ; Fernando Pérez-Miles, pers. comm.
32	**ISCHNOTHELIDAE****			
	Ischnothele	Web	*Mucor hiemalis*	Nentwig & Prillinger 1990
33	**LAMPONIDAE**			
	Lampona	Hunt	*Purpureocillium atypicola*	https://www.stuff.co.nz/environment/17344/Fungus-to-kill-white-tail-spiders-discovered
34	**LINYPHIIDAE**			
	Agyneta; Callitrichia; Centromerita; Centromerus; Collinsia; Erigone; Gongylidium; Leptorhoptrum; Leptyphantes; Oreoneta; Styloctetor; Walckenaeria	Web	*Beauveria bassiana; Cordyceps sp.; Gibellula leiopus; Gibellula nigelii; Gibellula pulchra; Gibellula* spp.; *Torrubiella albolanata;* N/A	Petch 1944, 1948; Bristowe 1948, 1958; Leatherdale 1970; Bosselaers 1984; Bishop 1990; Heinrichs 1994; Duffey 1997; Noordam et al. 1997; Meyling et al. 2011; Ruszkiewicz-Michalska et al. 2012; Costa 2014; Læssøe 2015; Kuephadungphan et al. 2022
35	**LIOCRANIDAE**			

	Agraecina	Hunt	*Aspergillus* spp.	Nováková et al. 2018a,b
36	**LYCOSIDAE**			
	Pardosa; Trochosa; N/A	Hunt	*Gibellula* spp.; *Cordyceps thaxteri; Purpureocillium atypicola; Conidiobolus* sp.	Van der Bijl 1922; Doidge 1950; Edgar 1969; Hywel-Jones & Sivichai 1995; Noordam et al. 1997; Keller and Wegensteiner 2010; Sandler 2016; Savić et al. 2016
37	**NEMESIIDAE**			
	Nemesia	Trapdoor	N/A	Isaia & Decae 2012
38	**NEPHILIDAE**			
	Trichonephila	Web	*Beauveria bassiana; Purpureocillium atypicola*	Nentwig 1985; Humber 2014; Internet source 8
39	**OONOPIDAE**			
	N/A	Hunt	*Basidiobolus* sp.	Henriksen et al. 2017
40	**OXYOPIDAE**			
	Hamataliwa; Peucetia; N/A	Hunt	*Gibellula trimorpha; Hevansia* sp.; *Purpureocillium atypicola*	Kuephadungphan et al. 2022; Internet source 9, Internet source 10
41	**PHILODROMIDAE**			
	Philodromus; Thanatus	Hunt	*Aspergillus* spp.; *Engyodontium* sp.; *Purpureocillium atypicola*	Rong & Grobbelaar 1998; Seth Ausubel, pers. comm.
42	**PHOLCIDAE**			
	Metagonia; Modisimus; Pholcus	Web	*Beauveria alba [=Engyodontium album]; Engyodontium aranearum; Gibellula pulchra; Gibellula* spp.; *Lecanicillium tenuipes; Mucor* sp.; *Torrubiella pulvinata*	Mercado et al. 1988; Cokendolpher 1993; Eiseman et al. 2010; Martynenko et al. 2012; Jent 2013; Costa 2014; Dubiel 2015; Humber 2014; Anonymous 2017; Kubátová 2017; Kuephadungphan et al. 2022
43	**PISAURIDAE**			
	N/A	Hunt	*Purpureocillium atypicola*	Internet source 11
44	PORRHOTHELIDAE			
	Porrhothele	Tunnel-shaped web	N/A	https://www.inaturalist.org/observations/138327035
45	**PYCNOTHELIDAE**			
	Stenoterommata	Trapdoor	*Lecanicillium*	Manfrino et al. 2017

			aphanocladii; Ophiocordyceps caloceroides	
46	**SALTICIDAE**			
	Afraflacilla; Corythalia; Euophrys; Heliophanus; Lyssomanes; Mopsus; Myrmarachne; Neon; Pelegrina; Phidippus; Portia; N/A	Hunt	*Acrodontium crateriforme; Akanthomyces* spp.; *Gibellula leiopus; Gibellula pulchra; Gibellula spp.; Granulomanus* sp.; *Engyodontium*; *Hymenostilbe* sp.; *Pseudogibellula* sp.; *Purpureocillium atypicola; Torrubiella* spp.	Williams 1921; Wolcott 1948; Edwards 1980; Evans & Samson 1987; Humber & Rombach 1987; Bishop 1990; Strongman 1991; Samson & Evans 1992; Rong & Botha 1993; Hywel-Jones 1996; Rong & Grobbelaar 1998; Meza 2004; Luangsa-Ard et al. 2008; Costa 2014; Durkin et al. 2021; Kuephadungphan et al. 2020, 2022; Abhijith et al. 2022; Saltamachia 2022; Charles Haddad, pers. comm.; Lisa Powers, pers. comm.; Steve & Alison Pearson, pers. comm.; Mary Jane Hatfield, pers. comm.
47	**SICARIIDAE**			
	Loxosceles	Hunt	*Metarhizium anisopliae; Purpureocillium atypicola*; N/A	Greenstone et al. 1987; Beys-da-Silva et al. 2013; https://www.inaturalist.org/observations/34934503
48	**SPARASSIDAE**			
	Caayguara; Heteropodus; Palystes	Hunt	*Gibellula* spp.; *Purpureocillium atypicola*	Rong & Grobbelaar 1998; Costa 2014; Hughes et al. 2016; Internet source 15
49	**SYNOTAXIDAE***			
	N/A	?	Fungal hyphae in Baltic amber	Wunderlich 2004
50	**TETRAGNATHIDAE**			
	Meta; Metellina; Pachygnatha; N/A	Web	*Aspergillus spp., Beauveria spp.; Engyodontium rectidentatum; Gibellula bang-bangus; Gibellula* cf. *leopus; Paecilomyces spp.; Penicillium vulpinum; Purpureocillium atypicola; Torrubiella leiopus; Torrubiella arachnophila;* N/A	Hywel-Jones & Sivichai 1995; Noordam et al. 1997; Yoder 2009; McNeil 2012; Kubátová 2017; Nováková et al. 2018a; Internet source 16
51	**THERAPHOSIDAE**			

	Aphonopelma; Avicularia; Grammostola; Pamphobeteus; Phormictopus; Pterinopelma; N/A	Hunt	*Aspergillus niger; Beauveria bassiana; Cordyceps ignota; Cordyceps nidus; Lecanicillium or Engyodontium; Ophiocordyceps caloceroides*	Mains 1954; Ortiz & Bertani 2005; Ayroza et al. 2012; Castillo et al. 2015; Barbosa et al. 2016; Guerrero 2019; Sherwood 2021; Daniel Winkler, pers. comm.
52	**THERIDIIDAE**			
	Achaearanea; Episinus; Helvibis; Hetschia; Janula; Latrodectus; Meotipa; Nesticodes; Theridion	Web	*Beauveria alba; Clathroconium sp.; Gibellula pulchra; Gibellula* spp.; *Mucor fragilis*	Chandrashekhar et al. 1981; Mercado et al. 1988; Gonzaga et al. 2006; Bibbs et al. 2013; Costa 2014; Kuephadungphan et al. 2022; Mongkolsamrit et al. 2022
53	**THOMISIDAE**			
	Amyciaea; Cebrenninus; Diaea; Indoxysticus; Synema; Tmarus	Hunt	*Gibellula pulchra; Gibellula* spp.; *Purpureocillium atypicola; Torrubiella* spp.	Petch 1944; Kobayasi & Shimizu 1982; Bishop 1990; Ruszkiewicz-Michalska et al. 2012, 2015; Costa 2014; Kuephadungphan et al. 2020, 2022; Mongkolsamrit et al. 2022; Tony DeSantis, pers. comm.
54	**TRACHELIDAE**			
	Trachelas	Hunt	*Gibellula leiopus; Gibellula spp.*	Costa 2014; Saltamachia 2022
55	**TRECHALEIDAE**			
	Cupiennius	Hunt	*Mucor hiemalis;* N/A	Nentwig & Prillinger 1990;https://www.inaturalist.org/observations/89466583; https://www.inaturalist.org/observations/93148799
56	**ULOBORIDAE**			
	Miagrammopes; Unident.	Web	*Gibellula dimorpha*	Kuephadungphan et al. 2022; Daniel Winkler, pers.comm.
57	**ZODARIIDAE**			
	Epicratinus; Storenomorpha	Hunt	*Gibellula* spp.	Costa 2014; Kuephadungphan et al. 2020, 2022

INTERNET SOURCES:

Internet source 1: http://analternativenaturalhistoryofsussex.blogspot.com/

Internet source 2: https://whyevolutionistrue.com/2020/05/12/readers-wildlife-photos-1013/

Internet source 3:

https://www.reddit.com/r/Entomology/comments/o32x4f/can_anyone_help_id_this_spider_killed_by/

Internet source 4: https://www.alexanderwild.com/Insects/InsectKilling-Fungi/i-MhDvdgb/A

Internet source 5 https://twitter.com/erincpow/status/1138628730803200002?lang=fr

Internet source 6: https://www.reddit.com/r/spiders/comments/ouo312/i_found_this_woodlouse_spider_overtaken_by_mold/

Internet source 7: https://bugguide.net/node/view/1209666

Internet source 8: https://www.flickr.com/photos/rainforests/40151443503

Internet source 9: https://rainforests.smugmug.com/Orders/Invertebrates/Orders/Cordyceps/i- FDVX5Kp/A

Internet source 10: https://bugguide.net/node/view/1208519/bgimage

Internet source 11: https://www.wikiwand.com/en/Beauveria_bassiana

Internet source 12: https://www.flickr.com/photos/rainforests/11307005053

Internet source 13: https://bugguide.net/node/view/36643

Internet source 14: https://www.flickr.com/photos/gillesarbour/24503554811/in/photostream/

Internet source 15: https://minibeastwildlife.blogspot.com/2011/03/killer-fungus.html

Internet source 16: https://www.bpww.at/de/artikel/mit-expertinnen-auf-artensuche

FIGURE CAPTIONS

Figure 1. – Fifty-two spider families containing species parasitized by fungi (see Table S1, Supplemental Materials for details). * fungus infections occurring exclusively under laboratory conditions. Extinct members of the families Anapidae, Gnaphosidae?, and Synotaxidae with fungi growing on their bodies – reported as amber inclusions (see Wunderlich 2004) – are not included here.

Figure 2. – **A.**– **G.** Cellar spiders (*Pholcus* spp.) infected by hypocrealean fungi (Cordycipitaceae). **A.** Observed in Cottage Grove, Wisconsin, USA (Photo by Kim Wood). **B.** In basement of an old house in Pennsylvania, USA (Photo by Lynn Lunger). **C.** Observed in Wayne, New Jersey, USA (Photo by Jeffrey J. Cook). **D.** Picture taken in Uxbridge, Ontario, Canada (Photo by J. Mass / "iNaturalist" CC BY-NC 4.0). **E.** On a water motor house in Gemunde, Portugal (Photo by Carlos M. Silva). **F.** Pholcid spider *Metagonia taruma* Huber, 2000 parasitized by fungus *Gibellula* sp. on leaf underside – Floresta Nacional de Tapajós, Brazil (Photo by Leonardo Sousa Carvalho).

Figure 3. – **A.** Linyphiid spider parasitized by *Gibellula pulchra* – vegetable plot in Denmark (Photo by Nicolai V. Meyling, University of Copenhagen). **B.** Linyphiid spider parasitized by *Torrubiella albolanata* – Denmark (Photo by Jens H. Petersen, "MycoKey"). **C.** Linyphiid spider parasitized by *Torrubiella albolanata* – Denmark (Photo by Thomas Læssøe, University of Copenhagen).

Figure 4. – **A.** *Pelegrina proterva* (Walckenaer, 1837) (Salticidae) parasitized by *Gibellula* cf. *leiopus* – Jefferson County Park, Iowa, USA (Photo by Mary Jane Hatfield). **B.** *Mopsus mormon* Karsch, 1878 (Salticidae) parasitized by *Gibellula* sp. (a member of the *Gibellula leiopus* complex) – Airlie Beach, Queensland, Australia (Photo by Steve & Alison Pearson). **C.** *Colonus* sp. (Salticidae) parasitized by *Gibellula* cf. *leiopus* – Athens/ Sandy Creek Nature Center, Georgia, USA (Photo by Carmen Champagne). **D.** *Phidippus putnami* (G. W. Peckham & E. G. Peckham, 1883) (Salticidae) parasitized by an immature *Gibellula* sp. – Bon Aqua, Tennessee, USA (Photo by Lisa Powers, "Froghaven Farm"). **E.** *Synema parvulum* (Hentz, 1847) (Thomisidae) parasitized by an immature hypocrealean fungus (most likely *Purpureocillium atypicola*) – Eno River State Park, North Carolina, USA (Photo by Tony DeSantis). **F.** *Philodromus* sp. (Philodromidae) parasitized by an immature hypocrealean fungus (most likely *Purpureocillium atypicola*) –Kakiat County Park, New York, USA (Photo by Seth Ausubel).

Figure 5. – **A.** *Trachelas* sp. (Trachelidae) parasitized by *Gibellula leiopus* – near Donalds, South Carolina, USA (photo by Kim Fleming). **B.** Pisaurid spider parasitized by an immature hypocrealean fungus (most likely *Purpureocillium atypicola*) – Mindo, Ecuador (Photo by Gilles Arbour / "NatureWeb"). **C.** *Peucetia viridans* (Hentz, 1832) (Oxyopidae) parasitized by an immature hypocrealean fungus (most likely *Purpureocillium atypicola*) – Okeechobee County, Florida, USA (Photo by Jeff Hollenbeck). **D.** *Arkys lancearius* Walckenaer, 1837 (Arkyidae) parasitized by an immature hypocrealean fungus (most likely *Gibellula* sp.) – Brisbane, Queensland, Australia (Photo by Tony Eales). **E.** Spider in the family Hersiliidae parasitized by a *Gibellula* sp. – Tambopata Research Centre, Peruvian Amazon (Photo by Paul Bertner). **F.** Spider in the family Uloboridae parasitized by a hypocrealean fungus (possibly *Engyodontium* or *Lecanicillium*) – Mocoa, Columbia (Photo by Daniel Winkler).

Figure 6. – Mygalomorph spiders infected by fungi (Photos by Daniel Winkler / "MushRoaming", Seattle, USA). **A.** Fruit body of *Purpureocillium atypicola* emerging from a unidentified mygalomorph spider carcass at Hongo, Bunkyo-ku, Tokyo, Japan (Photo by Sui-setz / "Wikipedia" CC BY-SA 3.0). **B.** Red fruit bodies (stromata) of *Cordyceps nidus* emerging from the underground burrow a dead trapdoor spider (family Idiopidae) – Chicaque Natural Park near Bogota, Colombia; the lid of the trapdoor has been pushed open by the emerging fruit bodies (Photo copyright: Daniel Winkler / "MushRoaming", Seattle, USA). **C.** Red fruit bodies (stromata) of *Cordyceps nidus* emerging from a dead unidentified trapdoor spider – Isla Escondida, Colombia (Photo copyright: Daniel Winkler). **D.** Fruit body of *Cordyceps cylindrica* emerging from an dead unidentified trapdoor spider – Chalalan, Bolivia (Photo copyright: Daniel Winkler). **E.** *Cordyceps calceroides* growing on a dead theraphosid (subfamily Theraphosinae) – Pitalito, Colombia (Photo copyright: Daniel Winkler).

Figure 7. – Percent composition of dominant fungus-infected spider groups in three different geographic regions: Europe, North America, and Tropics/Subtropics (combined data for Africa, Asia, Central & South America, and Oceania). Pie charts generated based on Table S1, Supplemental Materials.

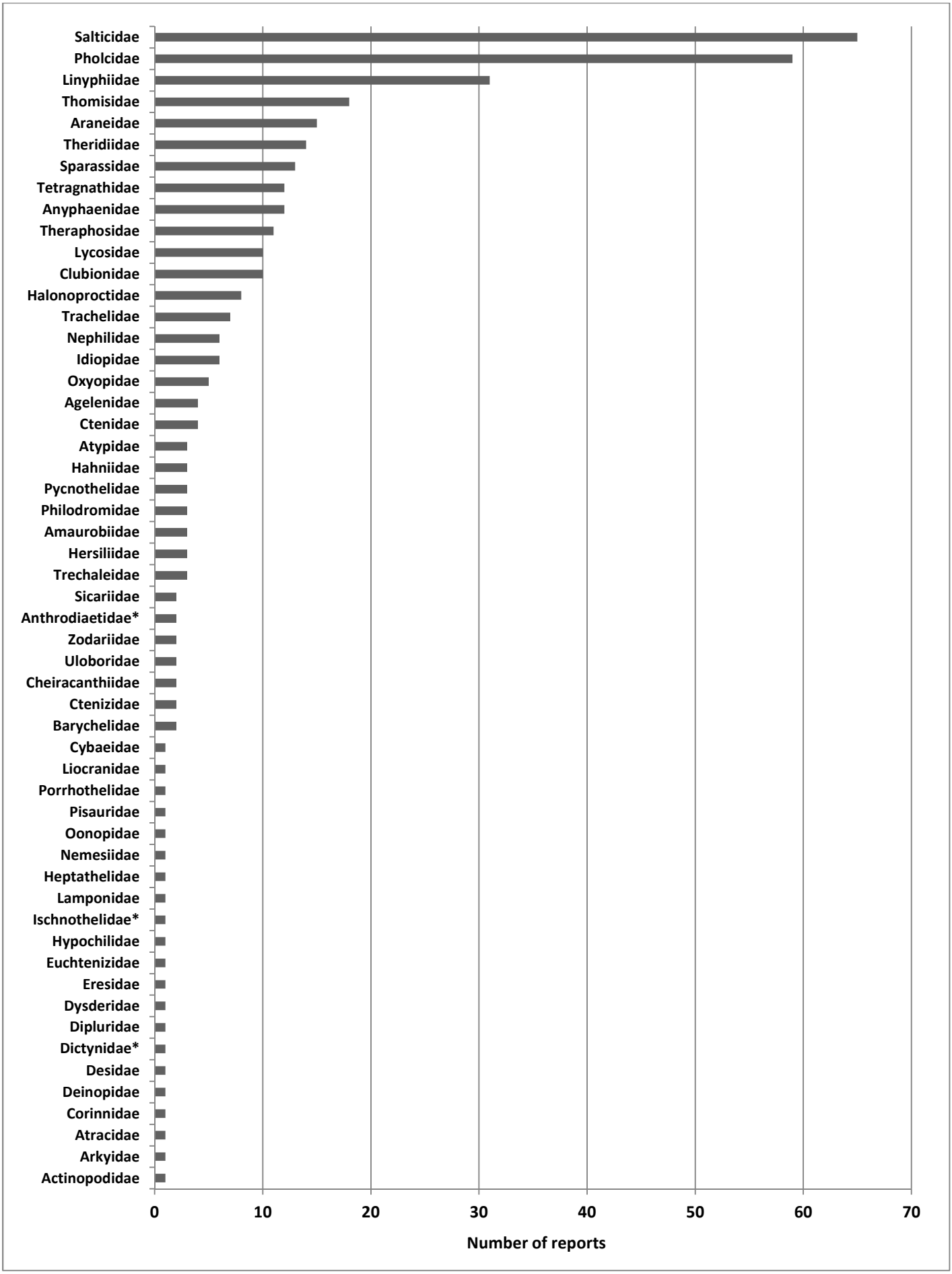
Salticidae
Pholcidae
Linyphiidae
Thomisidae
Araneidae
Theridiidae
Sparassidae
Tetragnathidae
Anyphaenidae
Theraphosidae
Lycosidae
Clubionidae
Halonoproctidae
Trachelidae
Nephilidae
Idiopidae
Oxyopidae
Agelenidae
Ctenidae
Atypidae
Hahniidae
Pycnothelidae
Philodromidae
Amaurobiidae
Hersiliidae
Trechaleidae
Sicariidae
Anthrodiaetidae*
Zodariidae
Uloboridae
Cheiracanthiidae
Ctenizidae
Barychelidae
Cybaeidae
Liocranidae
Porrhothelidae
Pisauridae
Oonopidae
Nemesiidae
Heptathelidae
Lamponidae
Ischnothelidae*
Hypochilidae
Euchtenizidae
Eresidae
Dysderidae
Dipluridae
Dictynidae*
Desidae
Deinopidae
Corinnidae
Atracidae
Arkyidae
Actinopodidae
0
10
20
30
40
50
60
70
Number of reports

Figure 1

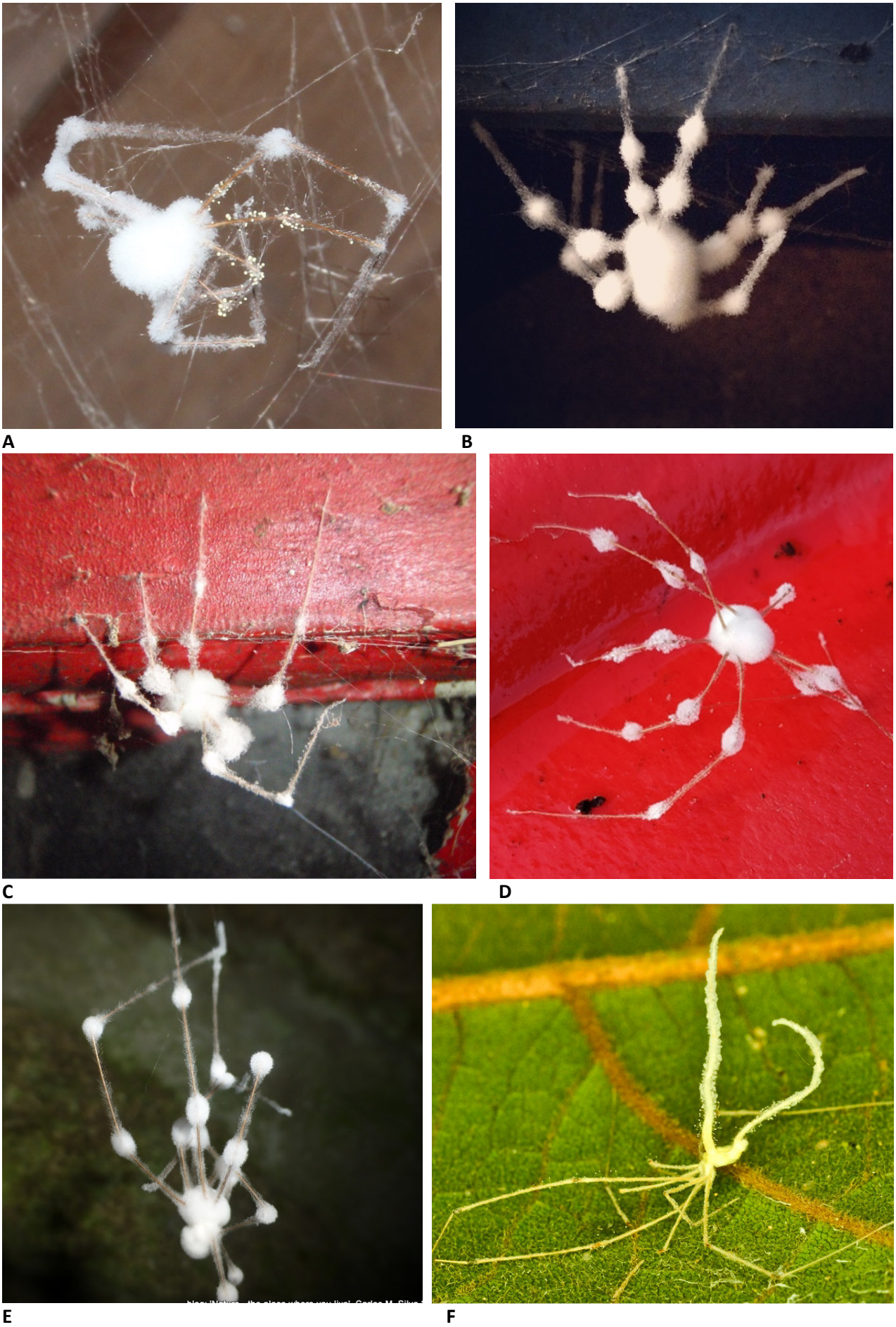

Figure 2

A

B

C

Figure 3

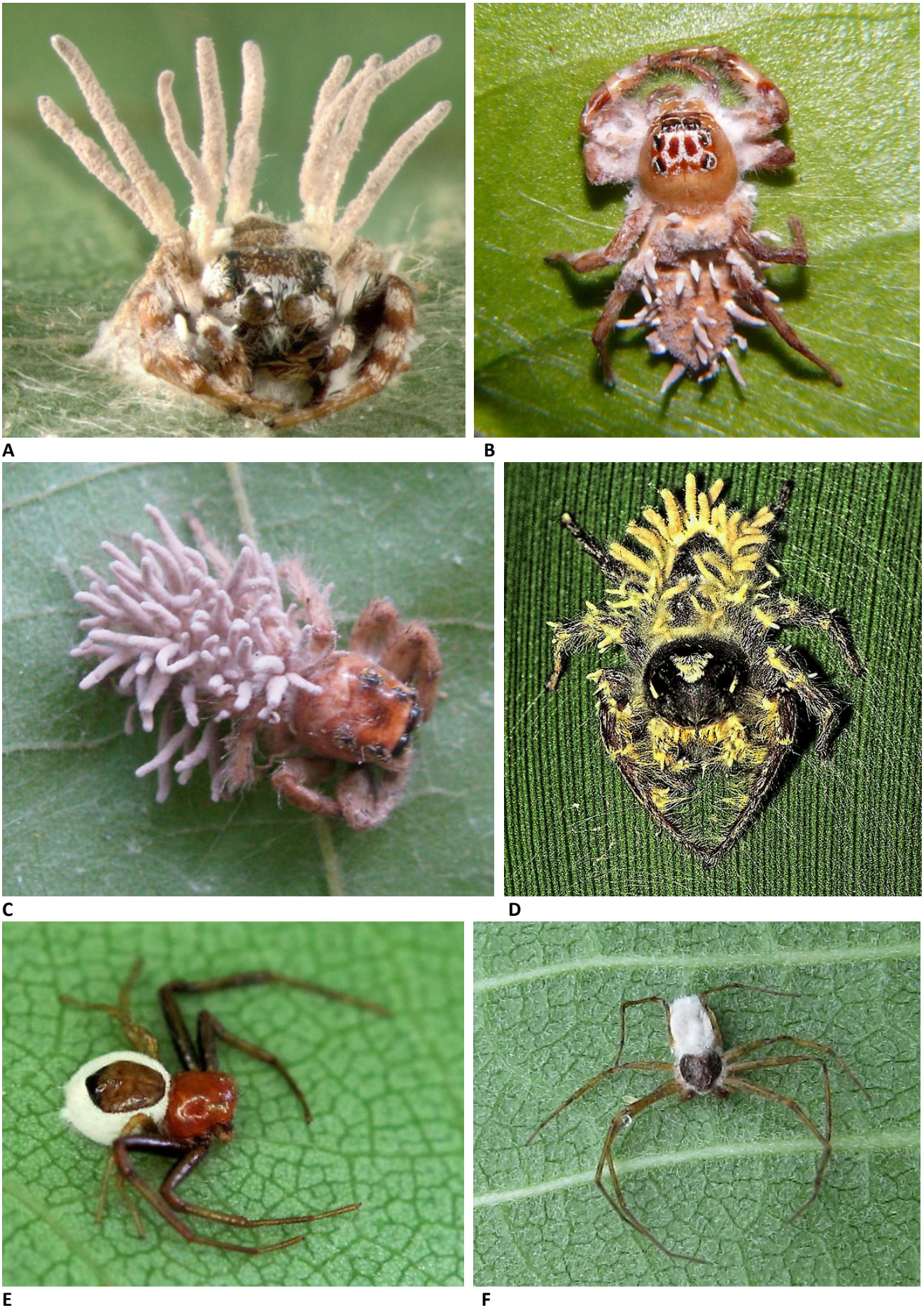

Figure 4

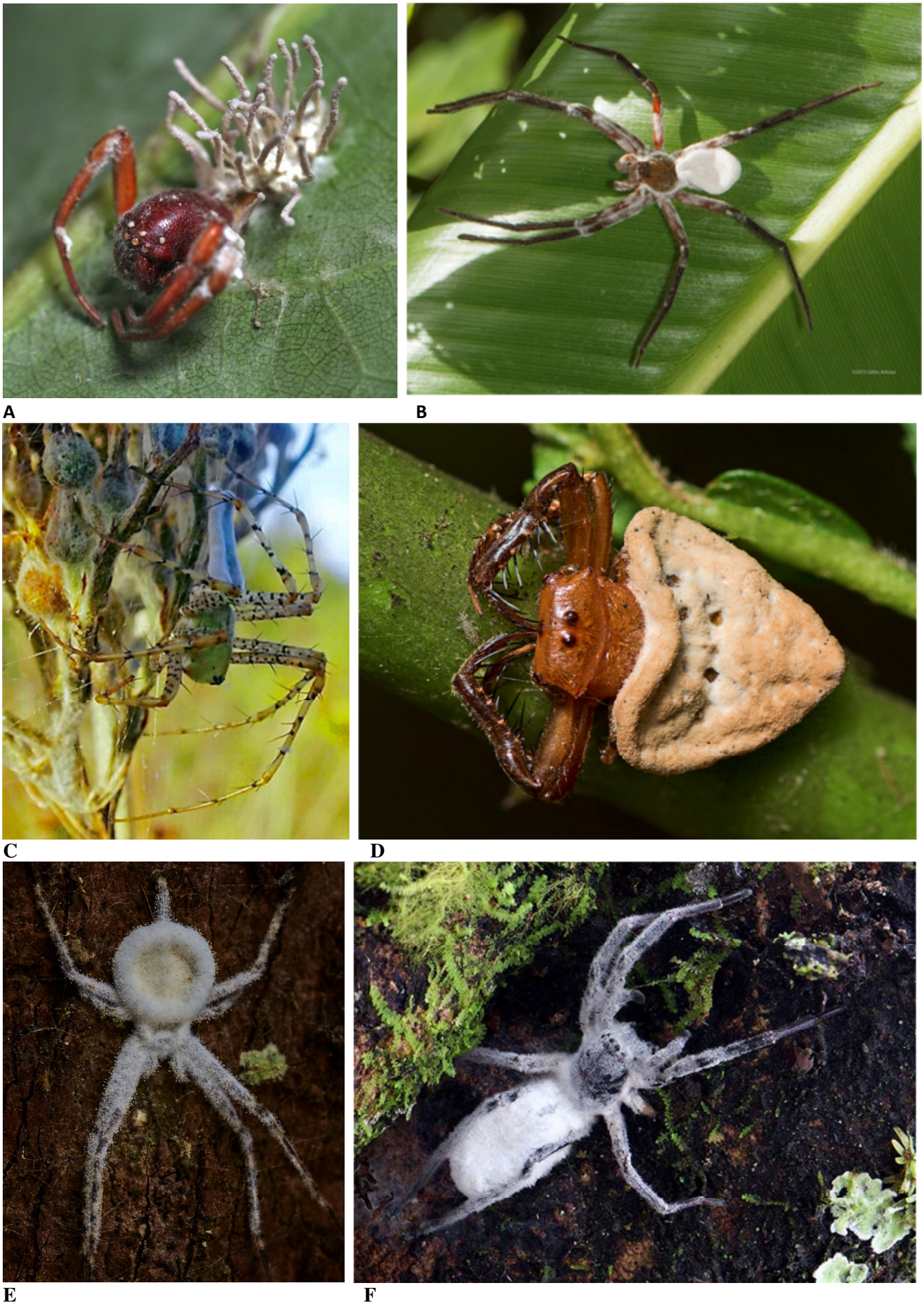

Figure 5

Figure 6

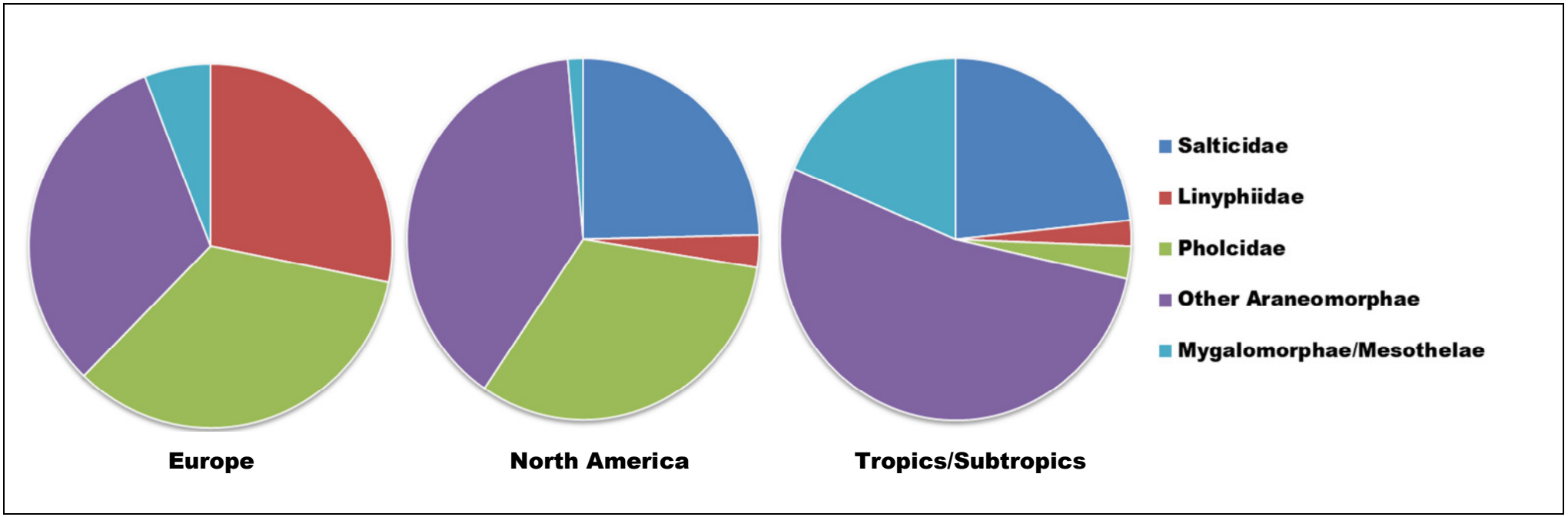
Salticidae
Linyphiidae
Pholcidae
Other Araneomorphae
Mygalomorphae/Mesothelae
Europe
North America
Tropics/Subtropics

Figure 7