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REVIEW

Spider-pathogenic fungi within Hypocreales (Ascomycota): their current nomenclature, diversity, and distribution

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Abstract

Spider-pathogenic fungi are widely distributed in the world. Our review shows at least eighty six spider- and harvestman-pathogenic fungi that are currently accommodated in genera *Akanthomyces* Lebert, *Beauveria* Vuill., *Clonostachys* Corda, *Cordyceps* Fr., *Engyodontium* de Hoog, *Gibellula* Cavara, *Hevansia* Luangsa-ard et al., *Hirsutella* Pat., *Hymenostilbe* Petch, *Lecanicillium* W. Gams & Zare, *Ophiocordyceps* Petch, *Purpureocillium* Luangsa-ard et al., and *Torrubiella* Boud. within Hypocreales. *Akanthomyces neoaraneogenum* (W.H. Chen, Y.F. Han, J.D. Liang, Z.Q. Liang & D.C. Jin) W.H. Chen, Y.F. Han & Z.Q. Liang, comb. nov. is also proposed here. Among the genera, *Gibellula*, *Hevansia*, *Torrubiella*, and *Akanthomyces* are exclusively or dominantly spider pathogens. *Gibellula pulchra*, *G. leiopus*, *P. atypicola*, *A. aranearum*, and *T. aranicida* are some of the cosmopolitan spider-pathogenic fungi. A total of twenty spider families and two harvestman families are known to be parasitized by hypocrealean fungi. Spider-pathogenic fungi are known from diverse areas of Europe, and Central and South America, but are only known from limited parts in Asia and Africa. However, east and southeast Asia shows the highest richness of spider-pathogenic fungi. Among three entomogenous families within Hypocreales, we show that the majority of the spider pathogens are distributed in Cordycipitaceae while a few in Ophiocordycipitaceae, but none in the family Clavicipitaceae. Through this review, we show that spiders constitute one of the major host groups of arthropod-associated fungi and hope a continuous interest will be generated to utilize such fungal resources through in vitro growth and extraction of useful bio-active secondary metabolites (extrolites).

Keywords Arachnids · Araneogenous fungi · Arthropod-pathogenic fungi · Fungal resource · New combination

Introduction

Different groups of fungi are associated with insects and spiders, among which the hypocrealeans (Ascomycota) are best known (Vega et al. 2012, Araújo and Hughes 2016). Spiders (phylum Arthropoda, class Arachnida, order Araneae), numbering more than 48,000 species (World Spider Catalog 2019), are found everywhere in the terrestrial regions, and are especially abundant around plants and under tree barks, dead leaves, fallen logs, or stones, or on the forest floor and underground burrows. Nearly-ninety hypocrealean pathogenic fungi have been identified on spiders. The spider-pathogenic fungi, by nature, cause mortality of spiders and produce small to occasionally large fruiting bodies on spider cadavers. The spider cadavers are usually found attached to the underside of leaves or on tree trunks, barks, decaying logs, and branches or on grass, leaf litters, and forest floors. Field observations have revealed a great diversity of spider-pathogenic fungi in the world (Petch 1923–1948; Mains

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1939–1955; Samson and Evans 1973–1992; Kobayasi and Shimizu 1976–1982b).

The first spider fungus was described on a *Ctinus* (*Ctenus*?) spider in Germany, which was attached to a piece of rotten wood with the help of white fungoid threads (Ditmar 1817; Gray 1858) (Fig. 1). The fungus *Isaria arachnophila* Ditmar was obscurely described as white, clavate, gregarious, simple, and subfasciculate with a wooly, loose texture. It was later renamed as *Hymenostilbe arachnophila* (Ditmar) Petch, with additional records from Denmark and Britain (Petch 1931). Mains (1950a, 1954) and Evans and Samson (1987) believed that Ditmar's fungus was actually *Akanthomyces aranearum* (Petch) Mains, the conidial stage of *Cordyceps thaxteri* Mains (Mains 1939), but not a *Hymenostilbe*. The second example of a spider fungus was *Isaria aranearum* Schwein. recorded in the USA (Schweinitz 1822), which was later synonymized with *Gibellula aranearum* P. Syd. by Petch (1932b). However, the identity of Schweinitz's fungus was doubted because of insufficient description (Mains 1950b; Samson and Evans 1992). Another spider-pathogenic fungus *Isaria gigantea* Mont. was reported by Montagne (1842) on *Mygale cubana* in Cuba, which was also treated as an incompletely described species (Massee 1895; Seaver 1910; Mains 1955). Interestingly, *Corethropsis pulchra* Sacc. was illustrated as a hyperparasitic fungus on spider and its isarioid clavae, producing loose mycelial covering with aspergillus-like, freely hanging, scattered conidiophores (Saccardo 1877) (Fig. 2). Cavara (1894), later, identified it as a new pathogen of spider and established a genus *Gibellula* based on it, naming Saccardo's fungus as *G. pulchra* (Sacc.) Cavara (Fig. 3). *Gibellula* species are some of the commonest spider pathogens in the world. *Isaria atypicola* Yasuda (Yasuda 1915, 1917), a common spider pathogen producing a 5–8-cm-tall light purple–colored asexual fruiting body, was first described in Japan as Ditmar's *I. arachnophila* (Yasuda 1894, Fig. 4). It is now classified in *Purpureocillium*, *P. atypicola* (Yasuda) Spatafora et al. (Spatafora et al. 2015).

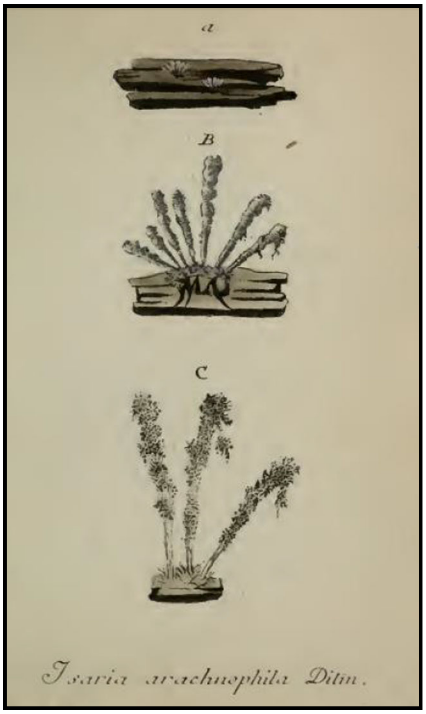

Fig. 1 *Isaria arachnophila* (Ditmar 1817)

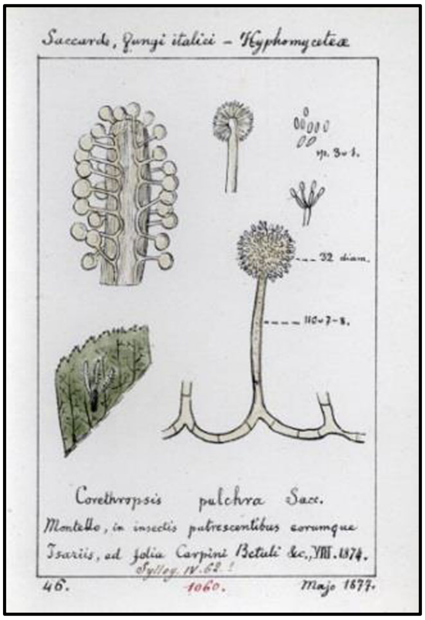

Fig. 2 *Corethropsis pulchra* (Saccardo 1877)

Besides the asexual morphs mentioned above, the first sexual morph on spider was described by Berkeley (1869) as *Cordyceps caloceroides* Berk. & M.A. Curtis in Cuba (Fig. 5). *Torrubiella aranicida* Boud. collected in France was another sexual morph on spider, but it completely lacked stromatic growth, in contrast with the well-developed stroma of *Cordyceps* (Boudier 1885; Boudier 1905–1910) (Fig. 6).

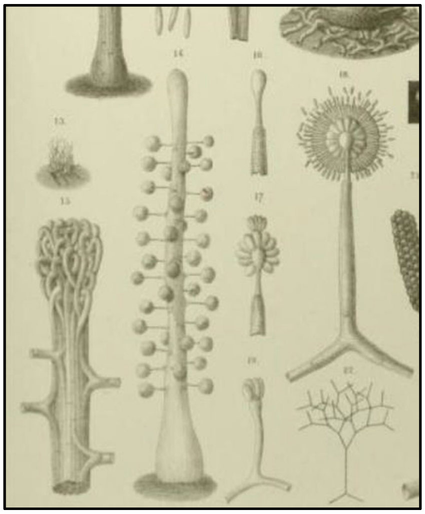

Fig. 3 *Gibellula pulchra* (Cavara 1894)

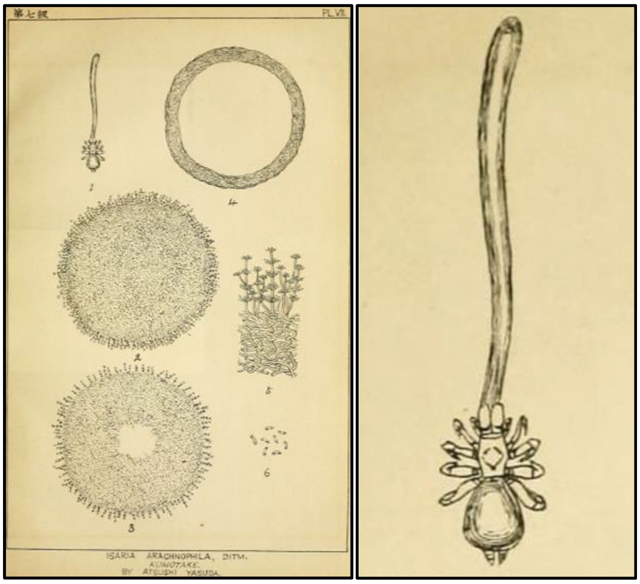

Fig. 4 *Isaria arachnophila* (Yasuda 1894; right, enlarged)

Apart from spiders, harvestmen (Class Arachnida, Order Opiliones) that resemble spiders and share similar ecological habitats are occasionally found parasitized by hypocrealean fungi. Nutritionally, spiders are mostly strict predators and feed on insects and other invertebrates, whereas harvestmen are omnivorous feeding on dead and decaying animal and plant materials including fungi (Coddington and Colwell 2001). Spider pathogens can be specifically termed araneogenous or araneopathogenic to show their host association different from insects (Evans and Samson 1987; Kubátová 2004).

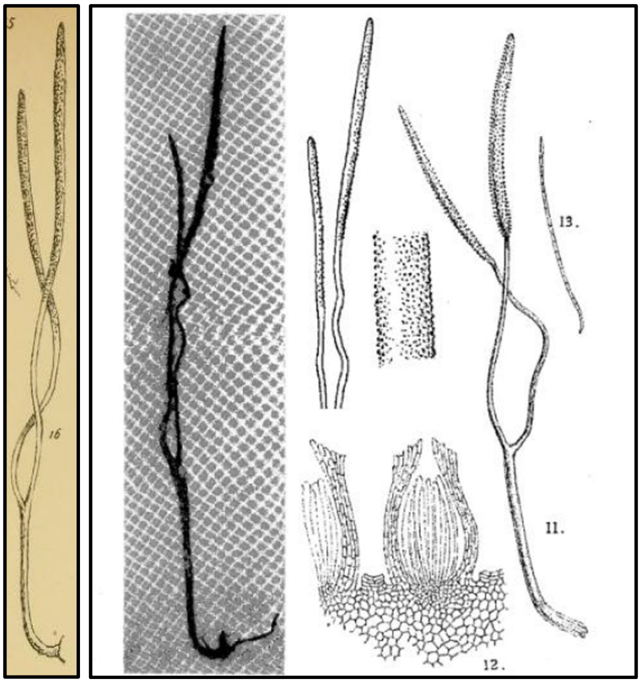

Fig. 5 *Cordyceps caloceroides* (left, Cooke 1892; right, Kobayasi 1977)

In this review, we have looked into the diversity of araneogenous fungi in order to get an overview of their current array of classification within Hypocreales. Currently, *Akanthomyces*, *Beauveria*, *Clonostachys*, *Cordyceps*, *Engyodontium*, *Gibellula*, *Hevansia*, *Hirsutella*, *Hymenostilbe*, *Lecanicillium*, *Ophiocordyceps*, *Purpureocillium*, and *Torrubiella* are described as spider-pathogenic genera within Hypocreales (Evans and Samson 1987; Evans 2013; Spatafora et al. 2015; Chen et al. 2016a; Kepler et al. 2017). The second objective is to know their distributions in the world based on the published literature and to analyze the micro-habitats where the spider cadavers are found, such as attachment to a particular tree or plant or occurrence in a special forest type.

Araneogenous genera within Hypocreales (Ascomycota)

Among the eleven families currently recognized in Hypocreales (Sun et al. 2017), araneogenous fungi are restricted to Cordycipitaceae and Ophiocordycipitaceae, with an exception in Bionectriaceae. Interestingly, no araneogenous fungus is known in another well-known entomopathogenic family, the Clavicipitaceae within Hypocreales. The araneogenous genera are arranged below alphabetically, regardless of their familial affinity.

Akanthomyces Lebert (Cordycipitaceae)

Akanthomyces is one of the oldest genera in Cordycipitaceae (Lebert 1858) that is morphologically characterized by white, cream, or flesh-colored cylindrical, attenuated synnematal growth covered by a hymenium-like layer of phialides producing catenulate conidia (Mains 1950a; Samson and Evans 1974; Hsieh et al. 1997). Currently, the genus is delimited to a clade accommodating its type species *A. aculeatus* Lebert that shows phylogenetic distinctness from *Cordyceps* and *Beauveria* (Kepler et al. 2017). The generic names *Lecanicillium* and *Torrubiella* are now synonymized with *Akanthomyces* (Kepler et al. 2017). On the other hand, akanthomyces-like species previously described on spiders are now mostly accommodated in a distinct genus *Hevansia* within Cordycipitaceae based on their phylogeny (Kepler et al. 2017). Recently, new spider pathogens with *Cordyceps*-, *Isaria*-, *Lecanicillium*-, or *Torrubiella*-like morphs have been described in *Akanthomyces* (Kepler et al. 2017; Mongkolsamrit et al. 2018). Here, we altogether list ten species of *Akanthomyces* on spiders (Table 1).

Akanthomyces aranearum (≡ *Hymenostilbe aranearum* Petch) is one of the earlier known spider pathogens with wide distribution and is connected with the sexual morph *Cordyceps thaxteri* (Petch 1932c) (Table 1).

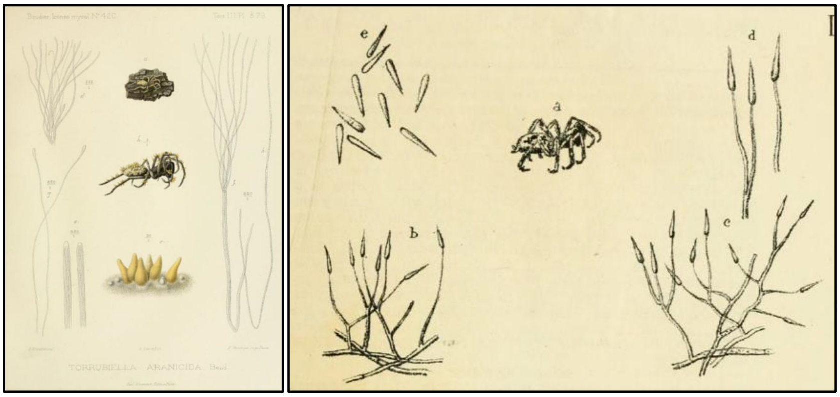

Fig. 6 *Torrubiella aranicida* (Boudier 1905–1910), left; *Isaria cuneispora* (Boudier 1887), right

Akanthomyces lecanii (Zimm.) Spatafora et al. (≡ *Cephalosporium lecanii* Zimm., = *Lecanicillium lecanii* (Zimm.) Zare and W. Gams) is another *Akanthomyces* species on spider (Evans and Samson 1982b) (Table 1). It is, however, a rare case that its sexual morph, *Cordyceps confragosa* (Mains) G.H. Sung et al., is recorded outside of arachnids, i.e., on a large scale-insect (class Insecta, order Hemiptera) in Brazil (Mains 1949; Sung et al. 2007) (Table 1). *Akanthomyces coccidioperitheciatus* (Kobayasi & Shimizu) Spatafora et al. (≡ *Cordyceps coccidioperitheciata* Kobayasi & Shimizu) and *A. ryukyuensis* (Kobayasi & Shimizu) Mongkolsamrit et al. (≡ *Torrubiella ryukyuensis* Kobayasi & Shimizu) are other previously recorded spider fungi (Kepler et al. 2017; Mongkolsamrit et al. 2018) (Table 1). Recently described *Akanthomyces* species on spiders include *A. kanyawimiae* Mongkolsamrit et al., *A. sulphureus* Mongkolsamrit et al., *A. thailandicus* Mongkolsamrit et al. and *A. waltergamsii* Mongkolsamrit et al. (Mongkolsamrit et al. 2018), and *A. araneogenum* Z.Q. Liang et al. (Chen et al. 2018) (Table 1). Among them, *A. sulphureus* and *A. thailandicus* are connected with *Torrubiella*-like sexual morphs.

Chen et al. (2017b) described *Lecanicillium araneogenum* W.H. Chen et al. on an *Araneus* spider. Based on its phylogenetic placement within the *Akanthomyces* clade (Zhou et al. 2018), a new combination for *L. araneogenum* in *Akanthomyces* is proposed here.

Akanthomyces neoaraneogenum (W.H. Chen, Y.F. Han, J.D. Liang, Z.Q. Liang & D.C. Jin) W.H. Chen, Y.F. Han & Z.Q. Liang, **comb. nov.**

Table 1 *Akanthomyces* spp. parasitizing spiders and their distribution

Akanthomyces spp.	Distribution
A. aranearum	Sri Lanka (Petch 1932c), USA (Mains 1950a), Britain (Leatherdale 1970), Ghana and the Netherlands (Samson and Evans 1974), Far East Russia (Koval 1974), Thailand (Hywel-Jones 1996), Taiwan (Hsieh et al. 1997), Republic of Serbia (Savić et al. 2016)
= *C. thaxteri*	US (Mains 1939, 1950a), Far East Russia (Koval 1974), Estonia and Ukraine (Kautman and Kautmanova 2009)
A. araneogenum	China (Chen et al. 2018)
A. coccidioperitheciatus ≡ *C. coccidioperitheciata*	Japan (Kobayasi and Shimizu 1982a)
A. kanyawimiae	Thailand (Mongkolsamrit et al. 2018)
A. lecanii = *C. confragosa*	Galápagos Islands, Ecuador (Evans and Samson 1982b) Brazil (Mains 1949)
A. neoaraneogenum	China (Chen et al. 2017b)
A. ryukyuensis ≡ *T. ryukyuensis*	Japan (Kobayasi and Shimizu 1982b)
A. sulphureus	Thailand (Mongkolsamrit et al. 2018)
A. thailandicus	Thailand (Mongkolsamrit et al. 2018)
A. waltergamsii	Thailand (Mongkolsamrit et al. 2018)

MycoBank: MB 831104.

Basionym: *Lecanicillium araneogenum* W.H. Chen, Y.F. Han, J.D. Liang, Z.Q. Liang & D.C. Jin, Phytotaxa 305: 30, 2017.

non *Akanthomyces araneogenum* Z.Q. Liang, W.H. Chen & Y.F. Han, Phytotaxa 379: 69, 2018.

Beauveria Vuill. (Cordycipitaceae)

Beauveria is one of the best known entomopathogenic genera within Hypocreales and parasitizes a wide range of insects. It forms a sister clade with *Cordyceps* in Cordycipitaceae (Kepler et al. 2017) and produces cordyceps-like sexual morphs where known (summarized in Shrestha et al. 2014a). Currently, more than twenty *Beauveria* species are recognized (Imoulan et al. 2016; Kepler et al. 2017). Despite its global distribution and a wide host range, *Beauveria* is rarely known on spiders (Evans and Samson 1987). *Beauveria araneola* W.H. Chen et al. is the only *Beauveria* species that is known as spider pathogen (Chen et al. 2017a). Besides it, *B. bassiana* (Bals.) Vuill., popularly known as a white muscardine fungus, was once reported on spider in Britain (Petch 1932a).

Clonostachys Corda (Bionectriaceae)

Clonostachys aranearum W.H. Chen et al. is the only spider fungus known outside Cordycipitaceae and Ophiocordycipitaceae within Hypocreales. It was recently described in China (Chen et al. 2016a).

Cordyceps Fr. (Cordycipitaceae)

In conventional sense, *Cordyceps* is described as a broad and cosmopolitan genus producing well-developed stipitate stroma on insects and spiders and a few fungi (Shrestha et al. 2014b). However, due to its polyphyletic nature, it was segregated into separate genera under 3 families of Hypocreales: Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae (Sung et al. 2007). *Cordyceps* s.s. is now delimited to a small clade in Cordycipitaceae that accommodates its type species *C. militaris* (L.) Fr. (Sung et al. 2007; Kepler et al. 2017).

During the recent phylogenetic revision of Cordycipitaceae, the use of the generic name *Isaria* was rejected in favor of *Cordyceps*, circumscribing some of its species to *Cordyceps* based on their phylogenetic placements (Kepler et al. 2017). In the past centuries, *Isaria* was very commonly used for asexual morphs growing not only on insects and spiders but also on other organic substrates such as animal excretes, soil, and fungal and plant parts (Saccardo 1886; Lindau 1910). After observing many isarioid forms, Petch (1932c, 1934) concluded *Isaria* as a form-genus consisting of a heterogeneous mixture of species, with little in common. Nearly 120 *Isaria* species were described as entomogenous that are now distributed among different hypocrealean genera *Akanthomyces*, *Beauveria*, *Gibellula*, *Hirsutella*, *Hymenostilbe*, and *Metarhizium* (Mains 1955; Koval 1984).

Eight spider-pathogenic fungi are currently described in *Cordyceps* that are mainly distributed in South America or east Asia (Table 2). Among them, *C. caloceroides* was the earliest known species on spider (Berkeley 1869) (Table 2) (Fig. 5). Based on the ascospore morphology, it was transferred to *Ophiocordyceps* as *O. caloceroides* (Berk. & M.A. Curtis) Petch (Petch 1933), but was recently resurrected to *Cordyceps* based on its phylogenetic affinity (Chiriví et al. 2017). *Cordyceps wittii* Henn., collected on a large *Mygale* spider (Hennings 1897) (Fig. 7), was synonymized with *C. caloceroides* (Petch 1933). Other *Cordyceps* species on spiders are *C. grenadensis* Mains, *C. singeri* Mains, and *C. ignota* Marchion. (Mains 1954) (Table 2). *Cordyceps arachnogena* Kobayasi (Kobayasi and Shimizu 1976), *C. ogurasanensis* Kobayasi & Shimizu, and *C. pseudonelumboides* Kobayasi & Shimizu (Kobayasi and Shimizu 1982a) are other species known on spiders. *Cordyceps nidus* T. Sanjuan et al. is a recently described species on young trapdoor spiders (Chiriví et al. 2017). Among *Cordyceps* species known on spiders, *C. arachnogena*, *C. grenadensis*, *C. ignota*, and *C. pseudonelumboides* are currently placed *incertae sedis* within Hypocreales (Sung et al. 2007). Besides above species, an unidentified species of *Cordyceps* was described on a linyphiid spider on the Arctic island Jan Mayen (Nentwig 1985). Cordyceps-like sexual morphs are also found associated with species of *Akanthomyces*, *Beauveria*, *Hevansia*, and *Purpureocillium*.

Engyodontium de Hoog (Cordycipitaceae)

Two *Engyodontium* species were previously described on spiders by Gams et al. (1984), both of which are now transferred to *Lecanicillium* (Zare and Gams 2001). They are *E. arachnophilum* H.C. Evans and Samson associated with *Torrubiella alba* Petch and *E. aranearum* (Cavara) W. Gams et al. *Engyodontium rectidentatum* (Matsush.) W. Gams et al., mainly occurring on soil, was recently found on a spider *Meta menardi* in Czech Republic (Kubátová 2017). Earlier, a species of *Engyodontium* was recorded on a crab spider *Thanatus* in South Africa (Rong & Grobbelaar 1998).

Gibellula Cavara (Cordycipitaceae)

Gibellula is an exclusively spider-pathogenic genus producing aspergillus-like conidiophores (Cavara 1894; Evans 2013). Its members form a monophyletic clade within Cordycipitaceae and are connected with *Torrubiella*-like sexual morphs where known (Evans 2013; Kepler et al. 2017). *Gibellula* species are distributed worldwide, but are mostly

Table 2 *Cordyceps* spp. parasitizing spiders and their distribution

Cordyceps spp.	Distribution
C. arachnogena	Papua New Guinea (Kobayasi and Shimizu 1976)
C. caloceroides	Bolivia, Colombia and Cuba (Berkeley 1869, Chiriví et al. 2017), Ecuador (Hennings 1897), Brazil (Barbosa et al. 2016), Argentina (Manfrino et al. 2017)
C. grenadensis	Grenada (Mains 1954)
C. ignota	Argentina (Mains 1954)
C. nidus	Colombia, Ecuador (Chiriví et al. 2017)
C. ogurasanensis	Japan (Kobayasi and Shimizu 1982a)
C. pseudonelumboides	Japan (Kobayasi and Shimizu 1982a)
C. singeri	Argentina (Mains 1954)

recorded from the tropics (Samson and Evans 1992). Some records of *Gibellula* species are also made from temperate regions of New Zealand, Southern Chile, and the Falkland Islands (Rong and Botha 1993).

Among seventeen *Gibellula* species, *G. pulchra*, the type species, is one of the most commonly distributed spider-pathogenic fungi in the world and is distributed from temperate to subtropical and tropical regions (Petch 1932b; Samson and Evans 1973, 1992) (Table 3). In Taiwan, it is the most predominant species, encountered throughout the year in all habitats, ranging from 200 to 2500 m asl (Tzean et al. 1997b). Many synonyms have been proposed for *G. pulchra*, causing its nomenclatural history long, complicated, and confusing (Table 3). We follow Mains (1950b) to enlist earlier synonyms of *G. pulchra* (Table 3). He recognized *Corethropsis australis* Speg., *G. suffulta* Speare, and *G. haygarthii* Van der Byl as synonyms of *G. pulchra*. *Gibellula arachnophila* Johnst. (non *G. arachnophila* (Ditmar) Vuill.), *G. arachnophila* f. *macropus* Vuill. ex Maubl., and *G. aranearum* were also synonymized with *G. pulchra* (Mains 1950b; Samson and Evans 1992). Apart from Mains's treatment, *G. tropicalis* Sawada was treated as a synonym of *G. pulchra* (Tzean et al. 1997b). *Gibellula globosa* Kobayasi & Shimizu associated with *Torrubiella globosa* Kobayasi & Shimizu and *G. globosostipitata* Kobayasi & Shimizu associated with *T. globosostipitata* Kobayasi & Shimizu were found indistinguishable from *G. pulchra* and thus synonymized with the latter (Samson and Evans 1992) (Table 3). Mains (1950b) named *T. arachnophila* var. *pulchra* Mains as the sexual morph of *G. pulchra*, which was later elevated to the species rank *T. pulchra* (Mains) Koval (Koval 1984).

Gibellula leiopus (Vuill.) Mains is another globally distributed spider fungus (Kubátová 2004) (Table 3). It is more common than *G. pulchra* in North America (Mains 1950b; Strongman 1991). *Gibellula leiopus*, originally described as *G. arachnophila* f. *leiopus* Vuill. ex Maubl. (Maublanc 1920), is associated with *Torrubiella arachnophila* (Johnst.) Mains var. *leiopus* Mains (Mains 1950b; Samson and Evans 1973), which was later elevated to the species rank *T. leiopus* (Mains) Kobayasi and Shimizu (Kobayasi and Shimizu 1977). Bałazy (1970) confirmed that *I. perexigua* Kobayasi (Kobayasi 1941), which was renamed as *Gibellula perexigua* (Kobayasi) Koval (Koval 1984), was identical with *G. leiopus* (Table 3). Tzean et al. (1997b) treated *Gibellula araneae* Sawada as another synonym of *G. leiopus* (Table 3).

Few more *Gibellula* species are described in Asia, Africa, and South America, including Oceania (Table 3). They are *G. alata* Petch, *G. clavulifera* (Petch) Samson and Evans (≡ *Spicaria clavulifera* Petch), *G. clavulifera* var. *major* Tzean et al., and *G. clavulifera* var. *alba* Humber & Rombach associated with *Torrubiella ratticaudata* Humber & Rombach (Table 3).

Gibellula brunnea Samson & Evans, *G. clavata* Samson & Evans associated with *Torrubiella clavata* Samson & Evans,

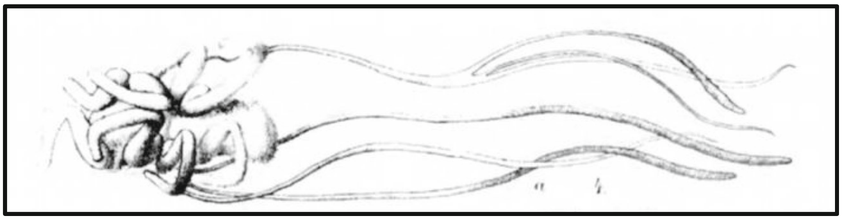

Fig. 7 *Cordyceps wittii* (Hennings 1897)

Table 3 *Gibellula* spp. and their distributions

Gibellula spp.	Distribution
G. alata	Sri Lanka (Petch 1932b), Ghana (Samson and Evans 1973)
G. brunnea	Brazil (Samson and Evans 1992)
G. clavata = *T. clavata*	Ecuador (Samson and Evans 1992)
G. clavispora	China (Chen et al. 2016b)
G. clavulifera	Sri Lanka (Petch 1932b), Ghana (Samson and Evans 1977), Thailand (Luangsa-ard et al. 2010), China (Chen et al. 2014)
G. clavulifera var. *alba* = *T. ratticaudata*	Solomon Islands (Humber and Rombach 1987)
G. clavulifera var. *major*	Taiwan (Tzean et al. 1997b), Mexico (López and García 2011)
G. curvispora	China (Han et al. 2013)
G. dabieshanensis = *T. dabieshanensis*	China (Huang et al. 1998a)
G. dimorpha = *T. dimorpha*	Taiwan (Tzean et al. 1998), Thailand (Luangsa-ard et al. 2010), Japan (?) (Okuzawa 2012), Brazil (Costa 2014)
G. gamsii	Thailand (Kuephadungphan et al. 2019)
G. leiopus	US and Canada (Mains 1950b), Czech Republic (Fassatiová 1960, Kubátová 2004), Poland (Bałazy 1970), Ghana (Samson and Evans 1973), Kuril islands of Russia (Koval 1974), Japan (Kobayasi and Shimizu 1977), Trinidad (Evans and Samson 1987), Mexico (Sánchez-Peña 1990), Taiwan (Tzean et al. 1997b), Sweden (Kubátová 2004), Austria (Tkaczuk et al. 2011), China (Chen et al. 2014), Brazil (Costa 2014), Republic of Serbia (Savić et al. 2016)
≡ *G. arachnophila* f. *leiopus*	Brazil (Maublanc 1920)
= *G. araneae*	Taiwan (Sawada 1928)
= *Isaria perexigua*	Japan (Kobayasi 1941), Far East Russia (Koval 1963)
= *G. perexigua*	Koval (1984)
= *T. arachnophila* var. *leiopus*	US (Mains 1950b), Ghana (Samson and Evans 1973)
= *T. leiopus*	Japan (Kobayasi and Shimizu 1977, McNeil 2012)
G. mainsii	Brazil (Samson and Evans 1992)
G. mirabilis	Ecuador (Samson and Evans 1992)
G. pulchra	US including Hawaii, Puerto Rico, Venezuela, Guyana, Trinidad, Chile, Papua New Guinea (Mains 1950b), Ghana (Samson and Evans 1973), Belgium (Bosselaers 1984), Solomon Islands (Humber and Rombach 1987), Mexico (Sánchez-Peña 1990), Canada (Strongman 1991), Ecuador and Brazil (Samson and Evans 1992), Spain (Santamaria and Girbal 1996), Taiwan (Tzean et al. 1997b), South Africa (Rong and Botha 1993), Poland (Bałazy 2004), Turkey (Selçuk et al. 2004), Austria (Tkaczuk et al. 2011), China (Chen et al. 2014), Brazil (Costa 2014)
≡ *Corethropsis pulchra*	Italy (Saccardo 1877)
= *Corethropsis australis*	Argentina (Spegazzini 1882)
= *G. suffulta*	Hawaii (Speare 1912), China (Gao 1981)
= *G. arachnophila* illeg.	Puerto Rico, Cuba (Johnston 1915)
= *G. arachnophila* f. *macropus*	Brazil (Maublanc 1920)
= *G. aranearum*	Papua New Guinea (Sydow 1922), Britain (Petch 1931, 1948), Far East Russia (Koval 1963)
= *G. haygarthii*	South Africa (Van der Byl 1922)
= *G. tropicalis*	Taiwan (Sawada 1959, Tzean et al. 1997b)
= *G. globosa*	Japan (Kobayasi and Shimizu 1982b)
= *G. globosostipitata*	Japan (Kobayasi and Shimizu 1982b)
= *T. arachnophila* var. *pulchra*	US (Mains 1950b), Ghana (Samson and Evans 1973)
= *T. pulchra*	Russia (Koval 1984)
G. shennongjiaensis	China (Zou et al. 2016)
G. unica	Taiwan (Tzean et al. 1997b), Thailand (Luangsa-ard et al. 2010), Japan (?) (Okuzawa 2012).

G. dabieshanensis Huang et al. associated with *T. dabieshanensis* Huang et al., *G. dimorpha* Tzean et al. associated with *T. dimorpha* Tzean et al., *G. clavispora* Z.Q. Liang et al., *G. curvispora* Y.F. Han et al., *G. gamsii*

Kuephadungphan et al., *G. mainsii* Samson & Evans, *G. mirabilis* Samson & Evans, *G. shennongjiaensis* X. Zou et al., and *G. unica* Tzean et al. are other *Gibellula* species described on spiders (Table 3). *Gibellula araneicola* Sawada was described on an *Aranea* spider by Sawada (1959) in Taiwan, but its identity was doubted by Tzean et al. (1997b) due to its isariod morph. Besides above *Gibellula* species, few more remain undescribed, especially those collected in Brazil (Costa 2014).

Hevansia Luangsa-ard et al. (Cordycipitaceae)

Hevansia is a recently established genus that is phylogenetically splitted from *Gibellula* (Kepler et al. 2017) and mostly accommodates asexual morphs on spiders that were previously described under *Akanthomyces*. It is also an exclusively spider-pathogenic genus and shows distribution mainly in Asia, Oceania, and Africa. Among eight *Hevansia* species, *H. arachnophila* (Petch) Luangsa-ard et al. (≡ *Trichosterigma arachnophilum* Petch, = *Akanthomyces arachnophilus* (Petch) Samson & H.C. Evans) connected with *Torrubiella flava* Petch (Petch 1923) is the earliest known species and is widely distributed (Table 4). Doi (1977) explained the asexual morph of *T. flava* as *Isaria*-like.

Hevansia novoguineensis (Samson & B.L. Brady) Luangsa-ard et al. (≡ *Akanthomyces novoguineensis* Samson & B.L. Brady) and *H. nelumboides* (Kobayasi & Shimizu) Luangsa-ard et al. (≡ *C. nelumboides* Kobayasi & Shimizu) are other widely distributed species (Table 4). Other *Hevansia* species are *H. ovalongata* (L.S. Hsieh et al.) Luangsa-ard et al. (≡ *A. ovalongatus* L.S. Hsieh et al.), *H. cinerea* (Hywel-Jones) Luangsa-ard et al. (≡ *A. cinereus* Hywel-Jones), *H. koratensis* (Hywel-Jones) Luangsa-ard et al. (≡ *A. koratensis* Hywel-Jones), *H. websteri* (Hywel-Jones) Luangsa-ard et al. (≡ *A. websteri* Hywel-Jones) and *H. longispora* (B. Huang et al.) Luangsa-ard et al. (≡ *A. longisporus* B. Huang et al.) (Table 4).

Hirsutella Pat. (Ophiocordycipitaceae)

Hirsutella is a large, heterogeneous, asexual genus with nearly hundred species that are awaiting phylogenetic revision (Spatafora et al. 2015). Majority of *Hirsutella* species have been shown to form a monophyletic clade with *Ophiocordyceps* within Ophiocordycipitaceae (Sung et al. 2007). Among *Hirsutella* fungi, *H. darwinii* H.C. Evans & Samson is the only recorded species on spider that was collected in Galápagos Islands (Evans and Samson 1982b).

Hymenostilbe Petch (Ophiocordycipitaceae)

Hymenostilbe kedrovensis Koval is the only *Hymenostilbe* sp. recorded on spider in Far East Russia (Koval 1967). Samson and Evans (1975), however, assumed the fungus as an *Akanthomyces* and is now awaiting for its correct phylogenetic position.

Lecanicillium Gams and Zare (Cordycipitaceae)

Lecanicillium is a heterogeneous genus, widely distributed within Cordycipitaceae, and is found parasitizing various hosts including arthropods, nematodes, plants, and fungi (Sukarno et al. 2009). Among *Lecanicillium* species currently placed *incertae sedis* within Cordycipitaceae, three species are recorded on spiders (Table 5). The first is *L. aranearum*

Table 4 *Hevansia* spp. parasitizing spiders and their distribution

Hevansia spp.	Distribution
H. arachnophila = *T. flava*	Sri Lanka (Petch 1923), Ghana (Samson and Evans 1974), Thailand (Hywel-Jones 1996)
	Sri Lanka (Petch 1923), Ghana (Samson and Evans 1974), Taiwan (Kobayasi and Shimizu 1981, Tzean et al. 1998), Japan (Kobayasi and Shimizu 1982b)
H. cinerea	Thailand (Hywel-Jones 1996)
H. koratensis	Thailand (Hywel-Jones 1996)
H. longispora	China (Huang et al. 2000)
H. nelumboides ≡ *C. nelumboides*	Japan (Kobayasi and Shimizu 1977), Taiwan (Kobayasi and Shimizu 1981), Thailand (Luangsa-ard et al. 2012), China (Qiu et al. 2012)
H. novoguineensis	Papua New Guinea (Samson and Brady 1982), Thailand (Hywel-Jones 1996), Taiwan (Hsieh et al. 1997), China (Huang et al. 1998c), Japan (Okuzawa 2012)
H. ovalongata	Taiwan (Hsieh et al. 1997), Japan (Okuzawa 2012)
H. websteri	Thailand (Hywel-Jones 1996)

Table 5 *Lecanicillium* spp. parasitizing spiders and their distribution

Lecanicillium spp.	Distribution
L. aranearum = *T. alba*	Sri Lanka (Petch 1932c), Ghana and India (Zare and Gams 2001)
L. araneicola	Indonesia (Sukarno et al. 2009)
L. tenuipes	US, Britain, Italy, Germany, France (Petch 1937), cosmopolitan (Gams et al. 1984), Spain (Zare and Gams 2001)

(Petch) Zare & W. Gams (≡ *Cephalosporium aranearum* Petch, = *Engyodontium arachnophilum*), associated with *Torrubiella alba* Petch (Table 5). Others are *L. tenuipes* (Petch) Zare & W. Gams (≡ *Acremonium tenuipes* Petch, = *Engyodontium aranearum*) and *L. araneicola* Sukarno & Kurihara. *Lecanicillium tenuipes* is widely distributed (Petch 1937; Gams et al. 1984) (Table 5). Chen et al. (2017b) recently described *Lecanicillium araneogenum* Wan H. Chen et al. on an *Araneus* spider. It is now transferred to *Akanthomyces* as *A. neoaraneogenum*.

Ophiocordyceps Petch (Ophiocordycipitaceae)

Ophiocordyceps is the largest genus among entomopathogenic genera within Hypocreales, with more than 200 species, majority of which were previously placed in *Cordyceps* (Sung et al. 2007; Spatafora et al. 2015; Shrestha et al. 2017a). Despite high species richness of *Ophiocordyceps*, only seven species are known on spiders (Table 6). Among them, *O. verrucosa* (Mains) B. Shrestha et al. (≡ *Hymenostilbe verrucosa* Mains) shows the widest distribution, followed by *O. engleriana* (Henn.) G.H. Sung et al. (≡ *C. engleriana* Henn., Table 6, Fig. 8). In addition to spider (Mains 1950a), *O. verrucosa* is also recorded on harvestmen of Phalangiidae (Leatherdale 1970). Similarly, an *Ophiocordyceps* sp., similar to *O. engleriana*, was described on free-living spiders in Ecuador (Evans 2013). Another species recorded on spider is *O. arachneicola* (Kobayasi) G.H. Sung et al. (≡ *C. arachneicola* Kobayasi) associated with *Hymenostilbe kobayasii* Koval (Table 6). *Ophiocordyceps mrciensis* (Aung et al.) G.H. Sung et al. (≡ *C. mrciensis* Aung et al.), *Ophiocordyceps aranearum* (Petch) B. Shrestha et al. (≡ *Synngliocladium aranearum* Petch), *O. ghanensis* (Samson & H.C. Evans) B. Shrestha et al. (≡ *Hymenostilbe ghanensis* Samson & H.C. Evans) and *O. spiculata* (B. Huang et al.) B. Shrestha et al. (≡ *Hymenostilbe spiculata* B. Huang et al.) are other species parasitic on spiders (Table 6).

Purpureocillium Luangsa-ard et al. (Ophiocordycipitaceae)

Purpureocillium was established based on *Penicillium lilacinum* Thom (Luangsa-ard et al. 2011). Among *Purpureocillium* species, *P. atypicola* (Yasuda) Spatafora et al. is the only species known on spider (Yasuda, 1915, 1917; Spatafora et al. 2015). It was first described in Japan as *Isaria arachnophila* by Yasuda (1894) (Fig. 3). Later, Yasuda (1915, 1917) himself showed that Japanese *I. arachnophila* was different from *I. arachnophila* of Ditmar, and hence renamed it *I. atypicola*. Petch (1939) transferred *I. atypicola* to *Spicaria*, *S. atypicola* (Yasuda) Petch, and Samson (1974) one more time transferred it to *Nomuraea*, *N. atypicola* (Yasuda) Samson. It is widely known from Central and South America, Africa, North America, and East Oceania besides Asia (Table 7) and sometimes viewed as a species complex (Evans 2013). Kobayasi (1941) reported it as most commonly found in the gardens and road sides in Japan. Greenstone et al. (1987) have shown a broad range of arachnids, spanning to 17 species in 10 families, susceptible to *P. atypicola*. Its sexual morph, *Cordyceps cylindrica* Petch (Petch 1937), is occasionally collected from Asia and Trinidad (Table 7). Li et al. (2005) considered *Spicaria araneae* Sawada collected in Japan (Sawada 1914) and Taiwan (Sawada 1919) as a synonym of *P. atypicola*.

Table 6 *Ophiocordyceps* spp. parasitizing spiders and their distribution

Ophiocordyceps spp.	Distribution
O. arachneicola = *H. kobayasii*	Japan (Kobayasi 1941), Far East Russia (Koval 1976)
O. aranearum ≡ *S. aranearum*	Britain (Petch 1932a)
O. engleriana	Cameroon (Hennings 1897), Guyana (Petch 1935)
O. ghanensis ≡ *H. ghanensis*	Ghana (Samson and Evans 1975)
O. mrciensis	Thailand (Aung et al. 2006)
O. spiculata ≡ *H. spiculata*	China (Huang et al. 1998b)
O. verrucosa ≡ *H. verrucosa*	US (Mains 1950a), Britain (Evans 1967), China (Peng et al. 2008)

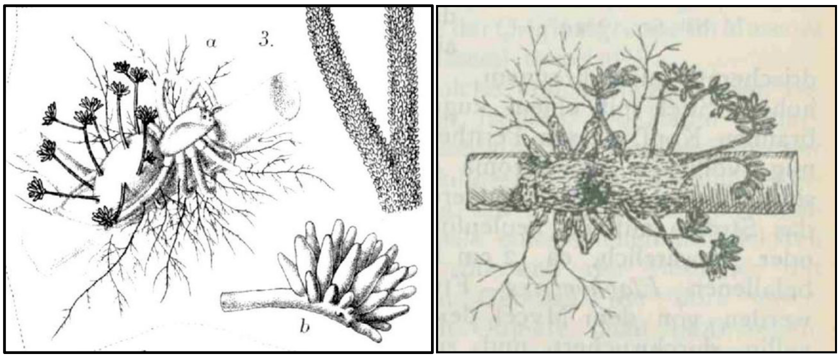

Fig. 8 *Cordyceps engleriana* (left, Hennings 1897; right, Hennings 1904)

Torrubiella Boud. s.l. (Cordycipitaceae)

Torrubiella is conceived as a large, sexual genus, producing superficial perithecia directly on the host surface without a definite stroma formation and principally parasitizing spiders and scale insects (Kobayasi and Shimizu 1982b). Due to its polyphyletic nature, *Torrubiella* was segregated into different genera under three families within Hypocreales, among which those on spiders are restricted to Cordycipitaceae (Johnson et al. 2009; Evans 2013). Currently, *Torrubiella*-like sexual morphs are found associated with members of *Akanthomyces Gibellula*, *Hevansia*, *Lecanicillium* etc. (Kepler et al. 2017).

Altogether, twenty-six *Torrubiella* species are known on spiders that currently remain *incertae sedis* within Cordycipitaceae and need phylogenetic revision (Johnson et al. 2009; Kepler et al. 2017) (Table 8). Among them, the first known species is *T. aranicida* associated with *Isaria cuneispora* Boud. (Boudier 1885, 1887) (Figs. 6 left, right). According to Doi (1977), the asexual morph of *T. aranicida* rather resembles *Cladobotryum*-like more than *Isaria*-like. *Torrubiella albolanata* Petch associated with *Cylindrophora aranearum* Petch is another earlier known *Torrubiella* species (Table 8). *Torrubiella flavoviridis* (Möller) Kobayasi (≡ *C. flavoviridis* Möller, Fig. 9), *T. pulvinata* Mains associated with *Spicaria pulvinata* Mains, and *T. falklandica* O'Donnell et al. are other species on spiders (Table 8). *Torrubiella pulvinata* was described on a pholcid spider (Cokendolpher 1993), not on a harvestman as initially reported by Mains (1949).

Kobayasi and Shimizu (1982b) have described many *Torrubiella* species on spiders, namely, *T. alboglobosa* Kobayasi and Shimizu, *T. aurantia* Kobayasi & Shimizu, *T. corniformis* Kobayasi & Shimizu, *T. ellipsoidea* Kobayasi & Shimizu, *T. farinacea* Kobayasi & Shimizu, *T. globosoides* Kobayasi & Shimizu, *T. inegoensis* Kobayasi & Shimizu, *T. longissimi* Kobayasi & Shimizu, *T. mammillata* Kobayasi & Shimizu, *T. minuta* Kobayasi & Shimizu, *T. miyagiana* Kobayasi & Shimizu, *T. neofusiformis* Kobayasi & Shimizu, *T. oblonga* Kobayasi & Shimizu, *T. ooaniensis* Kobayasi & Shimizu, *T. pallida* Kobayasi & Shimizu, *T. plana* Hirok. Sato et al. (= *T. minutissima* Kobayasi and Shimizu, non *T. minutissima* Lagarde), *T. rosea* Kobayasi & Shimizu, *T. ryogamimontana* Kobayasi & Shimizu, *T. formosana* Kobayasi & Shimizu, and *T. rokkiana* Kobayasi & Shimizu (Table 8). Among *Torrubiella* species, *T. gonylepticida* (Möller) Petch (≡ *C. gonylepticida* Möller, Fig. 10) is the only species growing on a harvestman *Gonyleptes*, associated with *Spicaria longipes* Petch (Table 8). It shows wider distribution ranging from South America and Caucasus region of Europe to east Asia (Table 8). Interestingly, almost all of the spider fungi in *Torrubiella* are described from Japan.

Table 7 *Purpureocillium atypicola* (with synonyms) and its distribution

Synonym	Distribution
I. atypicola	Japan (Yasuda 1915, 1917; Yakusiji and Kumazawa 1930; Kobayasi 1941)
S. atypicola	Costa Rica (Petch 1939)
N. atypicola	Ghana and US (Samson and Evans 1977), Panama (Nentwig 1985), Solomon Islands (Humber and Rombach 1987), Brazil (Greenstone et al. 1987), Argentina (Coyle et al. 1990; Catania et al. 2018), Mexico (Sánchez-Peña 1990), Thailand (Hywel-Jones and Sivichai 1995), Taiwan (Tzean et al. 1997a), China (Huang et al. 1998c), South Africa (Rong and Grobbelaar 1998), Ecuador (Evans 2013)
C. cylindrica	Trinidad (Petch 1937), Japan (Kobayasi and Shimizu 1977), Thailand (Hywel-Jones and Sivichai 1995), China (Li et al. 2005)

Table 8 *Torrubiella* species parasitizing spiders and their distribution

Torrubiella spp.	Distribution
T. aranicida = *Isaria cuneispora*	France (Boudier 1885), Cuba (Johnston 1918), China (Teng 1936), Britain (Petch 1939), Japan (Kobayasi and Shimizu 1982b)
T. alboglobosa	Japan (Kobayasi and Shimizu 1982b)
T. albolanata = *C. aranearum*	Britain (Petch 1944), Japan (Kobayasi and Shimizu 1982b)
T. aurantia	Japan (Kobayasi and Shimizu 1982b), Thailand (Luangsa-ard et al. 2012)
T. corniformis	Japan (Kobayasi and Shimizu 1982b)
T. ellipsoidea	Japan (Kobayasi and Shimizu 1982b)
T. falklandica	Falkland Islands (O'Donnell et al. 1977)
T. farinacea	Japan (Kobayasi and Shimizu 1982b)
T. flavoviridis	Brazil (Möller 1901), Guyana (Petch 1944)
T. formosana	Taiwan (Kobayasi and Shimizu 1982b)
T. globosoides	Japan (Kobayasi and Shimizu 1982b)
T. gonylepticida = *S. longipes*	Brazil (Möller 1901), Trinidad (Petch 1937), Russian Caucasus (Koval 1974), Taiwan (Tzean et al. 1998)
T. inegoensis	Japan (Kobayasi and Shimizu 1982b)
T. longissima	Japan (Kobayasi and Shimizu 1982b)
T. mammillata	Japan (Kobayasi and Shimizu 1982b)
T. minuta	Japan (Kobayasi and Shimizu 1982b)
T. miyagiana	Japan (Kobayasi and Shimizu 1982b)
T. neofusiformis	Japan (Kobayasi and Shimizu 1982b)
T. oblonga	Japan (Kobayasi and Shimizu 1982b)
T. ooaniensis	Japan (Kobayasi and Shimizu 1982b)
T. pallida	Japan (Kobayasi and Shimizu 1982b)
T. plana	Japan (Kobayasi and Shimizu 1982b; Sato et al. 2010), Taiwan (Tzean et al. 1998)
T. pulvinata = *S. pulvinata*	Hawaii (Mains 1949)
T. rokkiana	Taiwan (Kobayasi and Shimizu 1982b)
T. rosea	Japan (Kobayasi and Shimizu 1982b)
T. ryogamimontana	Japan (Kobayasi and Shimizu 1982b)

Fig. 9 *Cordyceps flavoviridis* (Möller 1901)

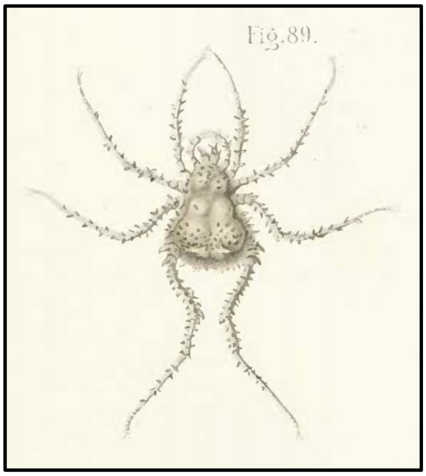

Fig. 10 *Cordyceps gonylepticida* (Möller 1901)

Spider and harvestman families parasitized by the hypocrealean fungi

In spite of rich and diverse fungal flora–parasitizing spiders, very few host spiders are definitely identified. In most cases, parasitized spiders are completely or almost completely covered by fungal growth, rendering the host identification very difficult (Evans 2013). In published literature, the host spiders are usually not identified, though some descriptive terms are sometimes used such as small or large spiders, free-living, jumping spiders, and ground-dwelling or trap-door spiders. Despite this limitation in host identity, available host information was analyzed to know major groups and subgroups of spiders and harvestmen that are parasitized by hypocrealean fungi.

Spiders

Two suborders of spiders, Araneomorphae and Mygalomorphae, are known to be parasitized by hypocrealean fungi.

Suborder Araneomorphae Araneomorphs account for over 90% of spider species and are sometimes known as true spiders (Humenik et al. 2011). Hypocrealean fungi are known to parasitize at least fifteen families of araneomorphs: Agelenidae, Anyphaenidae, Araneidae, Clubionidae, Corinnidae, Linyphiidae, Lycosidae, Pholcidae, Philodromidae, Salticidae, Sparassidae, Tetragnathidae, Theridiidae, Thomisidae, and Zodariidae (Table 9). Among them, Salticidae is the most common family, followed by Araneidae, Theridiidae, and Linyphiidae (Table 9). They are also the largest families among the araneomorphs (Coddington and Levi 1991).

Suborder Mygalomorphae It consists of mainly large-bodied spiders or trap-door spiders (Gillespie and Spagna 2009; Humenik et al. 2011) that generally live in burrows and forage (Coddington and Colwell 2001). Hypocrealean fungi are known to parasitize at least five mygalomorph families: Actinopodidae, Ctenizidae, Idiopidae, Nemesiidae, and Theraphosidae (Table 10). Among them, Ctenizidae is the most common family, followed by Theraphosidae (Table 10). *Cordyceps caloceroides* is a very special spider fungus that produces a long, brightly colored fruit-body (> 50 cm in length) on a large mygalomorph spider (Evans 2013).

Due to limited host information, understanding the extent of host specificity of spider fungi is difficult (Evans 1982). There are, however, a few records where a single spider genus or species plays a role of host for multiple fungal pathogens. For example, spiders belonging to *Araneus* are commonly parasitized by *A. araneogenum*, *L. araneogenum*, and *O. arachneicola* (Table 9). Similarly, *Gongylidium rufipes* is parasitized by two different pathogens, *G. pulchra* and *T. albolanata* (Table 9). On the other hand, a single fungal pathogen is found infecting a wide range of spiders. For instance, *P. atypicola* is recorded on four families of araneomorph spiders and three families of mygalomorph spiders (Tables 9 and 10). It was of interest to observe that fungal pathogens do not overlap between araneomorph and mygalomorph hosts except *P. atypicola* (Tables 9 and 10). For instance, *Gibellula*, *Akanthomyces*, and *Torrubiella* species are commonly recorded on araneomorph spiders (Table 9) but none on mygalomorph spiders (Table 10). Similarly, *Cordyceps* species are commonly recorded on mygalomorph spiders, but rarely on araneomorph spiders (Tables 9 and 10).

Harvestmen

Compared with spiders, hypocrealean fungi are very rarely known on harvestmen. Two suborders of the harvestmen, Laniatores and Eupnoi, are known to be parasitized by hypocrealean fungi.

Suborder Laniatores Members of this suborder are commonly known as armored harvestmen.

Family Gonyleptidae A species of *Gonyleptes* was the first example of a harvestman, parasitized by *Torrubiella gonylepticida* (Möller 1901). After a gap of more than one century, Barbosa et al. (2016) recently described *Torrubiella* cf. *aranicida* on an adult harvestman of *Acanthogonyleptes* in Brazil.

Suborder Eupnoi Members of this suborder are commonly known as daddy longlegs.

Family Phalangiidae A single example of a harvestman of Phalangiidae is known to be parasitized by *Ophiocordyceps verrucosa* in Britain (Leatherdale 1970).

Micro-habitat and distribution

Spiders seem to have preference for certain micro-habitats such as leaves, stems, tree trunks, barks, decaying logs and branch, and grass or leaf litters and forest floors, and even rice paddies. Table 11 shows different kinds of monocot, dicot, or coniferous plants and trees or grasses, mosses, ferns, lichens, and bamboo on which the parasitized spiders are found attached. The fact that many parasitized spiders are found on the under surface of leaves could be due to the manipulation of spider behavior by fungi (Hughes et al. 2016). Special mention can be made of spiders that are found attached to cacao leaves when parasitized by *Gibellula* species (Table 11).

Table 9 Hypocrealean fungi parasitizing araneomorph spiders

Family	Hypocrealean fungi known on araneomorph spiders
Agelenidae	*Gibellula leiopus* on *Urocoras longispinus* (Savić et al. 2016)
Anyphaenidae	*G. leiopus* on a anyphaenid spider (Costa 2014)
	Gibellula sp. on *Iguarima censoria* (Costa 2014)
Araneidae	*Akanthomyces araneogenum* on *Araneus* sp. (Chen et al. 2018)
	Gibellula sp. on *Eustala* (Costa 2014)
	Lecanicillium araneogenum on *Araneus* sp. (Chen et al. 2017b)
	Ophiocordyceps arachneicola on *Araneus ventricosus* (Kobayasi 1941)
	Purpureocillium atypicola on *Argiope* spp. and *Nephila* sp. (Nentwig 1985)
Clubionidae	*A. aranearum* on *Clubiona* sp. (Leatherdale 1970)
Corinnidae	*G. leiopus* on *Trachelas* aff. *robustus* (Costa 2014)
Linyphiidae	*Cordyceps* sp. on linyphiids (Nentwig 1985)
	G. pulchra on *Gongylidium rufipes* (Petch 1948)
	Gibellula sp. on a linyphiid (Costa 2014)
	Torrubiella albolanata on *Gongylidium rufipes* (Petch 1944)
Lycosidae	*A. aranearum* on a lycosid spider (Savić et al. 2016)
	G. pulchra on a lycosid spider (Van der Byl 1922)
	P. atypicola on a lycosid spider (Hywel-Jones and Sivichai 1995)
Pholcidae	*Gibellula* sp. on *Metagonia* aff. *beni* (Costa 2014)
	T. pulvinata on a pholcid spider (Cokendolpher 1993)
Philodromidae	*Engyodontium* sp. on *Thanatus* sp. (Rong and Grobbelaar 1998)
Salticidae	*G. brunnea*, *G. clavata*, *G. mainsii* and *G. mirabilis* possibly on free-living salticid spiders (Samson and Evans 1992)
	G. clavulifera on a salticid spider (Samson and Evans 1977)
	G. clavulifera var. *alba* on *Euophrys* nr. *trivittata* (Humber and Rombach 1987)
	G. pulchra on salticid spiders (Samson and Evans 1973) and *Neon nelli* (Strongman 1991)
	Gibellula sp. on *Corythalia* sp. (Costa 2014)
	Hevansia koratensis on a salticid spider (Hywel-Jones 1996)
Sparassidae	*Gibellula sp. on* Caayguara cupepema (Costa 2014)
	P. atypicola on *Palystes castaneus* (Rong and Grobbelaar 1998)
Tetragnathidae	*Gibellula* cf. *leiopus* on *Metellina* (= *Meta*) *merianae* (McNeil 2012)
	E. rectidentatum on *Meta menardi* (Kubátová 2017)
	P. atypicola on a tetragnathid spider (Hywel-Jones and Sivichai 1995)
Theridiidae	*Beauveria alba* on a theridiid spider (Nentwig 1985)
	Gibellula spp. on *Episinus cognatus*, *Hetschia gracilis*, *Janula bicorniger*, and *Theridion evexum* (Costa 2014)
Thomisidae	*Gibellula* spp. on *Tmarus* spp. (Costa 2014)
	T. albolanata on a thomisid spider (Petch 1944)
	T. neofusiformis on a thomisid spider (Kobayasi and Shimizu 1982b)
Zodariidae	*Gibellula* sp. on *Epicratinus* aff. *takutu* (Costa 2014)

Besides cocoa trees, spider hosts parasitized by *G. pulchra* are also found on other fruit and flowering plants, herbs and shrubs, grasses, and also on forest litters, decaying branch, pine cone, etc. (Table 11). Spider hosts parasitized by another common pathogen *Purpureocillium atypicola* are found in diverse habitats such as gardens and road sides or rice paddies and humus or underside of leaves or even boulders in rivers (Table 11). Mainly, adult spiders are parasitized by fungi, with rare records of egg-clusters (Petch 1937) or egg-cocoons (Petch 1944).

Discussion

This review shows a rich diversity of hypocrealean fungi that cause natural mortality of spiders. They are described as

Table 10 Hypocrealean fungi parasitizing mygalomorph spiders

Family	Hypocrealean fungi known on mygalomorph spiders
Actinopodidae	*Purpureocillium atypicola* on *Actinopus* sp. (Coyle et al. 1990)
Ctenizidae	*Cordyceps singeri* on *Latouchia* sp. (Mains 1954)
	Cordyceps cf. *singeri* on a small trapdoor spider (Evans 2013)
	P. atypicola on *Latouchia typica* and *L. japonica* (Yakushiji and Kumazawa 1930; Petch 1939; Kobayasi 1941; Coyle et al. 1990), and other trapdoor spiders (Petch 1937; Greenstone et al. 1987; Evans 2013)
Idiopidae	*C. nidus* on young trapdoor spiders (Chiriví et al. 2017)
Nemesiidae	*C. caloceroides* on *Stenoterommata platensis* (Manfrino et al. 2017)
	P. atypicola on a nemesiid spider (Catania et al. 2018)
Theraphosidae	*C. caloceroides* on *Mygale* sp. (Hennings 1897), *Grammostola* sp. and *Pterinopelma vitiosum* (Barbosa et al. 2016), and *Tarantula* spider (Chiriví et al. 2017)
	C. ignota on a large theraphosid spider (Mains 1954)

araneogenous or araneopathogenic (Evans and Samson 1987), or sometimes as arachnophilic (Rong and Grobbelaar 1998), arachnogenous (Kubátová 2004), or arachnophagous (Savić et al. 2016). Out of estimated 1000 entomopathogenic fungi reported on arthropods (Roberts & Humber 1981; McCoy et al. 1988; Vega et al. 2012), we have listed 86 spider-pathogenic fungi in the current review, all hypocrealeans. There is one more spider fungus, *Clathroconium arachnicola* Samson and H.C. Evans, recorded in Ghana (Samson and Evans 1982), but it is placed *incertae sedis* within Ascomycota. Besides hypocrealean spider pathogens, a species of *Aspergillus* has been recorded as a saprotroph on a crab spider of *Thanatus* (Rong & Grobbelaar 1998).

In agreement with Vega et al. (2012), our review shows that spider-pathogenic fungi are mainly concentrated in Cordycipitaceae of Hypocreales with 8 genera and 75 species out of 13 genera and 86 species, the remaining being distributed Ophiocordycipitaceae with one species in Bionectriaceae (Fig. 11). Spider-pathogenic genera within Cordycipitaceae (Kepler et al. 2017; Mongkolsamrit et al. 2018) are shown in Fig. 12.

The highest number of spider pathogens are comprised in *Torrubiella* (26 spp.), followed by *Gibellula* (17 spp.), *Akanthomyces* (10 spp.), *Cordyceps* (8 spp.), *Hevansia* (8 spp.), and *Ophiocordyceps* (7 spp.) (Fig. 11). Spider pathogens are also distributed in *Lecanicillium* (3 spp.), *Beauveria* (2 spp.), *Clonostachys* (1 sp.), *Engyodontium* (1 sp.), *Hirsutella* (1 sp.), *Hymenostilbe* (1 sp.), and *Purpureocillium* (1 sp.) (Fig. 11). Among the genera, *Akanthomyces*, *Gibellula*, *Hevansia*, and *Torrubiella* are exclusively or mostly spider pathogens. Other genera are, however, predominantly entomogenous. For example, *Ophiocordyceps* is a species-rich genus with more than 200 species, attacking members of Lepidoptera, Coleoptera, Hymenoptera, Hemiptera, Diptera, Orthoptera, and Odonata (Kobayasi 1941; Mains 1958; Evans and Samson 1982a, 1984; Shrestha et al. 2016, 2017b), of which only 7 species are known on spiders (Table 6). Similarly, despite wide host range of *Beauveria* covering more than 700 insect species (Toledo et al. 2008 and references therein), only *B. araneola* is described on spider (Chen et al. 2017a), with a rare instance of *B. bassiana* on spider (Petch 1932a). Besides *Beauveria*, another cosmopolitan entomopathogenic genus *Metarhizium* is also not observed on spiders (Evans and Samson 1987). Only one among nearly hundred species of *Hirsutella* is recorded on spider. Similarly, among species of *Clonostachys* and *Purpureocillium*, only *C. aranearum* and *P. atypicola* are known on spiders (Spatafora et al. 2015; Chen et al. 2016a).

Hypocrealean fungi–parasitizing spiders are cosmopolitan in distribution (Tables 1, 2, 3, 4, 5, 6, 7, and 8). In Europe, and Central and South America, they are recorded from wider parts, covering almost 18 and 16 countries respectively, whereas in Asia they are mainly known from east, southeast, and south regions such as Japan, China, Thailand, Sri Lanka, and Far East Russia (Kuril Islands), and in Africa mainly from Ghana, and occasionally from South Africa and Cameroon. Among the regions known for spider fungi, east and southeast Asia show the highest diversity, with Japan alone recorded for more than 30 species of spider-pathogenic fungi, and China and Thailand with nearly 20 species each. A few *Gibellula* and *Torrubiella* species are also recorded in Korea (Sung 1996). North America and Oceania are other parts of the world known for spider-pathogenic fungi. East and southeast Asia, South America and Africa are also well-known for insect-pathogenic fungi (Shrestha et al. 2016, 2017b). However, compared with spider pathogens, insect pathogens are less commonly recorded in Europe (Shrestha et al. 2016, 2017b).

Spider-pathogenic fungi are rarely reported from Australia and New Zealand although fungal pathogens of insects have long been known there. Among spider fungi, *Isaria abutii*

Table 11 Habitat of spider hosts parasitized by hypocrealean fungi

Hypocrealean fungi	Ecological habitat of the spider host
Akanthomyces aranearum	Spider on the forest floor of the oak/hornbeam forest (*Aculeato-Querco-Carpinetum*) (Savić et al. 2016) or buried in moss or concealed in cracks in the bark of trees (Petch 1932c)
A. araneogenum	Spider on pinewood (Chen et al. 2018)
A. kanyawimiae	Spider on stem of dicotyledonous plant or on underside of leaf of *Aglaia dookkoo* (Mongkolsamrit et al. 2018)
A. neoaraneogenum	Spider on pinewood (Chen et al. 2017b)
Cordyceps caloceroides	Spider buried in a tree stump (Evans 1982, 2013)
Gibellula alata	Spiders attached to the cocoa leaf surface (Samson and Evans 1973)
G. clavata	Spider on the under surface of cacao leaves (*Theobroma cacao*) (Samson and Evans 1992)
G. clavulifera	Spider on cocoa trees and forest shrubs (Samson and Evans 1977)
G. clavulifera var. *alba*	Spider attached to the upper sides of leaves of cacao (*Theobroma vulgaris*) (Humber and Rombach 1987)
G. leiopus	Spiders on the underside of bigger leaves of trees or forest herbaceous plants (Bałazy 1970), on the under-side of a lemon tree (*Citrus* sp.) leaf in an orchard (Sánchez-Peña 1990), on *Rubus* sp. (Tkaczuk et al. 2011), under decaying leaves of beech forest (*Tilio-Fagetum submontanum*) (Savić et al. 2016)
G. mainsii	Spider on cacao leaf (*Theobroma cacao*) (Samson and Evans 1992)
G. mirabilis	Spider on cacao leaf (*Theobroma cacao*) (Samson and Evans 1992)
G. pulchra	Spiders on guava (*Psidium guajava*) and *Casearia guianensis* trees (Johnston 1915), attached to grasses or to the underside of the leaves (Petch 1931, 1948), attached to underside of leaves of *Glochidion hongkongnense* (Sawada 1959), attached to the underside of cocoa leaves, less frequently on cocoa tree bark, particularly on the leaves of herbs and shrubs, also on forest litter (Samson and Evans 1973), on decaying branch (Kobayasi and Shimizu 1982b), on leaf litter under birch trees (Bosselaers 1984), attached to grass under cacao trees (Humber and Rombach 1987), on the underside of leaves and on the trunk of a feral orange tree in a tropical subperennial rain forest (Sánchez-Peña 1990), attached to the inside of an old pine cone in litter (Strongman 1991), on leaves of *Buxus sempervirens* (Selçuk et al. 2004) or on *Rubus* sp. (Tkaczuk et al. 2011)
Hevansia arachnophila	Spiders on underside of leaves of rubiaceous shrub (Samson and Evans 1974) or attached to underside of living leaves of zingiberaceous herb and Palmaceae (Hywel-Jones 1996)
H. nelumboides	Spider attached to the frond of *Polystichum tripteron* (Kobayasi and Shimizu 1977) or on *Helicia* leaves (Kobayasi and Shimizu 1981)
H. novoguineensis	Spider on *Hibiscus* leaf (Samson and Brady 1982)
Hirsutella darwinii	Small spider inside silk cocoon on a bracken frond (Evans and Samson 1982b)
Hymenostilbe kedrovensis	Spider on the leaf of wormwood (*Artemisia* sp.)
Lecanicillium araneicola	Spider attached under a leaf of a plant of Zingiberaceae on the forest floor of a primary lowland tropical rainforest (Sukarno et al. 2009)
L. tenuipes	On a spider's egg-cluster and on a spider attached to a living leaf (Petch 1937)
Ophiocordyceps mrciensis	Spider attached to a rotten culm of bamboo (Aung et al. 2006)
Purpureocillium atypicola	Spiders most commonly found in the gardens and road sides (Kobayasi 1941), in humus of a *Quercus polymorpha-Pinus* spp. forest (Sánchez-Peña 1990), spiders on rice paddies or attached to the underside leaves of forest herbs, saplings and trees or those inhabiting the underside of boulders in rivers (Hywel-Jones and Sivichai 1995)
Torrubiella albolanata	Spiders, spider's egg-cocoons in fen and reedswamp habitats (Petch 1944) or among *Cladium* (Petch 1948)
T. aranicida	Spider under the free lower edge of sheets of moss (Petch 1939), roadsides in beech forest (Doi 1977)
T. ellipsoidea	Spider on living leaf of fern *Polystichum tripteron* (Kobayasi and Shimizu 1982b)
T. falklandica	Spider on the thallus of a lichen *Pseudocyphellaria freycinetii* (O'Donnell et al. 1977)
T. farinacea	Spider on decorticated dead branch (Kobayasi and Shimizu 1982b)
T. formosana	Spider on fern *Hymenophyllum* sp. (Kobayasi and Shimizu 1982b)
T. globosoides	Spider on decaying log (Kobayasi and Shimizu 1982b)
T. gonylepticida	Harvestman on *Magnolia* leaves (Koval 1974)
T. longissima	Spider on *Rumohra standishii* leaf (Kobayasi and Shimizu 1982b)
T. pallida	Spider on *Rodgersia podophylla* leaf (Kobayasi and Shimizu 1982b)

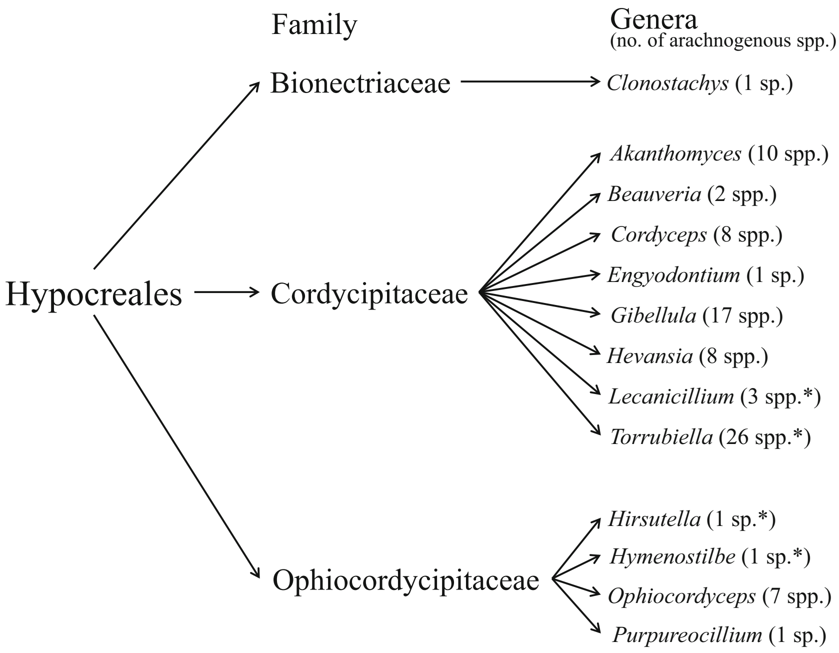

Fig. 11 Arachnogenous genera and species distributed within Hypocreales. *placed *incertae sedis* within Cordycipitaceae and Ophiocordycipitaceae

Lloyd, presumed to be *Gibellula aranearum*, was once reported from Australia (Petch 1933). Similarly, *Torrubiella gibellulae* Petch, considered to be a synonym of *T. arachnophila* (Johnston) Mains (Mains 1950b), was described in New Zealand by Dingley (1953). A rare record of a *Gibellula* species was also made in New Zealand (Rong and Botha 1993). Besides Australia and New Zealand, spider fungi are sporadically described from nearby regions such as Papua New Guinea (Sydow 1922; Kobayasi and Shimizu 1976; Samson and Brady 1982) and Solomon Islands (Humber and Rombach 1987).

The fungi recorded on harvestmen are very rare. Harvestmen are morphologically very similar to spiders and are often confused by non-experts. Mycologists, engaged in the study of fungi associated with spiders, need to take caution to distinguish between harvestmen and spiders. For example, Mains (1949) identified the host of *Torrubiella pulvinata* as a harvestman (Opilionoidea) in Hawaii, which Cokendolpher

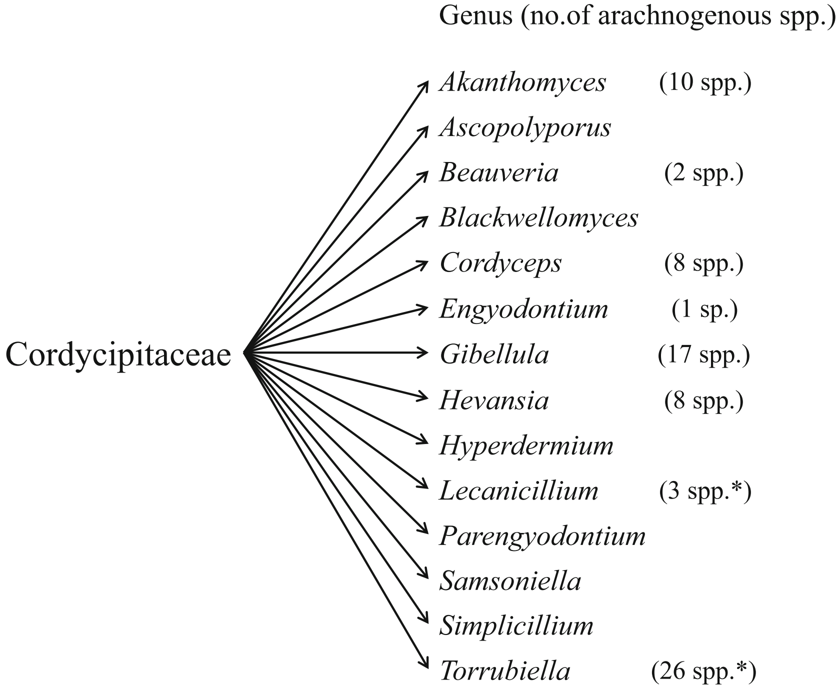

Fig. 12 Arachnogenous genera within Cordycipitaceae (Kepler et al. 2017; Mongkolsamrit et al. 2018). **incertae sedis* within Cordycipitaceae

(1993) later showed to be a pholcid spider. Gams et al. (1984) described *Engyodontium aranearum* as a cosmopolitan species on opilionids, but Cokendolpher (1993) again suggested that the hosts were spiders. Similarly, all the authors mentioned the host of *T. gonylepticida* as spider, though the specific epithet "*gonylepticida*" clearly indicate that the host was a harvestman, not a spider (Cokendolpher 1993). True host identification in cooperation with the experts could help increase our knowledge of fungal flora on harvestmen. Harvestmen number around 6000 species, more diverse among arachnids after mites and spiders (Shultz and Pinto-da-Rocha 2007).

As the hypocrealean fungi are well known to produce both sexual and asexual morphs, we analyzed whether hypocrealean spider fungi are dominantly sexual morphs or asexual morphs. Among 86 spider-pathogenic fungi reviewed here, we found that 33 species produce sexual morphs, 32 species produce asexual morphs, while the remaining 21 species produce both asexual and sexual morphs, though the ratio largely varies from genus to genus (Table 12). For example, *Torrubiella* and *Cordyceps* species are rarely known for asexual morphs whereas other genera rarely produce sexual morphs (Table 12).

We also analyzed which one between asexual morph and sexual morph shows wider distribution, in light of the general perception that the sexual morphs of the Hypocreales appear to be specialists with narrow distribution, while their asexual counterparts are generalists with wider distribution (Mora et al. 2017). *Gibellula* species, for instance, *G. pulchra* and *G. leiopus*, are widely distributed compared with their sexual counterparts *T. pulchra* and *T. leiopus*, respectively. Similarly, the asexual morph *A. aranearum* is found more widely, compared with its sexual morph *C. thaxteri*. *Purpureocillium atypicola* also shows worldwide distribution, but its sexual morph *C. cylindrica* is mainly known from Asia. Majority of species in *Torrubiella* are known only by sexual morphs and are known from limited locations, mainly in Asia. However, there is an exception. For example, no asexual morph is yet known for *C. caloceroides*, which shows wide distribution in Central and South America (Table 2).

Table 12 Number of spider-pathogenic fungi in different genera known for sexual morph, asexual morph, or both

Genus	Sexual morph	Asexual morph	Both morphs
Akanthomyces	2	4	4
Beauveria		1	1
Clonostachys		1	
Cordyceps	7		1
Engyodontium		1	
Gibellula		11	6
Hevansia		6	2
Hirsutella		1	
Hymenostilbe		1	
Lecanicillium		2	1
Ophiocordyceps	2	4	1
Purpureocillium			1
Torrubiella	22		4
Total	33	32	21

It has been shown that entomopathogenicity evolved in Clavicipitaceae, Cordycipitaceae, and Ophiocordycipitaceae within Hypocreales (Spatafora et al. 2007; Shang et al. 2016; Lovett and St. Leger 2017). Among the three entomopathogenic families within Hypocreales, our review shows that spider pathogens are restricted only to Cordycipitaceae and Ophiocordycipitaceae, but not Clavicipitaceae. Much less number of spider pathogens in Ophiocordycipitaceae and its sharing of sister-relationship with Clavicipitaceae within Hypocreales probably suggest that spider pathogenesis evolved more rapidly within Cordycipitaceae than Ophiocordycipitaceae.

Coleopterans, lepidopterans, and spiders are the major host groups of arthropod-pathogenic fungi within Hypocreales. In the past, we dealt with species of *Cordyceps* s.l. that parasitize members of insect orders Coleoptera, Lepidoptera, Hymenoptera, and Hemiptera (Shrestha et al. 2016, 2017b). In the current review, we have dealt with the hypocrealean fungi that parasitize spiders and harvestmen. It is hoped that the current review will regenerate interest among mycologists, arachnologists, and related experts and researchers for further exploration of spider pathogens, which also may lead to their potential use through novel secondary metabolites (Chiriví et al. 2017; Kuephadungphan et al. 2019). In this review, we have not however dealt with mechanism of spider infection by fungi, neither with the behavioral changes of hosts after fungal infection. Not much study seems to be carried out on fungus-induced behavioral changes in spiders (Hughes et al. 2016), though there are several studies carried out on insects (reviewed in Shang et al. 2015). With the description of new species on spiders in recent years including many more awaiting (Costa 2014), the number is expected to increase in future, revealing more diversity of spider pathogenic fungi. Mites and ticks are other members of Arachnida that are parasitized by different groups of fungi including hypocrealeans (Chandler et al. 2000).

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