



## Mycosphere Essay 19. *Cordyceps* species parasitizing hymenopteran and hemipteran insects

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### Abstract

Hymenoptera and Hemiptera are two major insect orders after Coleoptera and Lepidoptera that are parasitized by *Cordyceps* species. Among the 52 *Cordyceps* species parasitizing hymenopterans, the majority (50 species) are recorded on suborder Apocrita (ants, bees, wasps). Ant family Formicidae is the mostly parasitized family followed by Vespidae (wasps). *Ophiocordyceps uilaterialis*, *O. sphececephala*, *O. myrmecophila* and *Cordyceps australis* are some of the cosmopolitan species that parasitize ants and wasps. Among *Cordyceps* species recorded on hemipterans, the majority (34 species) are recorded on suborder Auchenorrhyncha (cicadas, spittlebugs, froghoppers), followed by six species on suborder Sternorrhyncha (scale insects) and four species on the suborder Heteroptera (true bugs). *Ophiocordyceps nutans* is recorded worldwide in Asia, Africa and South America and parasitizes more than 30 species of true bugs. Another worldwide species is *Ophiocordyceps sobolifera* that parasitizes six cicada species in Asia, Africa and South America. Pentatomidae (true bugs), Cicadidae (cicadas) and Acanthosomatidae (shield bugs) are major host families within Hemiptera. *Cordyceps* species parasitizing hemipteran insects are phylogenetically very diverse and are currently segregated into *Metarhizium*, *Ophiocordyceps*, *Polycephalomyces*, *Purpureocillium* and *Tolypocladium*. Many hymenopterans and hemipterans are important insect pests and have invaded new localities in the world, threatening agriculture and human life. The host information compiled in this review could be informative for their use as potential biocontrol agents of endemic insect pests belonging to Hymenoptera and Hemiptera, including invasive alien species.

**Key words** – biological control – insect hosts – medicinal fungus – *Ophiocordyceps*

## **Introduction**

*Cordyceps* is a hypocrealean entomogenous genus, parasitizing several orders of insects from larva to adult stages (Sung et al. 2007, Shrestha et al. 2014, Araújo & Hughes 2016). The most expensive biological commodity Chinese caterpillar fungus (*Cordyceps sinensis*, current name *Ophiocordyceps sinensis*) that parasitizes hepialid larvae in the alpine grasslands of the Himalayas and the Tibetan Plateau belongs to this broad genus (Sung et al. 2007, Shrestha et al. 2010). Recently, we catalogued *Cordyceps* species that parasitize coleopteran and lepidopteran insects (Shrestha et al. 2016). Here, we catalogue *Cordyceps* species parasitizing hymenopteran (ants, bees, wasps) and hemipteran (cicadas, true bugs) that include many agricultural pests and biting/stinging insects. We believe such compiling works help readers get a quick look into the host range of *Cordyceps* species and their potential as biocontrol agents of insect pests in agricultural lands, forests and recreation parks.

## **Materials and Methods**

*Cordyceps* species that parasitize hymenopteran and hemipteran insects are compiled from widely scattered literature, published in the last 170 years. The major subgroups of the two insect orders Hymenoptera and Hemiptera are briefly introduced, followed by *Cordyceps* species that parasitize them. The distributions of *Cordyceps* species are indicated here in the continental scale, though their records are mostly concentrated in a few countries within each continent. The hosts are also analyzed for life stages at which they are parasitized by *Cordyceps* species such as adult, nymph, pupa or larva.

Nomenclature of many *Cordyceps* species have recently changed after their transfer to older as well as newly established genera such as *Metarhizium* (Kepler et al. 2014), *Ophiocordyceps* (Sung et al. 2007), *Polycephalomyces* (Kepler et al. 2013), *Purpureocillium* (Ban et al. 2015), *Tolypocladium* (Quandt et al. 2014) and others (Spatafora et al. 2015). We have followed the current names of *Cordyceps* species in this review. Despite segregation of *Cordyceps* into several genera, we have frequently used the generic name *Cordyceps* in a wide sense throughout the text for the reason of simplicity. We have also included newly described species in *Ophiocordyceps* as far as they fit into the conventional sense of *Cordyceps* (Shrestha et al. 2014).

## **Order Hymenoptera**

Hymenoptera is the third-largest insect order, after Coleoptera and Lepidoptera. The common members of this group are ants, bees, wasps and sawflies. Many of them are economically important pollinators and agricultural pests. The members of Hymenoptera are classified into two suborders, Apocrita and Symphyta. Both suborders are parasitized by *Cordyceps* species (Tables 1, 2).

### **Suborder Apocrita**

Its members are ants, bees and wasps. Stinging wasps and ants are mostly carnivorous whereas bees feed on pollen and nectar. *Cordyceps* species parasitize three superfamilies of this suborder.

### **Superfamily Apoidea**

Its members are wasps and bees. Some of them are notable pests. Three families in this superfamily are known to be parasitized by *Ophiocordyceps* species.

### **Family Apidae**

It is a family of bees. They are widespread, mainly in Neotropical and Oriental regions. *Ophiocordyceps oxycephala* parasitizes *Bombus equestris* in Asia (Kobayasi 1941) (Table 1). Similarly, *O. sphecocephala* parasitizes a species of honey bee (*Apis*) in Africa (Moureau 1949)

**Table 1** *Cordyceps* species parasitizing order Hymenoptera.

| <i>Cordyceps</i> species       | Host family    | Host genus/species   | Host stage | Distribution                           |
|--------------------------------|----------------|--|------------|--|
| <i>Cordyceps coronilla</i>     | Tenthredinidae | -  | adult      | South America                          |
| <i>C. langloisii</i>           | Vespidae       | <i>Vespa muraria</i>   | larva      | North America                          |
| <i>C. odyneri</i>              | Vespidae       | <i>Odynerus</i> sp.  | larva      | Europe                                 |
| <i>C. phymatospora</i>         | Ichneumonidae  | -  | adult      | Asia                                   |
| <i>Ophiocordyceps ditmarii</i> | Ichneumonidae  | <i>Amblyteles armatorius</i>   | adult      | Europe                                 |
|                                | Siricidae      | <i>Sirex juvencus</i>  |            |  |
|                                | Vespidae       | <i>Dolichovespula sylvestris</i> , <i>Polistes gallicus</i> , <i>Vespa crabro</i> ,<br><i>Vespula germanica</i> , <i>Vespula vulgaris</i>  |            |  |
| <i>O. elongatistromata</i>     | Vespidae       | <i>Vespa</i> sp.   | adult      | Asia                                   |
| <i>O. gentilis</i>             | Sphecidae      | -  | adult      | Asia                                   |
| <i>O. humbertii</i>            | Vespidae       | <i>Vespa cincta</i>  | adult      | Africa, South America                  |
|                                | Mutillidae     | <i>Mutilla</i> sp.   |            |  |
|                                | Ichneumonidae  | -  |            |  |
| <i>O. lachnopoda</i>           | -              | -  | adult      | Asia                                   |
| <i>O. oxycephala</i>           | Apidae         | <i>Bombus equestris</i>  | adult      | Asia                                   |
|                                | Vespidae       | <i>Vespa velutina</i>  |            |  |
| <i>O. smithii</i>              | Vespidae       | -  | adult      | North America                          |
| <i>O. sphecocephala</i>        | Apidae         | <i>Apis</i> sp., <i>Xylocopa</i> sp.   | adult      | Africa, Asia,<br>Europe, South America |
|                                | Crabronidae    | <i>Tachytes chrysopiga</i>   |            |  |
|                                | Sphecidae      | <i>Pelopeus</i> sp.  |            |  |
|                                | Vespidae       | <i>Belonogaster</i> sp., <i>Gymnopolybia</i> sp., <i>Mischocyttarus cubensis</i> ,<br><i>Parapolybia orientalis</i> , <i>Polistes crinitus americanus</i> , <i>P. clavaria</i> , <i>P. hebraeus</i> , <i>P. lineatus</i> , <i>Polybia fasciata</i> , <i>Vespa auraria</i> , <i>V. mandarinia</i> , <i>Vespula vulgaris</i> |            |  |

and a species of carpenter bee (*Xylocopa*) in South America (Hennings 1902a) (Table 1).

### Family Crabronidae

Its members are wasps, generally solitary and predatory, preying on a wide range of insects and spiders. *Ophiocordyceps sphecocephala* parasitizes *Tachytes chrysopiga* in South America (van Vooren & Audibert 2005) (Table 1).

## Family Sphecidae

It is a cosmopolitan family of parasitoid wasps that prey on larvae of insects and spiders. *Ophiocordyceps sphecocephala* parasitizes a species of *Pelopeus* in Africa (Moureau 1949) (Table 1). Similarly, *O. gentilis* parasitizes a species of wasp of this family in Asia (Cesati 1879).

## Superfamily Ichneumonoidea

Wasps belonging to family Ichneumonidae are reported to be parasitized by three *Cordyceps* species. One of them is *Ophiocordyceps ditmarii* that parasitizes *Amblyteles armatorius* in Europe (Mornand et al. 2012) (Table 1). Besides family Ichneumonidae, *O. ditmarii* also parasitizes members of Vespidae (suborder Apocrita) and Siricidae (suborder Symphyta). Apart from Hymenoptera, *O. ditmarii* is also recorded on Diptera (Mornand et al. 2012). Other two species parasitizing family Ichneumonidae are *O. humbertii* in South America (Hennings 1902b) and *C. phymatospora* in Asia (Li et al. 2002) (Table 1).

**Table 2** *Cordyceps* species parasitizing family Formicidae of order Hymenoptera.

| <i>Cordyceps</i> species                      | Host species   | Distribution          |
|---|--|-----------------------|
| <i>Cordyceps australis</i>                    | <i>Bothroponera pachyderma</i> , <i>Megaponera foetens</i> , <i>Pachycondyla crassinoda</i> , <i>Pac. striata</i> , <i>Paltothyreus tarsatus</i> , <i>Paraponera clavata</i> , <i>Phrynoponera</i> sp. | Africa, South America |
| <i>C. carnata</i>                             | <i>Paltothyreus tarsatus</i>   | Africa                |
| <i>C. doiana</i>                              | <i>Paraponera clavata</i>  | South America         |
| <i>C. morakotii</i>                           | <i>Odontomachus</i> sp.  | Asia                  |
| <i>C. myrmecogena</i>                         | -  | Asia                  |
| <i>C. pilifera</i>                            | -  | South America         |
| <i>Ophiocordyceps camponoti-atricipis</i>     | <i>Camponotus atriceps</i>   | South America         |
| <i>O. camponoti-balzani</i>                   | <i>Camponotus balzani</i>  | South America         |
| <i>O. camponoti-bispinosi</i>                 | <i>Camponotus bispinosus</i>   | South America         |
| <i>O. camponoti-indiani</i>                   | <i>Camponotus indianus</i>   | South America         |
| <i>O. camponoti-leonardi</i>                  | <i>Camponotus leonardi</i>   | Asia                  |
| <i>O. camponoti-melanoticus</i>               | <i>Camponotus melanoticus</i>  | South America         |
| <i>O. camponoti-novogranadensis</i>           | <i>Camponotus novogranadensis</i>  | South America         |
| <i>O. camponoti-rufipedis</i>                 | <i>Camponotus rufipes</i>  | South America         |
| <i>O. camponoti-saundersi</i>                 | <i>Camponotus saundersi</i>  | Asia                  |
| <i>O. cucumispora</i>                         | <i>Cephalotes atratus</i>  | South America         |
| <i>O. cucumispora</i> var. <i>dolichoderi</i> | <i>Dolichoderus attelaboides</i>   | South America         |

|   |   |                                       |
|---|---|---------------------------------------|
| <i>O. evansii</i>                               | <i>Pachycondyla impressa</i>  | South America                         |
| <i>O. formicarum</i>                            | <i>Camponotus obscuripes</i> , <i>C. japonicus</i>  | Asia                                  |
| <i>O. halabalaensis</i>                         | <i>Camponotus gigas</i>   | Asia                                  |
| <i>O. irangiensis</i>                           | <i>Camponotus</i> sp., <i>Polyrhachis</i> sp.   | Africa, Asia                          |
| <i>O. japonensis</i>                            | <i>Camponotus</i> sp.   | Asia                                  |
| <i>O. kniphofioides</i>                         | <i>Cephalotes atratus</i>   | South America                         |
| <i>O. kniphofioides</i> var. <i>dolichoderi</i> | <i>Dolichoderus attelaboides</i>  | South America                         |
| <i>O. kniphofioides</i> var. <i>monacidis</i>   | <i>Monacis bispinosa</i>  | South America                         |
| <i>O. lloydii</i>                               | <i>Camponotus atriceps</i>  | South America                         |
| <i>O. lloydii</i> var. <i>binata</i>            | <i>Camponotus</i> sp.   | South America                         |
| <i>O. myrmecophila</i>                          | <i>Camponotus piceus</i> , <i>Dinoponera grandis</i> , <i>Formica fusca</i> , <i>F. polyctena</i> , <i>F. pratensis</i> , <i>F. rufa</i> , <i>F. sanguinea</i> , <i>Myrmica laevinodis</i> , <i>M. rufa</i> , <i>Paltothyreus tarsatus</i> , <i>Polyrhachis</i> sp.   | Asia, Europe, North and South America |
| <i>O. polyrhachis-furcata</i>                   | <i>Polyrhachis furcata</i>  | Asia                                  |
| <i>O. ponerinarum</i>                           | <i>Paraponera clavata</i> , <i>Dinoponera longipes</i>  | South America                         |
| <i>O. proliferans</i>                           | <i>Dinoponera grandis</i> , <i>Megaponera</i> sp.   | South America                         |
| <i>O. pseudolloydii</i>                         | <i>Dolichoderus bituberculatus</i>  | Asia                                  |
| <i>O. pulvinata</i>                             | <i>Camponotus obscuripes</i>  | Asia                                  |
| <i>O. rami</i>                                  | <i>Camponotus</i> sp.   | Asia                                  |
| <i>O. ridleyi</i>                               | <i>Camponotus gigas</i>   | Asia                                  |
| <i>O. septa</i>                                 | <i>Camponotus</i> sp.   | Asia                                  |
| <i>O. sessilis</i>                              | <i>Camponotus obscuripes</i>  | Asia                                  |
| <i>O. subunilateralis</i>                       | <i>Formica</i> sp.  | South America                         |
| <i>O. unilateralis</i>                          | <i>Atta cephalotes</i> , <i>Camponotus atriceps</i> , <i>C. brutus</i> , <i>C. americanus</i> , <i>C. leonardi</i> , <i>C. ligniperdus</i> , <i>C. pennsylvanicus</i> , <i>C. saundersi</i> , <i>C. sericeiventris</i> , <i>C. vividus</i> , <i>Echinopla melanarctos</i> , <i>Megaponera foetens</i> , <i>Phasmomyrmex aberrans</i> , <i>Ph. buchneri</i> , <i>Ph. paradoxus</i> , <i>Polyrhachis armata</i> , <i>P. decemdentata</i> , <i>P. fissa</i> , <i>P. furcata</i> , <i>P. hippomanes</i> , <i>P. laboriosa</i> , <i>P. latharis</i> , <i>P. latispina</i> , <i>P. militaris</i> , <i>P. monista</i> , <i>P. proxima</i> , <i>P. revoili</i> , <i>P. rufofemorata</i> , <i>P. sulcata</i> | Asia, North and South America         |
| <i>O. unilateralis</i> var. <i>clavata</i>      | <i>Polyrhachis lamellidens</i>  | Asia                                  |

### Superfamily Vespoidea

It includes common members such as ants and paper-nesting wasps. They are mostly tropical in distribution. Following three families are

parasitized by *Cordyceps* species.

### Family Formicidae

The common examples are ants. Out of 52 *Cordyceps* species that are known to parasitize hymenopterans, 40 species parasitize ants belonging to five subfamilies (Table 2).

Subfamily Dolichoderinae. *Ophiocordyceps cucumispora* var. *dolichoderi* and *O. kniphofioides* var. *dolichoderi* are recorded on *Dolichoderus attelaboides*, and *O. kniphofioides* var. *monacidis* on *Monacis bispinosa* in South America (Evans & Samson 1982) (Table 2). Similarly, *O. pseudolloydii* is recorded on *Dolichoderus bituberculatus* in Asia (Tzean et al. 1997) (Table 2).

Subfamily Formicinae. Five genera in this subfamily are known to be parasitized by *Ophiocordyceps* species. Among them, *Camponotus* is most commonly parasitized, followed by *Polyrhachis*, *Formica*, *Phasmomyrmex* and *Echinopla*.

*Camponotus* is a diverse ant genus. Twenty two *Ophiocordyceps* species parasitize *Camponotus* ants (Table 2). Among them, *O. unilateralis* parasitizes multiple *Camponotus* species, such as *C. atriceps* (Fawcett 1886) and *C. sericeiventris* (Evans & Samson 1984) in South America, *C. brutus* and *C. vividus* in Africa (Evans 1974), *C. pennsylvanicus* (Bequaert 1922) and *C. americanus* (Mains 1940) in North America, *C. leonardi* (Pontoppidan et al. 2009) and *C. saundersi* (Luangsa-Ard et al. 2011) in Asia, and *C. ligniperdus* (Bequaert 1922) in Europe and North America (Table 2). Similarly, *O. formicarum* parasitizes *Camponotus obscuripes* (Kobayasi 1939b) and *C. japonicus* (Kawamura 1955) in Asia (Table 2).

However, most other *Ophiocordyceps* species are recorded on distinct *Camponotus* ants (Table 2). For example, in South America, *O. camponoti-balzani* is recorded on *C. balzani* (Evans et al. 2011), and *O. camponoti-bispinosi* and *O. camponoti-indiani* on *C. bispinosus* and *C. indianus*, respectively (Araújo et al. 2015). Other species recorded on *Camponotus* ants in South America are *O. camponoti-melanotici* on *C. melanoticus*, *O. camponoti-novogranadensis* on *C. novogranadensis* and *O. camponoti-rufipedis* on *C. rufipes* (Evans et al. 2011). Similarly, *O. camponoti-leonardi* is recorded on *C. leonardi* and *O. camponoti-saundersi* on *C. saundersi* in Asia (Kobmoo et al. 2012) (Table 2). *Ophiocordyceps myrmecophila* is recorded on *Camponotus piceus* in Europe (Kautman & Kautmanová 2009).

In other cases, more than one species of *Ophiocordyceps* parasitize the same ant species (Table 2). For example, *O. camponoti-atricipis* (Araújo et al. 2015, Sobczak et al. 2017), and *O. lloydii* and *O. unilateralis* (Fawcett 1886) are recorded on *Camponotus atriceps* in South America. Similarly, *O. formicarum* (Kobayasi 1939b), *O. pulvinata* (Kepler et al. 2011) and *O. sessilis* (Kaitsu et al. 2013) are recorded on *C. obscuripes* in Asia. *Ophiocordyceps sessilis* is found hyperparasitizing *O. pulvinata* (Kaitsu et al. 2013). *Ophiocordyceps ridleyi* (Bequaert 1922) and *O. halabalaensis* (Luangsa-Ard et al. 2011) are recorded on *C. gigas* in Asia. *Ophiocordyceps lloydii* var. *binata* (Evans & Samson 1984) in South America, *O. irangiensis* (Moureau 1961) in Africa, and *O. japonensis* (Bequaert 1922), and *O. rami* and *O. septa* (Kobmoo et al. 2015) in Asia are other species that parasitize *Camponotus* species.

*Polyrhachis* is another diverse ant genus that is parasitized by several *Ophiocordyceps* species (Table 2). Among them, *Ophiocordyceps unilateralis* parasitizes *Polyrhachis decemdentata*, *P. fissa*, *P. laboriosa*, *P. latharis*, *P. latispina*, *P. militaris*, *P. monista*, *P. revoili* and *P. sulcata* in Africa (Evans 1974), and *P. armata*, *P. furcata*, *P. hippomanes*, *P. proxima* and *P. rufofemorata* in Asia (Fawcett 1886, Luangsa-Ard et al. 2011). *Ophiocordyceps unilateralis* var. *clavata* parasitizes *P. lamellidens* (Kobayasi 1939b) and *O. polyrhachis-furcata* parasitizes *P. furcata* (Kobmoo et al. 2012) in Asia. *Ophiocordyceps irangiensis* also parasitizes a species of *Polyrhachis* (Tzean et al. 1997), including an undetermined species of this subfamily (Hywel-Jones 1996). Another species recorded on *Polyrhachis* is *O. myrmecophila* (Tzean et al. 1997) in Asia. Earlier, Teng (1934), Kobayasi & Shimizu (1976) and Chen (1978) recorded *O. myrmecophila* in Asia, including New Guinea, on formicid ants. *Ophiocordyceps unilateralis* additionally parasitizes *Echinopla melanarctos* in Asia (Fawcett 1886), and *Phasmomyrmex aberrans*, *Ph. buchneri* and *Ph. paradoxus* in Africa (Evans 1974) (Table 2).

**Table 3** *Cordyceps* species parasitizing suborder Auchenorrhyncha of order Hemiptera.

| <i>Cordyceps</i> species                  | Host family   | Host Genus/species   | Host stage | Distribution                   |
|---|---------------|--|------------|--------------------------------|
| <i>Ophiocordyceps tricenri</i>            | Aphrophoridae | <i>Aphrophora flavomaculata</i> , <i>A. intermedia</i> , <i>A. rugosa</i> ,<br><i>Peuceptyelus medius</i>  | adult      | Asia                           |
| <i>Cordyceps atewensis</i>                | Cercopidae    | -  | adult      | Africa                         |
| <i>C. hesleri</i>                         | Cicadidae     | -  | nymph      | North America                  |
| <i>C. imagamiana</i>                      | Cicadidae     | -  | nymph      | Asia                           |
| <i>C. kobayasii</i>                       | Cicadidae     | <i>Meimuna opalifera</i>   | nymph      | Asia                           |
| <i>C. minuta</i>                          | Cicadidae     | <i>Oncotympana maculaticollis</i>  | adult      | Asia                           |
| <i>C. pluricapitata</i>                   | Cicadidae     | -  | nymph      | Asia                           |
| <i>C. polycephala</i>                     | Cicadidae     | <i>Euteropnosia iwasakii</i>   | nymph      | Asia                           |
| <i>C. zhejiangensis</i>                   | Cicadidae     | <i>Cicada flammata</i>   | nymph      | Asia                           |
| <i>Metarhizium guniujiangense</i>         | Cicadidae     | -  | nymph      | Asia                           |
| <i>M. owariense</i>                       | Cicadidae     | <i>Platypleura kaempferi</i>   | nymph      | Asia                           |
| <i>M. owariense f. viridescens</i>        | Cicadidae     | -  | nymph      | Asia                           |
| <i>Ophiocordyceps araracuarensis</i>      | Cicadidae     | -  | adult      | South America                  |
| <i>O. cicadicola</i>                      | Cicadidae     | -  | adult      | Asia                           |
| <i>O. evdorgeorgiae</i>                   | Cicadidae     | -  | adult      | Russia                         |
| <i>O. heteropoda</i>                      | Cicadidae     | <i>Tibicen bihamatus</i> , <i>T. japonicus</i> , <i>Graptopsaltria</i><br><i>nigrofuscata</i>  | nymph      | Asia                           |
| <i>O. heteropoda var. langyashanensis</i> | Cicadidae     | -  | nymph      | Asia                           |
| <i>O. longissima</i>                      | Cicadidae     | <i>Tanna japonensis</i>  | nymph      | Asia                           |
| <i>O. pseudolongissima</i>                | Cicadidae     | -  | nymph      | Asia                           |
| <i>O. sobolifera</i>                      | Cicadidae     | <i>Graptopsaltria nigrofuscata</i> , <i>Meimuna opalifera</i> ,<br><i>Platypleura kaempferi</i> , <i>Proalba chariclo</i> , <i>P. hilaris</i> , <i>Rihana</i><br><i>mesochlora</i> | nymph      | Asia, Africa,<br>South America |
| <i>O. takaoensis</i>                      | Cicadidae     | <i>Tanna japonensis</i>  | nymph      | Asia                           |
| <i>O. wuyishanensis</i>                   | Cicadidae     | -  | nymph      | Asia                           |
| <i>O. yakusimensis</i>                    | Cicadidae     | <i>Meimuna tsuchidai</i>   | nymph      | Asia                           |
| <i>Polycephalomyces kanzashianus</i>      | Cicadidae     | -  | nymph      | Asia                           |

|                                       |            |   |       |               |
|---------------------------------------|------------|---|-------|---------------|
| <i>P. nipponicus</i>                  | Cicadidae  | <i>Graptopsaltria nigrofuscata</i>                        | nymph | Asia          |
| <i>P. prolificus</i>                  | Cicadidae  | <i>Tanna japonensis</i>                                   | nymph | Asia          |
| <i>P. prolificus f. terminalis</i>    | Cicadidae  | <i>Tanna japonensis</i>                                   | nymph | Asia          |
| <i>P. ramosipulvinatus</i>            | Cicadidae  | -   | nymph | Asia          |
| <i>Purpleocillium takamizusanense</i> | Cicadidae  | <i>Oncotympana maculaticollis</i>                         | adult | Asia          |
| <i>Tolypocladium paradoxum</i>        | Cicadidae  | <i>Graptopsaltria nigrofuscata, Platypleura kaempferi</i> | nymph | Asia          |
| <i>T. toriharamontanum</i>            | Cicadidae  | <i>Tibicen bihamatus</i>                                  | nymph | Asia          |
| <i>T. inegoense</i>                   | Cicadidae  | <i>Oncotympana maculaticollis</i>                         | nymph | Asia          |
| <i>Ophiocordyceps lutea</i>           | Flatidae   | -   | adult | Africa        |
|                                       | Fulgoridae | -   |       |               |
| <i>O. fulgoromorphila</i>             | Fulgoridae | -   | adult | South America |

Among *Formica* species, *Ophiocordyceps myrmecophila* was originally recorded on *F. fusca* in Europe (Nylander 1869) and later on *F. polycytena*, *F. pratensis*, *F. rufa* and *F. sanguinea* (Nylander 1869, Kautman & Kautmanová 2009, Mornand et al. 2012) (Table 2). In South America, *Ophiocordyceps subunilateralis* is recorded on a species of *Formica* (Saccardo 1905).

Subfamily Myrmicinae. It is a cosmopolitan subfamily that is parasitized by several *Ophiocordyceps* species (Table 2). Among them, *O. unilateralis* parasitizes *Atta cephalotes* in South America (Tulasne & Tulasne 1865). Similarly, *O. kniphofioides* and *O. cucumispora* parasitize *Cephalotes atratus* (Evans & Samson 1982) in South America, and *O. myrmecophila* parasitizes *Myrmica laevinodis* (Kautman & Kautmanová 2009) and *M. rufa* (Fawcett 1886) in Europe and North America.

Subfamily Paraponerinae. *Cordyceps australis* (Sanjuán et al. 2001), *C. doiana* (Kobayasi 1981) and *Ophiocordyceps ponerinarum* (Sanjuán et al. 2015) are found to parasitize *Paraponera clavata* in South America (Table 2).

Subfamily Ponerinae. Several *Cordyceps* species are known to parasitize ponerine ants (Table 2). Among them, *Cordyceps australis* parasitizes *Bothroponera pachyderma* (Evans 1974), *Paltothyreus tarsatus* (Bequaert 1922) and *Phrynoponera* sp. (Evans 1982) in Africa, and *Pachycondyla crassinoda* (Evans 2001), *Pac. striata* (Spegazzini 1881) and *Megaponera foetens* (Petch 1932) in South America. Similarly, *Ophiocordyceps myrmecophila* parasitizes *Dinoponera grandis* in South America (Hennings 1904), and *Paltothyreus tarsatus* in Africa (Bequaert 1922). *Ophiocordyceps proliferans* is another species recorded on *Dinoponera grandis* (Hennings 1904) and a *Megaponera* species (Kobayasi 1941) in South America.

*Cordyceps carnata* (Evans 2001) is also recorded on *Paltothyreus tarsatus* in Africa. Other species recorded on this subfamily are *O. evansii* on *Pachycondyla impressa* and *O. ponerinarum* on *Dinoponera longipes* (Sanjuán et al. 2015) and *O. unilateralis* on *Megaponera foetens* (Petch 1934) in South America. Exceptionally, *Cordyceps morakotii* is recently recorded on pupa of a species of *Odontomachus* (Tasanathai et al. 2016) (Table 2). All other *Cordyceps* species are recorded on adult ants. Besides them, *C. myrmecogena* in Asia (Kobayasi & Shimizu 1978) and *C. pilifera* in South America (Kobayasi 1981) are recorded on adult formicid ants.



## Family Mutillidae

It is a group of wasps, with predominantly tropical distributions. *Ophiocordyceps humbertii* parasitizes a species of *Mutilla* in South America (Spegazzini 1889) (Table 1).

## Family Vespidae

Its members include solitary as well as eusocial wasps, with mainly tropical distributions. Some stinging wasps in this family are important agricultural pests. Several *Cordyceps* species are known to parasitize three subfamilies of this family.

Subfamily Eumeninae. The members are mostly solitary and few subsocial wasps. *Cordyceps odyneri* parasitizes larvae of a species of *Odynerus* in Europe (Saccardo 1891) (Table 1).

Subfamily Polistinae. All the members are eusocial wasps. *Ophiocordyceps sphecocephala* parasitizes eight species of this subfamily. They are *Belonogaster* sp. (Moureau 1949) in Africa, *Gynopolybia* sp. (Petch 1934), *Mischocyttarus cubensis* (Wolcott 1948), *Polistes crinitus americanus* (Kobayasi 1939b), *P. clavaria* (Tulasne & Tulasne 1865), *P. lineatus* (Johnston 1918) and *Polybia fasciata* (Kobayasi 1939b) in South America, and *Parapolybia orientalis* (Kawamura 1955) and *Polistes hebraeus* (Kobayasi 1939b) in Asia (Table 1). Similarly, *O. ditmarii* parasitizes *Polistes gallicus* in Europe (Cejp 1956) (Table 1).

Subfamily Vespinae. All the members are eusocial wasps. *Ophiocordyceps sphecocephala* parasitizes *Vespa auraria* (Kobayasi 1939b) and *V. mandarina* (Kawamura 1955) in Asia, and *Vespula vulgaris* (Kautman & Kautmanová 2009) in Europe (Table 1). Similarly, *O. ditmarii* parasitizes four species in Europe, *Dolichovespula sylvestris*, *Vespula germanica* and *V. vulgaris* (Cejp 1956), and *Vespa crabro* (Saccardo 1883) (Table 1). *Ophiocordyceps humbertii* is recorded on *Vespa cincta* (de Saussure 1853) in Africa and *O. oxycephala* on *Vespa velutina* (Penzig & Saccardo 1897) in Asia. Similarly, *Ophiocordyceps elongatistromata* is recorded on a species of *Vespa* in Asia (Kobayasi & Shimizu 1983). *Cordyceps langloisii* is recorded on a larva of *Vespa muraria* in North America (Saccardo 1895), the only larval stage among hymenopterans to be parasitized by *Cordyceps* species. Apart from them, *O. smithii* is recorded on a species of Vespidae in North America (Mains 1939). Similarly, *O. lachnopus* is recorded on an adult wasp in Asia (Penzig & Saccardo 1897) (Table 1).

## Suborder Symphyta

It is a small group that consists of sawflies, horntails, parasitic wood wasps, leaf feeders etc. Few of them cause economic damage to forest and cultivated plants. Two *Cordyceps* species are known to parasitize superfamilies Tenthredinoidea and Siricoidea in this suborder.

## Superfamily Tenthredinoidea

Its members are called leaf feeders and some of them are important agricultural pests. *Cordyceps coronilla* parasitizes a species of family Tenthredinidae in South America (Saccardo & Trotter 1913) (Table 1).

## Superfamily Siricoidea

Its members are xylophagous sawflies, horntails and wood wasps, some of which are important agricultural pests. *Ophiocordyceps ditmarii* parasitizes *Sirex juvencus* (family Siricidae) in Europe (Mornand et al. 2012) (Table 1).

## Order Hemiptera

Hemiptera is the fifth largest order of insects after Coleoptera, Lepidoptera, Hymenoptera and Diptera, and one of the major host orders of entomopathogenic fungi (Araújo & Hughes 2016). Commonly known members of this order are cicadas, aphids, true bugs, planthoppers, leafhoppers, scale insects, whiteflies etc. They are mostly phytophagous and are important pests in agriculture. Hemipterans are classified into four suborders Auchenorrhyncha, Coleorrhyncha, Heteroptera and

Sternorrhyncha, all of which except Coleorrhyncha are known to be parasitized by *Cordyceps* species (Tables 3–5).

**Table 4** *Ophiocordyceps* species parasitizing suborder Heteroptera of order Hemiptera.

| <i>Ophiocordyceps</i> species | Host family      | Host Genus/species   | Host stage | Distribution                            |
|-------------------------------|------------------|--|------------|---|
| <i>O. nigra</i>               | Reduviidae       | -  | nymph      | Africa                                  |
| <i>O. nutans</i>              | Acanthosomatidae | <i>Acanthosoma denticauda</i> , <i>A. forficula</i> , <i>A. haemorrhoidale angulata</i> , <i>A. labiduroides</i> , <i>Elasmucha putoni</i> , <i>Sastragala esakii</i> , <i>S. scutellata</i>   | Adult      | Africa, Asia, South America, New Guinea |
|                               | Coreidae         | <i>Molipteryx fuliginosa</i> , <i>Homoeocerus dilatatus</i> , <i>Ho. unipunctatus</i> , <i>Hygia lativentris</i> , <i>Hy. opaca</i>  |            |   |
|                               | Dinidoridae      | <i>Megymenum gracilicorne</i> , <i>M. tauriforme</i>   |            |   |
|                               | Pentatomidae     | <i>Caura pugillator</i> , <i>Dinorhynchus dybowskyi</i> , <i>Erthesina fullo</i> , <i>Gonopsis affinis</i> , <i>Halyomorpha halys</i> , <i>H. picus</i> , <i>Homalogonia obtusa</i> , <i>Lelia decempunctata</i> , <i>Nezara antennata</i> , <i>Pentatoma japonica</i> , <i>P. rufipes</i> , <i>Picromerus lewisi</i> , <i>Plautia stali</i> , <i>Tropicoris japonicus</i> |            |   |
|                               | Plataspidae      | <i>Coptosoma punctissimum</i>  |            |   |
|                               | Pyrrhocoridae    | <i>Callibaphus longirostris</i>  |            |   |
|                               | Reduviidae       | -  |            |   |
|                               | Tessaratomidae   | <i>Oncomeris</i> sp.   |            |   |
|                               | Urostylididae    | <i>Urostylis annulicornis</i>  |            |   |
| <i>O. pentatomae</i>          | Pentatomidae     | <i>Pentatoma semiannulata</i> , <i>Lelia decempunctata</i>   | adult      | Asia, Russia                            |
| <i>O. sichuanensis</i>        | Pentatomidae     | -  | adult      | Asia                                    |

### Suborder Auchenorrhyncha

Common members of this suborder are cicadas, leafhoppers, treehoppers, planthoppers, spittlebugs, frog hopper etc. that are distributed worldwide. All the members are plant-feeders. Two infraorders in this suborder are known to be parasitized by 34 *Cordyceps* species.

### Infraorder Cicadomorpha

The common members are cicadas, leafhoppers, treehoppers, frog hoppers and spittlebugs. They are distributed worldwide, but mainly in the tropical and subtropical zones. Two superfamilies are parasitized by *Cordyceps* species.

### Superfamily Cercopoidea

Its common members are spittlebugs and frog hoppers. Two families are known to be parasitized by *Cordyceps* species.

## Family Aphrophoridae

The members are spittlebugs and are mainly distributed in the Palaearctic and Oriental regions. They feed on xylem fluid and cause heavy economic losses to grass crops including rice, sugarcane, corn and pasture grasses. Adults of *Aphrophora flavomaculata*, *A. intermedia*, *A. rugosa* and *Peuceptyelus medius* are parasitized by *Ophiocordyceps tricenri* in Asia (Kobayasi 1941, Kawamura 1955) (Table 3).

## Family Cercopidae

The members are called froghoppers. *Cordyceps atewensis* parasitizes adults of this family in Africa (Samson et al. 1982) (Table 3).

## Superfamily Cicadoidea

Common members of this superfamily are cicadas. They are large, xylem-feeding insects on tree roots with long underground juvenile stages and brief aboveground adult lives. In summer, male cicadas produce calling songs for pair formation and courtship. Cicadas (family Cicadidae) have long been known to be parasitized by *Cordyceps* species in the Orient as well as the West (Kobayasi & Shimizu 1963). Many of them currently belong to *Metarhizium*, *Ophiocordyceps*, *Polycephalomyces*, *Purpureocillium* and *Tolypocladium* (Table 3). Altogether, 30 species (eleven *Ophiocordyceps* species, seven *Cordyceps* species, five *Polycephalomyces* species, three *Metarhizium* species, three *Tolypocladium* species and one species of *Purpureocillium*) are known to parasitize cicada species, mostly in Asia. Species recorded specifically outside of Asia are *Cordyceps hesleri* in North America (Mains 1939) and *Ophiocordyceps araracuarensis* in South America (Sanjuán et al. 2015).

Among *Cordyceps* species parasitizing cicadas, *Ophiocordyceps sobolifera* parasitizes several species such as *Graptopsaltria nigrofuscata*, *Meimuna opalifera*, *Platypleura kaempferi*, *Proalba chariclo*, *P. hilaris* and *Rihana mesochlora* distributed in South America, Africa and Asia (Kobayasi 1941, Kinjo et al. 2004) (Table 3). *Ophiocordyceps heteropoda* and *Tolypocladium paradoxum* are other species parasitizing multiple cicada species in Asia (Kobayasi 1939a). *Ophiocordyceps heteropoda* parasitizes *Graptopsaltria nigrofuscata*, *Tibicen bihamatus* and *T. japonicas* and *Tolypocladium paradoxum* parasitizes *Graptopsaltria nigrofuscata* and *Platypleura kaempferi* (Table 3).

Other *Cordyceps* species recorded on cicadas are *Cordyceps zhejiangensis* on *Cicada flammata* (Shing 1975), *C. kobayasi* on *Meimuna opalifera* (Kobayasi 1949), *C. polycephala* on *Euteropnosia iwasaki* (Kobayasi & Shimizu 1983), *Metarhizium owariense* on *Platypleura kaempferi* (Kobayasi 1939a), *O. yakusimensis* on *Meimuna tsuchidai* (Kobayasi & Shimizu 1963), *Po. nipponicus* on *Graptopsaltria nigrofuscata* (Kobayasi 1939a), and *T. toriharamontanum* on *Tibicen bihamatus* (Kobayasi & Shimizu 1963) (Table 3). Similarly, *O. longissima*, *Po. prolificus* and *Po. prolificus* f. *terminalis* (Kobayasi & Shimizu 1963) and *O. takaoensis* (Kobayasi 1939a) are recorded on *Tanna japonensis*. *Cordyceps minuta*, *Pu. takamizusanense* and *T. inegoense* are other species recorded on *Oncotympana maculaticollis* (Kobayasi & Shimizu 1963) (Table 3).

Few other *Cordyceps* species recorded on undetermined cicada species are *Cordyceps hesleri* (Mains 1939), *C. imagamiana* (Kobayasi & Shimizu 1983), *C. pluricapitata* (Kobayasi & Shimizu 1982a), *M. guniujiangense* (Li et al. 2010), *M. owariense* f. *viridescens* (Uchiyama & Udagawa 2002), *O. araracuarensis* (Sanjuán et al. 2015), *O. cicadicola* (Teng 1935), *O. evdodgeorgiae* (Koval 1961), *O. heteropoda* var. *langyashanensis* (Li et al. 2006), *O. pseudolongissima* (Kobayasi & Shimizu 1982b), *O. wuyishanensis* (Liang et al. 2002), *Po. kanzashianus* (Kobayasi & Shimizu 1982a) and *Po. ramosipulvinatus* (Kobayasi & Shimizu 1983) (Table 3).

Some cicadas are parasitized by multiple *Cordyceps* species (Table 3). For instance, *Tanna japonensis* is parasitized by *O. longissima*, *O. takaoensis*, *Po. prolificus* and *Po. prolificus* f. *terminalis* (Kobayasi 1939a, Kobayasi & Shimizu 1963), and *Graptopsaltria nigrofuscata* by *O. heteropoda*, *O. sobolifera*, *Po. nipponicus* and *T. paradoxum* (Kobayasi 1939a, Kinjo et al. 2004).

Similarly, *Oncotympana maculaticollis* is parasitized by *C. minuta*, *Pu. takamizusanense* and *T. inegoense* (Kobayasi & Shimizu 1963), *Platypleura kaempferi* by *M. owariense*, *O. sobolifera* and *T. paradoxum* (Kobayasi 1939a, Kobayasi 1941), *Meimuna opalifera* by *C. kobayasii* and *O. sobolifera* (Kobayasi 1949, Kinjo et al. 2004), and *Tibicen bihamatus* by *O. heteropoda* and *T. toriharamontanum* (Kobayasi 1939a, Kobayasi & Shimizu 1963). Among *Cordyceps* species parasitizing cicadas, *C. minuta*, *O. araracuarensis*, *O. cicadicola*, *O. evdogeorgiae* and *Pu. takamizusanense* parasitize adults, the remainings parasitize nymphs (Table 3).

**Table 5** *Cordyceps* species parasitizing suborder Sternorrhyncha of order Hemiptera

| <i>Cordyceps</i> species           | Host superfamily/<br>family | Host Genus/species  | Host<br>stage | Distribution             |
|------------------------------------|-----------------------------|---|---------------|--------------------------|
| <i>Cordyceps confragosa</i>        | Coccidae                    | -   | adult         | South America            |
| <i>C. yahagiana</i>                | Coccidae                    | -   | adult         | Asia                     |
| <i>Ophiocordyceps coccidiicola</i> | Coccidae                    | <i>Ceroplastes</i> sp.  | adult         | Asia                     |
| <i>O. clavulata</i>                | Coccidae                    | <i>Eulecanium coryli</i> ,<br><i>Lecanium persicae</i> ,<br><i>Coccus</i> sp. | adult         | Europe, North<br>America |
| <i>Cordyceps piperis</i>           | Coccoidea                   | -   | adult         | South America            |
| <i>C. novae-zelandiae</i>          | Coelostomidiidae            | <i>Coelostomidia</i> sp.  | adult         | New Zealand              |

### Infraorder Fulgoromorpha

Its common members are planthoppers and are mainly distributed in the tropical and subtropical zones. Two families (Flatidae and Fulgoridae) in superfamily Fulgoroidea are parasitized by *Cordyceps* species in Africa and South America. *Ophiocordyceps lutea* parasitizes adults of Flatidae and Fulgoridae in Africa (Moureau 1949) while *O. fulgoromorphila* parasitizes adults of Fulgoridae in South America (Sanjuán et al. 2015) (Table 3).

### Suborder Heteroptera

The members of Heteroptera are commonly known as true bugs. Two infraorders are parasitized by *Ophiocordyceps* species (Table 4).

### Infraorder Cimicomorpha

Nymphs and adults of family Reduviidae (superfamily Reduvioidea) of this infraorder are parasitized by *Ophiocordyceps nigra* (Samson et al. 1982) and *O. nutans* (Moureau 1949) in Africa (Table 4).

### Infraorder Pentatomomorpha

It is a large group of seed-eating stink bugs, flat bugs, seed bugs etc. Following superfamilies are parasitized by *Ophiocordyceps* species.

### Superfamily Coreoidea

*Ophiocordyceps nutans* parasitizes several members of family Coreidae of this superfamily in Asia. They are *Molipteryx fuliginosa*, *Homoeocerus unipunctatus* and *Hygia opaca* (Esaki 1929), *Ho. dilatatus* (Kawamura 1955) and *Hy. lativentris* (Sasaki et al. 2012) (Table 4).

### Superfamily Pentatomoidea

Its members are shield bugs, chust bugs or stink bugs and many of them are pests of economically important crops such as peach, apple, filbert nut, pear, wheat, grapes, small fruit, field corn, soybean, sorghum, sweet corn, tomato, pepper, okra and eggplant. Six families in this superfamily are parasitized by *Ophiocordyceps* species.

### **Family Acanthosomatidae**

Members of this family are known as shield bugs and mostly feed on developing fruits of conifers and flowering plants. *Acanthosoma denticauda*, *A. forficula*, *A. haemorrhoidale angulata*, *A. labiduroides*, *Elasmucha putoni*, *Sastragala esakii* and *S. scutellata* are parasitized by *Ophiocordyceps nutans* in Asia (Esaki 1929, Sasaki et al. 2012) (Table 4).

### **Family Dinidoridae**

Its members are large, colored bugs and are phytophagous. *Megymenum gracilicorne* and *M. tauriforme* are parasitized by *O. nutans* in Asia (Esaki 1929, Kawamura 1955) (Table 4).

### **Family Pentatomidae**

It is a cosmopolitan family of stink bugs. They are predacious and are important biocontrol agents. Some of them are also important pests of cultivated plants such as soybean, rice and wheat. Altogether 14 species in this family are known to be parasitized by *O. nutans* in Asia and Africa (Table 4). They are *Caura pugillator*, *Erthesina fullo*, *Halyomorpha halys*, *H. picus*, *Homalogonia obtusa*, *Lelia decempunctata*, *Nezara antennata*, *Pentatoma japonica*, *P. rufipes*, *Plautia stali* and *Tropicoris japonicas* in subfamily Pentatominae (Esaki 1929, Kobayasi 1949, Moureau 1949, Sasaki et al. 2012), *Dinorhynchus dybowskyi* and *Picromerus lewisi* in subfamily Asopinae (Esaki 1929, Yahagi 2008), and *Gonopsis affinis* in subfamily Phyllocephalinae (Esaki 1929). Among the parasitized bugs, only *Caura pugillator* is recorded in Africa (Moureau 1949), the rest in Asia. Koval (1974) also recorded *O. nutans* on *Pentatoma* sp. in Russia. Two more *Ophiocordyceps* species parasitize this family. They are *O. pentatomae* parasitizing *Pentatoma semiannulata* in Russia (Koval 1964) and *Lelia decempunctata* in Asia (Kobayasi & Shimizu 1978), and *O. sichuanensis* parasitizing a pentatomid bug in Asia (Liang et al. 2003) (Table 4).

### **Family Plataspididae**

Most species are distributed in the tropics, mainly in the Orient. They feed on soybean, kidney bean, other legume crops, sugarcane, sweet potato and rice. *Coptosoma punctissimum* is parasitized by *O. nutans* in Asia (Esaki 1929) (Table 4). In Africa, a *Coptosoma* sp. is found to be parasitized by *O. nutans* (Moureau 1949).

### **Family Tessaratomidae**

Its members are mainly found in the tropics and resemble stink bugs. A *Oncomeris* sp. is parasitized by *O. nutans* in New Guinea (Kobayasi & Shimizu 1976) (Table 4).

### **Family Urostylididae**

Members of this family attack ornamental trees in the Eastern Palaearctic region. *Urostylis annulicornis* is parasitized by *O. nutans* in Asia (Sasaki et al. 2012) (Table 4).

### **Superfamily Pyrrhocoroidea**

Its members are known as true bugs. *Callibaphus longirostris* in family Pyrrhocoridae is parasitized by *O. nutans* in Africa (Samson et al. 1982) (Table 4).

### **Suborder Sternorrhyncha**

The members of this suborder include aphids, whiteflies and scale insects that are cosmopolitan in distribution. They are sedentary and are firmly attached to the host plants. *Cordyceps* species parasitize scale insects of two families in superfamily Coccoidea (Table 5).

### **Family Coccidae**

Its members are known as soft scales, wax scales or tortoise scales. *Cordyceps confragosa* (Mains 1949) and *C. piperis* (Bischoff & White 2004) parasitize this family in South America (Table 5). Similarly, *C. yahagiana* and *O. coccidiicola* (on *Ceroplastes* sp.) are recorded on

members of this family in Asia (Kobayasi & Shimizu 1978, 1980) (Table 5). *Ophiocordyceps clavulata*, on the other hand, parasitizes *Eulecanium coryli*, *Lecanium persicae* and *Coccus* sp. in Europe and North America (Fawcett 1886, Ulvinen 1969) (Table 5).

### Family Coelostomidiidae

A single *Cordyceps* sp., *C. novae-zelandiae*, parasitizes *Coelostomidia* sp. in New Zealand (Dingley 1953) (Table 5).

### Discussion and Conclusion

Altogether 52 *Cordyceps* species are recorded on hymenopterans. All are recorded on suborder Apocrita except *Cordyceps coronilla* that is recorded on suborder Symphyta and *Ophiocordyceps ditmarii* recorded on both suborders (Tables 1, 2). Among them, 40 *Cordyceps* species are recorded on ants (Formicidae, Apocrita) alone. More than 80 ant species are parasitized by *Cordyceps* species (Table 2). Vespidae is another family of Hymenoptera, of which nearly 20 species are parasitized by *Ophiocordyceps sphecocephala*, *O. ditmarii* and others (Table 1).

*Ophiocordyceps unilateralis* is the most common species that is recorded on 29 ant species (Table 2). *Ophiocordyceps myrmecophila* is another species recorded on eleven ant species, followed by *C. australis* on seven ant species (Table 2). *Ophiocordyceps sphecocephala* is another common species, recorded on 16 species of bees and wasps in four families (Table 1). Similarly, *O. ditmarii* is another wasp fungus recorded on seven species of three wasp families (Table 1). Other filamentous fungi and yeasts are also rich in guts of honey bees (Moubasher et al. 2017).

Altogether 44 *Cordyceps* species are known to parasitize hemipterans. Among them, 34 *Cordyceps* species parasitize Auchenorrhyncha, six species parasitize Sternorrhyncha and four species parasitize Heteroptera. In suborder Heteroptera, nine families are parasitized by *Cordyceps* species (Table 4). Similarly, five families in suborder Auchenorrhyncha and at least two families in suborder Sternorrhyncha are parasitized by *Cordyceps* species (Tables 3, 5). Among all families in Hemiptera, Cicadidae is most commonly parasitized. Nearly 30 cicada species are parasitized by *Cordyceps* species (Table 3). Some of the commonly parasitized cicada species are *Tanna japonensis*, *Graptopsaltria nigrofuscata*, *Oncotympana maculaticollis*, *Platypleura kaempferi* and *Tibicen bihamatus* (Table 3). Pentatomidae is another family, of which 16 species are parasitized by *O. nutans*, including two other species (Table 4). Acanthosomatidae, Coreidae and Aphrophoridae are other commonly parasitized hemipteran families (Tables 3, 4).

Among *Cordyceps* species parasitizing hemipterans, *O. nutans* parasitizes 33 species in nine families in Asia, Africa and South America (Table 4). Phylogenetically distinct types have been shown for Asian *O. nutans* (Sasaki et al. 2012) that could possibly define *O. nutans* as a species complex in the global scale. *Ophiocordyceps clavulata*, *O. heteropoda*, *O. sobolifera* and *O. tricornis* are few other species parasitizing multiple species of Hemiptera (Tables 3, 5).

All scale insects are parasitized at adult stage (Table 5). Similarly, all host species in Aphrophoridae, Cercopidae, Flatidae and Fulgoridae are parasitized at adult stages (Table 3). Bugs are also mostly parasitized at adult stages (Table 4). However, nymph is the most common stage in cicada family, 25 out of 30 *Cordyceps* species parasitizing nymphs (Table 3).

In general, Asia, Africa and South America are common continents for *Cordyceps* species parasitizing hymenopterans, with rare reports from Europe and North America (Tables 1, 2). Similarly, most of *Cordyceps* species parasitizing hemipterans are recorded in Asia followed by Africa and South America (Tables 3–5). New Guinea, North America, Europe, New Zealand and Russia are rarely described for *Cordyceps* species on hemipterans.

Insects spend their lives in both agricultural lands and forests depending on season and life stages. Generally, insects spend their lives in forests for purposes such as reproduction, shelter etc. Forests provide optimum conditions for entomopathogenic fungi to parasitize insects by which they can overcome unfavorable environmental conditions by growing inside the body of the insect cadavers. The fungi sprout out of the cadavers when optimum environmental conditions prevail the following year and release spores from summer to early autumn. Spores of entomopathogenic fungi

on coming in contact with host surface germinate and produce germ-tubes that penetrate the hosts through the cuticular layer with the help of different enzymes such as proteases and chitinases but do not consume the exoskeleton. The cadavers remain intact with the internal organs being replaced by white compact fungal tissue (endosclerotium) of parasitizing *Cordyceps* species.

*Cordyceps* species have annual life cycles from the time of infection to its hosts till the fructification the following year. But, it remains curious how *Cordyceps* species that infect deeply earthed cicada nymphs as long as 50 cm deep manage to make a way out through the hard layers of soils the following year, leading to their fructification. In any case, the growth rate of *Cordyceps* species is presumed to be slow in nature. This is also observed in *in vitro* condition. Localized distributions of most of *Cordyceps* species could be a bottleneck for its use as wide biocontrol agents; however, there is a possibility of host-targeted propagule production to control agricultural pests. Since many hymenopterans and hemipterans are important agricultural pests, we believe this compiling work will regenerate interest among entomologists, biocontrol experts and specialists, and researchers for the application of insect fungi in conservation agriculture. Besides that, *Cordyceps* species are also valued for active metabolites that have a broad spectrum of biological activity (Wen et al. 2017).

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