

Review Article

Coleopteran and Lepidopteran Hosts of the Entomopathogenic Genus *Cordyceps* sensu lato

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Entomophthoralean and ascomycetous fungi are the two major groups known to parasitize arthropods in almost every terrestrial habitat of the earth. Within Ascomycota, *Cordyceps* sensu lato is a large genus with more than 400 spp. described on numerous orders of Arthropoda. Among the hosts of *Cordyceps*, Coleoptera and Lepidoptera are the two major orders. Out of the estimated 200 *Cordyceps* spp. recorded on coleopteran and lepidopteran hosts, we have documented 92 spp. based on the available information of their host species. Among coleopteran hosts, Scarabaeidae and Elateridae are the two major families. Similarly, among lepidopterans, Hepialidae is the largest host family. *Cordyceps militaris* shows the widest host range, extending to 2 orders, 13 families, and 32 spp. We hope such accumulative work will be useful as a quick reference for interested biologists, forest ecologists, biocontrol researchers, and fungal and insect taxonomists to apprehend host range and host specificities of *Cordyceps* fungi.

1. Introduction

Fungi play vital roles in the recycling of organic matter in the terrestrial habitat of the earth. Besides that, they also parasitize living organisms and cause various diseases on plants, animals, and insects. Estimates show 750–1000 fungal spp. parasitizing insects naturally [1, 2], although the extent of the diversity of the entomopathogenic fungi is not completely known [3, 4]. The entomopathogenic fungi mainly belong to two diverse groups within kingdom Fungi, Entomophthorales (Phylum Entomophthoromycota, formerly Zygomycota) and Hypocreales (Phylum Ascomycota). These fungi are distributed in wide terrestrial ecosystems of the world including Arctic Circle and Antarctica [5]. Entomophthoralean pathogens generally show narrow host range and are distributed in temperate forests [6] with rare reports from

tropical regions [7]. Hypocrealean pathogens, on the other hand, have narrow to very broad host range [4] and are dominantly distributed in humid tropical forests [7].

Cordyceps Fr. is one of the hypocrealean genera, comprising more than 400 spp. that parasitize a wide range of insects and few fungal genera. Externally, they produce clavate, cylindrical or thin filamentous, filiform stroma on the hosts. The history of exploring and identifying *Cordyceps* fungi is long and stretches back to the 17th century [8]. One of the most popular fungi is *Ophiocordyceps sinensis* (syn. *Cordyceps sinensis*) that grows on hepialid larvae in the alpine grasslands of the Himalayas and the Tibetan Plateau [9]. This host-fungus complex is traditionally highly revered for enhancing immunity, protecting lungs, enriching kidneys, restorative and tonic effects, treating impotence, and so forth [10–13].

Until the phylogenetic classification by Sung et al. [14], *Cordyceps* remained a big genus placed in family Clavicipitaceae of order Hypocreales. However, phylogenetic studies showed that neither *Cordyceps* nor Clavicipitaceae was monophyletic [14–18] and hence *Cordyceps* was segregated into several phylogenetic genera within three families of Hypocreales [14]. According to the phylogenetic classification, *Cordyceps* is now restricted to the clade containing the type species *C. militaris*, circumscribed to Cordycipitaceae [14]. Newly segregated genera *Ophiocordyceps* and *Elaphocordyceps* were placed under another family Ophiocordycipitaceae; the other two genera *Metacordyceps* and *Tyrannicordyceps* remained in Clavicipitaceae *sensu stricto* [14, 19].

Following the recent revision in the International Code of Nomenclature for algae, fungi, and plants (ICN), *Elaphocordyceps* is now synonymized with *Tolypocladium* [20] and *Metacordyceps* with *Metarhizium* [21]. *Drechmeria*, *Podocrella*, *Polycephalomyces*, and *Sphaerocordyceps* are other genera that consist of members that were formerly described under *Cordyceps*. *Cordyceps* along with the newly segregated genera is linked to many asexual insect-pathogenic genera distributed in all three families Clavicipitaceae s. s., Cordycipitaceae, and Ophiocordycipitaceae [4, 14, 20]. Further synonymizations of genera are recently proposed within Ophiocordycipitaceae following ICN [22].

The host range of *Cordyceps* in classical sense is very broad and includes several orders (Coleoptera, Lepidoptera, Hymenoptera, Hemiptera, Orthoptera, Araneae, Diptera, Blattodea, Mantodea, Dermaptera, Odonata, Phasmatodea, etc.). Based on the published literature, nearly 60% of the species of *Cordyceps* *sensu lato* are recorded on two orders Coleoptera and Lepidoptera. The other major host orders are Hymenoptera, Hemiptera, Orthoptera, and Araneae. The majority of hosts (more than 95%) in Lepidoptera (moths, butterflies) and Coleoptera (beetle) are larvae; the rest are adults or pupae, making the host identification difficult. In contrast, majority of hosts in other orders are adults such as spiders (Araneae), fly (Diptera), ant, bee, and wasp (Hymenoptera), grasshopper, locust, and cricket (Orthoptera), cicada, bug, scale-insect, and coccid (Hemiptera), cockroach and termite (Blattodea), mantis (Mantodea), earwig (Dermaptera), dragonfly (Odonata), and stick-insect (Phasmatodea). Why lepidopterans and coleopterans are mostly susceptible at larval stage while other orders are more susceptible at adult stage is not well understood.

2. Host-Pathogen Interaction

Cordyceps fungi range in habitat from aerial to epigeal to subterranean ones [74], based on their respective host species. When the host stage is adult, they grow on exposed environments such as leaf litter or are attached to some plant parts such as leaf and branch and in contrast to the larval or pupal stages that are buried in soil (hypogeal) or on wood up to nearly 50 cm, for example, *O. longissima* [75] and *O. xuefengensis* [76]. *Ophiocordyceps caloceroides* that is buried in the soil more than 50 cm is exceptional which grows on adult spiders [77].

The pathogenic fungi sometimes produce parasite manipulated behaviors on hosts, such as death grip or biting behavior [78–80]. Some of the parasitized ants always bite lower side veins but never the laminar blade or the upper surface [79, 80]. Similarly, some species of ants are attached to lower side of twigs whereas others are found attached to leaves [81]. In other cases, aphids, ants, grasshoppers, planthoppers, flies, and so forth shift to elevated position at the time of dying, known as summit disease [82, 83].

In this review, we present brief introductions of Coleoptera and Lepidoptera and their major subgroups parasitized by *Cordyceps* fungi. We hope the present review will serve as a reference for researchers and scholars to get a quick look at coleopteran and lepidopteran hosts of *Cordyceps* spp.

3. Materials and Methods

We accumulated host information from published literature and analysed the hosts that belonged to Coleoptera and Lepidoptera. We found that hosts of only 60% of *Cordyceps* fungi are known at family or genus/species ranks; the rest are known only at the order rank and hence no further discussions of the hosts could be done for them. Hence, in this review, we dealt with only those hosts that are known at family or infrafamily ranks within Coleoptera and Lepidoptera and tried to analyse the major taxonomic subgroups that are associated with *Cordyceps* fungi. We also analysed the host stage among coleopteran and lepidopteran hosts based on published literature.

4. Coleopteran Hosts

Coleoptera is currently the most species-rich group on this planet [84]. The order is classified into four suborders (Polyphaga, Adepaha, Myxophaga, and Archostemata) [85]. Polyphaga is the largest suborder covering 90% of total beetle species and is classified into more than 170 families. Adepaha is the second largest suborder, followed by Myxophaga and Archostemata. All the known coleopteran hosts belong to suborders Polyphaga and Adepaha under 8 superfamilies and 11 families. Short descriptions of host families are given below, followed by *Cordyceps* spp. recorded on them.

4.1. Superfamily Scarabaeoidea

4.1.1. *Scarabaeidae*. This is one of the largest families in Coleoptera and its members are commonly called scarabs or scarab beetles. Scarabaeid larvae (commonly called grubs) are short, thick, pale yellow or white, mostly live underground or under debris, and feed on dead organic matter (scavengers). Twenty-seven *Cordyceps* spp. are recorded in this family (Table 1). Among them, *C. brittlebankii* is recorded on *Heteronyx* sp., *C. brongniartii* on *Anomala cuprea*, *C. coxii* on *Lepidiota* sp., *C. pseudoinsignis* and *C. velutipes* on *Melolontha* sp., *Ophiocordyceps aphodii* on *Aphodius howitti* and *A. tasmaniae*, *O. melolonthae* on *Ancyloncha puncticollis*, *Lachnosterna fusca*, and *Melolontha* sp., *O. michiganensis* on *Scarabaeus* sp., *O. ravenelii* on *L. fusca*, *Phyllophaga*

TABLE 1: An aggregate list of coleopteran hosts (family/genus/species) of *Cordyceps* species.

S number	<i>Cordyceps</i> sp.	Family	Genus/species	Host stage
1	<i>C. aurantiaca</i>	Elateridae	—	Larva [23]
2	<i>C. brittlebankii</i>	Scarabaeidae	<i>Heteronyx</i> sp.	Larva [24]
3	<i>C. brongniartii</i>	Scarabaeidae	<i>Anomala cuprea</i>	Larva [25]
4	<i>C. coxii</i>	Scarabaeidae	<i>Lepidiota</i> sp.	Larva [26]
5	<i>C. erotyli</i>	Erotylidae	<i>Erotylus</i> sp.	Adult [27]
6	<i>C. geotrupis</i>	Geotrupidae	<i>Geotrupes</i> sp.	Adult [28]
7	<i>C. huntii</i>	Elateridae	—	Larva [29]
8	<i>C. memorabilis</i>	Staphylinidae	<i>Staphylinus</i> sp.	Adult [30]
9	<i>C. militaris</i>	Curculionidae Tenebrionidae	<i>Ips sexdentatus</i> <i>Tenebrio molitor</i>	Larva [31, 32]
10	<i>C. nikkoensis</i>	Carabidae	—	Larva [33]
11	<i>C. nirtolii</i>	Elateridae	<i>Melanotus communis</i>	Larva [34]
12	<i>C. obliquiordinata</i>	Scarabaeidae	—	Larva [35]
13	<i>C. pseudoinsignis</i>	Scarabaeidae	<i>Melolontha</i> sp.	Larva [36]
14	<i>C. rubra</i>	Elateridae	—	Larva [37]
15	<i>C. scarabaeicola</i>	Scarabaeidae	—	Adult [38]
16	<i>C. shanxiensis</i>	Elateridae	<i>Melanotus caudex</i> , <i>Pleonomus canaliculatus</i>	Larva [39]
17	<i>C. staphylinidicola</i>	Staphylinidae	—	Larva [40]
18	<i>C. velutipes</i>	Elateridae Scarabaeidae	— <i>Melolontha</i> sp.	Larva [36, 41]
19	<i>M. brittlebanksoides</i>	Scarabaeidae	—	Larva [42]
20	<i>M. campsosterni</i>	Elateridae	<i>Campsosternus auratus</i>	Larva [43]
21	<i>M. martiale</i>	Elateridae	<i>Hemirhipus</i> sp.	Larva [44]
22	<i>O. acicularis</i>	Tenebrionidae	<i>Nictobates</i> sp.	Larva [41]
23	<i>O. aphodii</i>	Scarabaeidae	<i>Aphodius howitti</i> , <i>A. tasmaniae</i>	Larva [45, 46]
24	<i>O. arbuscula</i>	Scarabaeidae	—	Larva [47]
25	<i>O. barnesii</i>	Scarabaeidae	—	Larva [41]
26	<i>O. brunneipunctata</i>	Elateridae	—	Larva [48]
27	<i>O. carabidicola</i>	Carabidae	—	Larva [49]
28	<i>O. curculionum</i>	Curculionidae	<i>Heilipus celsus</i>	Adult [41]
29	<i>O. dovei</i>	Cerambycidae	<i>Oemona hirta</i>	Larva [50]
30	<i>O. elateridicola</i>	Elateridae	—	Larva [33]
31	<i>O. elongatiperitheciata</i>	Scarabaeidae	—	Larva [51]
32	<i>O. entomorrhiza</i>	Carabidae Cerambycidae Chrysomelidae Curculionidae Staphylinidae Tenebrionidae	<i>Calathus</i> sp., <i>Calosoma</i> sp., <i>Carabus auronitens</i> , <i>C. coriaceus</i> , <i>C. glabratus</i> , <i>C. hortensis</i> , <i>C. intricatus</i> , <i>C. nemoralis</i> , <i>C. nemorensis</i> , <i>C. violaceus</i> , <i>Coptolabrus</i> sp., <i>Hadrocarabus problematicus</i> , <i>Pterostichus</i> sp. <i>Leptura</i> sp. <i>Diabrotica</i> sp. <i>Apion flavipes</i> <i>Ocytus</i> sp. <i>Meneristes laticollis</i>	Larva, adult [41, 50, 52–57]
33	<i>O. formosana</i>	Tenebrionidae	—	Larva [58]
34	<i>O. geniculata</i>	Scarabaeidae	—	Larva [59]
35	<i>O. gracilioides</i>	Elateridae	—	Larva [59]
36	<i>O. gracillima</i>	Scarabaeidae	—	Larva [60]

TABLE 1: Continued.

S number	<i>Cordyceps</i> sp.	Family	Genus/species	Host stage
37	<i>O. highlandensis</i>	Scarabaeidae	—	Larva [61]
38	<i>O. jiangxiensis</i>	Elateridae	<i>Campsosternus auratus</i> , <i>C. fruhstorferi</i>	Larva [62]
39	<i>O. konnoana</i>	Scarabaeidae	—	Larva [59]
40	<i>O. larvicola</i>	Cerambycidae	<i>Callidium</i> sp.	Larva
		Scarabaeidae	—	[36, 50, 63]
		Tenebrionidae	<i>Cylindronotus</i> sp., <i>Helops caraboides</i> , <i>H. lanipes</i>	
41	<i>O. macularis</i>	Scarabaeidae	—	Larva [64]
42	<i>O. melolonthae</i>	Scarabaeidae	<i>Ancyloncha puncticollis</i> , <i>Lachnosterna fusca</i> , <i>Melolontha</i> sp.	Larva [41, 65]
43	<i>O. michiganensis</i>	Carabidae	—	Larva [50, 66]
		Scarabaeidae	<i>Scarabaeus</i> sp.	
44	<i>O. neovolkiana</i>	Scarabaeidae	—	Larva [50]
45	<i>O. nigrella</i>	Scarabaeidae	—	Larva [33]
46	<i>O. purpureostromata</i>	Elateridae	—	Larva [51]
47	<i>O. ravenelii</i>	Scarabaeidae	<i>Lachnosterna fusca</i> , <i>Phyllophaga</i> sp., <i>Rhizotrogus</i> sp.	Larva [65, 67, 68]
48	<i>O. salebrosa</i>	Elateridae	—	Adult [69]
49	<i>O. scottiana</i>	Lucanidae	<i>Rhyssonotus nebulosus</i>	Larva [26]
50	<i>O. stylophora</i>	Carabidae	—	Larva
		Cerambycidae	<i>Phoracantha semipunctata</i>	[52, 70–72]
		Elateridae	<i>Denticollis linearis</i>	
51	<i>O. superficialis</i>	Scarabaeidae	<i>Costelytra zealandica</i>	Larva
		Chrysomelidae	—	[27, 49, 73]
		Staphylinidae	—	
		Scarabaeidae	—	
52	<i>O. variabilis</i>	Scarabaeidae	—	Larva [73]
53	<i>O. volkiana</i>	Carabidae	<i>Eripus heterogaster</i>	Larva [37]
54	<i>P. peltata</i>	Curculionidae	<i>Cryptorhynchus corticicolus</i>	Larva [68]
55	<i>S. palustris</i>	Scarabaeidae	—	Larva [37]

sp., and *Rhizotrogus* sp., and *O. stylophora* on *Costelytra zealandica* (Table 1). Other species recorded in this family are *C. obliquiordinata*, *C. scarabaeicola*, *Metarhizium brittlebankisoides*, *Ophiocordyceps arbuscula*, *O. barnesii*, *O. elongatiperitheciata*, *O. geniculata*, *O. gracillima*, *O. highlandensis*, *O. konnoana*, *O. larvicola*, *O. macularis*, *O. neovolkiana*, *O. nigrella*, *O. superficialis*, *O. variabilis*, and *Sphaerocordyceps palustris* (Table 1). Out of 27 *Cordyceps* spp., 26 are recorded on larvae except *C. scarabaeicola* that is recorded on adult (Table 1).

4.1.2. Geotrupidae. Members of this family are commonly called earth-boring dung beetles, which mostly excavate burrows to lay their eggs. They are normally detritivores but occasionally behave as coprophagous. *Cordyceps geotrupis* is recorded on an adult of *Geotrupes* sp. in this family (Table 1).

4.1.3. Lucanidae. Members of this family are commonly called stag beetles. The name stag beetle is derived from the distinctive mandibles found on the males that resemble the antlers of stags. The larvae feed on rotting deciduous wood for several years before pupating. *Ophiocordyceps scottiana* is recorded on *Rhyssonotus nebulosus* in this family (Table 1).

4.2. Superfamily Elateroidea

4.2.1. Elateridae. Members of this family are commonly called click beetles, elaters, snapping beetles, spring beetles, skipjacks, and so forth. The adults are typically nocturnal and phytophagous. Larvae are slender, elongate, cylindrical, or somewhat flattened, with relatively hard bodies, somewhat resembling mealworms. Fifteen spp. of *Cordyceps* have been recorded from this family (Table 1), all of which grow on larvae except *Ophiocordyceps salebrosa* that grows on an adult (Table 1). Six spp. are recorded on larvae of the following hosts: *Cordyceps nirtolii* on *Melanotus communis*, *C. shanxiensis* on *M. caudex* and *Pleonomus canaliculatus*, *Metarhizium campsosterni* on *Campsosternus auratus*, *M. martiale* on *Hemirhipus* sp., *Ophiocordyceps jiangxiensis* on *C. auratus* and *C. fruhstorferi*, and *O. stylophora* on *Denticollis linearis* (Table 1). Other spp. recorded in this family are *Cordyceps aurantiaca*, *C. huntii*, *C. rubra*, *C. velutipes*, *Ophiocordyceps brunneipunctata*, *O. elateridicola*, *O. gracilioides*, *O. purpureostromata*, and *O. salebrosa* (Table 1).

4.3. Superfamily Chrysomeloidea

4.3.1. Cerambycidae. The long-horned beetles, also known as longicorns, are cosmopolitan, typically characterized by

extremely long antennae, which are often as long as or longer than the beetle's body. The larvae, called roundheaded borers, bore into wood, where they can cause extensive damage to either living trees or untreated lumber. Four spp. are known from this family, all growing on larvae (Table 1). They are *Ophiocordyceps dovei* on *Oemona hirta*, *O. entomorrhiza* on *Leptura* sp., *O. larvicola* on *Callidium* sp., and *O. stylophora* on *Phoracantha semipunctata*.

4.3.2. *Chrysomelidae*. The family, commonly known as leaf beetle, is one of the largest beetle families. Adults and larvae feed on all sorts of plant tissues. Most chrysomelids are conspicuously colored, typically in glossy yellow to red or metallic blue-green hues. *Ophiocordyceps entomorrhiza* is recorded on adult of *Diabrotica* sp. and *O. superficialis* on a chrysomelid larva (Table 1).

4.4. Superfamily Cucujoidea

4.4.1. *Erotylidae*. It is a family of the pleasing fungus beetles. They feed on plant and fungal matter, a few of them being notable pests. *Cordyceps erotyli* is recorded on adult of *Erotylus* sp. in this family (Table 1).

4.5. Superfamily Curculionoidea

4.5.1. *Curculionidae*. It is the family of the true weevils or snout beetles. Weevils are almost entirely plant feeders. *Cordyceps militaris* is recorded on larva of *Ips sexdentatus*, *Ophiocordyceps curculionum* on adult of *Heilipus celsus*, *O. entomorrhiza* on adult of *Apion flavipes*, and *Podocrella peltata* on larva of *Cryptorhynchus corticicolus* (Table 1).

4.6. Superfamily Tenebrionoidea

4.6.1. *Tenebrionidae*. Tenebrionids are often referred to as darkling beetles as they have usually black or brown elytra and are nocturnal in habit. They are found worldwide though they are more diverse in semiarid and arid ecosystems. Adults of most species are saprophagous while larvae are mostly detritivores (litter feeders) or xylophagous. Five spp. are recorded on larvae of this family (Table 1): *C. militaris* on *Tenebrio molitor*, *O. acicularis* on *Nictobates* sp., *O. entomorrhiza* on *Meneristes laticollis*, and *O. larvicola* on *Cylindronotus* sp., *Helops caraboides*, and *H. lanipes*. *Ophiocordyceps formosana* is the fifth species recorded on larva of this family.

4.7. Superfamily Staphylinoidea

4.7.1. *Staphylinidae*. The rove beetles belong to family Staphylinidae, primarily distinguished by their short elytra. The group is currently recognized as the largest family of beetles. They are an ecologically and morphologically diverse group of beetles and commonly encountered in terrestrial ecosystems. *Cordyceps memorabilis* is recorded on adult of *Staphylinus* sp. whereas *Ophiocordyceps entomorrhiza* is recorded on larva of *Ocypus* sp. *Cordyceps staphylinidicola* and *O. superficialis* are other spp. recorded on larvae of this family (Table 1).

4.8. Superfamily Caraboidea

4.8.1. *Carabidae*. It is a large, cosmopolitan family. Its members are commonly known as ground beetles. They are mostly shiny black or metallic and have ridged wing covers (elytra). Common habitats are under the bark of trees, under logs, or among rocks or sand by the edge of ponds and rivers. Six spp. are known from this family (Table 1). Among them, *O. entomorrhiza* is recorded on adults and larvae of several species such as *Carabus auronitens*, *C. coriaceus*, *C. glabratus*, *C. hortensis*, *C. intricatus*, *C. nemoralis*, *C. nemorensis*, *C. violaceus*, *Calathus* sp., *Calosoma* sp., *Coptolabrus* sp., *Hadrocarabus problematicus*, and *Pterostichus* sp. *Ophiocordyceps volkiana* is recorded on larva of *Eripus heterogaster*. *Cordyceps nikkoensis*, *Ophiocordyceps carabidicola*, *O. michiganensis*, and *O. stylophora* are other species recorded on larvae of this family.

Among the coleopteran families, Scarabaeidae is parasitized by the highest number of *Cordyceps* fungi (27 spp.), followed by Elateridae (15 spp.) (Table 1). Among 55 parasitizing fungi (Table 1), we found that only few parasitize more than one family. For example, *Ophiocordyceps entomorrhiza* parasitizes 6 families, followed by *O. stylophora* (4 families), *O. larvicola* and *O. superficialis* (3 families each), and *C. militaris*, *C. velutipes*, and *O. michiganensis* (2 families each) (Table 1). From host range point of view, *Ophiocordyceps entomorrhiza* shows the widest range, infecting 13 spp. in Carabidae and one sp. in each Cerambycidae, Chrysomelidae, Curculionidae, Staphylinidae, and Tenebrionidae (Table 1). It is also exceptional in that it infects both larval and adult stages.

As mentioned earlier, larva is the most dominant host stage susceptible to *Cordyceps* pathogens in Coleoptera, with fewer adult stages being parasitized (Table 1). Besides *O. entomorrhiza*, six other spp. are recorded on coleopteran adults. They are *C. erotyli*, *C. geotrupis*, *C. memorabilis*, *O. curculionum*, *O. salebrosa*, and *C. scarabaeicola*; the remaining ones are recorded on larvae.

5. Lepidopteran Hosts

Lepidoptera is among the large orders of insects [121]. It has around 160,000 spp. that are classified into 4 suborders, 45 superfamilies, and 139 families [122]. Out of four suborders (Aglossata, Glossata, Heterobathmiina, and Zeugloptera), *Cordyceps* and allied genera are known only from Glossata. It is the largest suborder consisting of almost 99.9% of all described lepidopterans [122, 123]. It is further classified into six infraorders (Dacnonypha, Acanthoctesia, Lophocoronina, Neopseustina, Exoporia, and Heteroneura) [122]. Among them, *Cordyceps* hosts are known from two infraorders Exoporia and Heteroneura.

Lepidopterans have from three to more than a dozen larval instars (caterpillars), often five [123, 124], inhabiting as root- or stem-borers or foliage eaters and leaf-miners of angiosperms, usually within narrow range of host plants. Lepidopterans have distinct feeding habits, basically plant-feeding during larval stage and nectar-feeding during adult stage. Exoporia and Heteroneura are discussed below in short, followed by *Cordyceps* pathogens parasitizing them.

TABLE 2: *Cordyceps* species recorded on hepialid hosts (Lepidoptera, Glossata, Exoporia, and Hepialidae).

S number	<i>Cordyceps</i> species	Genus/species	Host stage
1	<i>C. cranstounii</i>	<i>Oxycanus dirempta</i> , <i>Abantiades</i> sp.	Larva [86]
2	<i>C. cuncunae</i>	—	Larva [87]
3	<i>C. hawkesii</i>	<i>Oxycanus</i> sp., <i>Trictena</i> sp., <i>Abantiades</i> sp.	Larva [26, 86]
4	<i>C. hepialidicola</i>	<i>Endoclita excrescens</i>	Larva [88]
5	<i>C. kurijimeansis</i>	<i>Thitarodes armoricanus</i>	Larva [34]
6	<i>C. militaris</i>	<i>Hepialus</i> sp.	Larva, pupa [89]
7	<i>D. gunnii</i>	<i>Abantiades labyrinthicus</i> , <i>Aoraia enysii</i> , <i>Oxycanus</i> sp., <i>Trictena atripalpis</i>	Larva, pupa [26, 46, 86]
8	<i>O. crassispora</i>	<i>Thitarodes baimaensis</i>	Larva [90]
9	<i>O. emeiensis</i>	—	Larva [91]
10	<i>O. gracilis</i>	<i>Ahamus altaicola</i> , <i>Hepialus humuli</i> , <i>Korscheltellus lupulina</i> , <i>Parahepialus nebulosus</i>	Larva [57, 92]
11	<i>O. robertsii</i>	<i>Aenetus virescens</i> , <i>Aoraia dinodes</i> , <i>A. ensyii</i> , <i>Dasypodia selenophora</i> , <i>Wiseana</i> spp.	Larva [46, 93, 94]
12	<i>O. sinensis</i>	<i>Ahamus anomopterus</i> , <i>A. gangcaensis</i> , <i>A. jianchuanensis</i> , <i>A. lijiangensis</i> , <i>A. luquensis</i> , <i>A. maquensis</i> , <i>A. sichuanus</i> , <i>A. yulongensis</i> , <i>A. yunlongensis</i> , <i>A. yunnanensis</i> , <i>A. yushuensis</i> , <i>A. zadoiensis</i> , <i>A. zhayuensis</i> , <i>Bipectilus yunnanensis</i> , <i>Endoclita davidi</i> , <i>Gazoryctra ganna</i> , <i>Hepialus xiaojinensis</i> , <i>Magnificus jiuzhiensis</i> , <i>M. zhiduoensis</i> , <i>Parahepialus nebulosus</i> , <i>Pharmacis carna</i> , <i>P. fusconebulosa</i> , <i>P. pyrenaicus</i> , <i>Thitarodes albipictus</i> , <i>T. armoricanus</i> , <i>T. baimaensis</i> , <i>T. baqingensis</i> , <i>T. bibelteus</i> , <i>T. biruensis</i> , <i>T. callinivalis</i> , <i>T. cingulatus</i> , <i>T. damxungensis</i> , <i>T. deqinensis</i> , <i>T. dongyuensis</i> , <i>T. ferrugineus</i> , <i>T. gonggaensis</i> , <i>T. jialangensis</i> , <i>T. jinshaensis</i> , <i>T. kangdingensis</i> , <i>T. kangdingroides</i> , <i>T. latitegumenus</i> , <i>T. litangensis</i> , <i>T. markamensis</i> , <i>T. meiliensis</i> , <i>T. namensis</i> , <i>T. namlinensis</i> , <i>T. oblifurcus</i> , <i>T. pratensis</i> , <i>T. pui</i> , <i>T. renzhiensis</i> , <i>T. varians</i> , <i>T. xunhuaensis</i> , <i>T. yeriensis</i> , <i>T. zaliensis</i> , <i>T. zhongzhiensis</i>	Larva [95, 96]
13	<i>O. taylorii</i>	<i>Trictena</i> sp.	Pupa [86]
14	<i>O. lanpingensis</i>	<i>Ahamus jianchuanensis</i> , <i>A. yunnanensis</i>	Larva [97]
15	<i>O. laojunshanensis</i>	<i>Ahamus yunnanensis</i>	Larva [98]
16	<i>O. ramosissimum</i>	<i>Endoclita nodus</i>	Larva [99]
17	<i>O. xuefengensis</i>	<i>Endoclita nodus</i>	Larva [76]

5.1. *Infraorder Exoporia*. It is a small infraorder consisting of 636 spp. that are classified into 2 superfamilies [122]. *Cordyceps* and allied genera are recorded only from the superfamily Hepialoidea. The superfamily comprises five families that are distributed in diverse vegetation such as forest, shrubland, grassland, tundra, swamp, and bog with the most varied diet habit among moth families [123, 125]. Among the families, *Cordyceps* spp. are recorded from family Hepialidae alone (Table 2).

Ophiocordyceps sinensis has the widest host range recorded on Hepialidae, covering 55 spp. [95, 96]. Among them, *Thitarodes* and *Ahamus* are the two major genera (Table 2). Thirty-two spp. of *Thitarodes* (*T. albipictus*, *T. armoricanus*, *T. baimaensis*, *T. baqingensis*, *T. bibelteus*, *T. biruensis*, *T. callinivalis*, *T. cingulatus*, *T. damxungensis*, *T.*

deqinensis, *T. dongyuensis*, *T. ferrugineus*, *T. gonggaensis*, *T. jialangensis*, *T. jinshaensis*, *T. kangdingensis*, *T. kangdingroides*, *T. latitegumenus*, *T. litangensis*, *T. markamensis*, *T. meiliensis*, *T. namensis*, *T. namlinensis*, *T. oblifurcus*, *T. pratensis*, *T. pui*, *T. renzhiensis*, *T. varians*, *T. xunhuaensis*, *T. yeriensis*, *T. zaliensis*, and *T. zhongzhiensis*) and 13 spp. of *Ahamus* (*A. anomopterus*, *A. gangcaensis*, *A. jianchuanensis*, *A. lijiangensis*, *A. luquensis*, *A. maquensis*, *A. sichuanus*, *A. yulongensis*, *A. yunlongensis*, *A. yunnanensis*, *A. yushuensis*, *A. zadoiensis*, and *A. zhayuensis*) are the host species of *Ophiocordyceps sinensis* (Table 2). The other host species are *Pharmacis carna*, *P. fusconebulosa*, *P. pyrenaicus*, *Magnificus jiuzhiensis*, *M. zhiduoensis*, *Bipectilus yunnanensis*, *Endoclita davidi*, *Gazoryctra ganna*, *Parahepialus nebulosus*, and *Hepialus xiaojinensis* (Table 2).

There are other species that share similar hosts as *Ophiocordyceps sinensis*. For example, *O. crassispora* and *C. kurijimeansis* are recorded on *Thitarodes baimaensis* and *T. armoricanus*, respectively (Table 2). *Ophiocordyceps gracilis*, *O. lanpingensis*, and *O. laojunshanensis* are recorded on *Ahamus altaicola*, *A. jianchuanensis*, and *A. yunnanensis*, respectively (Table 2). *Ophiocordyceps gracilis* is also recorded on three more hosts *Hepialus humuli*, *Korscheltellus lupulina*, and *Parahepialus nebulosus*. Similarly, *Cordyceps hepialidicola* is reported on *Endoclita excrescens* and *O. ramosissimum* and *O. xuefengensis* on *Endoclita nodus* (Table 2).

Many species are recorded in Australia and New Zealand on hepialid hosts. For instance, *Cordyceps cranstounii*, *C. hawkesii*, *D. gunnii*, *O. robertsii*, and *O. taylorii* are recorded on *Abantiades labyrinthicus* and other *Abantiades* spp., *Aenetus virescens*, *Aoraia dinodes*, *A. ensyii*, *Dasypodia selenophora*, *Oxycanus dirempta*, and other *Oxycanus* spp., *Trictena atripalpis* and other *Trictena* spp., *Wiseana* spp., and so forth (Table 2). Another *Cordyceps* sp. rarely described on *Hepialus* is *C. militaris* (Table 2). Besides that, *Cordyceps cuncunae* and *O. emeiensis* are also recorded on hepialid hosts (Table 2).

5.2. Infraorder Heteroneura. This infraorder consists of more than 98% of lepidopteran species [122]. Nine superfamilies among more than 30 in the infraorder are recorded as hosts of *Cordyceps* spp. Among the host families, Tineidae is the only microlepidopteran family; the rest are macrolepidopterans. Papilionidae and Pieridae are the two butterfly families, the rest being moths. The host families are briefly described below followed by *Cordyceps* spp. recorded on them.

5.2.1. Superfamily Noctuoidea

(1) *Erebidae*. It is the largest family in Lepidoptera with 24,569 described spp. [122]. Despite the high species richness, only two *Cordyceps* spp. are recorded on this family. Of them, *C. militaris* is recorded on *Calliteara pudibunda* and *Leucoma salicis* whereas *C. nikkoensis* is reported on a larva of the family (Table 3).

(2) *Noctuidae*. It is commonly known as owlet moths. *Cordyceps militaris* is recorded on 4 spp. of this family: *Arcte coerula*, *Colocasia coryli*, *Euxoa ochrogaster*, and *Panolis flammea* (Table 3). *Ophiocordyceps elongata* is recorded on *Acronicta americana*. Other species recorded in this family are *Cordyceps alpicola*, *C. bifusispora*, *C. bulolensis*, *C. cristata*, and *C. tuberculata* (Table 3).

(3) *Notodontidae*. Its members are mainly concentrated in the tropical areas. Some examples of this family are puss moths. *Cordyceps militaris* is recorded on 5 spp. of this family. They are *Fentonia ocypete*, *Lampronadata cristata*, *Phalera assimilis*, *P. bucephala*, and *Syntypistis punctatella* (Table 3).

5.2.2. Superfamily Zygaenoidea

(1) *Limacodidae* (*Cochlididae*). The members of this family are known as slug moths and are mostly tropical. *Ophiocordyceps*

cochlidicola is recorded on larva and pupa of this family (Table 3).

5.2.3. Superfamily Cossoidea

(1) *Cossidae*. The members are known as carpenter millers and are found worldwide. Four spp. are recorded in this family. Of them, *Metarhizium indigoticum* is recorded on *Yakudza vicarius*. Two recently described spp., *Ophiocordyceps arborescens* and *O. macroacicularis*, are recorded on *Cossus* sp. (Table 3). The other species recorded on this family is *Cordyceps bassiana*.

5.2.4. Superfamily Drepanoidea

(1) *Drepanidae*. The members of this family have worldwide distribution. *Cordyceps militaris* is recorded on 4 spp. of this family: *Achlya flavicornis*, *Ochropacha duplaris*, *Tethea ocularis*, and *Tetheella fluctuosa* (Table 3).

5.2.5. Superfamily Tineoidea

(1) *Tineidae*. The members are small to medium-sized moths. They are worldwide in distribution but are particularly common in the Palaearctic ecozone. *Cordyceps cardinalis* is recorded on larva of this family (Table 3).

5.2.6. Superfamily Papilionoidea

(1) *Papilionidae*. It is a family of colorful swallowtail butterflies. Some of the members are the largest butterflies in the world. The majority are distributed in the tropical region. *Cordyceps tuberculata* is reported on adult of this family (Table 3).

(2) *Pieridae*. It is a large family of butterfly, mostly distributed in the tropical parts of the world. Its members are mostly white, orange, or yellow in pigmentation. *Metarhizium taii* is reported on *Pieris rapae* in this family (Table 3).

5.2.7. Superfamily Geometroidea

(1) *Geometridae*. It is the second largest family in Lepidoptera with 23,002 spp. [122]. It is commonly known as inch worms. Some of the members are notorious pests. *Cordyceps militaris* and *C. riverae* are recorded from this family parasitizing *Biston panterinaria*, *Lycia hirtaria*, and *Triphosa* sp. (Table 3).

5.2.8. Superfamily Bombycoidea

(1) *Bombycidae*. It is known as silkworm family. The most well-known member is *Bombyx mori*, native to northern China. *Cordyceps militaris* is recorded on *B. mori* and *C. michaelisii* on a species of *Bombyx* (Table 3).

(2) *Endromidae*. This is a small family. *Cordyceps militaris* is recorded on *Andraca bipunctata* in this family (Table 3).

(3) *Saturniidae*. The members include giant silk moths, royal moths, and emperor moths. They are described worldwide

TABLE 3: *Cordyceps* species recorded on heteroneuran hosts (Lepidoptera, Glossata, and Heteroneura).

S number	<i>Cordyceps</i> sp.	Host family	Host genus/species	Host stage
1	<i>C. alpicola</i>	Noctuidae	—	Larva [38]
2	<i>C. bassiana</i>	Cossidae	—	Larva [100]
3	<i>C. bifusispora</i>	Noctuidae	—	Pupa [101]
4	<i>C. bulolensis</i>	Noctuidae	—	Larva [38]
5	<i>C. cardinalis</i>	Tineidae	—	Larva [102]
6	<i>C. cristata</i>	Noctuidae	—	Adult [37]
7	<i>C. flavobrunnescens</i>	Sphingidae	<i>Clanis bilineata</i>	Pupa [50]
8	<i>C. kyusyuensis</i>	Sphingidae	<i>Actias artemis</i>	Larva [103]
9	<i>C. longdongensis</i>	Saturniidae	<i>Bombyx</i> sp.	Pupa [91]
10	<i>C. michaelisii</i>	Bombycidae	<i>Bombyx mori</i>	Pupa [104]
		Bombycidae	<i>Andraca bipunctata</i>	
		Endromiidae	<i>Calliteara pudibunda</i> , <i>Leucoma salicis</i>	
		Erebidae	<i>Achlya flavicornis</i> , <i>Ochropacha duplaris</i> , <i>Tethea ocularis</i> , <i>Tetheella fluctuosa</i>	
		Drepanidae	<i>Biston panterinaria</i> , <i>Lycia hirtaria</i>	
		Geometridae	<i>Dendrolimus pini</i> , <i>D. superans</i> , <i>Macrothylacia rubi</i>	
		Lasiocampidae	<i>Arcte coerulea</i> , <i>Colocasia coryli</i> , <i>Euxoa ochrogaster</i> , <i>Panolis flammea</i>	
11	<i>C. militaris</i>	Noctuidae	<i>Fentonia ocypete</i> , <i>Lampronadata cristata</i> , <i>Phalera assimilis</i> , <i>P. bucephala</i> , <i>Syntypistis punctatella</i>	Larva, pupa [31, 32, 50, 105–113]
		Notodontidae	<i>Fentonia ocypete</i> , <i>Lampronadata cristata</i> , <i>Phalera assimilis</i> , <i>P. bucephala</i> , <i>Syntypistis punctatella</i>	
		Saturniidae	<i>Anisota senatoria</i>	
		Sphingidae	<i>Callambulyx tatarinovi</i> , <i>Laothoe populi</i> , <i>Marumba sperchius</i> , <i>Mimas tiliae</i> , <i>Hyles euphorbiae</i> , <i>Sphinx pinastri</i>	Larva [50]
12	<i>C. nikkoensis</i>	Erebidae	—	Larva, pupa [37]
13	<i>C. polyarthra</i>	Sphingidae	<i>Triphosa</i> sp.	Adult [114]
14	<i>C. riverae</i>	Geometridae	<i>Clanis bilineata</i>	Larva [115]
15	<i>C. taishanensis</i>	Sphingidae	<i>Clanis bilineata</i>	
		Noctuidae	—	
16	<i>C. tuberculata</i>	Papilionidae	—	Adult [50, 116–118]
		Sphingidae	<i>Amphipyra effusa</i> , <i>Amphophyx duponchel</i> , <i>A. jatrophae</i> , <i>Anceryx ello</i> , <i>Cocytus</i> sp., <i>Macroglossum insipida</i> , <i>Sphinx pinastri</i>	
17	<i>M. indigoticum</i>	Cossidae	<i>Yakudza vicarius</i>	Larva [119]
18	<i>M. taii</i>	Pieridae	<i>Pieris rapae</i>	Larva [57]
19	<i>O. cochlidicola</i>	Limacodidae	—	Larva, pupa [51]
20	<i>O. elongata</i>	Noctuidae	<i>Acronicta americana</i>	Larva, pupa [27]
21	<i>O. arborescens</i>	Cossidae	<i>Cossus</i> sp.	Larva [120]
22	<i>O. macroactularis</i>	Cossidae	<i>Cossus</i> sp.	Larva [120]

but are particularly known from tropical and subtropical regions. Some of the members are the largest moth species. *Cordyceps longdongensis* parasitizes *Actias artemis* whereas *C. militaris* parasitizes *Anisota senatoria* (Table 3).

(4) *Sphingidae*. The members of this family are commonly known as hawk moths or sphinx moths. They are moderate to large in size and are mainly described from the tropical parts. *Cordyceps militaris* is recorded on various species in this family such as *Callambulyx tatarinovii*, *Laothoe populi*, *Marumba sperchius*, *Mimas tiliae*, *Hyles euphorbiae*, and *Sphinx pinastri* and *C. tuberculata* on *Amphipyra effusa*, *Amphonyx duponchel*, *A. jatrophae*, *Anceryx ello*, *Cocytius* sp., *Macroglossum insipida*, and *S. pinastri*. Two other spp. *Cordyceps kyusyuensis* and *C. taishanensis* are recorded on *Clanis bilineata*. *Cordyceps flavobrunnescens* and *C. polyarthra* are other spp. recorded from this family.

5.2.9. Superfamily Lasiocampoidea

(1) *Lasiocampidae*. Its members are known as snout moths or lappet moths. They are large in size with broad wings and are known worldwide. *Cordyceps militaris* is reported on *Dendrolimus pini*, *D. superans*, and *Macrothylacia rubi* (Table 3).

Out of 22 spp. recorded on heteroneuran hosts (Table 3), *C. militaris* has the widest host range, extending to 2 infraorders, 6 superfamilies, 10 families, and 29 spp. (Table 3). It is a cosmopolitan species, distributed from sea level to more than 2000 m above sea level [126]. Probably due to its wide host range and adaptability to wider habitats, this species demonstrates rapid *in vitro* growth and fructifications [127]. *Cordyceps tuberculata* is another species recorded on multiple families. Larva is the most suitable host for *Cordyceps* spp. compared to pupa and adult (Table 3).

In total, 16 families in Lepidoptera (1 exoporian and 15 heteroneuran) are identified as host families of *Cordyceps* and allied genera. Hepialidae, though a small family, hosts 6 *Cordyceps* spp., 1 *Drechmeria* sp., and 10 *Ophiocordyceps* spp. (Table 2). They are mostly distributed in either Asia or Australia/New Zealand. After Hepialidae, Noctuidae and Sphingidae are the families mostly infected by *Cordyceps* spp. (Table 3).

Among heteroneuran families, Notodontidae, Drepanidae, and Lasiocampidae are known as hosts of *C. militaris* only (Table 3). Similarly, there are families identified as hosts for single *Cordyceps*/*Ophiocordyceps* spp., for example, Limacodidae (Cochlididae) for *O. cochliidiicola*, Tineidae for *C. cardinalis*, Papilionidae for *C. tuberculata*, and Pieridae for *C. taii*. In general, 11 families are known for just one or two *Cordyceps* spp. (Table 3). On the other hand, a single host species is infected by two spp. such as *Clanis bilineata* by *Cordyceps kyusyuensis* and *C. taishanensis*, *Sphinx pinastri* by *C. militaris* and *C. tuberculata*, *Ahamus yunnanensis* by *Ophiocordyceps lanpingensis* and *O. laojunshanensis*, and *Endoclita nodus* by *O. ramosissimum* and *O. xuefengensis*. From species richness point of view, Erebidae, Geometridae, and Noctuidae are the biggest families in Lepidoptera that occupy nearly 40% of the

total lepidopterans [122]. However, they are reported with fewer *Cordyceps* pathogens. For instance, only two *Cordyceps* spp. are recorded on each Erebidae and Geometridae, proportionately more on Noctuidae (7 spp.) (Table 3). In addition to Coleoptera and Lepidoptera, *C. militaris* is recorded on two more orders Diptera and Hymenoptera [126]. Similarly, the only other species growing on two orders Lepidoptera and Coleoptera is *C. nikkoensis*.

The analysis in the present review is based on the coleopteran and lepidopteran hosts that are identified at family or infrafamily ranks in the literature. Out of estimated 200 spp. reported on coleopteran and lepidopteran hosts, we have enlisted 92 spp. based on their host records in the literature. We could not include the remaining species because of lack of information on infraorder ranks of their hosts. Though the list is not complete for all Coleoptera and lepidopteran hosts, the overall scenario of the taxonomic distributions of the hosts within Coleoptera and Lepidoptera can be viewed in the present review.

6. Further Studies on Hosts of *Cordyceps* Pathogens

Cordyceps fungi with attached hosts have long been studied as botanical or mycological specimens. Mycologists have studied and identified fungal pathogens of insects based on morphological, ecological, and phylogenetic studies [14, 50, 128]. For interested readers, several color books on entomopathogenic fungi are available [59, 129–142]. However, identification of the host species is far from being complete. Some of the possible reasons for the less work on host identification are discussed here. First, the diseased/damaged/deformed insect specimens hinder the objectives of the insect biologists to study their diversity and life cycle and thus are disposed immediately after encountering them [77]. Second, insects are mostly attacked at larval stage, making the identification more difficult and time consuming. Larval stages are not yet described in most of insect species. However, molecular techniques have been recently developed to identify immature stages of insects [143]. Third, *Cordyceps* pathogens of insects rarely cause epizootic outbreaks on their hosts, hence causing no significant economic or ecological losses. Fourth, finding a *Cordyceps* pathogen requires much experience and patience and is out of sight for normal observers. Fifth, *Cordyceps* pathogens are specialists; that is, they are host specific; hence experts interested in one group of insects need not care about pathogens on insects of noninterest groups.

Exploring the potential economic benefit from *Cordyceps* fungi is a continuous objective of mycologists in collaboration with biotechnologists, pharmacologists, analytical chemists, medical scientists, and so forth. The most common example is *Ophiocordyceps sinensis*. This is the fungal entomopathogen collected every year in large quantities [144–148] and sold worldwide as the most expensive biological resource almost twice the value of gold by weight and hence commonly known as Himalayan Gold [149], Tibetan Gold (<http://mushrooming.com/content/yartsa-gunbu-article-national-geographic-magazine>), or Biological Gold [147].

The other potential species is *Cordyceps militaris* that has been successfully grown on artificial media for commercial purpose [126]. Antitumour, antimetastatic, immunomodulatory, antioxidant, anti-inflammatory, insecticidal, antimicrobial, hypolipidaemic, hypoglycaemic, antiaging, neuroprotective, and renoprotective effects are some of the main effects shown by *Cordyceps* fungi [150].

Insect specimens, decaying or mummified with natural enemies, such as virus, bacteria, and fungi, are the good sources of biological control agents of specific insect groups, especially in agriculture, forests, and other natural communities. For example, the susceptible stages of hosts in nature could be informative for the application of entomopathogenic fungi to control harmful insect and pests.

In conclusion, we believe such reviews will attract wider audience towards economic and ecological benefits of entomopathogenic fungi including *Cordyceps*, paving the way for interdisciplinary collaborations. Such reviews will also generate interest in a wider audience including field entomologists, ecologists, biocontrol researchers, and biotechnologists in utilization of entomopathogenic fungi. The accumulative work on host information of other orders parasitized by *Cordyceps* and its asexual genera is going on with the objective of expanding the insect-fungal pathogen index in future.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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