Phylogenetic classification of Cordyceps and the clavicipitaceous fungi

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Abstract: Cordyceps, comprising over 400 species, was historically classified in the Clavicipitaceae, based on cylindrical asci, thickened ascus apices and filiform ascospores, which often disarticulate into part-spores. Cordyceps was characterized by the production of well-developed often stipitate stromata and an ecology as a pathogen of arthropods and Elaphomyces with infrageneric classifications emphasizing arrangement of perithecia, ascospore morphology and host affiliation. To refine the classification of Cordyceps and the Clavicipitaceae, the phylogenetic relationships of 162 taxa were estimated based on analyses consisting of five to seven loci, including the nuclear ribosomal (nrLSU and nLSU), the elongation factor 1α (ef1α), β-tubulin (tub), and mitochondrial ATP6 (atp6). Our results strongly support the existence of three clavicipitaceous clades and reject the monophyly of both Cordyceps and Claviceps. Most diagnostic characters used in current classifications of Cordyceps (e.g., arrangement of perithecia, ascospore fragmentation, etc.) were not supported as being phylogenetically informative; the characters that were most consistent with the phylogeny were texture, pigmentation and morphology of stromata. Therefore, we revise the taxonomy of Cordyceps and the Clavicipitaceae to be consistent with the multi-gene phylogeny. The family Cordyceps is validated based on the type of Cordyceps, C. militaris, and includes most Cordyceps species that possess brightly coloured, fleshy stromata. The new family Ophiocordycipitaceae is proposed based on Ophiocordyces Petch, which we emend. The majority of species in this family produce darkly pigmented, tough to pliant stromata that often possess aperithecial apices. The new genus Elaphocrebrocords is proposed for a subclade of the Ophiocordycipitaceae, which includes all species of Cordyceps that parasitize the fungal genus Elaphomyces and some closely related species that parasitize arthropods.

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The family Clavicipitaceae s. s. is emended and includes the core clade of grass symbionts (e.g., Balasiana, Claviceps, Epichloë, etc.), and the entomopathogenic genus Hypocrella and relatives. In addition, the new genus Metacordyces is proposed for Cordyceps species that are closely related to the grass symbionts in the Clavicipitaceae s. s. Metacordyces includes teleomorphs linked to Metarhizium and other closely related anamorphs. Two new species are described, and lists of accepted names for species in Cordyceps, Elaphocrebrocords, Metacordyces and Ophiocordycipitaceae are provided.

TAXONOMIC NOVELTIES: NEW FAMILY: Ophiocordycipitaceae G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. NEW GENERA: Elaphocrebrocords G.H. Sung & Spatafora, Metacordyces G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora.
INTRODUCTION

Cordyceps Fr. is the most diverse genus in the family Clavicipitaceae in terms of number of species and host range (Kobayasi 1941, 1982, Mains 1957, 1958). There are estimated to be more than 400 species (Mains 1958, Kobayasi 1982, Stensrud et al. 2005) although this is expected to be an underestimation of the extent global diversity (Hawksworth & Rossman 1997). Its host range is broad, ranging from ten orders of arthropods to the truffle-like genus Elaphomycytes, although most species are restricted to a single host species or a set of closely related host species (Kobayasi 1941, 1982, Mains 1957, 1958). The distribution is cosmopolitan, including

Key words: Clavicipitaceae, Cordyceps, Cordycipitaceae, Elaphocordycipitaceae, Metarcondycipitaceae, multigene phylogeny, Ophiocordycipitaceae, Ophiocordycipitaceae.
all terrestrial regions except Antarctica, with the height of known species diversity occurring in subtropical and tropical regions, especially East and Southeast Asia (Kobayasi 1941, 1982, Samson et al. 1988). The genus is generally included in the family Clavicipitaceae, based on its cylindrical asci, thickened ascus apices, and filiform ascospores that often disarticulate into part-spores (Mains 1958, Kobayasi 1982, Rossman et al. 1999, Hywel-Jones et al. 2002). 

Cordyceps is characterized and distinguished from other genera of the family by its production of superficial to completely immersed perithecia on stipitate and often clavate to capitulate stromata and its ecology as a pathogen of arthropods and the fungal genus Elaphomyces (Kobayasi 1941, Mains 1957, 1958, Kobayasi & Shimizu 1960, Rogerson 1970).

Modern infrageneric classifications of Cordyceps have been based primarily on the taxonomic studies of Kobayasi (1941, 1982) and Mains (1958) (but see Masssee 1895). Kobayasi (1941, 1982) recognized three subgenera (C. subg. Cordyceps, C. subg. Ophiocordyceps, and C. subg. Neocordyceps), emphasizing arrangement of perithecia and morphology of asci, ascospores and part-spores. Species of C. subg. Cordyceps (type C. militaris) were characterized by the production of either immersed or superficial perithecia produced at approximately right angles (ordinal) to the surface of the stroma and ascospores that disarticulate into part-spores at maturity. Cordyceps subg. Ophiocordyceps (Petch) Kobayasi (type C. blattae Petch) was distinguished by the production of whole ascospores that do not disarticulate into part-spores and, in some species, ascii lacking pronounced apical hemispheric caps. Cordyceps subg. Neocordyceps Kobayasi (type C. sphecocephala (Klotzsch ex Berk.) Berk. & M.A. Curtis) was characterized by perithecia immersed at oblique angles in the clava region of the stroma and ascospores that disarticulate into part-spores upon maturity.

Mains (1958) expanded the infrageneric classification with a different emphasis on diagnostic characters and recognized two additional subgenera, C. subg. Racemella (Ces.) Sacc. and C. subg. Cryptocordyceps Mains. Cordyceps subg. Racemella (type C. memorabilis (Ces.) Šacc.) included species that produce superficial perithecia and ascii with hemispheric to short cylindrical caps. Cordyceps subg. Cryptocordyceps (type C. ravenelli Berk. & M.A. Curtis) was diagnosed by the production of brown, partly immersed to superficial perithecia in a palisade-like layer at more or less right angles to the surface of the stroma. Kobayasi and Mains also differed in their treatments of C. subg. Ophiocordyceps and C. subg. Neocordyceps. In contrast to Kobayasi (1941), who essentially adopted the diagnosis of Petch (1931) but at the rank of subgenus, Mains (1958) placed only C. blattae and C. peltata Wakef. in C. subg. Ophiocordyceps based on their lack of a thickened ascus apex, thus deemphasizing the importance of ascospore disarticulation at the subgeneric level. Furthermore, Mains (1958) did not recognize C. subg. Neocordyceps, rather he included species with oblique peritheca in C. subg. Cordyceps sect. Cremastocarpon subsect. Entomogena. Currently, the subgenus C. subg. Cordyceps, C. subg. Ophiocordyceps, and C. subg. Neocordyceps sensu Kobayasi (1941) have been arguably the most widely used infrageneric taxa of Cordyceps (Zang & Kinjo 1998, Artjariyasripong et al. 2001, Hywel-Jones 2002, Sung & Spatafora 2004, Stensrud et al. 2005) with the relatively recent addition of C. subg. Bolacordyceps O.E. Erikss., which is characterized by the production of bola-ascospores (Eriksson 1986). Although this ascospore form has been likened to the South American bola or the East Asian ninchuk (martial arts weapon), the overall form is best likened to that of a skipping rope. The two handles of the skipping rope are two terminal sets of four cells. The ‘rope’ is a slender hyphal thread, which appears to lack cytoplasm or, at most, has relic quantities.

In addition to the morphological characters discussed above, host affiliation has played an important role in the classification of Cordyceps (Masssee 1895, Kobayasi 1982). Cordyceps species that parasitize the truffle genus Elaphomyces have been recognized as a unique taxon. The genus Cordyli Fr. (1818) was once assigned for the mycogenous Cordyceps species (Masssee 1895) although it is a homonym of Cordyli Pers. 1807. Kobayasi (1941, 1982) also recognized the mycogenous Cordyceps species as taxonomic units (e.g., C. subg. Cordyceps sect. Cystocarpon subsect. Eucystocarpon ser. Mycogenae) and emphasized the utility of host affiliations in delimiting closely related species of arthropod pathogens. Mains (1958) adopted Kobayasi's treatment of the parasites of Elaphomyces, but questioned whether morphologically similar species on different insect hosts (e.g., C. irangiensis Moureau and C. sphecocephala attacking ants and wasps, respectively) are conspecific. The applicability of hosts as a taxonomic character is complicated, however, due to the difficulty in identifying immature hosts (e.g., larvae and pupae) and insufficient host identification for many herbarium collections.

Several phylogenetic studies employing ribosomal DNA (Artjariyasripong et al. 2001, Sung et al. 2001, Stensrud et al. 2005) have been conducted to test and refine the classification of Cordyceps. Such studies were restricted by both limited taxon sampling and the inadequate resolution power of ribosomal DNA, resulting in limited conclusions regarding systematics of the genus. Recent phylogenetic studies (Spatafora et al. 2007, Sung et al. 2007) based on multiple independent loci provided a greater level of resolution and support, and revealed that neither Cordyceps nor the family Clavicipitaceae is monophyletic. Three monophyletic groups of the clavicipitaceous fungi were recognized, all of which include species of Cordyceps. These results reject the current infrafamilial classification (Diehl 1950) and indicate that the phylogenetic diversity of Cordyceps is representative of the entire family Clavicipitaceae (Spatafora et al. 2007, Sung et al. 2007). Therefore, a new classification of Cordyceps and the Clavicipitaceae is necessary to reflect the current hypotheses of phylogenetic relationships and to be predictive in nature.
Here, we conducted the most extensive multi-gene phylogenetic analyses to provide a basis for the phylogenetic classification of *Cordyceps* and the clavicipitaceae fungi. The main objectives of this study are to 1) reassess the morphological traits used in the current classifications of *Cordyceps* in the context of phylogeny, 2) investigate the taxonomic utility of the anamorphic forms in classification of *Cordyceps* and better understand the teleomorph–anamorph connections, and 3) revise the classification of *Cordyceps* and *Clavicipitaceae* to be consistent with phylogenetic relationships.

**MATERIALS AND METHODS**

**Taxon and character sampling**

A total of 162 taxa were sampled from *Clavicipitaceae* and other families of *Hypocreales* with *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk (*Glomerellaceae*) and *Verticillium dahliae* Kleb. (*Plectosphaerellaceae*) included as outgroups (Table 1).

DNA extractions from cultures or herbarium specimens were conducted using a FastDNA kit (Qiagen) following the manufacturer’s instruction, with minor modifications. Polymerase chain and sequencing reactions were performed as previously described (Sung et al. 2007). DNA sequence data unique to this study were determined from five genes, including the nuclear ribosomal small and large subunits (*nrSSU* and *nrLSU*), the elongation factor 1α (*tef1*), and the largest second largest subunits of RNA polymerase II (*rpb1* and *rpb2*). These sequences were combined with data from 91 taxa, which were obtained from Sung et al. (2007). Information pertaining to voucher numbers concerning the sequences is provided in Table 1.

**Sequence alignment and phylogenetic analyses**

Sequences were edited using SeqEd 1.0.3 (Applied Biosystems Inc.) and contigs were assembled using CodonCode Aligner 1.4 (CodonCode Inc.). Sequences of each gene partition were initially aligned with Clustal W 1.64 (Thompson et al. 1994) and appended to an existing alignment (Sung et al. 2007). This initial alignment was manually edited as necessary in MacClade 4.0 (Maddison & Maddison 2000). All five gene regions sampled in this study were concatenated into a single, combined data set (162-taxon 5-gene data set) with ambiguously aligned regions excluded from phylogenetic analyses. Sequences from two additional gene regions, β-tubulin (*tub*) and mitochondrial ATP6 (*atp6*), from Sung et al. (2007) were also combined with the 162-taxon 5-gene data set to generate a supermatrix of 162-taxon 7-gene data set.

In order to detect incongruence among the five individual gene regions sampled in this study, bootstrap proportions were used for each individual data set with the 107 taxa that was complete for all five genes (Table 1). Bootstrap proportions (BP) were determined in a maximum-parsimony framework using the program PAUP* 4.0b10 (Swofford 2002). Only parsimony-informative characters were used with the following search options: 100 replicates of random sequence addition, TBR branch swapping, and MulTrees OFF. The incongruence was assumed to be significant if two different relationships for the same set of taxa were both supported with greater than 70 % bootstrap proportions by different genes (Mason-Gamer & Kellogg 1996, Wiens 1998). Previous studies revealed that *tub* was double copy in some clavicipitaceae species (Spatafora et al. 2007), and Sung et al. (2007) also showed that while *atp6* possessed conflicting data for a limited number of taxa, the conflict was localized and the locus simultaneously provided increased level of support for other nodes. Thus, although we focused our sampling and analyses of the five aforementioned loci, we also conducted phylogenetic supermatrix analyses with *tub* and *atp6* (162-taxon 7-gene) to detect any increased nodal support provided by those two loci.

Maximum parsimony (MP) analyses were conducted on the 162-taxon 5-gene and the 162-taxon 7-gene data set (Table 1, Fig. 3). All characters were equally weighted and unordered. MP analyses were performed using only parsimony-informative characters with the following settings: 100 replicates of random sequence addition, TBR branch swapping, and MulTrees ON. Phylogenetic confidence was assessed by nonparametric bootstrapping (Felsenstein 1985). A total of 200 bootstrap replicates were used to calculate bootstrap proportions; bootstrapping used the same search options with five replicates of random sequence addition per bootstrap replicate.

Maximum likelihood (ML) analyses were performed with RAxML-VI-HPC v2.2. using a GTRCAT model of evolution with 25 rate categories (Stamatakis al. 2005). The model was separately applied to each of the eleven partitions, which consisted of *nrSSU*, *nrLSU* and the nine codon positions of three protein-coding genes (*tef1*, *rpb1*, and *rpb2*). Nodal support was assessed with nonparametric bootstrapping using 200 replicates. Bayesian Metropolis coupled Markov chain Monte Carlo (B-MCMCMC) analyses were performed on combined datasets using MrBayes 3.0b4 (Huelsenbeck & Ronquist 2001). In estimating the likelihood of each tree, we used the general time-reversible model, with invariant sites and gamma distribution (GTR+I+Γ) and employed the model separately for each partition. In an initial analysis, a B-MCMCMC analysis with five million generations and four chains was conducted in order to test the convergence of log-likelihood. Trees were sampled every 100 generations, for a total of 50,000 trees. For a second analysis, five independent Bayesian runs with two million generations and random starting trees were conducted to reconfirm log-likelihood convergence and mixing of chains.

In addition to the analyses with 162-taxon 5-gene data set, a series of analyses were conducted in MP, ML, and Bayesian frameworks with different taxon samplings (107- and 152-taxon 5-gene data sets) to address the potential topological effects of missing data. Previous phylogenetic and simulation studies demonstrated that the phylogenetic analyses are often not negatively...
affected if less than 50% characters are missing for each taxon in the phylogenetic analyses (Wiens 2003, Philippe et al. 2004). In this study, we assumed that the phylogenetic analysis is not confounded if the taxa were complete for at least three out of five gene partitions. Therefore, ten taxa (Table 1) in the 162-taxon 5-gene data set that were complete for only two gene partitions were excluded to generate the 152-taxon 5-gene data set. A 107-taxon 5-gene data set that does not contain any missing data in gene partitions was also prepared to compare the phylogenetic relationships between 107-taxon and 152-taxon 5-gene analyses. MP, ML, and Bayesian analyses based on the 162-taxon 5-gene data set (Figs 1–2) showed that the *C. sphecocephala* clade is characterized by long-branch lengths relative to the rest of the clavicipitaceous fungi. To address the impact of the *C. sphecocephala* clade on the phylogenetic resolution, we excluded all members of the *C. sphecocephala* clade from the 152-taxon 5-gene data set and constructed a 147-taxon 5-gene data set.

**RESULTS**

Sequence alignment

The combined 162-taxon 5-gene dataset consisted of 4927 base pairs of sequence data (*nrSSU* 1102 bp, *nrLSU* 954 bp, *tef1* 1020 bp, *rpb1* 803 bp, *rpb2* 1048 bp). As a result of excluding ambiguously aligned regions, the final alignment comprised 4600 base pairs (*nrSSU* 1088 bp, *nrLSU* 767 bp, *tef1* 1020 bp, *rpb1* 677 bp, *rpb2* 1048 bp), 1882 of which were parsimony-informative (*nrSSU* 233 bp, *nrLSU* 220 bp, *tef1* 466 bp, *rpb1* 382 bp, *rpb2* 581 bp). A total of 107 taxa were complete for all five genes and the number of complete taxa for each gene was as follows: *nrSSU* 158 taxa, *nrLSU* 157 taxa, *tef1* 149 taxa, *rpb1* 143 taxa, *rpb2* 122 taxa (Table 1).

Phylogenetic analyses

The reciprocal comparisons of 70% bootstrap trees from individual data sets of the 162-taxon 5-gene dataset did not reveal any significantly supported contradictory nodes (data not shown). These results were interpreted as indicating that no strong incongruence existed among the individual data sets that would be indicative of different phylogenetic gene histories (e.g., lineage sorting or horizontal gene transfer). As a result, all five individual data sets were combined in simultaneous analyses.

MP analyses of the 162-taxon 5-gene data set resulted in 156 equally parsimonious trees. These trees were 21,323 steps with a consistency index (CI) of 0.1598 and a retention index (RI) of 0.6131. One of 156 equally parsimonious trees is shown in Fig. 1. Nodes that collapse in the strict consensus tree are denoted with asterisks. ML analyses of the 162-taxon 5-gene data set resulted in a tree with a log-likelihood (–ln) of 92019.95. In the Bayesian analyses, the five-million generation analysis converged on the log-likelihood (harmonic mean = –ln 99561.22) at approximately around 250,000 generations. The results from five of two-million generation analyses also showed a convergence on the log-likelihood at approximately 250,000 generations and the topologies were identical. As a result, the 3,000 trees from the first 300,000 generations were deleted from the five million generation analysis to generate a 50% majority-rule consensus tree.

A 50% majority consensus tree (Fig. 2) was generated from the 5 million generation analysis. Since the topology of ML analyses (tree not shown) was nearly identical to that of the Bayesian consensus tree of Fig. 2, the bootstrap proportions of ML analyses are provided above the corresponding nodes in Fig. 2. Previous studies have shown that in interpreting the supports of the phylogenetic estimates of relationships, the posterior probability tends to overestimate the phylogenetic confidence (Douady et al. 2003, Lutzoni et al. 2004, Reeb et al. 2004). As a result, the posterior probabilities were used as a supplementary indicator to bootstrap proportions. In this study, nodes were considered strongly supported when supported by both bootstrap proportions (BP ≥ 70%) and posterior probabilities (PP ≥ 0.95) (Lutzoni et al. 2004).

Phylogenetic relationships of the clavicipitaceous fungi

All MP, ML, and Bayesian analyses of the five-gene 162-taxon 5-gene data set recognized three well-supported clades of clavicipitaceous fungi (Figs 1–2), designated here as *Clavicipitaceae* clades A, B, and C (Figs 1–2), following the convention of the previous phylogenetic studies (Spatafora et al. 2007, Sung et al. 2007). These clades were statistically well supported by the bootstrap proportions of the MP (MP-BP) and ML (ML-BP) analyses and posterior probabilities (PP) of the Bayesian analyses (clade A: MP-BP = 98%, ML-BP = 99%, PP = 1.00; clade B: MP-BP = 93%, ML-BP = 98%, PP = 1.00; clade C: MP-BP = 100%, ML-BP = 100%, PP = 1.00). A sister-group relationship between clades A and B was also strongly supported (MP-BP = 72%, ML-BP = 90%, PP = 1.00). The monophyletic group of clade C and *Hypocreaceae* was moderately to strongly supported (MP-BP = 63%, ML-BP = 92%, PP = 1.00).

*Clavicipitaceae* clade A comprised five statistically well-supported subclades (Figs 1–2, 4). These were labelled in Figs 1, 2, and 4 as the *C. taii* clade (MP-BP = 73%, ML-BP = 78%, PP = 1.00), the *Claviceps* clade (MP-BP = 95%, ML-BP = 98%, PP = 1.00), the *Hypocrella* clade (MP-BP = 99%, ML-BP = 99%, PP = 1.00), the *Shimizuomyces* clade (MP-BP = 100%, ML-BP = 100%, PP = 1.00), and the *Torrubia luteorostrata* clade (MP-BP = 100%, ML-BP = 100%, PP = 1.00). As indicated previously by Sung et al. (2007), internal relationships among these five subclades were not strongly supported in MP and ML analyses (Figs 1–2, 4).

*Clavicipitaceae* clade B consisted of five major subclades designated as the *C. gunnii*, *C. ophiglossoides*, *C. sphecocephala*, *C. unilateralis*, and *Pa. lilacinus* clades (Figs 1–2, 6). Nearly all of
the subclades in clade B were strongly supported by bootstrap proportions and posterior probabilities (C. gunnii clade: MP-BP = 97 %, ML-BP = 100 %, PP = 1.00; C. ophioglossoides clade: MP-BP = 71 %, ML-BP = 88 %, PP = 1.00; C. sphecocephala clade: MP-BP = 100 %, ML-BP = 100 %, PP = 1.00). It should be noted, however, that the C. unilateralis subclade was not resolved in the MP analyses (Fig. 1). This lack of resolution was due to the instability of the C. unilateralis clade, which is characterized by long-branch lengths relative to the rest of the clavicipitaceous fungi. Multiple placements of the C. sphecocephala subclade, ranging from a basal lineage of the Clavicipitaceae clade B to a terminal clade nested within the C. unilateralis subclade, were present among the most parsimonious trees (data not shown). Our ML and Bayesian results (Fig. 3) indicate that the C. sphecocephala subclade is either a sister-group of the C. unilateralis subclade (107-taxon 5-gene data set) or in the terminal group of the C. unilateralis subclade (152-taxon 5-gene data set). In MP, ML, and Bayesian analyses with a supermatrix of 162-taxon 7-gene data set (Fig. 3), the C. sphecocephala subclade was placed as a terminal group of the C. unilateralis subclade with strong support (MP-BP = 89 %, ML-BP = 94 %, PP = 1.00) as seen in the previous analyses (Sung et al. 2007). In the light of long-branch attraction problems associated with the MP analyses (Fig. 1), we use the Bayesian tree (Fig. 2) to further discuss the relationships in clade B and we conclude that the C. sphecocephala subclade was best included as a member of the C. unilateralis subclade (Figs 2, 6). In interpreting the C. unilateralis subclade in terms of statistical support, we used the bootstrap proportions and posterior probabilities (MP-BP = 88 %, ML-BP = 88 %, PP = 1.00) based on the results of 147-taxon 5-gene data set (Fig. 3).
**DISCUSSION**

**Phylogenetic implications on the systematics of the genus Cordyceps**

The present and previous phylogenetic analyses (Spatapor et al. 2007, Sung et al. 2007) have revealed that species in the **Cordyceps** form three strongly supported monophyletic groups based on combined data sets of six or seven genes (the genes analyzed herein with and without *atp6*). Although more taxa were used in our study, these results were consistent with the previous studies, recognizing three monophyletic groups designated as **Cordyceps** clades A–C (Figs 1–2). In addition, our results also support the paraphyly of the **Cordyceps** as defined by the monophyly of **Cordyceps** clade C and **Hypocreales** (Figs 1–2). Although the paraphyly of the **Cordyceps** (clade C
+ Hypocreaceae) was moderately supported (MP-BP = 63%) in the 162-taxon 5-gene MP analyses (Fig. 1), it was strongly supported (ML-BP = 92%, PP = 1.00) in the ML and Bayesian analyses (Fig. 2) and more robustly addressed in the previous MP analyses, which investigated localized conflicts among gene partitions and compared bootstrap proportions among alternative sampling strategies (Sung et al. 2007).

The phylogenetic hypothesis presented here contradicts current infrafamilial classification of the Clavicipitaceae. Diehl (1950) proposed three subfamilies, Oomycetoideae, Clavicipitoideae, and Cordycipitoideae, based on the development of stromata, anamorphic characters and host affiliations. However, these three subfamilies do not coincide with the three clades of the Clavicipitaceae inferred in the present analyses (Figs 1–2). Clavicipitaceae clade A includes members of all three subfamilies (e.g., Claviceps of Clavicipitoideae, Cordyceps of Cordycipitoideae, and Hypocrella of Oomycetoideae), whereas the remaining clades only comprise members of Cordycipitoideae (e.g., Cordyceps and Torrubia). Importantly, all three major clades include members of Cordyceps, indicating that Cordyceps, like Clavicipitaceae, is not monophyletic (Figs 1–2). As a result, the three recognized well-supported clades (clades A–C) of the clavicipitaceous fungi represent a robust phylogenetic framework for the taxonomic revision of Cordyceps and the Clavicipitaceae.

In the current infrageneric classification of the genus, Cordyceps comprises four subgenera (C. subg. Bolacordyceps, C. subg. Cordyceps, C. subg.

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**Fig. 3.** Schematic diagrams of phylogenetic relationships from MP, ML, and Bayesian analyses that differ in character or taxon sampling. In addition to 162-taxon 5-gene and 7-gene data sets, 107-taxon and 152-taxon 5-gene data sets were generated with taxa complete for five genes (i.e., nrSSU, nrLSU, tef1, rp1 and rp2) and at least three genes, respectively. To address the impact of C. sphecocephala clade to nodal support of C. unilateralis clade in Fig. 1, a 147-taxon 5-gene data set was constructed after members of C. sphecocephala clade were excluded. Bootstrap proportions (BP ≥ 70%) or posterior probabilities (PP ≥ 0.95 in percentage) are shown above corresponding nodes and in a thicker line.
Fig. 4. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade A, to emphasize relationships within the clade. Respective subgenera of *Cordyceps* species in current classification are provided to the right of species. Known anamorphic genera of *Cordyceps* species are in parentheses. Tree description is the same as in Fig. 2.
Neocordyceps, and C. subg. Ophiocordyceps) based on ascospore morphology and arrangement of the perithecia in the stromata (Kobayasi 1941, 1982, Eriksson 1986). However, most of these characters are not consistent with the new phylogenetic hypothesis and are not diagnostic of monophyletic taxa (e.g., subgenera and genera) (Figs 1–2). For example, Kobayasi (1941, 1982) emphasized ascospore morphology and the lack of ascospore disarticulation into part-spores to delimit C. subg. Ophiocordyceps from the other subgenera. Species with non-disarticulating ascospores, however, are included in all three major clades (C. acicularis Ravenel of clade B, C. cardinals G.H. Sung & Spatafora of clade C, and Cordyceps sp. EFCC 2131 and 2135 of clade A described below as Metacordyceps yongmunensis) (Figs 1–2), indicating that non-disarticulating ascospores are not phylogenetically informative at this level (Figs 1–2). Therefore, a reassessment of diagnostic characters, in the previous and current classifications of Cordyceps, is necessary for the three major clades to provide a basis for taxonomic revisions of Cordyceps and the Clavicipitaceae.

Species in Clavicipitaceae clade A
Clavicipitaceae clade A comprises five well-supported subclades (Fig. 4). All known species of Cordyceps in the clade are included in the C. taii clade. Species of Cordyceps in the clade possess partially or completely immersed perithecia on clavate to cylindrical fertile parts of the stromata (Zang et al. 1982, Liang et al. 1991, Zare et al. 2001). They produce ascospores that either disarticulate or remain intact at maturity and include species that possess ordinal and obliquely embedded perithecia. In the current classification, clade A includes species of Cordyceps that were formerly classified in three subgenera of Cordyceps. Cordyceps liangshanensis M. Zang, D. Liu & R. Hu forms ordinal perithecia and possess disarticulating ascospores, consistent with C. subg. Cordyceps (Kobayasi 1982, Zang et al. 1982). Cordyceps chlamydosporia H.C. Evans possesses nondisarticulating ascospores, consistent with C. subg. Ophiocordyceps (Zare et al. 2001). Cordyceps taitii Z.Q. Liang & A.Y. Liu, a known teleomorph species linked to the anamorph genus Metarhizium Sorokin, produces disarticulating ascospores and obliquely embedded perithecia in the stromata, a trait used to recognize C. subg. Neocordyceps (Liang et al. 1991). Importantly, Cordyceps sp. EFCC 2131 and 2135 (described below as Metacordyceps yongmunensis) produce non-disarticulating ascospores and obliquely embedded perithecia in the stromata, characters inconsistent with any of the subgenera in the current classification.

These results suggest that ascospore morphology and arrangement of perithecia are not phylogenetically informative in recognizing either the C. taii clade, or higher clades of clavicipitaceous fungi. Rather, they are more useful at species level classification. For example, our phylogenetic analyses revealed that C. taiti is closely related to C. brittlebankisoides Z. Y. Liu, Z.Q. Liang, Whalley, Y.J. Yao & A.Y. Liu, the purported teleomorph of M. flavoviride (Huang et al. 2005). Although these species are similar to each other in macromorphology (e.g., greenish clavate stromata), they differ in the arrangement of the perithecia. C. brittlebankisoides possesses perithecia that are ordinally placed in the stromata, whereas C. taiti has obliquely embedded perithecia. These results therefore suggest that arrangement of the perithecia in the stromata is useful in delimiting these closely related species in the C. taiti clade (Fig. 4).

Fig. 5. A–E. Representative species of Cordyceps and its allies in Clavicipitaceae clade A. F-K. Morphology of Cordyceps sp. (described here as Metacordyceps yongmunensis sp. nov. below). A. C. liangshanensis on lepidopteran larva, EFCC 1452. B. Cordyceps sp. on lepidopteran pupa, EFCC 12285. C. Hypocrella schizostachyi on scale insect (Hemiptera). D. Shimizuomyces paradoxus on seed of plant (Smilax sieboldii: Smilacaceae). E. Metarhizium sp. on adult of cicada. F. Section of peritheci um, EFCC 2131. G. Asci and fascicle, EFCC 2131. H. Asci showing prominent ascus cap, EFCC 2131. I. Asci showing ascus foot, EFCC 2131. J. Ascospores showing indistinct septation, EFCC 2131. K. Discharged intact ascospores on SDAY agar, EFCC 2131. Scale bars: A–E = 10 mm, F = 200 μm, G = 100 μm, H–J = 10 μm, K = 100 μm.
Species in Clavicipitaceae clade B

Species of Cordyceps in Clavicipitaceae clade B possess disarticulating or non-disarticulating ascospores and produce superficial to completely immersed perithecia that are ordinarily or obliquely inserted in the stromata. As with the Cordyceps species of clade A, this clade also includes members of the former C. subg. Cordyceps (e.g., C. ophioglossoides (Ehrh.) Link and C. variabilis Petch), C. subg. Ophiocordyces (e.g., C. acicularis and C. uninodalis (Tul. & C. Tul.) Sacc.), and C. subg. Neocordyceps (e.g., C. nutans Pat. and C. sphecocephala). The majority of Cordyceps species in this clade produce wiry to pliant or fibrous stromata that typically are completely or partially darkly pigmented and parasitize subterranean or wood-inhabiting hosts, which are buried in soil or embedded in decaying wood. Exceptions to this morphology and ecology do exist, however; for example, C. melolonthae (Tul. & C. Tul.) Sacc. is pigmented bright yellow but stains darkly upon handling, and members of the C. sphecocephala clade parasitize adult insects.

Clade B consists of five subclades. All subclades include either species of Cordyceps or anamorphs with potential links to Cordyceps (e.g., Nomuraea atypicola (Yasuda) Samson linked to C. cylindrica Petch) (Fig. 6, Evans & Samson 1987). The well-resolved tree in the present study (Fig. 6) provides the basis to characterize three of the five subclades of clade B. Due to insufficient taxon sampling, it is not possible to characterize the members of the Cordyceps species in the C. gunnii and Pa. lilacinus subclades. In the light of this, we focus on the remaining three subclades that include sufficient numbers of Cordyceps species.

The C. ophioglossoides subclade primarily consists of Cordyceps species that parasitize species of the genus Elaphomyces (e.g., C. ophioglossoides and C. capitata (Holmsk.) Link) and the nymphs of cicadas (e.g., C. inequidens Kobayasi and C. paradoxa Kobayasi) buried in soil (Kobayasi 1939, Mains 1957, Kobayasi & Shimizu 1960, 1963). Species in this subclade produce partially or completely immersed perithecia, in clavate to capitate fertile parts of the stromata that are entirely or partially darkly pigmented, although some exceptions (e.g., C. melolonthae and C. variabilis) do exist, which produce brightly pigmented stromata (Mains 1958). Many species in the clade (e.g., C. brunneipunctata Hywel-Jones, C. stylophora Berk. & Broome, and C. uninodalis) are also differentiated by aperithecial stromatal apices while the production of perithecia occurs in subterminal regions of the stroma.

Similar to Cordyceps species in clade A, the C. uninodalis subclade includes species that produce disarticulating or non-disarticulating (intact) ascospores. For example, some species in the C. uninodalis subclade (e.g., C. sinensis (Berk.) Sacc. and C. uninodalis) were formerly classified in C. subg. Ophiocordyces. But these species are interspersed among other species (e.g., C. agriotidis A. Kawam. and C. robertsii (Hook.) Berk.) that are classified in C. subg. Cordyceps. This indicates that, while ascospore morphology is useful in delimiting closely related Cordyceps species and uniting others in species complexes, it is not diagnostic of the C. uninodalis subclade itself (Fig. 6). Most members of C. subg. Neocordyceps, as classically treated by Kobayasi (1941, 1982) and others (e.g., Artjariyasripong et al. 2001, Stensrud et al. 2005), form a monophyletic group labelled as the C. sphecocephala subclade within the C. uninodalis group (Fig. 6). The majority of species in the C. sphecocephala subclade produce long, thin, pliant, brightly coloured (or dark marasmioid in a few species) stromata,
Fig. 6. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade B, to emphasize relationships within the clade. Respective subgenera of Cordyceps species in current classification are provided to the right or below of species. Known anamorphic genera of Cordyceps species are in parentheses. Numbers above corresponding nodes are bootstrap proportions of ML analyses (before the backslash) and posterior probabilities (after the backslash) from 147-taxon 5-gene data set in Fig. 3. Numbers below corresponding nodes are bootstrap proportions of ML analyses (before the backslash) and posterior probabilities (after the backslash) from 162-taxon 5-gene data set in Fig. 2. Bootstrap proportions of ≥ 70 % or posterior probabilities of ≥ 0.95 (in percentage) are shown in corresponding nodes. Internodes in a thicker line are supported by the bootstrap proportions and posterior probabilities from either 147-taxon or 12-taxon 5-gene data sets. Numbers in a circle correspond to internode that is informative for placing the C. sphecocephala clade.
Phylogenetic classification of Cordyceps and the clavicipitaceous fungi

Fig. 7. A–S. Representative species of Cordyceps and its allies in Clavicipitaceae clade B. T–X. Ascus and ascospore of Cordyceps species in this clade. A. C. ophioglossoides on truffle (Elaphomycetes sp.: Eurotiomycetes). B. C. japonica on truffle (Elaphomycetes muniticus: Eurotiomycetes), OSC 110991. C. C. subsessilis on scarabaeid beetle in decaying wood (Coleoptera), OSC 128581. D. C. gracilis on lepidopteran larva, EFCC 10121. E. C. heteropoda on nymph of cicada (Hemiptera), EFCC 10125. F. C. nigrella on coleopteran larva, EFCC 3438. G. C. sobolifera on nymph of cicada (Hemiptera), EFCC 7768. H. C. longissima on nymph of cicada (Hemiptera), EFCC 8576. I. C. unilateralis on ant (Hymenoptera). J. C. cochlidicola on lepidopteran larva, EFCC 377. K. C. agritidis on coleopteran larva, EFCC 5274. L. C. sinensis on larva of Hepialus sp. (Lepidoptera), EFCC 3248. M. C. brunneipunctata on coleopteran larva. N. C. phaeocochlea on wasp (Hymenoptera). O. C. nutans on stink bug (Hemiptera). P. C. tricentri on adult of Tricentrus sp. (Hemiptera), EFCC 1001; bar = 10 mm. Q. Hymenostilbe odonatae on adult of dragonfly (Odonata), EFCC 12459; bar = 10 mm. R. Hirsutella sp. on wasp (Hymenoptera). S. Paecilomyces lilacinus. T. C. robertsii, ascus with disarticulating ascospores, MICH 28716. U. C. acicularis, ascus and nondisarticulating ascospores, OSC 110987. V. C. paludosa, non-disarticulating ascospores, MICH 14366. W. C. variabilis, disarticulated part-spores in ascus, and X. Part-spores, OSC 128581. Scale bars: A–B = 10 mm, C = 1 mm, D–H = 10 mm, I = 5 mm, J–S = 10 mm, T–X = 10 μm.
which terminate in clavate to elongated fertile parts, and possess ascospores that disarticulate into sixty-four part-spores (Kobayasi 1941, 1982, Hywel-Jones 2002). Species in this clade produce perithecia, which are partially or completely immersed in the stromata at strongly oblique angles (Kobayasi 1941, 1982, Mains 1958, Hywel-Jones 1996). This clade is one of the best characterized by its morphology (obliquely embedded perithecia in a well-defined clava) and its ecology of parasitizing adult stages of insects.

Species in Clavicipitaceae clade C
Clavicipitaceae clade C includes C. militaris, the type species of the genus Cordyceps (Fig. 8). Most Cordyceps species in this clade are currently classified in C. subg. Cordyceps (Kobayasi 1941, 1982). This clade also contains the members of the former C. subg. Ophiocordyceps and C. subg. Bolocordyceps, resulting in C. subg. Cordyceps being paraphyletic within clade C (Eriksson 1982, Hywel-Jones 1994, Sung & Spatafora 2004). Species of Cordyceps in this clade produce three ascospore types, including disarticulating ascospores (e.g., C. militaris), intact ascospores (e.g., C. cardinalis and C. pseudomilitaris Hywel-Jones & Sivichai), and bola-ascospores (e.g., C. bifusispora O.E. Erikss.). Of particular note, this clade includes Phytocordyceps ninchukispora C.H. Su & H.-H. Wang in the unspecific genus Phytocordyceps C.H. Su & H.-H. Wang. The genus Phytocordyceps was originally described based on bola-ascospores and its host affiliation as a pathogen of Beilschmiedia erythrophloia Hayata (Lauraceae) plant seeds (Su & Wang 1986).

Morphologically, this species is most similar to C. bifusispora in that it produces bola-ascospores typical of C. subg. Bolocordyceps. However, the phylogenetic analyses in this study reveal that species producing bola-ascospores (e.g., C. bifusispora and P. ninchukispora) do not form a monophyletic group (Fig. 8). Rather, they are interspersed among other Cordyceps species possessing disarticulating ascospores, most notably C. militaris.

Species of Cordyceps in clade C produce superficial to partially immersed perithecia on fleshystromata that are dappled to brightly pigmented. This is in contrast to Cordyceps species in clade B, which produce darkly pigmented, wiry to pliant or fibrous stromata. This suggests that pigmentation and texture of stromata may be phylogenetically informative at a higher level of classification. It should be noted, however, that some Cordyceps species in clade C are morphologically similar to distantly related Cordyceps species (e.g., C. melolonthae and C. variabilis) in stromatal pigmentation. Although these characters are useful in recognizing Cordyceps species of clade C, the utility of these characters for any future infrageneric classification is probably limited (Fig. 8). For example, C. militaris is macroscopically similar to C. cardinalis and C. pseudomilitaris. All three species produce orangish to red-coloured and fleshy stromata; however, these species differ in ascospore and anamorph morphology (Sung & Spatafora 2004). Furthermore, C. militaris is known as exhibiting considerable variability in stroma morphology (Sung & Spatafora 2004). Potentially conspecific species, such as C. roseostromata Kobayasi & Shimizu and C. kyusyuensis A. Kawam., differ in stroma morphology, but are closely related to C. militaris and possess identical ascospore and ascus morphologies (Fig. 8, Hywel-Jones 1994, Sung & Spatafora 2004).

The variation in ascospore morphology of Clavicipitaceae clade C combined with old descriptions and unavailable type material complicates species identification for many taxa, as is the case for many of Cordyceps. For example, this study reveals a close relationship between the anamorphic species, Mariannae pruinosa Z.Q. Liang from China, C. pruinosa from Korea and Thailand, and Phytocordyceps ninchukispora from Taiwan (Fig. 8). The teleomorph of M. pruinosa is C. pruinosa Petch, which was originally described as producing disarticulating ascospores and reddish orange stromata, parasitizing lepidopteran cocoons (Petch 1924, Kobayasi 1941, Liang 1991). Although the isolate of M. pruinosa was obtained from ascospores (Liang 1991), the morphology of the ascospores was not well characterized. The species was identified primarily based on its host affiliation and macroscopic characters. In our study, C. pruinosa EFCC 5197 and N.H.J. 10627 were collected from the same host family (Lepidoptera, Limacodidae) in Korea and Thailand. They are also closely related and produce reddish orange stroma (Fig. 8) and bola-ascospores and not the typical C. subg. Cordyceps part-spores. It should be noted, however, that Petch did not provide any drawings or images of ascospores and it is possible that the terminal cells of bola-ascospores could easily be interpreted as part-spores. Thus, at this time we use the name C. pruinosa for the Chinese, Korean and Thai collections and, if further attempts fail to locate type material for C. pruinosa, one of these may have to be designated a neotype. The C. pruinosa collections are closely related to and morphologically indistinguishable from P. ninchukispora with the exception of host affiliation, suggesting the possibility of host misidentification in the original description of P. ninchukispora. Because the tree topology of the C. pruinosa/P. ninchukispora complex is indicative of greater phylogenetic species diversity, i.e., the Korean, Thai, and Taiwanese material may represent unique phylogenetic species (Fig. 8), we retain the use of both names until more detailed sampling and analyses have been conducted.

Clavicipitaceae clade C not only includes members of Cordyceps but also species of the genus Torrubiella, which generally parasitize spiders and scale insects (Kobayasi & Shimizu 1982). The genus Torrubiella is morphologically characterized by the production of superficial perithea on a mycelial subiculum that partially or completely surrounds the host (Kobayasi & Shimizu 1982, Humber & Rombach 1987). Species of Torrubiella also produce disarticulating (e.g., T. ratticaudata Humber & Rombach) and intact (e.g., T. wallacei) ascospores. Among species of Cordyceps, C. tuberculata (Lebert) Maire, a pathogen of adult
Fig. 8. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade C, to emphasize relationships within the clade. Respective subgenera of Cordyceps species in previous classification are provided to the right of the species. Known anamorphic genera of Cordyceps species are in parentheses. Tree description is the same as in Fig. 2.
The taxonomic utility of anamorphic forms in classification of Cordyceps

The genus *Cordyceps* is characterized by a diverse assemblage of more than 25 anamorph genera (e.g., *Beauveria Vuill.*, *Hirsutella Pat.*, *Hymenostilbe Petch, Isaria Fr.*, *Lecanicillium W. Gams & Zare, Metarhizium, and Tolypocladium W. Gams*) (Kobayasi 1982, Samson et al. 1988, Gams & Zare 2003, Hodge 2003). The anamorph genera of *Cordyceps* are hyphomycetes with conidigenous cells that are hyaline to brightly coloured and produce conidia in dry chains or slimy drops (Samson et al. 1988). Some anamorph genera (e.g., *Hymenostilbe*) are known as a useful diagnostic character in recognizing monophyletic groups of *Cordyceps* species (Artjaryasripong et al. 2001, Kobayasi 1941, 1982), while other anamorph morphologies and genera are placed in more than one clade of the *Clavicipitaceae*. Therefore, the distribution of anamorphic forms is discussed to evaluate their phylogenetic utility in characterizing the three clades of *Cordyceps* and *Clavicipitaceae* and to better understand teleomorph–anamorph connections.

**Anamorphs of Clavicipitaceae clade A**

*Clavicipitaceae* clade A includes isolates of the anamorph genera *Aschersonia* Mont., *Metarhizium*, *Nomuraea* Maublanc, *Pochonia* Bat. & O.M. Fonseca, *Paecilomyces s. l.*, *Rotiferophthora* G.L. Barron, *Tolypocladium W. Gams*, and *verticillium-like* (Fig. 4). *Nomuraea*, *Paecilomyces*, and *Tolypocladium* are found in other clades of *Clavicipitaceae* (Figs 1–2). Significantly, *Verticillium* s. s. is known from the *Plectosphaerellaceae*, which is closely related with the *Glomerellaceae* in the Sordariomycetidae (Zare et al. 2007). *Paecilomyces* s. s. is in the *Eurotiales* (*Eurotiomycetidae*), but species of *Paecilomyces* s. I. are also present elsewhere in the *Hypocreales* (Luangsa-ard et al. 2004). In contrast, the anamorph genera *Aschersonia, Metarhizium, Pochonia* and *Rotiferophthora* are restricted to clade A (Figs 1–2).

Anamorph taxa of the *C. taii* subclade include *Nomuraea rileyi* (Farl.) Samson, *Paecilomyces carneus* (Duché & R. Heim) A.H.S. Brown & G. Smith and *Pa. marquandii* (Massée) S. Hughes, *Pochonia, Tolypocladium parasiticum*, and *Metarhizium* (Fig. 4). The genera *Nomuraea, Pochonia* and *Tolypocladium* are not monophyletic, although *Pochonia* is restricted to clade A. *Nomuraea rileyi* and *Metarhizium* are entomogenous; *Pa. carneus* is a common soil fungus considered a weak insect pathogen, while *Pa. marquandii*, *Pochonia* and *T. parasiticum* are also common soil fungi and can be parasitic on nematodes. *Metarhizium* is the only monophyletic anamorph genus of clade A (Fig. 4). The conidigenous cells in the genus *Metarhizium* are cylindrical to clavate without a neck and produced in candelabrum-like or palisade-like fashion (Rombach et al. 1986, Driver et al. 2000, Evans 2003). The genus is most similar to *Nomuraea* and differs in the compact conidiophores that form a hymenial layer (Evans 2003). *Nomuraea rileyi* groups with species of *Metarhizium*, while *N. atypicola* (Yasuda) Samson belongs to the *Pa. lilacinus* clade.
in clade B. Interestingly, *N. rileyi* produces greenish-coloured conidia, as do species of *Metarhizium* in the *C. taii* subclade, while *N. atypica* possesses lavender-coloured conidia similar to those of *Pa. lilacinus* (Coyle *et al.* 1990, Hywel-Jones & Sivichai 1995, Evans 2003). Currently, three teleomorphic species of *Metarhizium* (C. brittlebankisoides, C. camposterni, and *C. taii*) have been reported (Liang *et al.* 1991, Liu *et al.* 2001, Zhang *et al.* 2004). The species *M. taii* was described with its teleomorph species, *C. taii* (Liang *et al.* 1991) and recently synonymized with *M. anisoplae var. majus* (Huang *et al.* 2005). *Cordyceps brittlebankisoides* was once also considered to have the anamorph *M. anisoplae var. omajus* (Liu *et al.* 2001), but it is likened to *M. flavoviride* (Huang *et al.* 2005). In general, *Metarhizium* species show extensive variation in size and colour of conidia (Driver *et al.* 2000, Evans 2003) and more intensive sampling of anamorphs and teleomorphs is needed for this group.

The genus *Tolypocladium* is characterized by producing single or whorled (verticillate) conidiogenous cells (phialides), which are flask-shaped with enlarged bases that taper into a needle-like neck usually bent from the axis of the phialides (Gams 1971, Bissett 1983). The type of the genus *Tolypocladium, T. inflatum* W. Gams, is linked to the teleomorph *C. subsessilis* (Hodge *et al.* 1996, Gams & Zare 2003). *Tolypocladium inflatum* is placed in clade B and is distantly related to *T. parasiticum* in the *C. taii* clade. *Tolypocladium parasiticum* was described from the rotifer host *Adineta* and described with underwater conidiation (Barron 1980). Morphologically, *T. parasiticum* differs from other species of *Tolypocladium*, as it is the only member of the genus that produces chlamydospores in vivo (Barron 1980) and in culture (Bissett 1983, Zare *et al.* 2001, Gams & Zare 2003). In a recent treatment of *Verticillium* sect. *Prostrata* W. Gams, the genus *Pochonia* was also reclassified based on production of dictyochlamydsospores or at least swollen hyphal cells (Gams & Zare 2001, Zare *et al.* 2001), supporting the close phylogenetic relationship of *T. parasiticum* and *Pochonia* species demonstrated in this study (Fig. 4). Hence, *T. parasiticum* is transferred to *Pochonia* below, rendering the remaining species in *Tolypocladium* monophyletic. *Paecilomyces marquandii* also produces infrogenous chlamydospores in culture, as does the anamorph of *Metacordyceps yongmunensis* sp. nov. (discussed below). As suggested by Barron & Onions (1966), the presence of chlamydospores can be a taxonomically informative character.

The genus *Aschersonia* is a monophyletic lineage labelled as *Hypocrella* subclade (Fig. 4). The genus *Aschersonia* is characterized by its pycnidial or acervular conidioma with hymenial phialides and its ecology of parasitizing only the nymphs of scale insects and whiteflies (Petch 1921, Hywel-Jones & Evans 1993). The teleomorphs of *Aschersonia* have long been linked to the species of *Hypocrella* and *Aschersonia*, these findings corroborate that the unique morphology of *Aschersonia* is phylogenetically informative and diagnostic of a monophyletic group of clavicipitaceous fungi (Fig. 4).

### Anamorphs of Clavicipitaceae clade B

Clavicipitaceae clade B includes several anamorph genera including *Haptocillium* W. Gams & Zare, *Hirsutella*, *Hymenostilbe* and *Tolypocladium* (Fig. 6). Several of the anamorphic forms in the clade are phylogenetically informative. *Hirsutella* and *Hymenostilbe* occur dominantly in the *C. unilateralis* subclade.

*Hirsutella* is characterized by its typical basally-subulate phialides, narrowing into one (usually) or more (occasionally) very slender needle-like necks, on synnemata or mononematos mycelium (Hodge 1998, Gams & Zare 2003). *Hirsutella* species normally produce a few (<5) conidia in mucus and the phialides are not usually bent in their needle-like necks such as in the genus *Tolypocladium*, but also single conidia as in *H. thompsonii* F.E. Fisher. Not all *Cordyceps* species in the *C. unilateralis* subclade are connected to *Hirsutella* anamorphs. Some are connected to *Paecilomyces* s. i., *Parasaria* Samson & B.L. Brady, and *Syngliocladium* Petch, whereas anamorphic forms are not known for many of the *Cordyceps* species, especially in the *C. ravenellii* subclade (e.g., *C. heteropoda* Kobayasi). However, most *Cordyceps* species in the rest of the *C. unilateralis* subclade have been linked to *Hirsutella* anamorphs (Fig. 6). These results suggest that *Hirsutella* anamorphs are phylogenetically informative for at least part of the *C. unilateralis* subclade or possibly symplesiomorphic for the *C. unilateralis* subclade as a whole.

The taxonomic utility of *Hirsutella* anamorphs is exemplified by the teleomorph–anamorph connection of the genus *Cordycepioideus* Stijfer, a termite pathogen, which does not have typical ascospore and ascus morphologies of clavicipitaceous fungi (Blackwell & Gilbertson 1984, Suh *et al.* 1998). It possesses thick-walled multisepatate ellipsoid ascospores and its ascii lack the thickened ascus tip characteristic of most clavicipitaceous fungi (Blackwell & Gilbertson 1984, Ochiel *et al.* 1997). The anamorph of *Cordycepioideus bisporus* Stijfer is a synnematus *Hirsutella* that is either conspecific with or closely related to *H. thompsonii* (Ochiel *et al.* 1997, Suh *et al.* 1998, Sung *et al.* 2001). Although *Cordycepioideus bisporus* differs greatly from other members of the *C. unilateralis* subclade in its teleomorphic characters, molecular data strongly support it as a member of the *C. unilateralis* subclade, a finding consistent with its *Hirsutella* anamorph. It should be noted that species of *Cordyceps* outside of clade B have been described with atypical *Hirsutella* anamorphs (e.g., *C. pseudomilitaris*), but upon further investigation were more accurately characterized in other anamorph genera (e.g., *Simplicillium* W. Gams & Zare).

The *C. unilateralis* clade includes the members of the *C. sphecocephala* subclade, which possess a *Hymenostilbe* anamorph. The genus *Hymenostilbe* usually produces cylindrical to clavate conidiogenous cells, which are produced in a more or less dense
palisade in synnemata (Samson et al. 1988). It is differentiated from closely related genera (e.g., Akanthomyces Lebert and Hirsutella) by its polyblastic conidiogenous cells, which holoblastically produce single conidia on short denticles or scars (Samson et al. 1988, Hywel-Jones 1996). The results from the present study indicate that Hymenostilbe anamorphs may be derived from within Hirsutella (Fig. 6). The close phylogenetic relationship between Hirsutella and Hymenostilbe anamorphs is exemplified by the morphologically intermediate synnematos Hirsutella Hymenostilbe species. For example, Hy. licanicol (Jaap) Mains, the anamorph of C. clavulata (Schwein.) Ellis & Everh. (Hodge 1998), was previously classified in Hirsutella although it possesses extensively polyphialidic conidiogenous cells in a discontinuous layer (Mains 1950, 1958, Samson & Evans 1975, Hodge 1998). In addition, some Hirsutella species (e.g., Hi. rubripunctate Samson, H.C. Evans & Hoekstra) produce only a single conidium without a mucous sheath on denticles of extensively polyphialidic conidiogenous cells. Therefore, the modes of asexual reproduction in Hirsutella and Hymenostilbe may overlap to some extent and additional work is necessary to address the relationships between the two genera (Hodge 1998, Gams & Zare 2003).

In addition to the C. unilateralis subclade, the remaining three subclades contain Haptocillium, Tolypocladium and verticillum-like anamorphs. The genus Haptocillium was reclassified from the former Verticillum sect. Prostrata primarily based on its adhesive conidia and its ability to parasitize free-living nematodes (Zare & Gams 2001b). This study shows that the genus is a monophyletic group in the C. gunnii subclade (Fig. 6). However, the teleomorph–anamorph connection has not been established for any of the species in the clade or its close relative, C. gunnii, and thus its taxonomic utility remains unclear. The C. ophioglossoides and Pa. lilacinus subclades contain anamorphic forms of Paecilomyces s. l., Nomu-raea, Tolypocladium, and verticillum-like, all of which are polyphyletic as previously discussed (Figs 1–2; Obornik et al. 2001, Luangsaa-ard et al. 2004, 2005). Several teleomorph–anamorph connections have been reported for Cordyceps species in the C. ophioglossoides and Pa. lilacinus subclades although their taxonomic utility is limited. Cordyceps subsessilis is known to be the teleomorph of Tolypocladium inflatum (Hodge et al. 1996) and C. ophioglossoides produces a verticillum-like anamorph (Gams 1971). In the Pa. lilacinus subclade, N. atypica is linked to C. cylindrica (Evans & Samson 1987, Hywel-Jones & Sivichai 1995).

**Anamorphs of Clavicipitaceae clade C**

The anamorph genera sampled that are members of clade C include Beauveria, Isaria, Lecanicillium, Microhilum H.Y. Yip & A.C. Rath, and Simplicillium. Species of Lecanicillium and Simplicillium were previously placed in Verticillum sect. Prostrata and recently reclassified based on the phylogenetic studies of Sung et al. (2001) and Zare & Gams (2001a, b). The genus Lecanicillium is characterized by producing slender aculeate phialides that are produced singly or in whorls and usually arise from prostrate aerial hyphae (Zare & Gams 2001a). Conidia are mostly produced at the tip of phialides and attached in heads or fascicles (Zare & Gams 2001a). The morphological delimitation of Simplicillium from Lecanicillium is difficult although the species of Simplicillium tend to produce phialides that more or less arise singly from prostrate aerial hyphae (Zare & Gams 2001a). This study shows again that the species of Lecanicillium form a paraphyletic group, as species of other well-delimited anamorphic genera (e.g., Beauveria, Engyodontium G.S. de Hoog, and Isaria) are interspersed among species of Lecanicillium (Fig. 8).

Some Lecanicillium species are known to be anamorphic forms of Cordyceps and Torrubiella (Petch 1932, Evans & Samson 1982, Zare & Gams 2001a). For example, C. militaris produces a Lecanicillium anamorph in culture (Zare & Gams 2001a) and the anamorph of Torrubiella alba Petch is L. araneorum (Petch) Zare & W. Gams (Petch 1932). The type species of Lecanicillium is L. licanii (Zimm.) Zare & W. Gams, which is connected to the teleomorph T. confragosa Mains, a pathogen of scale insects (Evans & Samson 1982), which we transfer here to Cordyceps. In addition to Lecanicillium anamorphs, other genera (e.g., Akanthomyces, Gibellula Cava, Hirsutella, Paecilomyces (Isaria), and Simplicillium) have also been linked to Torrubiella (Kobayasi & Shimizu 1982, Samson et al. 1988, 1989, Zare & Gams 2001a).

**Clavicipitaceae clade C** also includes the species of Isaria, the generic name of which has been conserved with I. farinosa (Holmsk.) Fr. as the type, for some of the clavicipitaceous Paecilomyces species (Gams et al. 2005, Luangsaa-ard et al. 2005). The genus Paecilomyces was a diverse genus, with molecular studies indicating its polyphyletic status (Obornik et al. 2001, Luangsaa-ard et al. 2004, 2005). The type species, Pa. variotii Bainier, belongs to the order Eurotiales (Ascomycota) and is distantly related to the clavicipitaceous Paecilomyces species that were previously classified in Paecilomyces sect. Isariaidea (Samson 1974, Luangsaa-ard et al. 2004). The previous taxonomy of Paecilomyces was primarily based on the monographic study by Samson (1974), which included approximately 22 species in Paecilomyces sect. Isariaidea. In a recent molecular study, Luangsaa-ard et al. (2005) demonstrated that species in Paecilomyces sect. Isariaidea are subdivided into four monophyletic groups, three of which are statistically supported. As a result, eleven species of Paecilomyces sect. Isariaidea were reclassified in Isaria (e.g., I. fumosorosea Wize, I. javenica (Frieder, & Bally) Samson & Hywel-Jones and I. tenuipes Peck) (Luangsaa-ard et al. 2005). The present study indicates that the four isolates of Isaria do not form a monophyletic group in clade C, as they are interspersed among other anamorphic forms in the clade. Thus, the taxonomic utility of Isaria anamorph is limited to clade C, as seen with Lecanicillium and Simplicillium anamorphs. Furthermore, few connections have been made between teleomorphs of the Clavicipitaceae and species of Isaria. Kobayasi
(1941) reported that the anamorph of C. takaomontana Yakush. & Kumaz. is Isaria japonica Yasuda, which Samson (1974) synonymized with Pa. tenuipes (= I. tenuipes). Isaria farinosa is the anamorph of C. memorabilis (Pacioci & Frizzi 1978), but was once mistakenly linked to C. militaris (Petch 1936). Isaria farinosa was also connected to two Torrubiella species, T. gonylecttica (A. Möller) Petch and T. pulvinata Mains. The anamorph of the latter was reported as Spicaria pulvinata Mains, and Petch described the conidial state of T. gonylecttica as Spicaria longipes Petch, two Spicaria species that Samson (1974) synonymized with Paecilomyces farinosus (= I. farinosa). Although T. gonylecttica was originally described in combination with Cordyceps, Petch (1937) transferred the species to its current combination and redescribed the species. Isaria farinosa has been reported to occur on six insect orders (Lepidoptera, Coleoptera, Hemiptera, Homoptera, Diptera, and Hymenoptera) and also on spiders (Araneae). The simplicity and plasticity in the morphology of most Isaria species make it difficult to set boundaries among and between sister-taxa and the search for better markers in species delimitation must be a goal for further studies.

The closely related species, C. scarabaeicola Kobayasi and C. staphylinidica Kobayasi & Shimizu produce Beauveria anamorphs (Fig. 8; Sung 1996), and C. bassiana Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan and C. bronniartii Shimazu are known as teleomorphs of B. bassiana (Bals.) Vuill. and B. bronniartii (Sacc.) Petch, respectively (Shimazu et al. 1998; Li et al. 2001). The genus Beauveria is morphologically well-characterized by producing basally-inflated conidiogenous cells that sympodially produce conidia on divergent denticles (MacLeod 1954, de Hoog 1972). Beauveria has a cosmopolitan distribution with a quite a broad host range (Mugnai et al. 1989; Evans 2003, Rehner & Buckley 2005). A recent molecular study (Rehner & Buckley 2005) that included 87 isolates of five Beauveria species (B. amorpha (Höhn.) Samson & H.C. Evans, B. bassiana, B. bronniartii, B. caledonica Bissett & Widden, and B. vermicionia de Hoog & V. Rao) demonstrated that the genus is monophyletic and one of the more phylogenetically-informative anamorphs of clade C.

In fungal systematics, the naming of anamorphic forms is allowed for Phyla Ascomycota and Basidiomycota by Article 9 of the International Code of Botanical Nomenclature (McNeill et al. 2006) and multiple names exist for the same organisms of teleomorphic and anamorphic taxa. Recently, molecular phylogenetics has played an important role in integrating teleomorphic and anamorphic forms in a unified classification system in the clavicipitaceous fungi (Reynolds & Taylor 1993, Sung et al. 2001, Luangsa-ard et al. 2005). In such efforts, Verticillium sect. Prostrata and Paecilomyces sect. Isarioidae have recently been reclassified into several anamorphic genera (e.g., Haptocillium, Isaria, Lecanicillium, Pochonia, Rotiferophthora, and Simplicillium) to be consistent with the current hypotheses of relationships (Zare & Gams 2001a, Zare et al. 2001, Luangsa-ard et al. 2005). The phylogeny presented here further improves our understanding of the teleomorph–anamorph connections in Cordyceps and implies that several anamorphic genera (e.g., Beauveria, Hirsutella, Hymenostilbe, and Metarhizium) are more restricted in their phylogenetic distribution and therefore phylogenetically informative in characterizing Cordyceps species (Figs 4, 6, 8).

**TAXONOMIC REVISION**

The present phylogenetic analyses reveal three strongly supported monophyletic groups (i.e., Clavicipitaceae clades A, B, and C) of clavicipitaceous fungi (Figs 1–2), a result consistent with studies involving fewer taxa (Spatafora et al. 2007, Sung et al. 2007). In reviewing the diagnostic characters used in previous classification schemes, most characters are not consistent with the phylology presented here. Therefore, the phylogenetic relationships of Cordyceps and the related clavicipitaceous fungi provide the evidence for rejecting most of the previous classifications of Cordyceps and Clavicipitaceae (Kobayasi 1941, 1982, Diehl 1950, Mains 1958). Here, we propose a new phylogenetic classification for Cordyceps and Clavicipitaceae as follows (Fig. 10).

**Clavicipitaceae Clade A**

Clavicipitaceae clade A is a well-supported monophyletic group that represents the Clavicipitaceae s. s. (MP-BP = 98 %, ML-BP = 99 %, PP = 1.00 in Figs 1–2, 10). The name Clavicipitaceae was first used in 1901 by Earle for the former Hypocreaceae subfam. Clavicipitaceae Lindau (Earle 1901). However, Earle (1901) used it without description and without reference to its basionym. The name was then invalidly used by subsequent workers, such as Nannfeldt (1932) and Diehl (1950), until it was validated by Rogerson (1970) as confirmed by Eriksson & Hawksworth (1985). Although Clavicipitaceae is well characterized by cylindrical asci, thickened ascus apices, and filiform ascospores that tend to disarticulate at maturity as in the original description, we restrict the application of Clavicipitaceae s. s. to the members of Clavicipitaceae cladeA because of the non-monophyly of Clavicipitaceae s. l. (Fig. 10). These findings suggest that the character states of cylindrical asci and filiform ascospores that disarticulate at maturity are plesiomorphic for the Clavicipitaceae s. l./Hypocreaceae clade. Importantly, the Hypocreaceae also possesses cylindrical asci and while its ascospores are subglobose to fusiform and easily distinguished from those of Clavicipitaceae s. l., they show a similarly high frequency of disarticulation (Rogerson 1970, Rossman et al. 1999).

The family Clavicipitaceae s. s. includes the grass-associated genera Balansia Speg., Claviceps, Epichloë (Fr.) Tul. & C. Tul., and Myriogenospora G.F. Atk., which were classified in Clavicipitaceae subfam. Clavicipitaceae sensu Diehl 1950 (Fig. 10). Recent molecular studies show that Aciculosporium I. Miyake, Atkinsonella Diehl, Heteroëpichloë E. Tanaka, C.
Fig. 9. A–M. Representative species of Cordyceps and its allies in Clavicipitaceae clade C. N–S. Perithecia, asci, and ascospores. A. *C. militaris* on lepidopteran pupa, EFCC 5192. B. *C. kyusyuënsis* on lepidopteran larva, EFCC 10985. C. *C. chichibuënsis* on coleopteran pupa, EFCC 422. D. *C. cf. ochraceostromata* on lepidopteran larva, EFCC 11846. E. *C. scarabaecicola* on scarabaenid beetle (Coleoptera), EFCC 5014. F. *C. staphylindicola* on coleopteran larva, EFCC 783. G. *C. bifusispora* on lepidopteran pupa, EFCC 2626. H. *C. cf. pruinosa* on lepidopteran pupa (Limagadidae), EFCC 11756. I. *C. cardinals* on lepidopteran larva, EFCC 12212. J. *C. tuberculata* on adult of moth (Lepidoptera), EFCC 2067. K. *Torrubiella* sp. on spider (Arachnida), EFCC 10882. L. *Beauveria* sp. on adult of beetle (Coleoptera), EFCC 1357. M. *Isaria tenuipes* on lepidopteran pupa, EFCC 1497. N. *C. cardinals*, section of perithecia in stroma, OSC 93609. O. *C. militaris*, ascus with disarticulating ascospores, OSC 93623. P. *C. cardinals*, ascus with nondisarticulating ascospores, OSC 93609. Q. *C. cf. pruinosa*, fusiform terminal parts of ascospores in ascus, EFCC 7481. R. *C. militaris*, multisepctated ascospores in ascus, OSC 93623. S. *C. cf. pruinosa*, thread-like structures connecting fusiform terminal parts of ascospores, EFCC 7481. Scale bars: A–M = 10 mm, N = 100 μm, O–S = 5 μm.
Tanaka, Gafur & Tsuda, Neoclaviceps J.F. White, Bills, S.C. Alderman & Spatafora, and Parepichloë J.F. White & P.V. Reddy are also members of this clade, thus supporting their classification in the Clavicipitaceae s. s. (White & Reddy 1998, Sullivan et al. 2001, Tanaka et al. 2002). Clavicipitaceae s. s. also includes the plant-associated Shimizuomyces paradoxus Kobayasi, which occurs on seeds of Smilax (Smilacaceae). In addition to plant-associated fungi, Clavicipitaceae s. s. contains four arthropod-associated lineages. Three of the four arthropod-associated lineages are characterized as pathogens of scale insects, including Hypocrella (pathogens of scale insects and white flies; Hywel-Jones & Evans 1993, Hywel-Jones & Samuels 1998), Regiocrella P. Chaverry & K.T. Hodge (pathogen of scale insects; Chaverry et al. 2006), and Torrubiella luteorostra Zimm. (pathogen of scale insects; Hywel-Jones 1993). The fourth lineage is described here as Metacordyceps; it comprises former species of Cordyceps and their related anamorphs and as a genus displays relatively broad arthropod host associations.

**CLAVICIPITACEAE** (Lindau) Earle ex Rogerson, Mycologia 62 : 900. 1970, emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

Stromata or subiculum darkly or brightly coloured, fleshy or tough. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Ascus cylindrical with thickened ascus apex. Ascospores immersed in stromata, ordinal or oblique in arrangement.

**Type**: Claviceps Tul., Ann. Sci. Nat. Bot., Sér. 3, 20: 43. 1853.

**Teleomorphic genera**: Aciculosporium, Atkinsonella, Balansia, Claviceps, Epichloë, Heteropichloë, Hypocrella, Metacordyceps gen. nov., Myriogenospora, Neoclaviceps, Parepichloë, Regiocrella, Shimizuomyces.

**Anamorphic genera**: Aschersonia, Ephelis Fr., Metarhizium, Neotyphodium A.E. Glenn, C.W. Bacon & Hanlin, Nomuraea, paecilomyces-like, Pochonia, Sphacelia Lév., verticillium-like.

**METACORDYCEPS** G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, gen. nov. MycoBank MB504182.

Stromata solitaria vel nonnulla aggregata, simplicia vel ramosa. Stipes carnosus vel tenax, albidus, viridi-luteus vel viridulus, cylindrical vel sursum dilatatus. Pars fertlis cylindrica vel clavata. Perithecia partim vel omnino in stromate immersa, perpendicularia vel oblique inserta. Ascii cylindrici, apice inspissato. Ascosporeae cylindricae, multiseptatae, in cellulas diffrangentes vel maturae integrae remanentes.

Stromata solitaria vel nonnulla aggregata, simplicia vel ramosa. Stipes carnosus vel tenax, albidus, viridi-luteus vel viridulus, cylindrical vel sursum dilatatus. Pars fertlis cylindrica vel clavata. Perithecia partim vel omnino in stromate immersa, perpendicularia vel oblique inserta. Ascii cylindrici, apice inspissato. Ascosporeae cylindricae, multiseptatae, in cellulas diffrangentes vel maturae integrae remanentes.

Stromata solitaria vel nonnulla aggregata, simplicia vel ramosa. Stipes carnosus vel tenax, albidus, viridi-luteus vel viridulus, cylindrical vel sursum dilatatus. Pars fertlis cylindrica vel clavata. Perithecia partim vel omnino in stromate immersa, perpendicularia vel oblique inserta. Ascii cylindrici, apice inspissato. Ascosporeae cylindricae, multiseptatae, in cellulas diffrangentes vel maturae integrae remanentes.

**Type**: Cordyceps taii Z.Q. Liang & A.Y. Liu

**Etymology**: Greek *meta* = behind, a genus close to *Cordyceps* (and suggesting relationship to Metarhizium).

**Anamorphic genera**: Metarhizium, Nomuraea, paecilomyces-like, Pochonia.

**Commentary**: The genus Metacordyceps is proposed for species of *Cordyceps* s. l. in the Clavicipitaceae s. s. based on the phylogenetic placement of *C. taii* (Figs 1–2, 10). The genus is applied to the C. *taii* clade, which is strongly supported (MP-BP = 73 %, ML-BP = 78 %, PP = 1.00 in Figs 1–2, 10). Among the members of the clade, the best-known taxon is the anamorphic genus *Metarhizium*, because of its importance in biological control (Samson et al. 1988, Evans 2003). Currently, three species of *Cordyceps* (viz., C. britlebankisoides, C. campososterni, and C. *taii*) are known as telemorphs of *Metarhizium* (Liang et al. 1991, Liu et al. 2001, Zhang et al. 2004). The genus name *Metacordyceps* is here used to emphasize that the clade includes the species of *Cordyceps* s. l. that produce *Metarhizium* anamorphs although other species of *Cordyceps* (e.g., *C. chlamydospora*) in the clade are not connected to *Metarhizium* anamorphs.

**Metacordyceps yongmunensis** G.H. Sung, J.M. Sung & Spatafora, sp. nov. MycoBank MB504183. Figs 5B, 5F-K, 11A-G.

**Anamorph**: pochonia-like.

Stromata nonnulla vel raro singula, clavata, simplicia vel saepius ramosa, in chrysalidibus Lepidopterarum. Pars fertlis alba vel dilute lutea, a stipite haud distincta. Perithecia sparsa vel dense aggregata, partim immersa, brunneo-lutea, dilute brunnea vel aurantio-brunnea, oblique inserta, fusiformia vel clavata, 550–800 × 450–500 μm. Ascii 8-spori, hyalini, cylindrici, 205–360 × 5–7 μm, apice conspicue inspissato. Ascosporeae filiformes, hyalinae, inconspicue multiseptatae, haud fragmentatae, 180–345 × 1 μm. Anamorph *Pochonia* similis.

Stromata several or rarely solitary, clavate, simple or more usually branched, on pupa of Lepidoptera. Fertile area white to pale yellow, not differentiated from stipe. Perithecia scattered or crowded, loosely immersed, brownish yellow, pale brown to orangish brown, oblique in arrangement, fusiform to clavate, 550–800 × 450–500 μm. Ascii 8-spori, hyaline, cylindrical, 205–360 × 5–7 μm, possessing a prominent apical cap. Ascospores filiform, hyaline, multiseptate with indistinct septation, not fragmenting into part-spores, 180–345 μm. Anamorph *Pochonia* similis.

**Etymology**: Yongmunensis in reference to the known locality of the first record of the species being Mt. Yongmun, Republic of Korea.
| Species                                      | Voucher Info. | Host/Substratum                      | GenBank Accession Number |
|---------------------------------------------|---------------|--------------------------------------|--------------------------|
| Aphysostronia stercorenorum                 | HCC 001       | Cow dung                             | EF51004, EF51005         |
| Aphysostronia budia                        | HCC 002       | Cow dung                             | EF51006, EF51007         |
| Aphysostronia piccola                       | HCC 003       | Cow dung                             | EF51008, EF51009         |
| Aphysostronia citrinum                      | HCC 004       | Cow dung                             | EF51010, EF51011         |
| Aphysostronia atrata                        | HCC 005       | Cow dung                             | EF51012, EF51013         |

Table 1. Taxa used in molecular phylogenetic analyses. (\(^a\)) **Authentic material**, (\(^t\)) **ex-type culture**.

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**Notes:**
- **Host/Substratum:** Species of the hosts or substrata are listed in parentheses.
- **GenBank Accession Number:** Accession numbers are provided for each species, indicating the GenBank record associated with the species.
- **Voucher Info.:** Voucher information is included to help trace the source of the material.

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**References:**
- Sung et al. (2023). Molecular phylogenetic analysis of asexually reproducing species of the genus Aphysostronia. *Mycol Res* 127(1): 1-14.
| Species                          | Voucher Info. | Host/Substratum                   | nrSSU     | nLSU  | tef1  | rpb1  | rpb2  | tub  | atp6 |
|---------------------------------|---------------|------------------------------------|-----------|-------|-------|-------|-------|------|------|
| *Cordyceps fracta*              | OSC 110990    | Elaphomyces sp. (Eurotiomycetes)   | DQ52345   | DQ518759 | DQ523238 | DQ522373 | DQ522425 | DQ522487 | EF469009 |
| *Cordyceps gracilis*            | EFCC 3101     | Lepidopteran larva                 | EF468655  | EF468810 | EF468750 | EF468858 | EF468913 |
| *Cordyceps gracilis*            | EFCC 8572     | Lepidopteran larva                 | EF468956  | EF468811 | EF468751 | EF468859 | EF468912 |
| *Cordyceps gunnii*              | OSC 76404     | Lepidopteran larva                 | AF339572  | AF339522 | AY489616 | AY489650 | DQ522426 | DQ522488 | AY489582 |
| *Cordyceps heteropoda*          | EFCC 10125    | Nymph of cicada (Hemiptera)        | EF468957  | EF468812 | EF468752 | EF468860 | EF468914 |
| *Cordyceps heteropoda*          | OSC 106404    | Nymph of cicada (Hemiptera)        | AY489690  | AY489722 | AY489617 | AY489651 |
| *Cordyceps ineoënsis*           |               | Nymph of cicada (Hemiptera)        | AB027322  | AB027368 |          |        |        |      |      |
| *Cordyceps irangiensis*         | OSC 128577    | Ant (Hymenoptera)                  | DQ522546  | DQ518760 | DQ522329 | DQ522427 | DQ522489 |
| *Cordyceps irangiensis*         | OSC 128579    | Ant (Hymenoptera)                  | EF469123  | EF469076 | EF469060 | EF469089 | EF469107 | EF469138 |
| *Cordyceps japonica*            | OSC 110991    | Elaphomyces sp. (Eurotiomycetes)   | DQ522547  | DQ518761 | DQ522330 | DQ522375 | DQ522428 | DQ522490 | EF469010 |
| *Cordyceps jezoënsis*           | EFCC 7295     | Coleopteran larva                  | EF468958  | EF468862 | EF468915 |
| *Cordyceps konnoana*            | EFCC 7315     | Coleopteran larva                  | EF468959  | EF468753 | EF468681 | EF468916 |
| *Cordyceps kyusuënsis*          | EFCC 5886     | Lepidopteran larva                 | EF468960  | EF468813 | EF468754 | EF468863 | EF468917 |
| *Cordyceps liangshenensis*      | EFCC 1452     | Lepidopteran pupa                  | EF468962  | EF468815 | EF468756 |
| *Cordyceps liangshenensis*      | EFCC 1523     | Lepidopteran pupa                  | EF468961  | EF468814 | EF468755 | EF468918 |
| *Cordyceps longisegmentis*      | OSC 110992    | Elaphomyces sp. (Eurotiomycetes)   |               |       |       |       |       | EF468816 | EF468864 | EF468919 |
| *Cordyceps longissima*          | EFCC 6814     | Nymph of cicada (Hemiptera)        |               |       |       |       |       |       | EF468817 | EF468757 | EF468865 |
| *Cordyceps melolonthae*         | OSC 110993    | Scarabaeid larva (Coleoptera)      | DQ522548  | DQ518762 | DQ522331 | DQ522376 | DQ522491 | EF469011 |
| *Cordyceps militaris*           | OSC 93623     | Lepidopteran pupa                  | AY184977  | AY184966 | DQ522332 | DQ522377 | AY545732 | DQ522492 | EF469012 |
| *Cordyceps nigrilla*            | EFCC 9247     | Lepidopteran larva                 | EF468963  | EF468818 | EF468758 | EF468866 | EF468920 |
| *Cordyceps nutans*              | OSC 110994    | Stink bug (Hemiptera)              | DQ522549  | DQ518763 | DQ522333 | DQ522378 | DQ522493 |
| *Cordyceps cf. ochraceostromata*| ARSEF 5691    | Lepidoptera                        | EF468964  | EF468819 | EF468759 | EF468867 | EF468921 |
| *Cordyceps ophioglossoides*     | OSC 106405    | Elaphomyces sp. (Eurotiomycetes)   | AY489691  | AY489723 | AY489618 | AY489652 | DQ522429 | DQ522494 | AY489583 |
| *Cordyceps paradoxa*            |               | Nymph of cicada (Hemiptera)        | AB027323  | AB027369 |          |        |        |      |      |
| *Cordyceps cf. pruinosa*        | EFCC 5197     | limacodid pupa (Lepidoptera)       | EF468965  | EF468820 | EF468760 | EF468868 |
| *Cordyceps cf. pruinosa*        | EFCC 5693     | limacodid pupa (Lepidoptera)       | EF468966  | EF468821 | EF468762 | EF468869 |
| *Cordyceps cf. pruinosa*        | N.H.J. 10627  | limacodid pupa (Lepidoptera)       | EF468967  | EF468822 | EF468763 | EF468870 |
| Species                          | Voucher Info. | Host/Substratum                         | nrSSU      | nrLSU   | tef1     | rpb1     | rpb2     | tub   | atp6   |
|----------------------------------|---------------|----------------------------------------|------------|---------|----------|----------|----------|-------|--------|
| Cordyceps cf. pruinosa           | N.H.J. 10684  | Limacodid pupa (Lepidoptera)           | EF468968   | EF468823 | EF468761 | EF468871 |
| Cordyceps ravenellii             | OSC 110995    | Coleopteran larva                      | DQ522550   | DQ521764 | DQ522334 | DQ522379 | DQ522430 | DQ522495 |
| Cordyceps rhizoidea              | N.H.J. 12522  | Termite (Isoptera)                     | EF468970   | EF468825 | EF468764 | EF468873 | EF468923 |
| Cordyceps rhizoidea              | N.H.J. 12529  | Termite (Isoptera)                     | EF468969   | EF468824 | EF468765 | EF468872 | EF468922 |
| Cordyceps robertsi               | KEW 27083     | Lepidoptera                            | EF468826   | EF468766 |
| Cordyceps scarabaeicola          | ARSEF 5689    | Scarabaeid adult (Coleoptera)          | AF339574   | AF339524 | DQ522335 | DQ522380 | DQ522431 | DQ522496 | EF469013 |
| Cordyceps sinensis               | EFCC 7287     | Lepidopteran pupa                      | EF468971   | EF468827 | EF468767 | EF468874 | EF468924 |
| Cordyceps sobolifera             | KEW 78842     | Nymph of cicada (Hemiptera)            | EF468972   | EF468828 | EF468875 | EF468925 |
| Cordyceps sphecocephala          | OSC 110998    | Wasp (Hymenoptera)                     | DQ522551   | DQ521765 | DQ522336 | DQ522381 | DQ522432 | EF469014 |
| Cordyceps staphylinidicola       | ARSEF 5718    | Staphylinid pupa (Coleoptera)          | EF468981   | EF468836 | EF468776 | EF468881 |
| Cordyceps stylophora             | OSC 110999    | Coleopteran larva                      | EF468982   | EF468837 | EF468777 | EF468882 | EF468931 |
| Cordyceps stylophora             | OSC 111000    | Elaterid larva (Coleoptera)            | DQ522552   | DQ521766 | DQ522337 | DQ522382 | DQ522433 | DQ522497 |
| Cordyceps subsessilis            | OSC 71235     | Scarabaeid larva (Coleoptera)          | EF469124   | EF469077 | EF469090 | EF469108 | EF469139 | EF469015 |
| Cordyceps superficialis          | MICH 36253    | Coleopteran larva                      | EF468983   | EF468883 |
| Cordyceps taii                   | ARSEF 5714    | Lepidoptera                            | AF543763   | AF543787 | AF543775 | DQ522383 | DQ522434 | DQ522498 | EF469016 |
| Cordyceps takaomontana           | N.H.J. 12623  | Lepidoptera                            | AB044631   | AB044637 |
| Cordyceps cf. takaomontana       | N.H.J. 12623  | Lepidoptera                            | EF468984   | EF468838 | EF468778 | EF468884 | EF468932 |
| Cordyceps tricentri              | AB027330      | Spittlebug (Hemiptera)                 | AB027330   | AB027376 |
| Cordyceps tuberculata            | OSC 111002    | Lepidoptera                            | DQ522553   | DQ521767 | DQ522338 | DQ522384 | DQ522435 | DQ522499 | EF469017 |
| Cordyceps unilateralis           | OSC 128574    | Ant (Hymenoptera)                      | DQ522554   | DQ521768 | DQ522339 | DQ522385 | DQ522436 |
| Cordyceps variabilis             | ARSEF 5365    | Dipteran larva                         | DQ522555   | DQ521769 | DQ522340 | DQ522386 | DQ522437 | DQ522500 | EF469018 |
| Cordyceps variabilis             | OSC 111003    | Dipteran larva                         | EF468985   | EF468839 | EF468779 | EF468885 | EF468933 |
| Cordyceps yakusimensis           | MICH 323      | Nymph of cicada (Hemiptera)            | AB044632   | AB044633 |
| Cordyceps sp.                    | EFCC 2131     | Lepidopteran pupa                      | EF468977   | EF468833 | EF468770 | EF468876 |
| Cordyceps sp.                    | EFCC 2135     | Lepidopteran pupa                      | EF468979   | EF468834 | EF468769 | EF468877 |
| Cordyceps sp.                    | EFCC 2535     | Coleoptera                             | EF468980   | EF468835 | EF468772 |
| Cordyceps sp.                    | N.H.J. 12118  | Lepidoptera                            | EF468978   | EF468829 | EF468768 | EF468878 | EF468927 |
| Cordyceps sp.                    | N.H.J. 12581  | Termite (Isoptera)                     | EF468973   | EF468831 | EF468775 | EF468930 |
| Cordyceps sp.                    | N.H.J. 12582  | Termite (Isoptera)                     | EF468975   | EF468830 | EF468771 | EF468926 |
| Species                                      | Voucher Info. | Host/Substratum         | GenBank Accession Number |
|----------------------------------------------|---------------|-------------------------|--------------------------|
| **Phylogenetic classification of Cordyceps and the clavicipitaceous fungi** |
| **Species**                                  |               |                         |                          |
| Cordyceps sp.                               | OSC 110996    | Lepidoptera             | EF468974 EF468832 EF468773 EF468880 EF468928 |
| Cordyceps sp.                               | OSC 110997    | Ant (Hymenoptera)       | EF468976 EF468774 EF468879 EF468929 |
| Cosmospora coccinea                         | CBS 114050    | Inonotus nodulosus (Hymenomycetes) | AY489702 AY489734 AY489629 AY489667 DQ522248 DQ522501 AY489596 |
| Engyodontium araneum                        | CBS 309.8     | Spider (Arachnida)      | AF339576 AF339526 DQ522341 DQ522287 DQ522439 DQ522502 EF469019 |
| Epichloë typhina                            | ATCC 56429    | Festuca rubra (Poaceae) | U32405 U17396 F543777 AY489563 DQ522440 DQ522503 AY489584 |
| Glomerella cingulata                        | CBS 114054    | Fragaria sp. (Rosaceae) | AF543762 AF543786 AF543773 AY489569 DQ522441 DQ522504 AY489590 |
| Glomerella cingulata                        | F.A.U. 513    | Fragaria rp. (Rosaceae)  | U48427 U48428 F543772 DQ58454 AY489545 EF469140 EF469020 |
| Haptopodium balanoides                      | CBS 250.82    | Nematode                | AF339588 AF339539 DQ522342 DQ522388 DQ522442 DQ522505 EF469021 |
| Haptopodium sinense                         | CBS 567.95    | Nematode                | AF339594 AF339545 DQ522343 DQ522389 DQ522443 DQ522506 EF469022 |
| Haptopodium zeosporum                       | CBS 335.80    | Nematode                | AF339589 AF339540 EF469062 EF469091 EF469109 EF469141 EF469023 |
| Hirutella sp.                               | N.H.J. 12525  | Hemipteran adult        | EF469125 EF469078 EF469063 EF469092 EF469111 EF469142 |
| Hirutella sp.                               | OSC 128575    | Hemipteran adult        | EF469126 EF469079 EF469064 EF469093 EF469110 EF469143 |
| Hydropisphaera erubescens                   | ATCC 36903    | Cordyline banksii (Laxmanniaceae) | AY545722 AY545726 DQ522344 DQ522390 AY545731 DQ522358 EF469024 |
| Hydropisphaera pezzia                        | CBS 102038    | On bark                 | AY489698 AY489730 AY489625 AY489661 DQ522444 DQ522507 AY489591 |
| Hymenostilbe aurantiaca                     | OSC 128578    | Ant (Hymenoptera)       | DQ522556 DQ518770 DQ522345 DQ522391 DQ522445 DQ522508 |
| Hypocrea lutea                              | ATCC 208838   | On decorticated conifer wood | AF543768 AF543791 AF543781 AY489562 DQ522446 DQ522509 AY489592 |
| Hypocrella schizostachyi                    | BCC 14.123    | Scale insect (Hemiptera) | DQ522557 DQ518771 DQ522346 DQ522392 DQ522447 DQ522510 EF469025 |
| Hypocrella sp.                              | G.J.S. 89-104 | Scale insect (Hemiptera) | U32409 U47832 DQ522347 DQ522448 DQ522511 EF469026 |
| Hypomyces polyborinus                       | ATCC 76479    | Trametes versicolor (Hymenomycetes) | AF543771 AF543793 AF543784 AY489663 AY489593 |
| Isaria cf. farinosa                         | OSC 111004    | Lepidopteran pupa       | EF468866 EF468840 EF468780 EF468886 |
| Isaria farinosa                              | OSC 111005    | Lepidopteran pupa       | DQ522558 DQ518772 DQ522348 DQ522394 DQ522512 EF469028 |
| Isaria farinosa                              | OSC 111005    | Lepidopteran pupa       | EF469127 EF469080 EF469065 EF469094 EF469144 EF469027 |
| Isaria tenupes                               | OSC 111007    | Lepidopteran pupa       | DQ522559 DQ518773 DQ522349 DQ522395 DQ522449 DQ522513 EF469029 |
| Lecanicillium antillanum                    | CBS 350.85 T  | Agaric (Hymenomycetes)  | AF339565 AF339536 DQ522350 DQ522396 DQ522450 DQ522514 EF469030 |
| Lecanicillium araneanum                     | CBS 726.73a   | Spider (Arachnida)      | AF339566 AF339537 EF468781 EF468876 EF468934 |
| Lecanicillium attenuatum                    | CBS 402.78    | Leaf litter of Acer saccharum | AF339614 AF339565 EF468782 EF468888 EF468935 |
| Lecanicillium dimorphum                     | CBS 363.86 T  | Agaricus bisporus (Hymenomycetes) | AF339608 AF339559 EF468784 EF468890 |
| Lecanicillium fusioperon                     | CBS 164.70 T  | Coltricia perennis (Hymenomycetes) | AF339598 AF339549 EF468873 EF468889 |
| Lecanicillium psalliota                     | CBS 101270    | Soil                    | EF469128 EF469081 EF469066 EF469095 EF469113 EF469146 EF469031 |
| Lecanicillium psalliota                     | CBS 532.81    | Soil                    | EF339609 EF339560 EF469067 EF46906 EF469112 EF469145 EF469032 |
| Leuconectria clusiae                        | ATCC 22228 T  | Soil                    | AY489700 AY489732 AY489627 AY489664 EF469114 AY489595 |
| Mariannaea pruinosa                         | ARSEF 5413 AUT | Iragoides fasciata (Lepidoptera) | AY184979 AY184968 DQ522351 DQ522397 DQ522451 DQ522515 EF469033 |
| Metarhizium album                           | ARSEF 2082    | Cofana spectra (Hemiptera) | DQ522560 DQ518775 DQ522352 DQ522398 DQ522452 DQ522516 EF469034 |
| Species                        | Voucher Info. | Host/Substratum                           | nrSSU       | nLSU       | tef1       | rpb1       | rpb2       | tub       | atp6       |
|-------------------------------|---------------|-------------------------------------------|-------------|------------|------------|------------|------------|-----------|------------|
| Metarhizium anisopliae       | ARSEF 3145    | Oryctes rhinoceros (Coleoptera)            | AF339579    | AF339530   | AF543774   | DQ522399   | DQ522453   | DQ522536   | EF469035   |
| Metarhizium flavoviride      | ARSEF 2037\(\) | Nilaparvata lugens (Hemiptera)             | AF339580    | AF339531   | DQ522353   | DQ522400   | DQ522454   | DQ522517   | EF469036   |
| Microhilum oncoperae         | AFSEF 4358\(\) | Oncopera intricata (Lepidoptera)           | AF339581    | AF339532   | EF468785   | EF468911   | EF468936   |            |            |
| Myrothecium atramentosum     | A.E.G. 96-32  | Andropogan virginicus (Poaceae)            | AY489701    | AY489733   | AY489628   | AY489665   | DQ522455   | DQ522518   |            |
| Nectria cinnabarina          | CBS 114055    | Betula sp. (Betulaceae)                    | U32412      | U00748     | AF543785   | AY489666   | DQ522456   | DQ522519   | EF469037   |
| Nomuraea 'typica'            | CBS 744.73    | Spider (Arachnida)                         | EF468987    | EF468841   | EF468786   | EF468892   |            |            |            |
| Nomuraea rileyi              | CBS 806.71    | Lepidoptera                                | AY624205    | AY624250   | EF468787   | EF468893   | EF468937   |            |            |
| Ophiocordycipitella atramentosobora | CBS 10987   | On llana                                  | AF543766    | AF543790   | AY489669   | DQ522457   | DQ522520   | EF469039   |
| Paecilomyces carneus         | CBS 239.32\(\) | Sand dune                                 | EF468988    | EF468843   | EF468789   | EF468894   | EF468938   |            |            |
| Paecilomyces carneus         | CBS 399.59    | Soil                                      | EF468989    | EF468842   | EF468788   | EF468895   | EF468939   |            |            |
| Paecilomyces cinus           | ARSEF 2181    | Meloidogynesp. (Nematoda)                  | AF339534    | AF468790   | EF468896   |            |            |            |            |
| Paecilomyces lilacinus       | CBS 284.36\(\) | Soil                                      | AY624188    | AY624227   | EF468792   | EF468941   |            |            |            |
| Paecilomyces lilacinus       | CBS 431.87    | Meloidogynesp. (Nematoda)                  | AY624188    | EF468844   | EF468791   | EF46897    | EF468940   |            |            |
| Paecilomyces marquandii      | CBS 182.27\(\) | Soil                                      | EF468990    | EF468845   | EF468793   | EF46899    | EF468942   |            |            |
| Phytophthora rheinhardiana   | E.G.S. 38.165 | Belischmia erythroploia (Lauraceae)        | EF468981    | EF468846   | EF468795   | EF468900   |            |            |            |
| Phytophthora rheinhardiana   | E.G.S. 38.166 | Belischmia erythroploia (Lauraceae)        | EF468982    | EF468847   | EF468794   | EF468901   |            |            |            |
| Pochonia bulbillosa          | CBS 145.70    | Root of Picea abies                        | AF339591    | AF339542   | EF468796   | EF468902   | EF468943   |            |            |
| Pochonia chlamydosporia      | CBS 504.66\(\) | Nematode                                  | AF339593    | AF339544   | EF469069   | EF469098   | EF469120   | EF469149   | EF469040   |
| Pochonia gonioides           | CBS 891.72    | Nematode                                  | AF339599    | AF339550   | DQ522354   | DQ522401   | DQ522458   | DQ522521   | EF469041   |
| Pochonia rubescens           | CBS 464.88\(\) | Heterodera avenae (Nematoda)               | AF339615    | AF339566   | EF468797   | EF468903   | EF468944   |            |            |
| Pseudonectria rousseilliana  | CBS 114049    | Buxus sempervirens (Buxaceae)              | AF543767    | U17416     | AY489670   | DQ522459   | DQ522522   | AY489598   |
| Rotifer (Rotifera)           | CBS 101437    | Rotifer                                    | AF339584    | AF339535   | DQ522402   | DQ22460    | DQ522523   | EF469042   |
| Globoidea rostochiensis (Nematoda) | CBS 346.85 | DQ522451   | DQ522403   | DQ522456   | DQ522524   | EF469043   |            |            |
| Globoboida rostochiensis (Nematoda) | CBS 10429 | EF469129   | EF469082   | EF469070   | EF469099   | EF469116   | EF469150   | EF469044   |
| Shimizumomyces paradoxus      | EFCC 6279     | Smaiaxie buildi (Similaceaceae)            | EF469131    | EF469084   | EF469071   | EF469100   | EF469117   | EF469151   | EF469046   |
| Shimizumomyces paradoxus      | EFCC 6564     | Smaiaxie buildi (Similaceaceae)            | EF469130    | EF469083   | EF469072   | EF469101   | EF469118   | EF469152   | EF469045   |
| Simplicillium lamellicola     | CBS 116.25\(\) | A garicis bisp_Back{Hymenomycetes}         | AF339601    | AF339552   | DQ522356   | DQ522404   | DQ522524   | DQ522552   | EF469047   |
| Simplicillium lasuosinicum    | CBS 101267    | Hemileia vastatixi (Uredinales)            | AF339603    | AF339554   | DQ522357   | DQ522405   | DQ522463   | DQ522526   | EF469048   |
| Simplicillium lasuosinicum    | CBS 704.86    | Hemileia vastatixi (Uredinales)            | AF339602    | AF339553   | DQ522358   | DQ522406   | DQ522464   | DQ522527   | EF469049   |
| Simplicillium obiavatum       | CBS 311.74\(\) | Air above sugarcane field                  | AF339567    | AF339517   | EF468798   |            |            |            |            |
| Sphaerostilbella berkeleyana | CBS 102308    | Polypore (Hymenomycetes)                   | AF543770    | U00756     | AF543783   | AY489671   | DQ522465   | DQ522528   | EF469050   |
## Phylogenetic classification of Cordyceps and the clavicipitaceous fungi

### Known distribution: Republic of Korea.

**Specimens examined:** Mt. Yongmun, Gyunggi Province, Republic of Korea: 13 June 1998, EFCC 2131 (holotype); 13 June 1998, EFCC 2134; 13 June 1998, EFCC 2135; 30 June 1999, EFCC 3379; 30 June 1999, EFCC 3380; 29 Aug. 1999, EFCC 4342; 8 Aug. 1999, EFCC 4343; 8 June 2000, EFCC 4951; 30 June 2004, EFCC 12287; 30 June 2004, EFCC 12288; 30 June 2004, EFCC 12291; 8 Aug. 2004, EFCC 12467. Mt. Chiaik, Kangwon Province, Republic of Korea: 8 Aug. 2000, EFCC 5750. Bukbang-myun, Kangwon Province, Republic of Korea: 21 June 2002, EFCC 8808. Living culture in EFCC.

**Commentary:** Most specimens of *M. yongmunensis* possess several stromata (up to 10), on a large pupa of Lepidoptera deeply buried in soil (Fig. 5B). Stroma of the species is typically branched in a dichotomous way at its basal or upper regions (Fig. 5B). Perithecia are usually obliquely inserted in the stromata with a few exceptions that are ordinarily arranged, i.e. at right angles to the surface of the stromata (Fig. 5B). While some perithecia are characterized by an acute narrowing of the perithecium at the ostiole, producing a narrow terminal end (Fig. 5F), others are not significantly narrowed (Fig. 11B). In the asci the ascospores are arranged parallel for their entire length and almost reach the ascus foot, suggesting that ascospores are of approximately the same length as the ascii (Figs 5I, 11A). Unlike the distinct septation of ascospores as seen in *C. militaris* (Fig. 9O), the septa of the ascospores are indistinct and discharged ascospores do not disarticulate into part-spores (Figs 5K, 11A).

In the anamorph of *M. yongmunensis*, cultures derived from ascospores are moderately fast growing in SDAY (Sabouraud-dextrose-yeast extract agar) and the colonies reach 25–35 mm diam at 25 °C in 10 d. Colonies are slightly cottony without zonation and white with a green margin, remaining greenish brown at the reverse side of the cultures. Conidiophores are erect and produced in prostrate aerial hyphae. Phialides are solitary, not in whors, broader at the base and tapering towards the end, measuring 20–28 × 2.0–2.2 μm (Fig. 11C). Conidia are in slimy heads (with usually 2 or 3 conidia) and ellipsoidal to oblong, measuring 2.3–2.5 × 1.5–2.4 μm (Fig. 11C). In submerged areas of the cultures, chlamydospores are developed in chains or reduced to intercalary swollen structures (Figs 11E–G). The anamorph of *M. yongmunensis* is best classified as pachonnia-like because of its subulate phialides and production of chlamydospores, although verticillium-like whorls of phialides were not observed (Zare et al. 2001). In *Metacordyceps*, *M. yongmunensis* is most similar to *C. chlamydospora* (= *C. chlamydomyspora*) in the shape of perithecia and its anamorph. Both species produce brownish perithecia that possess long terminal ends in white or pale yellow stroma (Zare et al. 2001). The anamorph of *C. chlamydospora* is identical with the type of *Pochonia*. Thus the production of chlamydospores can be informative for recognizing some species of *Metacordyceps*.
Accepted names and new combinations for Metacordyceps
The following taxa are accepted species of Metacordyceps based on their inclusion in molecular phylogenies presented herein1 (see Table 1) or morphological descriptions matching the characters described above2. The known anamorph connection is provided for the species of Metacordyceps.

2Metacordyceps brittlebankisioides (ZuoY. Liu, Z.Q. Liang, Whalley, Y.-J. Yao & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504184.
≡ Cordyceps brittlebankisioides ZuoY. Liu, Z.Q. Liang, Whalley, Y.-J. Yao & A.Y. Liu, J. Invert. Pathol. 78: 179. 2001.
Anamorph: Metarhizium

3Metacordyceps campsosterni (W.M. Zhang & T.H. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504185
≡ Cordyceps campsosterni W.M. Zhang & T.H. Li, Fungal Diversity 17: 240. 2004. [as C. 'campsosterna'].
Anamorph: Metarhizium

1Metacordyceps chlamydosporia (H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504186.
≡ Cordyceps chlamydosporia H.C. Evans, in Zare et al., Nova Hedwigia 73: 59. 2001.
Anamorph: Pochonia chlamydosporia (Goddard) Zare & W. Gams

1Metacordyceps liangshanensis (M. Zang, D. Liu & R. Hu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504187.
≡ Cordyceps liangshanensis M. Zang, D. Liu & R. Hu, Acta Bot. Yunnanica 4: 174. 1982.

1Metacordyceps taimii (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones, Spatafora, comb. nov. MycoBank MB0504188.
≡ Cordyceps taimii Z.Q. Liang & A.Y. Liu, Acta Mycol. Sin. 10: 257. 1991.
Anamorph: Metarhizium anisopliae var. anisopliae (Metschn.) Sorokin

1Metacordyceps yongmunensis G.H. Sung, J.M. Sung, Spatafora, sp. nov., see p. 27.
Anamorph: pochonia-like

New combinations for anamorphs associated with Metacordyceps
T. parasiticum is transferred to the genus Pochonia based on molecular phylogenies presented herein1. Pochonia parasitica (G.L. Barron) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504189.
≡ Tolypocladium parasiticum G.L. Barron, Canad. J. Bot. 58: 439. 1980.

CLAVICITACEAE Clade B
Clavicipitaceae clade B is strongly supported (MP-BP = 93 %, ML-BP = 98 %, PP = 1.00 in Figs 1–2, 10) and the family Ophiocordycipitaceae is proposed for it with the type genus Ophiocordyces Petch. Most species of the Ophiocordycipitaceae produce darkly pigmented stromata that are pliant to wiry, or fibrous to tough in texture. Ecologically, many species of the family are known as pathogens of subterranean or wood-inhabiting hosts, buried in soil or embedded in decaying wood. Notable exceptions do exist to these traits with brightly coloured species that may or may not attack adult stages of hosts and occur in exposed habitats.

OPHIOCORDYCIPITACEAE G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, fam. nov. MycoBank MB0504190.
Stromata vel subiculum fusca vel raro laete colorata, tenacia, fibrosa vel flexibilia, raro carnosa, sape ostiolis peritheciorum prominentibus, summa sape peritheciis carentia. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem vel oblique inserta. Ascii cylindri, apice inspissato. Ascosporae cylindricae, multiseptatae, maturae in cellulas diffrangentes vel integrae remanentes.
Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous to pliant, rarely fleshy, often with aperithecial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Ascii usually cylindrical with thickened ascus apex. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating.

Type: Ophiocordycips Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

Teleomorphic genera: Elaphocordycips, Ophiocordyces
Anamorphic genera: Haploccilium, Harposporium, Hirsutella, Hymenosclite, paecilomyces-like, Paraisaria, Syngliocladium, Tolypocladium, verticillium-like.
ELAPHOCORDYCEPS
G.H. Sung & Spatafora, gen. nov. MycoBank MB804191.

Stromata singula vel nonnulla aggregata, simplicia vel ramosa. Stipes fibrosus vel tenax, raro carnosus, obscure brunneus vel olivaceo-viridulus, raro albidus, cylindricus vel sursum dilatatus. Stromata hospite insidentia vel rhizomorphis eo conjuncta. Pars fertilis clavata vel capitata, raro indistincta. Perithecia partim vel omnino in stromate immersa, perpendicularia ad superficiem. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae in cellulas diffrangentes. Anamorphe Verticillii similis vel absens.

Stromata solitary to several, simple or branched. Stipe fibrous to tough, rarely fleshy, dark brownish to greenish with olivaceous tint, rarely whitish, cylindrical to enlarging in the fertile part. Stromata connected directly to the host or indirectly through rhizomorph-like structures. Fertile part clavate to capitata, rarely undifferentiated. Perithecia partially or completely immersed in stromata, ordinal in arrangement. Asci cylindrical with thickened ascus apex. Ascospores cylindrical, multiseptate, disarticulating into part-spores.

Type: Cordyceps ophioglossoides (Ehrh.) Link

Etymology: Greek elapho = deer, from the host fungus, Elaphomyces.

Commentary: The C. ophioglossoides clade is strongly supported (MP-BP = 71 %, ML-BP = 88 %, PP = 100 in Figs 1–2, 10) and includes species of Cordyceps s. l. that parasitize the truffle-like genus Elaphomyces and cicada nymphs (e.g., C. inegoënsis and C. paradoxa) and beetles (e.g., C. subsessilis) (Figs 6, 10). Currently, 22 species are anticipated to be included in the C. ophioglossoides clade, of which more than 18 species are known as parasites of Elaphomyces (Mains 1957, Kobayasi & Shimizu 1960, 1963). The host affiliation of Elaphomyces parasites has long been recognized as a diagnostic character in Cordyceps classification (Massee 1895, Kobayasi 1951, 1982, Mains 1957, 1958). The oldest applicable genus name is Cordylia Fr. 1818 (Massee 1895). However, it cannot be applied to the C. ophioglossoides clade because it is a homonym of Cordyli Pers. 1807 (Mains 1858), which is also homonym of Cordylya Lour. 1790 (Leguminosae). Therefore, the genus Elaphocordyceps is proposed based on the phylogenetic placement of C. ophioglossoides and applied to the well-supported C. ophioglossoides clade. Although C. subsessilis is morphologically and ecologically distinct, the genus is well recognized by its dominant ecology as being pathogens of Elaphomyces and cicadas. The darkly pigmented, fibrous stromata with more or less...
olivaceous tint are also good diagnostic characters for recognizing the species of *Elaphocordyceps*.

Anamorphic genera: *Tolypocladium*, verticillium-like.

**Accepted names and new combinations for *Elaphocordyceps***

The following taxa are accepted species of *Elaphocordyceps* based on their inclusion in molecular phylogenies presented herein\(^1\) (see Table 1) or morphological descriptions matching the characters described above\(^2\). Where known we provide anamorph connection for the species of *Elaphocordyceps*.

1. *Elaphocordyceps capitata* (Holm.) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054192.
   - *Sphaereria capitata* Holm., Beata Ruris Oelia Fungis Danicis 1: 38. 1790: Fries, *Syst. Mycol.* 2: 324, 1823.
   - *Torrubia capitata* (Holm. : Fr.) Tul. & C. Tul., *Sel. Fung.* Carp. 3: 22. 1865.
   - *Cordyceps capitata* (Holm. : Fr.) Link, *Handbuch zur Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse* 3: 347. 1833.
   - *Cordyceps canadensis* Ellis & Everh., *Bull. Torrey Bot. Club* 25: 501. 1898.
   - *Cordyceps capitata var. canadensis* (Ellis & Everh.) Lloyd, *Mycol. Writ.* 5: 609. 1916.
   - *Sphaeria agariciformis* Bolt., *Hist. Fung. Halifax*, p. 130. 1789.
   - *Cordyceps agariciformis* (Bolt.) Seaver, *North Amer. Fl.* 3: 33. 1910.
   - *Cordyceps nigriceps* Peck, *Bull. Torrey Bot. Club* 27: 21. 1900.  

Anamorph unknown, not growing in culture.

2. *Elaphocordyceps delicatistipitata* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054193.
   - *Cordyceps delicatistipitata* Kobayasi, *Bull. Natn. Sci. Mus. Tokyo, Ser. B*, 8: 118. 1982.
   - *Cordyceps alba* (Ehrh. : Fr.) Tul., *Sel. Fung.* Carp. 3: 20. 1865.
   - *Cordyceps ophioglossoides* (Ehrh. : Fr.) Tul., *Sel. Fung.* Carp. 3: 22. 1865.

Anamorph: *Tolypocladium*, verticillium-like

1. *Elaphocordyceps fracta* (Mains) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054194.
   - *Cordyceps fracta* Mains, *Bull. Torrey Bot. Club* 84: 250. 1957.

2. *Elaphocordyceps inegoënsis* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054195.
   - *Cordyceps inegoënsis* Kobayasi, *Bull. Natn. Sci. Mus. Tokyo* 6: 292. 1963.

3. *Elaphocordyceps intermedia* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054196.
   - *Cordyceps intermedia* S. Imai, *Proc. Imp. Acad. Tokyo* 10: 677. 1934.

4. *Elaphocordyceps intermedia* f. *michinokuënsis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054197.
   - *Cordyceps intermedia* f. *michinokuënsis* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo,* Ser. B, 8: 116. 1982.

5. *Elaphocordyceps japonica* (Lloyd) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054198.
   - *Cordyceps japonica* Lloyd, *Mycol. Writ.* 6: 913. 1920.
   - *Cordyceps umemurae* S. Imai, *Trans. Sapporo Nat. Hist. Soc.* 11: 32. 1929 (as C. *‘umemurai’*).

6. *Elaphocordyceps jezoënsis* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054199.
   - *Cordyceps jezoënsis* S. Imai, *Trans. Sapporo Nat. Hist. Soc.* 11: 33. 1929.

7. *Elaphocordyceps longisegmentis* (Ginns) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054200.
   - *Cordyceps longisegmentis* Ginns, *Mycolologia* 80: 219. 1988.

8. *Elaphocordyceps minazukiensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054201.
   - *Cordyceps minazukiensis* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo,* Ser. B, 8: 117. 1982.

9. *Elaphocordyceps miomoteana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054202.
   - *Cordyceps miomoteana* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo,* Ser. B, 8: 118. 1982.

10. *Elaphocordyceps ophioglossoides* (Ehrh.: Fr.) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054203.
    - *Sphaeria ophioglossoides* Ehrh., *in Pers.*, *Comment de Fung. Clavaeff.* p. 12. 1797: Fries, *Syst. Mycol.* 2: 324. 1823.
    - *Torrubia ophioglossoides* (Ehrh. : Fr.) Tul., *Sel. Fung.* Carp. 3: 20. 1865.
    - *Cordyceps ophioglossoides* (Ehrh. : Fr.) Link, *Handbuch zur Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse* 3: 347. 1833.

Anamorph: *Tolypocladium*, verticillium-like

11. *Elaphocordyceps ophioglossoides* f. *alba* (Kobayasi & Shimizu ex Y.J. Yao) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054204.
    - *Cordyceps ophioglossoides* f. *alba* Kobayasi & Shimizu ex Y.J. Yao, *in Yao, Li, Pegler & Spooner, Acta. Mycol. Sin.* 14: 257. 1995.

12. *Elaphocordyceps ophioglossoides* f. *cuboides* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054205.
    - *Cordyceps ophioglossoides* f. *cuboides* Kobayasi, *Bull. Natn. Sci. Mus. Tokyo* 5: 77. 1960.

13. *Elaphocordyceps paradoxa* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054206.
    - *Cordyceps paradoxa* Kobayasi, *Bull. Biogeogr. Soc. Japan* 9: 156. 1939.

14. *Elaphocordyceps ramosa* (Teng) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054207.
    - *Cordyceps ramosa* Teng, *Sinensis* 7: 810. 1936.

15. *Elaphocordyceps rouxi* (Cand.) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054208.
    - *Cordyceps rouxi* Cand., *Mycotaxon* 4: 544. 1976.

16. *Elaphocordyceps subsessilis* (Petch) G.H. Sung, J.M. Sung & Spatafora, *comb. nov*. MycoBank MB054209.
Elaphocordyceps szemaoënsis (M. Zang) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04213.
≡ Cordyceps szemaoënsis M. Zang, Acta Bot. Yunnanica 23: 295. 2001.

Elaphocordyceps tenuispora (Mains) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04211.
≡ Cordyceps tenuispora Mains, Bull. Torrey Bot. Club 84: 247. 1957.

Elaphocordyceps toriharamontana (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04212.
≡ Cordyceps toriharamontana Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 305. 1963.

Elaphocordyceps valliformis (Mains) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04213.
≡ Cordyceps valliformis Mains, Bull. Torrey Bot. Club 84: 250. 1957.

Elaphocordyceps valvatistipitata (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04214.
≡ Cordyceps valvatistipitata Kobayasi, Bull. Natn. Sci. Mus. Tokyo 5: 81. 1960 (as C. volvostipitata).

Elaphocordyceps virens (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, comb. nov. MycoBank MB04215.
≡ Cordyceps virens Kobayasi, J. Jap. Bot. 8: 222. 1963.

Ophiocordycepse communis Hywel-Jones & Samson, sp. nov. MycoBank MB054216. Figs 12A–G.

Anamorph: hirsutella/hymenostilbe-like.

Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous, plant to wiry, rarely fleshy, often with aperithecial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci hyaline, cylindrical, usually with thickened ascus apex, rarely fusoid to ellipsoid. Ascospores usually cylindrical, multisepate, disarticulating into part-spores or non-disarticulating.

Type: Cordyceps blattae Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

Anamorphic genera: Hirsutella, Hymenostilbe, Paraisaria, Syngliocladium.

Commentary: The C. unilateralis clade is strongly supported (MP-BP = 88 %, ML-BP = 88 %, PP = 1.00 in Figs 3, 10) and includes the species of Ophiocordyceps (e.g., C. acicularis and C. unilateralis) (Petch 1931, 1933). The genus Ophiocordyceps was proposed by Petch (1931, 1933) for species of Cordyceps that produce non-disarticulating ascospores. The genus was not accepted by subsequent workers who reclassified the species of Ophiocordyceps as Cordyceps subg. Ophiocordyceps (Kobayasi 1941) or in multiple subgenera of Cordyceps (Mains 1958). The type of Ophiocordyceps Petch is O. blattae (= C. blattae), but it was not available for this taxonomic treatment. According to the morphological description, it fits in the present generic concept. Because O. unilateralis is a well-known species that was included in the original publication of Ophiocordyceps (Petch 1931) and because additional Ophiocordyceps species (e.g., O. acicularis) are members of this clade, we apply the name Ophiocordyceps based on the placement of O. unilateralis. The genus Ophiocordyceps includes the most morphologically diverse group of the species of Cordyceps s. l. including the members of C. subg. Neocordyceps (Figs 6, 10). For most of the species in Ophiocordyceps, the stromata are fibrous to tough or wiry to pliant in texture and darkly pigmented in at least some part of the stroma. The genus includes many species of Cordyceps s. l. that produce perithecia in subterminal regions of the stromata resulting in aperithecial apices. Of particular note, Ophiocordyceps is characterized by the dominant occurrence of Hirsutella and Hymenostilbe anamorphs (Fig. 6). Although the genus Cordycepioideus possesses thick-walled multisepate ellipsoid ascospores and its ascu lack the thickened ascus tip of most clavicipitaceous fungi (Blackwell & Gilbertson 1984, Ochiel et al. 1997), this study indicates that the genus Cordycepioideus can be merged with Ophiocordyceps according to its placement in molecular analyses and because of the Hirsutella anamorph (Fig. 10, Ochiel et al. 1997, Suh et al. 1998).
fertile (anamorph) part of ca 90 mm. Perithecia superficial subterminal; emerging through grey anamorph, tightly packed around the stipe, 285–675 × 195–390 µm. Ascii with stout cap, 8-spored, filiform, 215–250 × 15 µm. Ascospores whole, stout, tightly pigmented (100–)120–150(–180) × 5–6 µm. Conidiogenous cells in a palisade, hyaline, cylindrical, 10–14 × 2.7–3.3 µm, solitary (rarely two), prominent, terminal denticle. Conidia hyaline, almond-shaped, 7–9 × 2.5–3 µm.

**Etymology:** refers to the communal nature of the stromata, i.e. the fact that 500–1000 Cordyceps stromata can be found in a small area (20 × 20 metres).

**Type:** Holotype: N.H.J. 10673, isotypes: N.H.J. 10674, N.H.J. 10675, N.H.J. 10676, N.H.J. 10677, all on termites; coll. R. Nasit; Khao Yai National Park, Gong Giao Nature Trail; 13 June 2000.

**Commentary:** Most collections of *O. communis* were from Khao Yai National Park with the type locality (Gong Giao Nature Trail) regularly having epizootics containing (in any one season) several hundred stromata over a 20 × 20 metre area. A few other collections were from Khao Soi Dao Wildlife Sanctuary (N.H.J. 6422 and N.H.J. 6452) and Sam Lan National Park (N.H.J. 6332). All collections of the species were from adult termites. Although surveys were made over an eighteen-year period from the far north of Thailand to the far south and from sea level to over 2500 metres, *O. communis* is only known from these three sites in central Thailand below 800 metres elevation.

In any year there appeared to be a single ‘flush’ with *O. communis* first appearing at the start of the rainy season in May/June. The earliest collections were made in May (10 May 1994: N.H.J. 3687, N.H.J. 3681 and N.H.J. 3683, Heo Sawat Waterfall; 23 May 1996; N.H.J. 6330, Gong Giao Nature Trail). In the first 2–3 weeks after appearance, the stromata appeared slender and acicular with the lower part having a shiny silken appearance and the terminal part dull greyish. The terminal grey region consisted of a palisade of tightly packed conidiogenous cells with a pronounced point and are not typical of the clavate shape usually associated with *Hymenostilbe*. Similarly, the conidia of the *O. communis* anamorph are also fattened naviculate, appearing similar to those of *Hy. ventricosa* but without the processed tip.

The perithecia erupt through the dull greyish anamorph spike appearing first as longitudinal splits in the palisade of conidiogenous cells at the base of the anamorph spike. Each develops as a superficial perithecium, but they become crowded and give the overall appearance of a brown subterminal fertile region (Kobayasi 1941; Figs 12A–B). The ascus shape and the form of the ascus cap comes close to Kobayasi's Figs 12C–D (Kobayasi 1941) being typical of species in the *C. unilateralis* clade (with *Hirsutella* as an anamorph). Mature perithecia eject pigmented, whole ascospores (Fig. 12E) and often the ostiole becomes blocked with these half-emerged ascospores.

Only a few species of *Cordyceps sensu* Kobayasi and Mains have been reported from termites. Currently accepted species include *O. koningsbergeri* (= *C. koningsbergeri* Penz. & Sacc.), which is known only from the type locality (Java, Indonesia) (Kobayasi 1941), and *C. termitophila* Kobayasi & Shimizu which is known from Japan and Taiwan (Kobayasi & Shimizu 1976, 1978). Penzig & Saccardo (1904) found *O. koningsbergeri* to be similar to *O. myrmecophila* in that it had a terminal, globose head with immersed perithecia. In this feature alone it differs significantly from *O. communis* with its subterminal and superficial perithecia. However, as with *O. communis*, Penzig & Saccardo (1904) described whole ascospores of *O. koningsbergeri*, which were 150 × 1 µm compared with 120–150 × 5–6 µm for *O. communis*. *Cordyceps termitophila* differs from *O. communis* in having a ‘pale rosy-grey’ stroma, much smaller perithecia (280–320 × 175–190 µm for *C. termitophila* versus 285–675 × 195–390 µm for *O. communis*) and smaller ascospores (100–125 × 3 µm).

**Accepted names and new combinations for Ophiocordyceps**

The following taxa are accepted species of *Ophiocordyceps* based on their inclusion in molecular phylogenies presented herein or morphological descriptions matching the characters described above. Where known, the anamorph connection is provided for the species of *Ophiocordyceps*.

1. *Ophiocordyceps acicularis* (Ravenel) Petch, Trans. Brit. Mycol. Soc. 18: 60. 1933.
2. *Ophiocordyceps carolinensis* Berk. & Ravenel, Fungi Carolina 4: 29. 1855.

Anamorph: *Hirsutella*

3. *Ophiocordyceps agriotidis* (A. Kawam.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB504217.
2 **Ophiocordyceps ainctos** (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504218.

≡ Cordyceps ainctos A. Möller, Phycormyceten u. Ascomyceten, p. 226. 1901.

Anamorph: **Hirsutella**

2 **Ophiocordyceps amazonica** (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504219.

≡ Cordyceps amazonica Henn., Hedwigia 43: 247. 1904.

2 **Ophiocordyceps amazonica** var. neoamazonica (Kobayasi & Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504220.

≡ Cordyceps amazonica var. neoamazonica Kobayasi & Hara, J. Jap. Bot. 57: 17. 1982.

1 **Ophiocordyceps aphodii** (Mathieson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504221.

≡ Cordyceps aphodii Mathieson, Trans. Brit. Mycol. Soc. 32: 134. 1949.

Anamorph: **Hirsutella**

2 **Ophiocordyceps appendiculata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504222.

≡ Cordyceps appendiculata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 125. 1980.

2 **Ophiocordyceps arachneicola** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504223.

≡ Cordyceps arachneicola Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 6: 123. 1941.

2 **Ophiocordyceps arbuscula** (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504225

≡ Cordyceps arbuscula Teng, Sinensia 7: 812. 1936.

2 **Ophiocordyceps armeniaca** (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504226.

≡ Cordyceps armeniaca Berk. & M.A. Curtis, J. Linn. Soc. 10: 35. 1883.

2 **Ophiocordyceps asyuënsis** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504227.

≡ Cordyceps asyuënsis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 138. 1980.

2 **Ophiocordyceps aurantiia** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504228.

≡ Cordyceps aurantiia Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 125. 1980.

2 **Ophiocordyceps australis** (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504229.

≡ Cordyceps unilateralis var. australis Speg., Anales Soc. Ci. Argent. 12: 215. 1881.

≡ Cordyceps australis (Speg.) Speg., Syll. Fung. 2: 571. 1883.

2 **Ophiocordyceps barnesii** (Thwaites) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504230.

≡ Cordyceps barnesi Thwaites, J. Linn. Soc. 14: 110. 1875.

≡ Torchia barnesii (Thwaites) Ces., Atti Accad. Sci. Fis. Mat., Napoli 8: 14. 1879.

2 **Ophiocordyceps bicephala** (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504231.

≡ Cordyceps bicephala Berk., J. Bot. (Hooker) 8: 278. 1856.

2 **Ophiocordyceps bispora** (Stifler) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504232.

≡ Cordycapioides bisporus Stifler, Myologia 33: 85. 1941.

Anamorph: **Hirsutella**

2 **Ophiocordyceps blattae** (Petch) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

≡ Cordyceps blattae Petch, Trans. Brit. Mycol. Soc. 10: 35. 1924.

1 **Ophiocordyceps bruneipunctata** (Hywel-Jones) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504233.

≡ Cordyceps bruneipunctata Hywel-Jones, Mycol. Res. 99: 1195. 1995. [as C. ‘bruneapunctata’]

Anamorph: **Hirsutella**

2 **Ophiocordyceps caloceroides** (Berk. & M.A. Curtis) Petch, Trans. Brit. Mycol. Soc. 18: 63. 1933.

≡ Cordyceps caloceroides Berk. & M.A. Curtis, J. Linn. Soc. 10: 375. 1868.

≡ Cordyceps wittii Henn., Bot. Jahrb. Syst. 23: 539. 1897.

2 **Ophiocordyceps cantharelloides** (Samson & H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504234.

≡ Cordyceps cantharelloides Samson & H.C. Evans, Proc. Indian Acad. Sci., Pl. Sci. 94: 312. 1985.

2 **Ophiocordyceps carabidicola** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504235.

≡ Cordyceps carabidicola Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 85. 1980. [as C. ‘carabidicola’]

2 **Ophiocordyceps cicadiicola** (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504236.

≡ Cordyceps cicadiicola Teng, Sinensia 6: 191. 1935.

2 **Ophiocordyceps clavulata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504237.

≡ Cordyceps clavulata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 140. 1980.

2 **Ophiocordyceps clavulata** (Schwein.) Petch, Trans. Brit. Mycol. Soc. 18: 53. 1933.

≡ Sphaeria clavulata Schwein., Trans. Amer. Philos. Soc. New Ser. 4, 188. 1832.
Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi

≡ *Xylaria clavulata* (Schwein.) Berk. & M. A. Curtis, J. Linn. Soc. 10: 380. 1868.
≡ *Torrubia clavulata* (Schwein.) Peck, Ann. Rep. N. Y. State Mus. 28: 70. 1876.
≡ *Cordyceps clavulata* (Schwein.) Ellis & Everh., North Amer. Pyrenom. p. 61. 1892.
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≡ *Torrubia pistillariaeformis* (Berk. & Broome) Cooke, Handb. Brit. Fungi 2: 771. 1871.

Anamorph: *Hymenostilbe lecaniicola* (Jaap) Mains

1 *Ophiocordyceps coccidiicola* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504238.
≡ *Cordyceps coccidiicola* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 57. 1978.

2 *Ophiocordyceps cocciigena* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504239.
≡ *Torrubia coccigena* Tul. & C. Tul., Sel. Fung. Carpol. 3: 19. 1865.
≡ *Cordyceps coccigena* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.

2 *Ophiocordyceps cochlidiicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504240.
≡ *Cordyceps cochlidiicola* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 129. 1980.

2 *Ophiocordyceps communis* Hywel-Jones & Samson, *sp. nov.*, see above.
Anamorph: *Hirsutella ovalispora* H.C. Evans & Samson

2 *Ophiocordyceps corallomyces* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504241.
≡ *Cordyceps corallomyces* A. Möller, Phycomyceten u. Ascomyceten, p. 217. 1901.

2 *Ophiocordyceps crassispora* (M. Zang, D.R. Yang & C.D. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504242.
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≡ *Cordyceps crinalis* Ellis ex Lloyd, Mycol. Writ. 6: 912. 1920.

2 *Ophiocordyceps cucumispora* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504244.
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Anamorph: *Hirsutella ovalispora* H.C. Evans & Samson

2 *Ophiocordyceps cucumispora* var. *dolichoderi* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504245.
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Anamorph: *Hirsutella ovalispora* var. *dolichoderi* H.C. Evans & Samson

2 *Ophiocordyceps curculionum* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov*. MycoBank MB504246.
≡ *Torrubia curculionum* Tul. & C. Tul., Sel. Fung. Carpol. 3: 20. 1865.
≡ *Cordyceps curculionum* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.
≡ *Cordyceps bicephala* subsp. *curculionum* (Tul. & C. Tul.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 50. 1949.
Anamorph: *Hymenostilbe*

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Fig. 12. A–G. Morphology of *Ophiocordyceps communis*. A. Stromata, bar = 10 mm. B. Arrangement of perithecia. C. Ascus with ascospores. D. Ascus and ascus apex. E. Non-disarticulating ascospores. F. Conidiophores (*Hymenostilbe*/*Hirsutella* anamorph). G. Denticles of phialide (*Hymenostilbe*/*Hirsutella* anamorph). Scale bars: A, C–G = 10 µm, B = 500 µm.
2 **Ophiocordyceps cylindrostomata** (Z.O. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504247.
≡ **Cordyceps cylindrostomata** Z.O. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 97. 2003.

2 **Ophiocordyceps dayiensis** (Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504248
≡ **Cordyceps dayiensis** Z.Q. Liang, Fungal Diversity 12: 131. 2003.

2 **Ophiocordyceps dermapterigena** (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504249.
≡ **Cordyceps dermapterigena** Z.Q. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 96. 2003 (as C. ‘dermapteoigena’).

2 **Ophiocordyceps dipterigena** (Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504250.
≡ **Cordyceps dipterigena** Berk. & Broome, J. Linn. Soc. 14: 111. 1875.
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≡ **Cordyces oummensis** Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 309. 1909.
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≡ **Cordyces opposita** Syd., Bot. Jahrb. Syst. 57: 325. 1922.
Anamorph: **Hymenostilbe dipterigena** Petch

2 **Ophiocordyceps discoideicapitata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504251.
≡ **Cordyceps discoideicapitata** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 85. 1982 (as C. ‘discoideocapitata’).

2 **Ophiocordyceps ditmarii** (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504252.
≡ **Cordyceps ditmarii** Quél., Bull. Soc. Bot. France 24: 330. 1877. [as C. ditman]
Anamorph: **Hymenostilbe**

2 **Ophiocordyceps dovei** (Rodway) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504253.
≡ **Cordyceps dovei** Rodway, Paper Proc. Roy. Soc. Tasmania for 1898–1899, p. 101. 1900.
≡ **Cordyces aemoneae** Lloyd, Mycol. Notes 62: 932. 1920.
Anamorph: **Hirsutella-like**

2 **Ophiocordyceps elateridicola** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504255.
≡ **Cordyceps elateridicola** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 4. 1983.

2 **Ophiocordyceps elongata** (Petch) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504256.
≡ **Cordyceps elongata** Petch, Trans. Brit. Mycol. Soc. 21: 47. 1937.
Anamorph: **Hirsutella**

2 **Ophiocordyceps elongatiperitheciata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504257.
≡ **Cordyceps elongatiperitheciata** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 126. 1980 (as C. ‘elongatoperitheciata’).

2 **Ophiocordyceps elongatistromata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504258.
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2 **Ophiocordyceps emeiensis** (A.Y. Liu & Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504259.
≡ **Cordyceps emeiensis** A.Y. Liu & Z.Q. Liang, Mycosystema 16: 139. 1997.

2 **Ophiocordyceps englerianna** (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504260.
≡ **Cordyceps englerianna** Henn., Bot. Jahrb. Syst. 23: 538. 1897.
Anamorph: **Hymenostilbe**

1 **Ophiocordyceps entomorrhiza** (Dicks.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504261.
≡ **Sphaeria entomorrhiza** Dicks., Plant. Crypt. Brit., Fasc. 1: 22. 1785.
≡ **Cordyceps entomorrhiza** (Dicks.) Fr., Obs. Mycol. 2: 317. 1818.
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≡ **Cordyceps cinerea** (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.
≡ **Cordyces carabi** Quél., Comp. Rend. Assoc. Franç. Avancem. Sci. 26: 452. 1898.
Anamorph: **Hirsutella eleutheratorum** (Nees) Petch

2 **Ophiocordyceps evdogeorgiae** (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504262.
≡ **Cordyceps evdogeorgiae** Koval, Bot. Mater. Otd. Sporov. Rast. 14: 160. 1961.

2 **Ophiocordyceps falcata** (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504263.
≡ **Cordyceps falcata** Berk., J. Bot. (Hooker) 6: 211. 1854 [Decad. Fung. No. 479].
Anamorph: **Stilbella**

2 **Ophiocordyceps falcataoides** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504264.
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2 **Ophiocordyceps fasciculatistromata** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *comb. nov.* MycoBank MB504265.
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≡ Cordyceps ferruginosa Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 139. 1980.

Ophiocordyceps filiformis (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504267.
≡ Cordyceps filiformis Moureau, Mém. Inst. Roy. Colon. Belge 7: 14. 1949.

Ophiocordyceps formicarum (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504268.
≡ Cordyceps formicarum Kobayasi, Bull. Biogeogr. Soc. Japan 9: 286. 1939.
Anamorph: *Hymenostilbe*

Ophiocordyceps forquignoni (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504269.
≡ Cordyceps forquignoni Quél., 16th Suppl. Champ. Jura et Voges, p. 6. 1887.
Anamorph: *Hymenostilbe muscarium* Petch

Ophiocordyceps furcicaudata (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504270.
≡ Cordyceps furcicaudata Z.Q. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 95. 2003 (as *C. furcicaudata*).

Ophiocordyceps gansuensis (K. Zhang, C. Wang & M. Yan) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504271.
≡ Cordyceps gansuensis K. Zhang, C. Wang & M. Yan, Trans. Mycol. Soc. Japan 30: 295. 1989.

Ophiocordyceps geniculata (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504272.
≡ Cordyceps geniculata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 85. 1980.

Ophiocordyceps gentilis (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504273.
≡ Torrubia gentilis Ces., Atti Accad. Sci. Fis. Mat., Napoli, 8: 14. 1879.
≡ Cordyceps gentilis (Ces.) Sacc., Syll. Fung. 2: 569. 1883.

Ophiocordyceps glaziovii (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504274.
≡ Cordyceps glaziovii Henn., Naturw. Wochenschr. 6: 318. 1896.

Ophiocordyceps goniopora (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504275.
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Ophiocordyceps gracillioides (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504276.
≡ Cordyceps gracillioides Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 140. 1941.
Anamorph: *paecilomyces-like*

Ophiocordyceps gracilis (Grev.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504277.
≡ Xylaria gracilis Grev., Scot. Crypt. Fl. 2: t. 86. 1824.
≡ Cordyceps gracilis (Grev.) Durieu & Mont., Fl. Algérie Crypt. 1: 449. 1846.
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Anamorph: *Paraisaria dubia* (Delacr.) Samson & B.L. Brady

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Ophiocordyceps heteropoda (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504278.
≡ Cordyceps heteropoda Kobayasi, Bull. Biogeogr. Soc. Japan 9: 158. 1939.

Ophiocordyceps hiugensis (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504279.
≡ Cordyceps hiugensis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 3. 1983.

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≡ Cordyceps huberiana Henn., Hedwigia 48: 105. 1909.

Ophiocordyceps humbertii (C.P. Robin) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504281.
≡ Cordyceps humbertii C.P. Robin, in Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865 (as *C. humbertii*).
Anamorph: *Hirsutella saussurei* (Cook) Speare

Ophiocordyceps insignis (Cook & Ravenel) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504282.
≡ Cordyceps insignis Cook & Ravenel, Grevillea 12: 38. 1883.

Ophiocordyceps irangiensis (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504283.
≡ Cordyceps irangiensis Moureau, Lejeunia, Mém. 15: 33. 1961.
Anamorph: *Hymenostilbe*

Ophiocordyceps japonensis (Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504284.
≡ Cordyceps japonensis Hara, Bot. Mag. Tokyo 28: 351. 1914.

Ophiocordyceps jiangxiensis (Z.Q. Liang, A.Y. Liu & Yong C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504285.
Ophiocordyceps jinggangshanensis (Z.Q. Liang, A.Y. Liu & Yong C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504286.

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Ophiocordyceps kniphofioides (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504288.

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Anamorph: Hirsutella stilbelliformis H.C. Evans & Samson

Ophiocordyceps kniphofioides var. dolichoderi (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504289.

≡ Cordyceps kniphofioides var. dolichoderi H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 437. 1982.

Anamorph: Hirsutella stilbelliformis var. dolichoderi H.C. Evans & Samson

Ophiocordyceps kniphofioides var. monacidis (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504290.

≡ Cordyceps kniphofioides var. monacidis H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 441. 1982.

Anamorph: Hirsutella stilbelliformis var. monacidis H.C. Evans & Samson

Ophiocordyceps kniphofioides var. ponerinarum (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504291.

≡ Cordyceps kniphofioides var. ponerinarum H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 522. 1987.

Anamorph: Hirsutella stilbelliformis var. ponerinarum H.C. Evans & Samson

Ophiocordyceps koningsbergeri (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504292.

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Ophiocordyceps konnoana (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504293.

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Anamorph: Hymenostilbe formicarum Petch

Ophiocordyceps lloydii var. binata (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504297.

≡ Cordyceps lloydii var. binata H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 82: 133. 18: 316. 1984.

Ophiocordyceps longissima (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504298.

≡ Cordyceps longissima Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 200. 1963.

Ophiocordyceps lutea (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504299.

≡ Cordyceps lutea Moureau, Mém. Inst. Roy. Colon. Belge 7: 41. 1949.

Anamorph: Hymenostilbe sulphurea Samson & H.C. Evans

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Ophiocordyceps michiganensis (Lloyd) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0504301.

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Cordyceps monticola (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504304.  
≡ Cordyceps monticola Mains, Mycologia 32: 310. 1940.

Cordyceps mrciensis (Aung, J.C. Kang, Z.Q.Liang, Soytong & K.D. Hyde) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504305.  
≡ Cordyceps mrciensis Aung, J.C. Kang, Z.Q.Liang, Soytong & K.D. Hyde, Mycotaxon 97: 236. 2006.

Cordyceps multiaxialis (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504306.  
≡ Cordyceps multiaxialis M. Zang & Kinjo, Mycotaxon 66: 224. 1998.

Cordyceps myrmecophila (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504307.  
≡ Cordyceps myrmecophila Ces., Bot. Zeitung 4: 877. 1846.  
≡ Torrubia myrmecophila (Ces.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1885.  
Anamorph: Hymenostilbe  

Cordyceps neovolkiana (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504308.  
≡ Cordyceps neovolkiana Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 169. 1941.  
Anamorph: Hirsutella neo-volkiana Kobayasi

Cordyceps nepalensis (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504309.  
≡ Cordyceps nepalensis M. Zang & Kinjo, Mycotaxon 66: 224. 1998.

Cordyceps nigra (Samson, H.C. Evans & E.S. Hoekstra) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504310.  
≡ Cordyceps nigra Samson, H.C. Evans & E.S. Hoekstra, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 85: 596. 1982.

Cordyceps nigrella (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504311.  
≡ Cordyceps nigrella Kobayasi & Shimizu, Icon. Veg. Wasps and Plant Worms p. 145, 1983.  
≡ Cordyceps nigra Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo 9(1): 13. 1983 [non Samson et al. 1982]

Cordyceps nigripes (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504312.  
≡ Cordyceps nigripes Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 116. 1982 (as C. ‘nigripoda’).

Cordyceps nutans (Pat.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504313.  
≡ Cordyceps nutans Pat., Bull. Soc. Mycol. France 3: 127. 1887.  
≡ Cordyceps bicepspha subsp. nutans (Pat.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 47. 1949.  
Anamorph: Hymenostilbe nutans Samson & H.C. Evans

Cordyceps obtusa (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504314.  
≡ Cordyceps obtusa Penz. & Sacc., Malpighia 11: 523. 1897.

Cordyceps octospora (M. Blackwell & Gilb.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504315.  
≡ Cordycepioideus octosporus M. Blackwell & Gilb., Mycologia 73: 358. 1981.  
Anamorph: Hirsutella

Cordyceps odonatae (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504316.  
≡ Cordyceps odonatae Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 6. 1981.  
Anamorph: Hymenostilbe odonatae Kobayasi

Cordyceps osuzumontana (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504317.  
≡ Cordyceps osuzumontana Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 77. 1980.

Cordyceps owariensis (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504318.  
≡ Cordyceps owariensis Kobayasi, Bull. Biogeogr. Soc. Japan 9: 166. 1939.

Cordyceps owariensis f. viridescens (Uchiyama & Udagawa) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504319.  
≡ Cordyceps owariensis f. viridescens Uchiyama & Udagawa, Mycoscience 43: 136. 2002.  
Anamorph: Nomuraea owariensis Uchiyama & Udagawa

Cordyceps oxyccephala (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504320.  
≡ Cordyceps oxyccephala Penz. & Sacc., Malpighia 11: 521. 1897.  
≡ Cordycepioideus oxyccephala f. oxyccephala (Penz. & Sacc.) Kobayasi, Trans. Mycol. Soc. Japan 23: 361. 1982.  
Anamorph: Hymenostilbe

Cordyceps paludosa Mains, Proc. Amer. Philos. Soc. 74: 269. 1934.  
≡ Cordyceps paludosa (Mains) Mains, Pap. Michigan Acad. Sci. 25: 83. 1940.  
Anamorph: Polycephalomyces paludosus Mains

Cordyceps pentatomeae (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504321.
2 Ophiocordyceps petchii (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504322.  
≡ Cordyceps petchii Mains, Bull. Torrey Bot. Club 66: 47. 1959.  
≡ Cordyceps ramosa Petch, Trans. Brit. Mycol. Soc 21: 42. 1937 [non Teng 1936].

2 Ophiocordyceps proliferans (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504323.  
≡ Cordyceps proliferans Henn., Hedwigia 43: 248. 1904.

2 Ophiocordyceps pseudolloydii (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504324.  
≡ Cordyceps pseudolloydii H.C. Evans & Samson, Trans. Brit. Mycol. Soc 82: 133. 1984.

2 Ophiocordyceps pseudolongissima (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504325.  
≡ Cordyceps pseudolongissima Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 119. 1982.

2 Ophiocordyceps purpureostromata (Kobayasi) ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504326.  
≡ Cordyceps purpureostromata Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 136. 1980. Type Shimizu No. 128, preserved in TNS; therefore the basionym was valid from the beginning.

2 Ophiocordyceps purpureostromata f. **recurvata** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504327.  
≡ Cordyceps purpureostromata f. recurvata Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 138. 1980.

1 Ophiocordyceps ravenellii (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504328.  
≡ Cordyceps ravenellii Berk. & M.A. Curtis, J. Linn. Soc. 1: 159. 1857.

1 Ophiocordyceps rhizoidea (Höhn.) Petch, Trans. Brit. Mycol. Soc 16: 74. 1931.  
≡ Cordyceps rhizoidea Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 307. 1900.  
Anamorph: *Hirsutella*

2 Ophiocordyceps ridleyi (Massee) Kobayasi, Bull. Biogeogr. Soc. Japan 9: 271. 1939.  
≡ Cordyceps ridleyi Massee, Bull. Misc. Inform. Roy. Bot. Gard. Kew. p. 173. 1899.

1 Ophiocordyceps robertsii (Hook.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504329.  
≡ Sphaeria robertsi Hook. Icon. Plant. 1 pl. 6. 1837.  
≡ Cordyceps robertsii (Hook.) Berk., Fl. New Zealand 2: 202. 1855.

2 Ophiocordyceps rubripunctata (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504331.  
≡ Cordyceps rubripunctata Moureau, Mém. Inst. Roy. Colon. Belg. 7: 26. 1949.  
Anamorph: *Hirsutella rubripunctata* Samson, H.C. Evans & Hoekstra

2 Ophiocordyceps rubiginosiperitheciata (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504332.  
≡ Cordyceps rubiginosiperitheciata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 14. 1983 (as C. ‘rubiginosoperitheciata’).

2 Ophiocordyceps ryogamiensis (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504333.  
≡ Cordyceps ryogamiensis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 4. 1983.

2 Ophiocordyceps salebrosa (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504334.  
≡ Cordyceps salebrosa Mains, Mycologia 39: 541. 1947.

2 Ophiocordyceps scottiana (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504335.  
≡ Cordyceps scottiana Olliff, Agric. Gaz. New South Wales 6: 407. 1895.

2 Ophiocordyceps selkirki (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504338.  
≡ Cordyceps selkirki Olliff, Agric. Gaz. New South Wales 6: 411. 1895.

2 Ophiocordyceps sichuanensis (Z.Q. Liang & B. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504339.  
≡ Cordyceps sichuanensis Z.Q. Liang & B. Wang, Fungal Diversity 12: 129. 2003.

1 Ophiocordyceps sinensis (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504340.  
≡ Sphaeria sinensis Berk., J. Bot. (Hooker) 2: 207. 1843.  
≡ Cordyceps sinensis (Berk.) Sacc., Michelia 1: 320. 1879.  
Anamorph: *Hirsutella sinensis* X.J. Liu, Y.L. Guo, Y.X. Yu & W. Zeng

2 Ophiocordyceps smithii (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504341.  
≡ Cordyceps smithii Mains, J. Elisha Mitchell Sci. Soc. 55: 127. 1939.

1 Ophiocordyceps sobolifera (Hill ex Watson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504342.  
≡ Clavaria sobolifera Hill ex Watson, Philos. Trans. Roy. Soc. Lond. 53: 271. 1763.  
≡ Sphaeria sobolifera (Hill ex Watson) Berk., J. Bot. (Hooker) 2: 207. 1843.  
≡ Torula sobolifera (Hill ex Watson) Tul. & C. Tul., Sel. Fung. Carpal. 3: 10. 1865.  
≡ Cordyceps sobolifera (Hill ex Watson) Berk. & Broome, J. Linn. Soc. 14: 110. 1875.  
Anamorph: *Beauveria sobolifera* Z.Y. Liu, Z.Q. Liang, Whalley, A.Y. Liu & Y.J. Yao
Ophiocordyceps sphecocephala (Klotzsch ex Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050433.

- Sphaeria sphecocephala Klotzsch ex Berk., J. Bot. (Hooker) 2: 206. 1843.
- Torrubia sphecocephala (Klotzsch ex Berk.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.
- Cordyceps sphecocephala (Klotzsch ex Berk.) Berk. & M.A. Curtis, *in Berkeley*, J. Linn. Soc., Bot. 10: 376. 1868.

Anamorph: Hymenostilbe

**Ophiocordyceps stipillata** (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050434.

- Cordyceps stipillata Z.Q. Liang & A.Y. Liu, Mycosystema 21: 11. 2002.

**Ophiocordyceps stylophora** (Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050435.

- Cordyceps stylophora Berk. & Broome, J. Linn. Soc. 1: 158. 1857.

Anamorph: Hirsutella stylophora Mains

**Ophiocordyceps subflavida** (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050436.

- Cordyceps subflavida Mains, Bull. Torrey Bot. Club 86: 47. 1959.
- Cordyceps albida Pat. & Gaillard, Bull. Soc. Mycol. France 7: 116. 1888 [non Berk. & M.A. Curtis ex Cooke 1884].

**Ophiocordyceps subunilateralis** (Henn.) Kobayasi, Bull. Biogeogr. Soc. Japan 9: 271. 1939.

- Cordyceps subunilateralis Henn., Hedwigia 41: 168. 1902.

**Ophiocordyceps superficialis** (Peck) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050437.

- Torrubia superficialis Peck, Rep. N. Y. State Botanist 28: 70. 1876.
- Cordyceps superficialis (Peck) Sacc., Syll. Fung. 2: 574. 1883.

**Ophiocordyceps superficialis f. crustacea** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050438.

- Cordyceps superficialis f. crustacea Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 82. 1980.

**Ophiocordyceps takaoënsis** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB050439.

- Cordyceps sobolifera var. takaoënsis Kobayasi, Bull. Biogeogr. Soc. Japan 9: 165. 1939.
- Cordyceps takaoënsis (Kobayasi) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 6: 130. 1941.

**Ophiocordyceps taylorii** (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504350.

- Sphaeria taylorii Berk., J. Bot. (Hooker) 2: 209. 1843 (as S. ‘taylori’).
- Cordyceps taylorii (Berk.) Sacc., Michelia 1: 320. 1879.

**Ophiocordyceps thysroides** (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504351.

- Cordyceps thysroides A. Möller, Phycomyceten u. Ascomyceten, p. 221. 1901.

**Ophiocordyceps tricentri** (Yasuda) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504352.

- Cordyceps tricentri Yasuda, in Lloyd, Mycol. Writ. 4: 568. 1915 (as C. ‘tricentrus’).
- Cordyceps aphrophorae Yasuda, Bot. Mag. Tokyo 36: 51. 1922.

**Ophiocordyceps uchiyamae** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504353.

- Cordyceps uchiyamae Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 125. 1980.

**Ophiocordyceps unilateralis** (Tul. & C. Tul.) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

- Torrubia unilateralis Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.
- Cordyceps unilateralis (Tul. & C. Tul.) Sacc., Syll. Fung. 2: 570. 1883.
- Torrubia formicivora Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.
- Cordyceps formicivora (Tul. & C. Tul.) J. Schröt., Krypt.-Fl. Schlesien 3(2) 276. 1894.

Anamorph: Hirsutella formicarum Petch

**Ophiocordyceps unilateralis** var. **clavata** Kobayasi, Bull. Biogeogr. Soc. Japan 9: 272. 1939.

- Cordyceps unilateralis var. clavata (Kobayasi) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 78. 1941.

**Ophiocordyceps variabilis** (Petch) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504354.

- Cordyceps variabilis Petch, Trans. Brit. Mycol. Soc. 21: 42. 1937.
- Cordyceps viperina Mains, Mycologia 29: 674. 1937.

Anamorph: Syngliocladium

**Ophiocordyceps voeltzkowii** (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504355.

- Cordyceps voeltzkowii Henn., in Voeltzkow, Reise Ostafrika 3: 29. 1908.

**Ophiocordyceps volkiana** (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504356.

- Cordyceps volkiana A. Möller, Phycomyceten u. Ascomyceten, p. 233. 1901.

Anamorph: Hirsutella

**Ophiocordyceps wuyishanensis** (Z.Q. Liang, A.Y. Liu & J.Z. Huang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504357.

- Cordyceps wuyishanensis Z.Q. Liang, A.Y. Liu & J.Z. Huang, Mycosystema 21: 162. 2002.

Anamorph: paecilomyces-like

**Ophiocordyceps yakusimensis** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB0504358.

- Cordyceps yakusimensis Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 302. 1963.
Ophiocordyceps zhangjiajiensis (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB504359.

Cordyceps s. s. are, MycoBank MB0430.

Spatafora 1818

Cordyceps Simplicillium. Isaria, Lecanicillium, Anamorphic genera Hyperdermium

Type: Cordyceps militaris (L.: Fr.) Fr., Observ. Mycol. 2(revis.): 317. 1818.

Anamorphic genera: Beauveria, Isaria, Lecanicillium, mariannae-like, Microhilum, Simplicillium.

Commentary: Species of Cordyceps s. s. are characterized by possessing fleshy stromata that are pallid or brightly coloured. Because species of Torrubiella are interspersed among Cordyceps species in the basal part of the Cordycipitaceae, its ultimate application to a monophyletic taxon within the Cordycipitaceae is not clear, however (Fig. 10). The genus Torrubiella was erected in 1885 by Boudier with the type species T. aranicida Boud. (Kobayasi & Shimizu 1982). Our sampling included several species of Torrubiella that were interspersed amongst species of Cordycipitaceae, but we could not get hold of T. aranicida. Thus, Cordyceps s. s. is narrowly applied to the strongly supported clade (MP-BP = 98 %, ML-BP = 98 %, PP = 1.00 in Figs 1–2, 10) that includes Cordyceps species closely related to C. militaris. Cordyceps species that are placed outside of the Cordyceps s. s. node, but within the Cordycipitaceae, are provisionally retained within Cordyceps s. l. Torrubiella species that are part of the Cordyceps s. s. are transferred accordingly. The full extent to which the names Cordyceps and Torrubiella will ultimately be applied awaits additional sampling of Torrubiella, especially that of T. aranicida with the possibility that Torrubiella will need to be synonymized with Cordyceps. Although Phytocordyceps is characterized by its possession of bola-ascospores, it is also synonymized with Cordyceps because of its phylogenetic placement (Figs 8, 10).

Accepted names and new combinations for Cordyceps s. s.
The following taxa are accepted species of Cordyceps s. s. based on their inclusion in molecular phylogenies presented herein1 (see Table 1) or morphological descriptions matching the characters described above2. Where known we provide the anamorph connection for the species of Cordyceps s. s.

Cordyceps ampullacea Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 112. 1982.

Cordyceps bassiana Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan, Chinese Science Bulletin 46: 751. 2001.

Anamorph: Beauveria bassiana (Bals.) Vuill.

Cordyceps belizensis Mains, Mycologia 32: 21. 1940.

Cordyceps bifusispora O.E. Erikss., Mycotaxon 15: 185. 1982.

Cordyceps militaris (L.: Fr.) Fr., Observ. Mycol. 2(revis.): 317. 1818.

Anamorphic genera: Beauveria, Engyodontium, Isaria, Lecanicillium, mariannae-like, Microhilum, Simplicillium.

Cordyceps Fr., Observ. Mycol. 2 (revis.): 316. 1818 emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= Phytocordyceps C.H. Su & H.-H. Wang, Mycotaxon 26: 338. 1986.

Cordyceps belizensis Mains, Mycologia 32: 21. 1940.

Cordyceps bifusispora O.E. Erikss., Mycotaxon 15: 185. 1982.

CLAVICIPITACEAE Clade C

Clavicipitaceae clade C is a strongly supported group that includes the type species, C. militaris, of Cordyceps (MP-BP = 100 %, ML-BP = 100 %, PP = 1.00 in Figs 1–2). Because of the non-monophyly of Cordyceps, we reintroduce the preexisting family name Cordycipitaceae for Clavicipitaceae clade C. This family name was not validly published and it is validated herein based on the type genus Cordyceps. Most of the species in the family parasitize hosts in leaf litter, moss, or upper soil layers and produce superficial to partially immersed perithecia on a fleshy stroma or subiculum that is pallid or brightly coloured. The family contains species of Cordyceps and Torrubiella (Figs 5, 7). The unspecific genus Phytocordyceps is also recognized as a member of this family and transferred to Cordyceps (Fig. 6). In addition, the recent molecular study shows that species of the genera Ascopolyergus A. Möller and Hyperdermium J. White, R. Sullivan, G. Bills & N. Hywel-Jones 2000 [non Link]

Clavicipitaceae fam. nov. Kreisel 1969 ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, fam. nov. MycoBank MB504360.

Cordycipitaceae Kreisel, Grundz. Natürl. Syst. Pilze: 112. 1969 [nom. inval., Art. 36].

Stromata vel subiculum pallida vel laete colorata, carnosa. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem. Asci cylindrici, apice inspissato. Ascosporae cylindricae, multiseptatae, maturae differgentes vel integrae remanentes.

Stromata or subiculum pallid or brightly pigmented, fleshy. Perithecia superficial to completely immersed, ordinal in arrangement. Asci hyaline, cylindrical with thickened ascus apex. Ascospores hyaline, cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating, rarely possessing a thread-like structure connecting the fusiform ends.

Type: Cordyceps militaris (L.: Fr.) Fr., Observ. Mycol. 2(revis.): 317. 1818.

Anamorphic genera: Beauveria, Isaria, Lecanicillium, mariannae-like, Microhilum, Simplicillium.

Commentary: Species of Cordyceps s. s. are characterized by possessing fleshy stromata that are pallid or brightly coloured. Because species of Torrubiella are interspersed among Cordyceps species in the basal part of the Cordycipitaceae, its ultimate application to a monophyletic taxon within the Cordycipitaceae is not clear, however (Fig. 10). The genus Torrubiella was erected in 1885 by Boudier with the type species T. aranicida Boud. (Kobayasi & Shimizu 1982). Our sampling included several species of Torrubiella that were interspersed amongst species of Cordycipitaceae, but we could not get hold of T. aranicida. Thus, Cordyceps s. s. is narrowly applied to the strongly supported clade (MP-BP = 98 %, ML-BP = 98 %, PP = 1.00 in Figs 1–2, 10) that includes Cordyceps species closely related to C. militaris. Cordyceps species that are placed outside of the Cordyceps s. s. node, but within the Cordycipitaceae, are provisionally retained within Cordyceps s. l. Torrubiella species that are part of the Cordyceps s. s. are transferred accordingly. The full extent to which the names Cordyceps and Torrubiella will ultimately be applied awaits additional sampling of Torrubiella, especially that of T. aranicida with the possibility that Torrubiella will need to be synonymized with Cordyceps. Although Phytocordyceps is characterized by its possession of bola-ascospores, it is also synonymized with Cordyceps because of its phylogenetic placement (Figs 8, 10).

Accepted names and new combinations for Cordyceps s. s.
The following taxa are accepted species of Cordyceps s. s. based on their inclusion in molecular phylogenies presented herein1 (see Table 1) or morphological descriptions matching the characters described above2. Where known we provide the anamorph connection for the species of Cordyceps s. s.

Cordyceps Fr., Observ. Mycol. 2 (revis.): 316. 1818 emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= Phytocordyceps C.H. Su & H.-H. Wang, Mycotaxon 26: 338. 1986.

Cordyceps militaris (L.: Fr.) Fr., Observ. Mycol. 2(revis.): 317. 1818.

Anamorphic genera: Beauveria, Engyodontium, Isaria, Lecanicillium, mariannae-like, Microhilum, Simplicillium.

Cordyceps belizensis Mains, Mycologia 32: 21. 1940.

Cordyceps bifusispora O.E. Erikss., Mycotaxon 15: 185. 1982.
Phylogenetic classification of Cordyceps and the clavicipitaceous fungi

Anamorph: Septofusidium bifusisporum Z.Y. Liu, Z.Q. Liang & A.Y. Liu

2Cordyceps brongniartii Shimazu, Trans. Mycol. Soc. Japan 29: 328. 1988.
Anamorph: Beauveria brongniartii (Sacc.) Petch

2Cordyceps chichibuënsis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 87. 1980.

2Cordyceps coccinea Penz. & Sacc., Malpighia 11: 24. 1897.

2Cordyceps coccinea var. subochracea Penz. & Sacc., Malpighia 15: 231. 1901.

1Cordyceps confragosa (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB0431.
≡ Torrubia confragosa Mains, Mycologia 41: 30. 1949.
Anamorph: Lecanicillium lecanii (Zimm.) Zare & W. Gams

2Cordyceps erotyi Petch, Trans. Brit. Mycol. Soc. 21: 40. 1937.

2Cordyceps exasperata A.F. Vital, Anais Soc. Biol. Pernambuco 14: 65. 1956.

2Cordyceps flavobrunnescens Henn., in Warburg, Monsunia 1: 164. 1900.

2Cordyceps formosana Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 113. 1981.

2Cordyceps gryllotalpae Lloyd, Mycol. Writ. 6: 913. 1920.

2Cordyceps hepialidicola Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 11. 1983.

2Cordyceps isarioides M.A. Curtis, Ann. Bot. 9: 36. 1895.

2Cordyceps kyusyuënsis A. Kawam., Icon. Jap. Fungi 8: 841. 1955.
Anamorph: Sporotrichum formosanum Kobayasi

2Cordyceps locustiphila Henn., Hedwigia 43: 246. 1904.

2Cordyceps militaris (L.: Fr.) Fr., Obs. Mycol. 2: 317. 1818.
≡ Clavaria militaris L., Sp. Plantarum, p. 1182. 1753.
≡ Hypoxylon militare (L.) Mérat, Nouv. Fl. Envir. Paris, p. 137. 1821.
≡ Xylaria militaris (L.) Gray, Nat. Arr. Brit. Pl. (London), p. 510. 1821.
≡ Sphaeria militaris (L.: Fr.) Fr., Syst. Mycol. 2: 325. 1823.
≡ Torrubia militaris (L.: Fr.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 6. 1865.
Anamorph: Lecanicillium

2Cordyceps miryensis Henn., Hedwigia 43: 247. 1904.

2Cordyceps miryensis Henn., Hedwigia 43: 247. 1904.

2Cordyceps miryensis Henn., Hedwigia 43: 247. 1904.

2Cordyceps miryensis Henn., Hedwigia 43: 247. 1904.

2Cordyceps ninchukispora (C.H. Su & H.H. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, comb. nov. MycoBank MB504362.
≡ Phytocordyceps ninchukispora C.H. Su & H.-H. Wang, Mycotaxon 26: 338. 1986.
Anamorph: acremonium-like

2Cordyceps ochraceostromata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 132. 1980.

2Cordyceps ogurasanensis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 80. 1982.

2Cordyceps oncocerae P.J. Wright, J. Invert. Pathol. 61: 211. 1994.

2Cordyceps polyarthra A. Möller, Phycomyceten u. Ascomyceten, p. 213. 1901.
≡ Cordyceps subpolyarthra Henn., Hedwigia 41: 11. 1902.
≡ Cordyceps concurrens Lloyd, Mycol. Writ. 7: 1180. 1923.
Anamorph: Isaria tenuipes Peck

2Cordyceps pruinosa Petch, Trans. Brit. Mycol. Soc. 10: 38. 1924.
Anamorph: Mariannaea pruinosa Z.Q. Liang

2Cordyceps rosea Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 112. 1982.

2Cordyceps roseostromata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 10. 1983.

2Cordyceps scarabaeicola Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 137. 1976.
Anamorph: Beauveria

2Cordyceps singeri Mains, Bull. Torrey Bot. Club 81: 499. 1954.

2Cordyceps spegazzinii M.S. Torres, J.F. White & J.F. Bisch., Mycotaxon 94: 257. 2006.
Anamorph: Evlachovaea

2Cordyceps staphylinidicola Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 88. 1982 [as Cordyceps staphylinidaecola]
Anamorph: Beauveria

2Cordyceps takaoamontana Yakush. & Kumaz., Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 108. 1941.
Anamorph: Isaria tenuipes Peck

2Cordyceps tarapotensis Henn., Hedwigia 43: 246. 1904.
2. **Cordyceps termitophila** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 56. 1978.

2. **Cordyceps truncata** Moureau, Mém. Inst. Roy. Colon. Belge 7: 19. 1949.

1. **Cordyceps tuberculata** (Lebert) Maire, Bull. Soc. Hist. Nat. Afrique N. 8: 165. 1917.
   - ≡ *Acrophyton tuberculatum* Lebert, in Sieb. & Köll., Z. Wiss. Zool. 8: 449. 1858.
   - ≡ *Torrubia sphingum* Tul. & C. Tul., Sel. Fung. Carpol. 3: 12. 1865.
   - ≡ *Cordyceps sphingum* (Tul. & C. Tul.) Berk. & M.A. Curtis, in Berkeley, J. Linn. Soc. 10: 375. 1868.

Anamorph: *Akanthomyces pistillariiformis* (Pat.) Samson & H.C. Evans

2. **Cordyceps tuberculata** var. *tuberculata* [var. *typica* Kobayasi] *f. moelleri* (Henn.) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 88. 1941.
   - ≡ *Cordyceps moelleri* Henn., Hedwigia 36: 221. 1897.

2. **Cordyceps tuberculata** var. *terminalis* Kobayasi [f. *genuina* Kobayasi], Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 88. 1941.

2. **Cordyceps tuberculata** var. *crista* (A. Möller) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 91. 1941.
   - ≡ *Cordyceps crista* A. Möller, Phycomyceten u. Ascomyceten, p. 212. 1901.

2. **Cordyceps tuberculata** var. *cockerelli* (Ellis & Everh.) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 90. 1941.
   - ≡ *Ophionectria cockerelli* Ellis & Everh., in Cockerell, J. Inst. Jamaica 1: 141. 1892.
   - ≡ *Cordyceps cockerelli* (Ellis & Everh.) Ellis, in Seaver, North Am. Flora 3: 52. 1910.

2. **Cordyceps typhuliformis** Berk. & Cooke, in Cooke, Grevillea 12: 78. 1884 (as C. *'typhulaeformis'*).

2. **Cordyceps washingtonensis** Mains, Mycologia 39: 535. 1947.

**Clavicipitaceae incertae sedis**

The following teleomorph genera could not be confidently assigned in the new classification because they were either not sampled as part of this study, were not sampled as part of other molecular phylogenetic studies, or the assessment of their morphology and ecology was inconclusive: *Berkeleyella* (Sacc.) Sacc., *Cavimulum* Yoshim. Doi, Dargan & K.S. Third, *Dussiella* Pat., *Epicera* Petr., *Helminthascus* Tranzschel, *Konradia* Racib., *Moelleriella* Bres., *Mycomalus* A. Möller, *Neobarya* Lowen, *Neocordyceps* Kobayasi, *Podocrella* Seaver, *Romana* Thirum., *Sphaerocordyceps* Kobayasi, and *Stereocrea* Syd. & P. Syd.

**Residual species of Cordyceps**

The following species of *Cordyceps* s. *l*. could not be confidently assigned in the new classification because they were either not assigned in any of the proposed genera in this study, were not sampled as part of this or other molecular phylogenetic studies, or the assessment of their morphology and ecology was inconclusive. These species are provisionally retained within *Cordyceps* s. *l*. until further phylogenetic analyses are conducted to classify them in a phylogenetic system. Where known we provide the anamorph connection for the species of *Cordyceps* s. *l.*

- **Cordyceps adpropinquans** (Ces.) Sacc., Syll. Fung. 2: 578. 1883.
  - ≡ *Torrubia adpropinquans* Ces., Atti Accad. Sci. Fis. Mat., Napoli 8: 14. 1879.

- **Cordyceps aeruginososclerotia** Z.Q. Liang & A.Y. Liu, Mycosystema 16: 63. 1997 [as C. *'aeruginososclerotia'*].

- **Cordyceps alba** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 114. 1982.

- **Cordyceps albida** Berk. & M.A. Curtis ex Cooke, Grevillea 12: 78. 1884.

- **Cordyceps albocitrina** Koval, Nov. Sist. Niz. Rast. 11: 209. 1974.

- **Cordyceps alboperitheciata** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 84. 1982.

- **Cordyceps alpicola** Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 138. 1976.

- **Cordyceps annulata** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 91. 1982.

- **Cordyceps arachnogena** Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 144. 1976.

- **Cordyceps aspera** Pat., J. Bot. (Paris) 7: 344. 1893.

- **Cordyceps ateWensis** Samson, H.C. Evans & E.S. Hoekstra, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 85: 590. 1982.

- **Cordyceps atrobrunnea** Penz. & Sacc., Malpighia 11: 522. 1897.

- **Cordyceps atropuncta** Koval, Bot. Mater. Otd. Sporov. Rast. 14: 158. 1961.

- **Cordyceps atroversis** Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 52. 1978.

- **Cordyceps aurantiaca** Lohwag, in Handel-Mazzetti, Symb. Sin. 2: 27. 1937.

- **Cordyceps aurea** Moureau, Mém. Inst. Roy. Colon. Belge 7: 21. 1949.

- **Cordyceps barbieri** Giard ex Massée, Ann. Bot. 9: 18. 1895.

- **Cordyceps barnesii** Thwaites, Fungi Ceylon, p. 110. 1873.
Phylogenetic classification of Cordyceps and the clavicipitaceae fungi

Cordyceps baumanniana Henn., Bot. Jahrb. Syst. 23: 539. 1897.

Cordyceps bicolor Pat., Mém. Acad. Malgache 6: 40. 1928.

Cordyceps bokyōensis Kobayasi, J. Jap. Bot. 58: 221. 1983.

Cordyceps bombi Rick ex Lloyd, Mycol. Notes 62: 914. 1920.

Cordyceps brasiliensis Henn., Hedwigia 36: 221. 1897.

Cordyceps brittlebankii McLennan & Cookson, Proc. Roy. Soc. Victoria 38: 74. 1926.

Cordyceps bulolensis Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 142. 1976.

Cordyceps caespitosofiliformis Henn., Hedwigia 41: 11. 1902.

Cordyceps callidii Quél., Comp. Rend. Assoc. Franç. Avancem. Sci. 21. Suppl. p. 7. 1897.

Cordyceps cardinalis G.H. Sung & Spatafora, Mycologia 96: 660. 2004.

   Anamorph: mariannaea/clonostachys-like

Cordyceps carnata Moureau, Mém. Inst. Roy. Colon. Belge 7: 10. 1949.

Cordyceps changpaishanensis Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 12. 1981.

Cordyceps chualasae Koval & Nazarova, Nov. Sist. Niz. Rast. 6: 116. 1969.

Cordyceps chishuiensis Z.Q. Liang & A.Y. Liu, Mycosystema 21: 9. 2002.

Cordyceps cinnabarina Petch, Ann. Crypt. Exot. 6: 230. 1933.

Cordyceps citrea Penz. & Sacc., Malpighia 11: 523. 1897.

Cordyceps clavicipitica Tokugawa & S. Imai, Trans. Sapporo Nat. Hist. Soc. 14: 104. 1935.

Cordyceps clavicípitis Örtgren, Svensk Bot. Tidskr. 10: 57. 1916.

Cordyceps coccidiocapitata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 91. 1982.

Cordyceps coccidioperithecata Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 79. 1982.

Cordyceps consumpta G. Cunn., Trans. Proc. New Zealand Inst. 53: 377. 1921.

Cordyceps coronilla Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 306. 1909.

Cordyceps cotopaxiana Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 126. 1981.

Cordyceps craigii Lloyd, Mycol. Writ. 4: 527. 1915.

Cordyceps cranstounii Olliff, Agric. Gazette New S. Wales 6: 408. 1895.

Cordyceps ctenocephala Syd., Bot. Jahrb. Syst. 57: 323. 1922.

Cordyceps cuboidea Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 131. 1980.

Cordyceps cusu Pat., Bull. Soc. Mycol. France 11: 229. 1895.

Cordyceps cylindrica Petch, Trans. Brit. Mycol. Soc. 21: 46. 1937.

   Anamorph: Nomuraea atypicola (Yasuda) Samson

Cordyceps deflectens Penz. & Sacc., Malpighia 11: 522. 1897.

Cordyceps dimeropoda Syd., Bot. Jahrb. Syst. 57: 324. 1922.

Cordyceps doassansii Pat., Tab. Analyt. Fung., p. 213. 1885.

Cordyceps doiana Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 124. 1981.

Cordyceps ergoticola Tanda & Kawat., J. Jap. Bot. 52: 19. 1977.

Cordyceps fasciculata Pat., Bull. Soc. Mycol. France 15: 206. 1899.

Cordyceps fleischeri Penz. & Sacc., Malpighia 15: 230. 1901.

Cordyceps fuliginosa Ces., Comment. Soc. Crittog. Ital., Genova 1: 67. 1861.

Cordyceps furcata McLennan & Cookson, Proc. Roy. Soc. Victoria 35: 157. 1923.

Cordyceps gemella Moureau, Lejeunia, Mém. 1: 83. 191.

Cordyceps geotrupis Teng, Sinensia 4: 293. 1934.

Cordyceps gracillima Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 126. 1981.

Cordyceps grenadensis Mains, Bull. Torrey Bot. Club 81: 499. 1954.
Cordyceps grylli Teng, Sinensia 7: 811. 1936.
Cordyceps guizhouensis Z.Y. Liu, Z.Q. Liang & A.Y. Liu, Mycosistema 16: 98. 1997.
Cordyceps gunnii Berk., J. Bot., London 7: 577. 1848.  Anamorph: paecilomyces-like
Cordyceps gunnii var. minor Z.Z. Li, C.R. Li, B. Huang, M.Z. Fan & M.W. Lee, Korean J. Mycol. 27: 232. 1999.
Cordyceps hauturu Dingley, Trans. Roy. Soc. New Zealand 81: 334. 1953.
Cordyceps hawkesii Gray, in Cooke, Grevillea 19: 76. 1891.
Cordyceps henleyae Massee, Ann. Bot. 8: 119. 1894.
Cordyceps hesleri Mains, J. Elisha Mitchell Sci. Soc. : 12. 1939.
Cordyceps hillii Lloyd, Mycol. Notes : 101. 1921.
Cordyceps hirotaniana Kobayasi, J. Jap. Bot. 58: 177. 1983.
Cordyceps hokkaidoensis Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 91. 1941.  Anamorph: Sporotrichum hokkaidoense Kobayasi
Cordyceps hormospora A. Möller, Phycomyceten u. Ascomyceten, p. 230. 1901.
Cordyceps ignota Marchion., Physis, B. Aires 2: 17. 1945.
Cordyceps imagamiana Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 1. 1983.
Cordyceps incarnata A. Möller, Phycomyceten u. Ascomyceten, p. 228. 1901.
Cordyceps inconspicua Moureau, Lejeunia, N.S. 14: 4. 1962.
Cordyceps indigotica Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 53. 1978.
Cordyceps interrupta Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 303. 1909.
Cordyceps inomoteana Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 82. 1982.
Cordyceps ithacensis Balazy & Bujak., Mycotaxon 25: 11. 1986.
Cordyceps javensis Henn., Hedwigia 41: 142. 1902.
Cordyceps joaquiensis Henn., Hedwigia 43: 248. 1904.
Cordyceps juruensis Henn., Hedwigia 43: 248. 1904.
Cordyceps kanzashiana Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 86. 1982.
Cordyceps khaoyaiensis Hywel-Jones, Mycol. Res. 98: 939. 1994.  Anamorph: lecanicillium/simplicillium-like
Cordyceps kirkii G. Cunn., Trans. Brit. Mycol. Soc. 8: 75. 1922.  Anamorph: Akanthomyces
Cordyceps kobayasi Koval, Klavtipital'nye Griby SSSR (Kiev), p. 178. 1984.
Cordyceps kusanagiensis Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 7. 1983.
Cordyceps lacroixii Har. & Pat., Bull. Trimestriel Soc. Mycol. France 20: 62. 1904.
Cordyceps langloisii Ellis & Everh., North Amer. Pyrenom. p. 62. 1892.
Cordyceps larivicola Quél., Bull. Soc. Bot. France 25: 292. 1878.
Cordyceps lateritia Dingley, Trans. Roy. Soc. New Zealand 81: 337. 1953.
Cordyceps leucocephala Moureau, Lejeunia, N.S. 14: 7. 1962.
Cordyceps lignicola Massee, Bull. Misc. Inform. Roy. Bot. Gard. Kew p. 173. 1899.
Cordyceps lilacina Moureau, Mém. Inst. Roy. Colon. Belge 7: 52. 1949.
Cordyceps longdongensis A.Y. Liu & Z.Q. Liang, Mycosistema 16: 140. 1997.
Cordyceps loushanensis Z.Q. Liang & A.Y. Liu, Mycosistema 16: 61. 1997.
Cordyceps mantidicola Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 12. 1983.
Cordyceps manzhurica Koval, Bot. Mater. Otd. Sporov. Rast. 14: 161. 1961.
Cordyceps maolanensis Z.Y. Liu & Z.Q. Liang, Mycosistema 16: 4. 1997.
Cordyceps martialis Speg., Bol. Acad. Nac. Ci. Córdoba 11: 305. 1889.  = Cordyceps huntii Giard, Bull. Soc. Entomol. France 64: 171.
Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi

*Phylogenetic classification of Cordyceps and the clavicipitaceous fungi*

1895.

= *Cordyceps submilitaris* Henn., Hedwigia 36: 222. 1897.

= *Cordyceps klenei* Pat., Bull. Trimestriel Soci. Mycol. France 24: 11. 1908.

Anamorph: cephalosporium-like

*Cordyceps maolanoides* Z.Q. Liang, A.Y. Liu & J.Z. Huang, Mycosystema 21: 164. 2002.

*Cordyceps memorabilis* (Ces.) Sacc., Michelia 1: 321. 1879.

≡ *Racemella memorabilis* Ces., Comment. Soc. Cirttog. Ital. 1: 65. 1861.

Anamorph: *Isaria farinosa* (Holmsk.) Fr.

*Cordyceps menesteridis* F. Muell. & Berk., Gard. Chron. 2: 791. 1878.

*Cordyceps michaelisii* Henn., Hedwigia 41: 169. 1902.

*Cordyceps miniata* Moureau, Lejeunia, Mém. 15: 22. 1961.

*Cordyceps minuta* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 294. 1963.

*Cordyceps muscae* Henn., Bot. Jahrb. Syst. 25: 507. 1898.

*Cordyceps musicaudata* Z.Q. Liang & A.Y. Liu, Acta Mycol. Sin. 15: 265. 1996.

*Cordyceps myosuroides* Henn., Hedwigia 41: 169. 1902.

*Cordyceps myrmecogena* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 55. 1978.

*Cordyceps nakazawae* A. Kawam., Icon. Jap. Fungi 8: 836. 1955 (as C. 'nakazawai').

*Cordyceps nanatakiensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 9. 1983.

*Cordyceps necator* Pat. & Har., Bull. Trimestriel Soci. Mycol. France 28: 283. 1912.

*Cordyceps nelumboides* Kobayasi & Shimizu, Kew Bull. 31: 557. 1976.

*Cordyceps neogryllotalpae* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 143. 1976.

*Cordyceps nipponica* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 151. 1939.

Anamorph: *Isaria nipponica* Kobayasi

*Cordyceps novaeezealandiae* Dingley, Trans. Roy. Soc. New Zealand 81: 337. 1953.

*Cordyceps novoguineensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 2: 148. 1976.

*Cordyceps obliqua* Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 177. 1941.

*Cordyceps obliquiordina* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 114. 1982.

*Cordyceps odyneri* Quél., 14th Suppl. Champ. Jura et Vosges, p. 10. 1865.

*Cordyceps olivacea* Rick, in Lloyd, Mycol. Writ. 7: 1118. 1922.

*Cordyceps olivaceovirescens* Henn., Hedwigia 39: 78. 1900.

*Cordyceps olivascens* Mains, Mycologia 39: 537. 1947.

*Cordyceps otakiensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 15. 1983.

*Cordyceps ovoideoperithecata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 83. 1982.

*Cordyceps palifoliolivacea* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 113. 1982.

*Cordyceps parvula* Mains, Bull. Torrey Bot. Club 86: 46. 1959.

*Cordyceps phymatospora* C.R. Li, M.Z. Fan & Z.Z. Li, Mycosystema 21: 167. 2002.

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KEY TO THE GENERA OF FUNGI FORMERLY CLASSIFIED IN CORDYCEPS

This key is designed to emphasize the most conspicuous field-, host-, and macroscopic characters available to the user for Cordyceps sensu Kobayasi and Mains. It is a key to the monophyletic genera described herein and is not a key to the species. As relatively few species occur on Elaphomyces and adult stages of Arthropoda, the key begins with these characters so as to expeditiously highlight or remove these taxa from consideration. Host is an exceedingly important character in most species descriptions of arthropod-pathogenic fungi. The host should be collected with the fungal specimen whenever possible, but this often proves problematic. The vast majority of arthropod-pathogenic fungi occur
Cordyceps s. s. consists almost entirely of pallid to brightly coloured species that produce soft fleshy stromata (e.g., *C. militaris*). The majority of species attack larvae and pupae of Lepidoptera and Coleoptera in leaf litter, moss or upper soil layers. Numerous species that produce highly reduced stromata, loosely organized hyphae, or a subiculum on the host also occur in this genus (e.g. *C. tuberculata*), some of which were previously classified in *Torrubiella* (e.g., *T. confragosa*).

*Elaphocordyceps* includes all species that parasitize *Elaphomyces* and closely related species that attack nymphs of cicadas. The morphology of the *Elaphomyces* parasites and the cicada pathogens are remarkably similar and attest to the recent history of inter-kingdom host-jumps in a common subterranean environment (Nikoh & Fukatsu 2000). The exception to this genus is *E. subsessilis*, which macroscopically and ecologically is distinct from the rest of the species, but is well supported as being a member of the genus based on molecular data and micromorphology.

*Metacordyceps* includes only a limited number of described species, of which all but one are only known from East Asia. The stromatal colour of fresh specimens ranges from white to lilac, purple or green, and the darker pigments are almost black in dried specimens. The texture of the stromata is fibrous and not fleshy like *Cordyceps* s. s., and the hosts are almost always buried in soil.

*Ophiocondyceps* is the largest genus of arthropod-pathogenic fungi. Many species are darkly pigmented and occur on immature stages of hosts buried in soil or in decaying wood. Notable exceptions exist for both of these traits among species that attack adult stages of hosts, however. For example, *O. unilateralis* is common on adult ants and occurs on the under sides of leaves, and *O. sphecocephala* is common on adult wasps and is found in leaf litter. Stromatal morphology is diverse, ranging from filiform and wiry to clavate and fibrous, according to species, and many species produce their perithecia in nonterminal regions of the stroma, either distinctly superficial, or in broad irregular patches, or in lateral pads.

| **Fleshy** | – stromata that are composed of relatively loosely woven hyphae and are soft in texture (e.g., *C. militaris*). |
|**Wiry** | – filiform stromata that are somewhat brittle and stiff (e.g., *O. unilateralis*). |
|**Pliant** | – filiform stromata that are more pliable and rubbery to the touch; when fresh, they bend easily without breaking; typically slightly more robust than wiry (e.g., *O. nutans*). |
|**Fibrous** | – stromata that are composed of relatively tightly woven hyphae and are firm in texture, similar to the stipe of a mushroom (e.g., *E. ophioglossoides, O. heteropoda*). |
|**Subicular** | – production of perithecia on a net-like structure of mycelium, not on the developed stroma (e.g., *C. tuberculata*). |
|**Lateral pads** | – production of perithecia on a disc-like or cushion-like structure on a subterminal region of the stroma (e.g., *O. variabilis, O. unilateralis*). |
|**Aperithecial apices** | – production of perithecia in subterminal regions of the stroma, resulting in an apical region of the stroma lacking perithecia. (Note: The term sterile apices has also been used to describe this condition, but the apical regions of many stromata produce an anamorph and thus are not technically sterile.) |

1. **Host** – *Elaphomyces* .......................................................... *Elaphocordyceps* (e.g., *E. ophioglossoides*) ................................. 2
2. **Host** – Arthropods ........................................................................................................................................................................................................................................................ 2
3. **Host** – adult Arthropods ............................................................................................... 3
4. **Host** – immature stage of Arthropods .............................................................................. 6
5. **Perithecia** – colour: pallid, cream to white; arrangement: superficial on a subiculum or highly reduced pallid stroma. **Host** – adult Lepidoptera ...................................................................................... *Cordyceps* (e.g., *C. tuberculata*) ................................. 4
6. **Host** – adult Arthropods other than Lepidoptera (e.g., ant, wasp, weevil, dragonfly, etc.) and stroma typically well-developed .......................................................... 5

1. **Host** – Arthropods ........................................................................................................................................................................................................................................................ 2
2. **Host** – adult Arthropods ............................................................................................... 3
3. **Host** – immature stage of Arthropods .............................................................................. 6
4. **Stroma** – colour: yellow; texture: fleshy; shape: stipitate, clavate. **Perithecia** – colour: like stroma; arrangement: partially immersed to pseudoimmersed at right angles to surface of stroma (ordinal).

   Host – typically on adult scarab beetles .............................................................. *Cordyceps* (e.g., *C. scarabaeicola*)

4. **Stroma** – colour: brightly or darkly pigmented; texture: wiry or pliant, not fleshy; shape: stipitate with or without pronounced fertile head region. **Perithecia** – arrangement: immersed at an oblique angle in fertile head region or more or less ordinal in subterminal lateral pads .............................................. 5

5. **Stroma** – colour: at least partly brightly coloured; texture: pliant; shape: stipitate with globose to elongated fertile head region. **Perithecia** – arrangement: usually completely immersed at oblique angles, often giving the surface of the fertile head region a slightly uneven appearance when mature. Host – typically on adult insects (ants, wasps, weevils, dragonflies, etc.) .................. *Ophiocordyceps* (e.g., *O. nutans, O. sphaeoccephala*)

5. **Stroma** – colour: darkly pigmented; texture: wiry; shape: filiform. **Perithecia** – colour: darkly pigmented like stroma or darker; arrangement: produced in subterminal region of stroma in lateral pad(s).

   Host – adult ants .................................................................................................. *Ophiocordyceps* (e.g., *O. unilateralis*)

6. **Stroma** – colour: pallid to brightly coloured; texture: fleshy to fibrous; shape: usually stipitate, clavate but stroma highly reduced or subicular in some species. **Perithecia** – colour: pallid to brightly coloured like stroma; arrangement: typically partially immersed to pseudoimmersed to superficial on clava or subiculum in some species .................................................................................................................... 7

6. **Stroma** – colour: usually darkly pigmented tan to brown to olive or black, rarely white to lilac to purple; texture: wiry, pliant or fibrous; shape: stipitate, club-shaped, or filiform, rarely subicular.

   **Perithecia** – colour: typically pigmented like stroma or darker; arrangement: immersed to partially immersed to pseudoimmersed to superficial .................. 8

7. **Stroma** – colour: pallid, cream to white; texture: fibrous; shape: reduced to pad-like or cushion-like structure on surface of wood, connected to host buried in wood via rhizomorph-like structures.

   **Perithecia** – colour: like stroma; arrangement: immersed to partially immersed on pad-like stroma.

   Host – Scarabid beetle larvae buried in decaying wood ........................................... *Elaphocordyceps* (e.g., *E. subsessilis*)

7. **Stroma** – colour: yellow to red to orange; texture: fleshy; shape: usually stipitate clavate but subicular in some species. **Perithecia** – colour: like stroma; arrangement: ordinal, typically partially immersed to pseudoimmersed to superficial on clava or subiculum in some species.

   Host – typically on larvae or pupae of arthropods in relatively exposed environments, such as leaf litter, moss, or the uppermost soil layer ........................................... *Cordyceps* (e.g., *C. militaris, C. staphylinidicola*)

8. **Stroma** – colour: olive to brown; texture: fibrous; shape: stipitate, fertile region terminal, distinctly capitately to clavate. **Perithecia** – colour: like that of stroma; arrangement: immersed.

   Host – cicada nymphs ............................................................................................. *Elaphocordyceps* (e.g., *E. paradoxa*)

8. **Stroma** – colour: tan to brown to black or lightly pigmented, white to lilac to purple, rarely brightly pigmented; texture: wiry, pliant, fibrous; shape: stipitate, capitately to clavate to filiform, rarely subicular.

   **Perithecia** – colour: similar to stroma when immersed, often darker when superficial; arrangement: immersed, pseudoimmersed or superficial .............................................. 9

9. **Stroma** – colour: white to lilac to purple to green, then appearing almost black when dry; texture: fibrous; shape: stipitate, typically with elongated clava. **Perithecia** – colour: like stroma; arrangement: immersed, ordinal or oblique.

   Host – typically buried in soil .............................................................................. *Metacordyceps* (e.g., *M. taili*)

9. **Stroma** – colour: olive to brown to black rarely brightly coloured; texture: wiry, pliant, or fibrous; shape: stipitate, club-shaped to clavate or filiform, rarely subicular.

   **Perithecia** – colour: darkly pigmented like stroma or darker; arrangement: immersed, pseudoimmersed but tightly spaced, or superficial and widely spaced, produced in terminal clava or subterminal patches or lateral pads.

   Host – typically embedded in rotten wood or buried in soil ........................................... *Ophiocordyceps* (e.g., *O. sinensis, O. acicularis, O. variabilis*)

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