

Phylogenetic-based nomenclatural proposals for *Ophiocordycipitaceae* (*Hypocreales*) with new combinations in *Tolypocladium*

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Abstract: *Ophiocordycipitaceae* is a diverse family comprising ecologically, economically, medicinally, and culturally important fungi. The family was recognized due to the polyphyly of the genus *Cordyceps* and the broad diversity of the mostly arthropod-pathogenic lineages of *Hypocreales*. The other two cordyceps-like families, *Cordycipitaceae* and *Clavicipitaceae*, will be revised taxonomically elsewhere. Historically, many species were placed in *Cordyceps*, but other genera have been described in this family as well, including several based on anamorphic features. Currently there are 24 generic names in use across both asexual and sexual life stages for species of *Ophiocordycipitaceae*. To reflect changes in Art. 59 in the *International Code of Nomenclature for algae, fungi, and plants* (ICN), we propose to protect and to suppress names within *Ophiocordycipitaceae*, and to present taxonomic revisions in the genus *Tolypocladium*, based on rigorous and extensively sampled molecular phylogenetic analyses. When approaching this task, we considered the principles of priority, monophyly, minimizing taxonomic revisions, and the practical utility of these fungi within the wider biological research community.

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BACKGROUND

The revision of Art. 59 in the *International Code of Nomenclature for algae, fungi, and plants* (ICN; McNeill *et al.* 2012) has created a major task for mycologists, who must now reconcile under one name various possible names existing for different morphs of the same species of fungus

(Hibbett & Taylor 2013). Groups have already begun to propose names which should be protected or suppressed within *Hypocreales* in accordance with the 'one fungus one name' policy (Geiser *et al.* 2013, Rossman *et al.* 2013, Leuchtman *et al.* 2014, Johnston *et al.* 2014, Kepler *et al.* 2014) and others are in progress. Here, we seek to retain names in *Ophiocordycipitaceae* with the goal of harmonizing

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priority, monophyly, simplicity of taxonomic revisions, and minimization of disruption to the research community.

The family *Ophiocordycipitaceae* was described by Sung *et al.* (2007) to accommodate species that were determined to be phylogenetically distinct from *Cordycipitaceae* and *Clavicipitaceae* *s.str.* Asexual morphologies in *Ophiocordycipitaceae* show a tremendous range of variation, some of which are restricted in their phylogenetic distribution while others are often found in disparate lineages. For example, *Verticillium* is a common asexual morph of many species in several hypocrealean families, including *Ophiocordycipitaceae*, *Cordycipitaceae* and *Clavicipitaceae* (see Zare *et al.* 2000, Sung *et al.* 2001, 2007, and Gams & Zare 2001).

Ophiocordyceps is the most speciose genus of the family, and was described originally by Petch (1931a) for species of *Cordyceps* that have septate ascospores that do not disarticulate into part-spores at maturity and asci with inconspicuous apical caps (Petch 1931a, 1933). Kobayasi (1941) later used *Ophiocordyceps* as a subgeneric classification of the genus *Cordyceps*, but Sung *et al.* (2007) restored *Ophiocordyceps* to the rank of genus to include those *Cordyceps* species within *Ophiocordycipitaceae* forming a sister clade with the genus *Elaphocordyceps* (see below). The type of the genus is *O. blattae*, a rarely collected cockroach pathogen for which no culture or molecular data are available.

Asexual generic names associated with *Ophiocordyceps* include *Sorospora*, the oldest name still in use for species in the clade, *Hirsutella*, *Hymenostilbe*, *Stilbella*, *Syngliocladium*, and *Paraisaria*. *Hirsutella* species typically produce one to several conidia in a limited mucus droplet borne on basally subulate phialides that taper into slender necks (Gams & Zare 2003). *Hymenostilbe* was proposed by Petch (1931b), and there is some evidence to support restricting its use within the genus *Ophiocordyceps* to the '*O. sphecocephala* clade', most species of which sporulate from adult insects (Sung *et al.* 2007, Luangsa-ard *et al.* 2011a). These taxa produce conidia singly from multiple denticles on conidiogenous cells forming a palisade-like layer along the entire outer surface of synnemata (Mains 1950). The *Stilbella* morphology has been applied broadly among species associated with *Ophiocordyceps*, as well as to fungi later reclassified in other genera (Seifert 1985, Gräfenhan *et al.* 2011). *Stilbella* species often produce aggregate synnemata with a fertile, terminal head of conidia. *Syngliocladium* spp. often have laterally arising conidiophores similar in morphology to the hypocreaceous asexual morph *Gliocladium*, and they may be either synnematosous or mononematous on their arthropod hosts (Petch 1932, Hodge *et al.* 1998). *Sorospora*, a chlamydospore producing spore state, has been linked as a synasexual morph of *Syngliocladium* (Speare 1917, 1920), but the two morphologies are not always produced by all species (Hodge *et al.* 1998, Evans & Shah 2002). Species of *Paraisaria* possess feathery synnemata which fruit from arthropod hosts, and several species have been linked via cultural and molecular data to the *O. gracilis* clade (Samson & Brady 1983, Sung *et al.* 2007, Evans *et al.* 2010). Names of genera associated with *Ophiocordyceps* whose types are located outside of *Hypocreales* include *Tilachlidiopsis*

and *Podonectria*, members of the *Agaricomycetes* and *Dothideomycetes*, respectively (Rossman 1978, Stalpers *et al.* 1991, Hughes *et al.* 2001, Boonmee *et al.* 2011). Despite the large number of taxa associated with *Ophiocordyceps*, a lack of support for internal nodes resulting in equivocal topologies has limited inferences about relationships within the genus in previous studies (Sung *et al.* 2007).

The most notable species in the *Ophiocordyceps* clade is *O. sinensis*, which is nearly double the price of gold by weight (Stone 2008, Shrestha & Bawa 2013) and the subject of intense research, especially in China (Shrestha *et al.* 2010, Hu *et al.* 2013, Ren & Yao 2013, Bushley *et al.* 2013a, *etc.*). Almost exclusively found parasitizing the larvae of ghost moths (*Hepialidae: Thitarodes*) in the alpine and sub-alpine pastures of the Tibetan plateau and the Himalayas, this species is undergoing heavy, possibly unsustainable, and destructive harvesting (Cannon *et al.* 2009, Shrestha & Bawa 2013).

The recently described genus *Elaphocordyceps* is typified by *E. ophioglossoides*, one of the first *Cordyceps* species to be described. Species in *Elaphocordyceps* are mostly parasites of the ectomycorrhizal truffle genus *Elaphomyces* (*Ascomycota, Eurotiales*). The majority of *Elaphocordyceps* species have no known asexual morph, but where known they produce ones which are verticillium-like or *Tolypocladium* (Sung *et al.* 2007). There are a few *Elaphocordyceps* species known to be entomopathogens, including three cicada pathogens (*E. inegoensis*, *E. paradoxa*, and *E. toriharamontana*), and one beetle pathogen, *E. subsessilis* (syn. *Tolypocladium inflatum*) (Hodge *et al.* 1996, Sung *et al.* 2007). *Tolypocladium inflatum* (a name conserved by the rejection of *Pachybasium niveum*; Dreyfuss & Gams 1994), is a medicinally important fungus and the subject of much research due to its production of the immunosuppressant drug, cyclosporin A (Survase *et al.* 2011, Bushley *et al.* 2013b). The other species of *Tolypocladium* have no known sexual morphs and have mainly been isolated from soil (Gams 1971, Bissett 1983) or observed parasitizing rotifers or insects (Barron 1980, 1981, 1983, Samson & Soares 1984, Weiser *et al.* 1991). The asexually typified genus *Chaunopycnis* is also related to this clade (Bills *et al.* 2002) and has been isolated mainly from soil samples (Gams 1980, Bills *et al.* 2002), although one species was isolated from epilithic Antarctic lichens (Möller & Gams 1993). The similarity of conidiogenesis between *Chaunopycnis* and *Tolypocladium* was noted in the original description of *Chaunopycnis* (Gams 1980), and its phialides often taper in a manner similar to those of *Tolypocladium*. Interestingly, these two genera have also been linked by their shared production of cyclosporin A (Traber & Dreyfuss 1996). Two of the described *Chaunopycnis* species produce loosely enclosed conidiomata, a morphology not seen in other members of the clade or within *Ophiocordycipitaceae* as a whole.

The relationships among the species of the *Purpureocillium* clade were recently reviewed by Luangsa-ard *et al.* (2011b). The genus was proposed to encompass taxa closely related to *Purpureocillium lilacinum* (syn. *Paecilomyces lilacinus*) and consists of species with purple-hued conidia, including *Nomuraea atypicola* and *Isaria*

takamizusanensis. The type of *Nomuraea* is *N. rileyi* (syn. *N. prasina*), which has recently been synonymized with *Metarhizium* (Kepler *et al.* 2014). The type of *Isaria* is a member of *Cordycipitaceae* (Gams *et al.* 2005, Hodge *et al.* 2005, Luangsa-ard *et al.* 2011b). While *N. atypicola* and *I. takamizusanensis* have not been addressed taxonomically, other studies found close relationships between these taxa and *Purpureocillium* (Sung *et al.* 2007, Perdomo *et al.* 2013). *Nomuraea atypicola* is the asexual morph of *C. cylindrica* (Hywel-Jones & Sivichai 1995), the only sexual morph described for this clade and one of the “residual” *Cordyceps* s. lat. left without reassignment to any phylogenetically redefined genus by Sung *et al.* (2007).

Nematode pathogens have been described in many genera throughout *Hypocreales*. The largest and oldest of these is the asexually typified genus *Harposporium*. Most *Harposporium* species produce crescent-shaped or helicoid conidia that are ingested by their hosts and become lodged in the upper portions of the digestive tract (Barron 1977). Conidia are produced on spherical conidiogenous cells, and several species are known to produce hirsutella-like synasexual morphs (Hodge *et al.* 1997, Chaverri *et al.* 2005, Li *et al.* 2005). While the majority of *Harposporium* species are known from nematodes, these fungi are common in the soil and several studies have reported an entomopathogenic ecology as well (e.g., Shimazu & Glockling 1997, Evans & Whitehead 2005). In 2005, Chaverri *et al.* reported the asexual-sexual morph connection between *Harposporium* and *Podocrella*, an arthropod-pathogenic genus. Several researchers initially described nematophagous taxa in the originally plant-pathogenic genus *Meria* (Vuillemin 1896, Drechsler 1941), but this genus was found to be polyphyletic (Gams & Jansson 1985), and for this reason *Drechmeria* was erected for the nematophagous meria-like taxa in *Hypocreales*. The type of *Drechmeria*, *D. coniospora*, has cone-shaped conidia whose conidiogenous cells are not basally swollen as in *Harposporium*. One protozoan-infecting species of *Drechmeria*, *D. harposporioides*, produces crescent-shaped conidia similar to those of *Harposporium* (Barron & Szijarto 1982). *Haptocillium* was erected for asexual nematode pathogens bearing verticillate phialides and whose conidia are not ingested but adhere to the surface of their hosts (Zare & Gams 2001).

Polycephalomyces represents a diverse clade that is currently *incertae sedis* within *Hypocreales*, as its placement has lacked support in previous molecular studies (Kepler *et al.* 2013). Of particular uncertainty was whether *Polycephalomyces* and its closest related taxon, *C. pleuricapitata*, formed a sister clade to *Ophiocordycipitaceae*, or if it was more closely related to *Clavicipitaceae*. Many morphological characters are shared between *Ophiocordycipitaceae* and *Polycephalomyces*. For example, numerous species in both clades produce hirsutella-like anamorphs with conidia often borne in a slimy mass (Seifert 1985). In addition, sexual sporing structures of *Polycephalomyces* often possess a wiry, tough, carbonaceous stipe which is a common morphology of *Ophiocordyceps* (Kepler *et al.* 2013). Many species within this genus are known mycoparasites of other hypocrealean entomopathogens and myxomycetes, but there are also several species of

entomopathogens. *Cordyceps pleuricapitata* was deemed a residual species of *Cordyceps* of uncertain placement by Kepler *et al.* (2013), due to a lack of statistical support joining that species and *Polycephalomyces*.

In this paper we expand the taxon sampling presented in Sung *et al.* (2007) by 222 hypocrealean isolates. This includes sexual and asexual states which provide the framework for addressing the nomenclatural issues demanded by changes to the most recent ICN.

MATERIALS AND METHODS

Sequences from five nuclear loci, including the small and large subunits of the rDNA (SSU and LSU), the transcription elongation factor-1 α (TEF), and the first and second largest subunits of RNA polymerase II (RPB1 and RPB2) were used for phylogenetic analyses. DNA extraction and PCR amplification were carried out as previously described (Kepler *et al.* 2013). Sequencing reactions were performed at the University of Washington High-Throughput Genomics Center (Seattle, WA) with the primers used for the initial amplifications. All other sequences were collected from GenBank. Efforts were made for all specimens to have data for at least three of the five genes to be considered in our analyses. However, certain taxa for which only one or two genes were available were included due to the importance in addressing the taxonomic issues at hand (Table 1).

Raw sequences were processed, aligned, and gaps excluded as in Kepler *et al.* (2013), using the programs MAFFT v. 6 (Kato *et al.* 2002, Kato & Toh 2008), Geneious v. 7.0.6 (Biomatters, available <http://www.geneious.com>), and Gblocks (Talavera & Castresana 2007). The final alignment length was 4570 nucleotides - 1023 for SSU, 879 for LSU, 987 for TEF, 646 for RPB1, and 1035 for RPB2. RAxML v. 7.6.6 (Stamatakis 2006) was used to perform Maximum likelihood (ML) estimation of the phylogeny with 500 bootstrap replicates on the concatenated dataset using eleven data partitions. These included one each for SSU and LSU, and three for each of the three codon positions of the protein coding genes, TEF, RPB1, and RPB2. The GTR-GAMMA model of nucleotide substitution was used.

RESULTS AND DISCUSSION

Our results are in agreement with the overall phylogenetic structure of the order *Hypocreales* put forth by Sung *et al.* (2007). Nomenclatural issues for taxa in the other two families of cordyceps-like organisms, *Cordycipitaceae* and *Clavicipitaceae*, will be presented elsewhere or have already been published (Leuchtman *et al.* 2014, Kepler *et al.* 2014). Based on this exhaustive phylogenetic reconstruction (Fig. 1), we recognize six genera within *Ophiocordycipitaceae* *Ophiocordyceps*, *Tolypocladium*, *Purpureocillium*, *Harposporium*, *Drechmeria*, and *Polycephalomyces* (Table 2). This framework will provide clarity for researchers, ease of communication for instructors, and phylogenetic taxonomy around which to investigate the evolution of life histories (e.g. morphology, ecology).

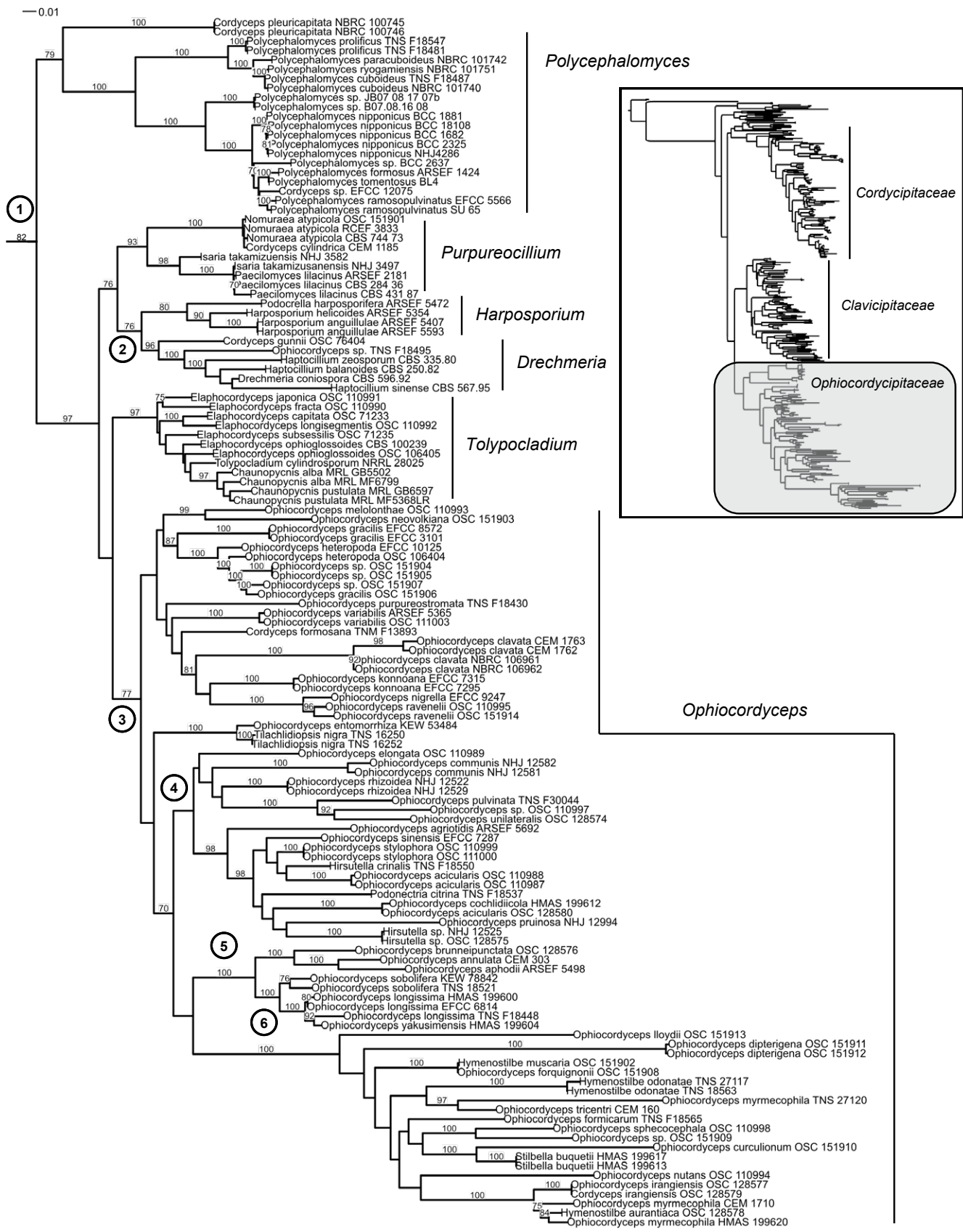


Fig. 1. ML tree of *Ophiocordycipitaceae* obtained using RAxML to analyze the concatenated five gene dataset (SSU, LSU, TEF, RPB1, and RPB2). Proposed genus level names to protect are delimited, but names of individual species have not been changed on the leaves of the tree, to demonstrate the diversity of taxa sampled. Values above branches represent MLBP proportions greater than or equal to 70 % from 500 replicates. Inset tree shows the larger phylogeny of *Hypocreales*.

TAXONOMY

***Ophiocordyceps* Petch 1931**

Ophiocordyceps sensu Sung *et al.* (2007) is resolved as a well-supported (MLBP=77) clade (Fig. 1, Node 3). This clade is speciose, diverse, and almost exclusively comprises insect pathogens. In spite of increased taxon sampling, current reconstructions fail to find strong statistical support at the internal nodes, and therefore we refrain from defining infrageneric groupings (Fig. 1). While *Sorospora* is the oldest name for any members in this clade, there are only two described species, and Evans & Shah (2002) argued *Sorospora* should be synonymized with *Syngliocladium* instead of being recognized as an asexual morph, as *Synnematium* was previously treated with respect to *Hirsutella* (Evans & Samson 1982). We propose, therefore, to suppress the use of *Sorospora* for this clade. *Hirsutella* is the next oldest name, but the type, *H. entomophila*, which was described growing from adult Coleoptera, has not been sampled and no culture of this species is available. Sung *et al.* (2007) argued that the *Hirsutella* morphology was phylogenetically informative for the ‘*O. unilateralis* group’ which they resolved as paraphyletic, a topology recovered in the current analyses as well (Fig 1, Nodes 4 and 5). However, the *Hirsutella* morphology is observed in other clades (e.g. *Harposporium*, *Polycephalomyces*, *Clavicipitaceae*), and while it is difficult to place the type species based on morphology alone, it appears from its original description to be morphologically and ecologically (as a parasite of adults) similar to species of *Hymenostilbe* found in the ‘*O. sphecocephala*’ clade and not *Hirsutella* of the ‘*O. unilateralis* group’ (Patouillard 1892). Another reason for suppressing the use of *Hirsutella* for this clade is the larger number of new combinations that would have to be made – 178 for *Ophiocordyceps* vs. 77 for *Hirsutella* – as the vast majority of species encompassed here are currently described as *Ophiocordyceps*. Also, preservation of the name “cordyceps” within the name of *O. sinensis* is considered paramount given its economic, medicinal, and cultural importance in addition to being the most widely known and researched species in the clade (Shrestha *et al.* 2010).

At this time, we also propose to suppress the use of the other names proposed for taxa in this clade, including *Hymenostilbe*, *Syngliocladium*, and *Paraisaria*, because these names are younger, and they contain fewer associated taxa than either *Ophiocordyceps* or *Hirsutella*. Our results suggest the restriction of *Hymenostilbe* to the ‘*O. sphecocephala* clade’ (Fig. 1, Node 6) which occupies a long branch and has strong support (MLBP=100), however, because the other internal nodes of the clade do not receive support, we refrain from making this distinction now as it would result in a paraphyletic *Ophiocordyceps*. These analyses place one species of *Stilbella*, *S. buquetii*, in this clade, while other studies (Seifert 1985, Gräfenhan *et al.* 2011) have placed other *Stilbella* species in *Nectriaceae*, *Bionectriaceae*, or *Polycephalomyces*, and the current placement of *Stilbella* remains *Hypocreales incertae sedis* (Kirk *et al.* 2008). The type of *Stilbella*, a coprophile, has yet to be considered in a phylogenetic context, and for these reasons we do not address that name here, but reject the use of that name for

this clade. Therefore, we propose to protect *Ophiocordyceps* as the genus name for the entire clade, while acknowledging that future studies including more data and taxonomic sampling may provide better resolution of the relationships within the genus and a narrower concept of *Ophiocordyceps*.

***Tolypocladium* W. Gams 1971**

Tolypocladium is proposed for protection over the other two generic names in the clade, *Elaphocordyceps* and *Chaunopycnis*. The clade itself is well supported (MLBP=97) in this and other published analyses (Sung *et al.* 2007, Kepler *et al.* 2013). However, relationships between species in this clade are very sensitive to taxon sampling, and there is little bootstrap support for internal branches from the current data to justify more than one name for this clade. The asexual-sexual morph connection between *Tolypocladium* and some *Elaphocordyceps* species has been known for several years (Hodge *et al.* 1996), although where known most *Elaphocordyceps* spp. do not possess the morphology associated with *Tolypocladium* (Sung *et al.* 2007). While this may cause some short-term confusion, the alternative would be to name the clade *Elaphocordyceps* (which would cause the fewest name changes, 12 vs. 26 for *Tolypocladium*) and suppress *Tolypocladium*, a much more widely known, medicinally important, and older name, and therefore we find this a poor option. In this analysis the *Chaunopycnis* species sampled form a monophyletic clade which is the most divergent group within the clade. However, this may be the result of limited taxon and genetic sampling; only small subunit rDNA data for the sampled *Chaunopycnis* species was available for these analyses.

Here, we present a list of 26 new combinations within the genus *Tolypocladium*, which we emend to include species whose anamorphic forms do not possess inflated phialide bases, but that do form a single monophyletic clade encompassing a large number of truffle parasites, several insect pathogens, rotifer pathogens, and several fungi isolated to date only from soil.

***Tolypocladium* W. Gams, *Persoonia* 6: 185 (1971).**

Synonyms: *Chaunopycnis* W. Gams, *Persoonia* 11: 75 (1980).

Elaphocordyceps G.H. Sung & Spatafora, *Stud. Mycol.* 57: 36 (2007).

Circumscription: The genus *Tolypocladium* is emended here to apply to all descendants of the node defined in the reference phylogeny (Fig. 1) as the terminal *Tolypocladium* clade. It is the least inclusive clade containing *T. album*, *T. capitatum*, *T. cylindrosporium*, *T. fractum*, *T. inflatum*, *T. japonicum*, *T. longisegmentum*, *T. ophioglossoides*, and *T. pustulatum*. No definitive synapomorphies are known for the clade. Morphologies associated with sexual reproductive states include robust stipitate stroma with clavate to capitate clava (e.g. *T. capitatum*) to highly reduced stroma comprising rhizomorphs and aggregated perithecia (e.g. *T. inflatum*); perithecia may be immersed and ordinal to the long axis of the stroma or superficial and produced on a highly reduced stromatic pad; asci are single-walled, long and cylindrical with a pronounced apical cap; ascospores

are filiform, approximately as long as asci, septate and typically disarticulate into part-spores. Where known, asexual states include morphologies described as *Tolypocladium sensu* Gams (1970), *Chaunopycnis sensu* Gams (1979), or verticillium-like. Ecologies include parasites and pathogens of insects, rotifers and fungi, as well as, soil-inhabiting.

Type: *Tolypocladium inflatum* W. Gams 1971.

Tolypocladium inflatum W. Gams, *Persoonia* **6**: 185 (1971), *nom. cons.*

Synonyms: *Cordyceps subsessilis* Petch, *Trans. Brit. Mycol. Soc.* **21**: 39 (1937).

Elaphocordyceps subsessilis (Petch) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Cordyceps facis Kobayasi & Shimizu, *Trans. Mycol. Soc. Japan* **23**: 361 (1982); as '*Codyceps*'.

Tolypocladium album (W. Gams) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808698

Basionym: *Chaunopycnis alba* W. Gams, *Persoonia* **11**: 75 (1979).

Tolypocladium capitatum (Holmsk. : Fr.) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808699

Basionym: *Clavaria capitata* Holmsk., *Beata Ruris Otia Fung. Dan.* **1**: 38 (1790).

Synonyms: *Sphaeria capitata* (Holmsk. : Fr.) Pers., *Comm. Fung. Clav.*: **13** (1797); Fr., *Syst. Mycol.* **2**: 324 (1822).

Cordyceps capitata (Holmsk.: Fr.) Link, *Handb. Erk. Gew.* **3**: 347 (1833).

Torrubia capitata (Holmsk. : Fr.) Tul. & C. Tul., *Sel. Fung. Carpol.* **3**: 22 (1865).

Elaphocordyceps capitata (Holmsk. : Fr.) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Sphaeria agariciformis Bolton, *Hist. Fung. Halifax*: 130 (1789).

Cordyceps agariciformis (Bolton) Seaver, *N. Amer. Fl.* **3**: 53 (1910).

Cordyceps canadensis Ellis & Everh., *Bull. Torrey Bot. Club* **25**: 501 (1898).

Cordyceps capitata var. *canadensis* (Ellis & Everh.) Lloyd, *Mycol. Writ.* **5**: 609 (1916).

Cordyceps nigriceps Peck, *Bull. Torrey Bot. Club* **27**: 21 (1900).

Tolypocladium delicatistipitatum (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808700

Basionym: *Cordyceps delicatistipitata* Kobayasi, *Bull. Natn. Sci. Mus., Tokyo* **5** (2, no. 47): 79 (1960); as '*delicatostipitata*'.

Synonym: *Elaphocordyceps delicatistipitata* (Kobayasi) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Tolypocladium fractum (Mains) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808701

Basionym: *Cordyceps fracta* Mains, *Bull. Torrey. Bot. Club* **84**: 250 (1957).

Synonym: *Elaphocordyceps fracta* (Mains) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Tolypocladium inegoense (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808702

Basionym: *Cordyceps inegoensis* Kobayasi, *Bull. Natn. Sci. Mus., Tokyo* **6**: 292 (1963)

Synonyms: *Elaphocordyceps inegoensis* (Kobayasi) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007); as '*inegoensis*'.

Tolypocladium intermedium (S. Imai) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808703

Basionym: *Cordyceps intermedia* S. Imai, *Proc. Imp. Acad. Japan* **10**: 677 (1934).

Synonyms: *Elaphocordyceps intermedia* (S. Imai) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Tolypocladium intermedium f. michinokuense (Kobayasi & Shimizu) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808704

Basionym: *Cordyceps intermedia* f. *michinokuensis* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus., Tokyo*, B **8**: 116 (1982).

Synonym: *Elaphocordyceps intermedia* f. *michinokuensis* (Kobayasi & Shimizu) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007); as '*michinokuensis*'.

Tolypocladium japonicum (Lloyd) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808705

Basionym: *Cordyceps japonica* Lloyd, *Mycol. Writ.* **6** (Letter 62): 913 (1920).

Synonyms: *Elaphocordyceps japonica* (Lloyd) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Cordyceps umemurae S. Imai, *Trans. Sapporo Nat. Hist. Soc.* **11**: 32 (1930) [1929]; as '*umemurai*'.

Tolypocladium jezoense (S. Imai) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808706

Basionym: *Cordyceps jezoensis* S. Imai, *Trans. Sapporo Nat. Hist. Soc.* **11**: 33 (1930) [1929].

Synonym: *Elaphocordyceps jezoensis* (S. Imai) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007); as '*jezoensis*'.

Tolypocladium longisegmentum (Ginns) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808856

Basionym: *Cordyceps longisegmentis* Ginns, *Mycologia* **80**: 219 (1988).

Synonym: *Elaphocordyceps longisegmentis* (Ginns) G.H. Sung et al., *Stud. Mycol.* **57**: 37 (2007).

Tolypocladium minazukiense (Kobayasi & Shimizu) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808857

Basionym: *Cordyceps minazukiensis* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus., Tokyo*, B 8: 117 (1982).

Synonym: *Elaphocordyceps minazukiensis* (Kobayasi & Shimizu) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (1982).

Tolypocladium miomoteanum (Kobayasi & Shimizu) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808858

Basionym: *Cordyceps miomoteana* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus., Tokyo*, B 8: 118 (1982).

Synonym: *Elaphocordyceps miomoteana* (Kobayasi & Shimizu) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (1982).

Tolypocladium ophioglossoides (Ehrh. ex J.F. Gmel.) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808859

Basionym: *Sphaeria ophioglossoides* Ehrh. ex J.F. Gmel., *Syst. Na.*, 13th edn 2: 1474 (1792).

Synonyms: *Sphaeria ophioglossoides* Ehrh., *Pl. Crypt. Exs.* fasc. 16 no. 160 (1789); nom. inval. (Art. 38.1).

Cordyceps ophioglossoides (Ehrh. ex G.F. Gmel.) Link, *Handb. Erk. Gew.* 3: 347 (1833) : Fr., *Syst. Mycol.* 2: 324 (1822).

Torrubia ophioglossoides (Ehrh. ex G.F. Gmel.) Tul. & C. Tul., *Sel. Fung. Carp.* 3: 20 (1865).

Elaphocordyceps ophioglossoides (Ehrh. ex G.F. Gmel.) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Clavaria parasitica Willd., *Fl. Berol. Prodr.*: 405 (1787).

Cordyceps parasitica (Willd.) Henn., *Nerthus* 6: 4 (1904).

Tolypocladium ophioglossoides f. album (Kobayasi & Shimizu ex Y.J. Yao) Quandt, Kepler & Spatafora, **comb. nov.**

MycoBank MB808860

Basionym: *Cordyceps ophioglossoides f. alba* Kobayasi & Shimizu ex Y.J. Yao, *Acta Mycol. Sin.* 14: 257 (1995).

Synonym: *Elaphocordyceps ophioglossoides f. alba* (Kobayasi & Shimizu ex Y.J. Yao) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Tolypocladium ophioglossoides f. cuboides (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808861

Basionym: *Cordyceps ophioglossoides f. cuboides* Kobayasi, *Bull. Natn. Sci. Mus., Tokyo* 5 (2, no. 47): 77 (1960).

Synonym: *Elaphocordyceps ophioglossoides f. cuboides* (Kobayasi) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Tolypocladium ovalisporum (C. Möller & W. Gams) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808862

Basionym: *Chaunopycnis ovalispora* C. Möller & W. Gams, *Mycotaxon* 48: 442 (1993).

Tolypocladium paradoxum (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808863

Basionym: *Cordyceps paradoxa* Kobayasi, *Bulletin of the Biogeogr. Soc. Jap.* 9: 156 (1939).

Synonym: *Elaphocordyceps paradoxa* (Kobayasi) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Tolypocladium pustulatum (Bills *et al.*) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808864

Basionym: *Chaunopycnis pustulata* Bills *et al.*, *Mycol. Progr.* 1: 8 (2002).

Tolypocladium ramosum (Teng) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808865

Basionym: *Cordyceps ramosa* Teng, *Sinensia* 7: 810 (1936).

Synonym: *Elaphocordyceps ramosa* (Teng) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Tolypocladium rouxii (Cand.) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808866

Basionym: *Cordyceps rouxii* Cand., *Mycotaxon* 4: 544 (1976).

Synonym: *Elaphocordyceps rouxii* (Cand.) G.H. Sung *et al.*, *Stud. Mycol.* 57: 37 (2007).

Tolypocladium szemaoense (M. Zang) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808867

Basionym: *Cordyceps szemaoensis* M. Zang, *Acta Bot. Yunn.* 23: 295 (2001).

Synonym: *Elaphocordyceps szemaoensis* (M. Zang) G.H. Sung *et al.*, *Stud. Mycol.* 57: 38 (2007); as 'szemaoënsis'.

Tolypocladium tenuisporum (Mains) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808868

Basionym: *Cordyceps tenuispora* Mains, *Bull. Torrey Bot. Club* 84: 247 (1957).

Synonym: *Elaphocordyceps tenuispora* (Mains) G.H. Sung *et al.*, *Stud. Mycol.* 57: 38 (2007).

Tolypocladium toriharamontanum (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808869

Basionym: *Cordyceps toriharamontana* Kobayasi, *Bull. Natn. Sci. Mus., Tokyo* 6: 305 (1963).

Synonym: *Elaphocordyceps toriharamontana* (Kobayasi) G.H. Sung *et al.*, *Stud. Mycol.* 57: 38 (2007).

Tolypocladium valliforme (Mains) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808870

Basionym: *Cordyceps valliformis* Mains, *Bull. Torrey Bot. Club* 84: 250 (1957).

Synonym: *Elaphocordyceps valliformis* (Mains) G.H. Sung *et al.*, *Stud. Mycol.* 57: 38 (2007).

Tolypocladium valvatistipitatum (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**

Mycobank MB808871

Basionym: Cordyceps valvatistipitata Kobayasi, *Bull. Natn. Sci. Mus., Tokyo* 5(2, no. 47): 81 (1960); as 'valvatostipitata'.*Synonym: Elaphocordyceps valvatistipitata* (Kobayasi) G.H. Sung et al., *Stud. Mycol.* 57: 38 (2007).**Tolypocladium virens** (Kobayasi) Quandt, Kepler & Spatafora, **comb. nov.**

Mycobank MB808872

Basionym: Cordyceps virens Kobayasi, *J. Jap. Bot.* 58: 222 (1983).*Synonym: Elaphocordyceps virens* (Kobayasi) G.H. Sung et al., *Stud. Mycol.* 57: 38 (2007).**Purpureocillium Luangsa-ard et al. 2011**

Our findings support those reported by Luangsa-ard et al. (2011b) for the *Purpureocillium* clade, and the change in Art. 59 allows for the inclusion of *N. atypicola* (syn. *Cordyceps cylindrica*) and *Isaria takamizusanensis* within this genus. Shared characters for this clade include purple-hued conidia and pathogenesis of arthropods, although *P. lilacinum* and *P. lavendulum* have been cultured from various substrates (Perdomo et al. 2013), and *P. lilacinum* can cause keratitis and other mycoses in humans and other vertebrates (Pastor & Guarro 2006, Rodríguez et al. 2010). Because this genus is well supported (MLBP=76) as sister to the nematode pathogen clade (Fig. 1), it is important to mention that *P. lilacinum* is frequently collected from nematodes (Luangsa-ard et al. 2011b), and has been used in the biocontrol of plant pathogenic nematodes (Kalele et al. 2006, Castillo et al. 2013).

Harposporium Lohde 1874 and Drechmeria W. Gams & H.-B. Jansson 1985

Our analyses reconstruct a well-supported (MLBP=76) monophyletic origin of the mostly nematophagous clade of *Ophiocordycipitaceae* (Fig. 1 Node 2). Within this clade, there is strong phylogenetic support for two clades: one containing *Harposporium* and *Podocrella*, and the other consisting of *Drechmeria*, *Haptocillium*, and *Cordyceps gunnii*. The relationship between *Harposporium* and *Podocrella* has already been described (Chaverri et al. 2005), but the revision of Art. 59 requires that one name be chosen for this genus. *Harposporium* is an older name, and the morphology of at least somewhat crescent-shaped conidia is a shared character for this clade. Suppression of *Podocrella* also requires the fewest taxonomic revisions (3 vs 30). For these reasons, we propose to protect *Harposporium* over *Podocrella* (Table 2).

Within the other nematophagous subclade, *Drechmeria* is an older name than *Haptocillium*, and the isolate included in these analyses is nested within the *Haptocillium* isolates sampled. For this reason, we propose to protect *Drechmeria* over *Haptocillium*. The inclusion of *C. gunnii* in this clade also provides a name for this residual taxon of *Cordyceps*. Most species however, are nematophagous (*C. gunnii* being the exception), and conidia may be cone-shaped, formed on conidiogenous cells in rosettes or verticils, or in the case

of *C. gunnii*, paecilomyces-like. We did not have access to molecular data from *D. harposporioides*, but given our finding that the two nematophagous clades in *Ophiocordycipitaceae* are monophyletic in origin, it will be interesting to see if this species, a protozoan pathogen with helical conidia, is truly a member of the *Drechmeria* clade or in fact a species within *Harposporium* that simply lacks the basally swollen conidiogenous cells.

Polycephalomyces Kobayasi 1941

This study is the first to have definitive ML support (MLBP=82) for the sister relationship between the *Polycephalomyces* clade and *Ophiocordycipitaceae* (Fig. 1 Node 1). Support for this relationship remains even with the exclusion of *C. pleuricapitata*, which is on an early-diverging, long branch within the clade. Two options remain to deal with this finding. Either a new family must be erected to account for this clade, or *Polycephalomyces* and related taxa must be moved into *Ophiocordycipitaceae*. We propose to accept *Polycephalomyces* and *C. pleuricapitata* in *Ophiocordycipitaceae*, where it will be the earliest diverging lineage of the family. The taxonomy of *C. pleuricapitata* will be addressed elsewhere.

CONCLUSIONS

We present a concise, thorough, phylogenetically relevant, and taxonomically accurate revision of the family *Ophiocordycipitaceae* with the aim of complying with the changes to Art. 59 of the ICN. With the criteria of naming monophyletic taxa, and where possible, of adhering to priority while avoiding changes that would be disruptive to the wider community of researchers, we have proposed to protect six genera within *Ophiocordycipitaceae*, including incorporation of the genus *Polycephalomyces* within the family. We have also formally revised the genus *Tolypocladium*, to reflect the nomenclature suggested by our results.

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Table 1. Specimen information and GenBank accession numbers for sequences used in this study.

Species	Voucher Information	SSU	LSU	TEF	RPB1	RPB2
<i>Chaunopycnis alba</i>	MRL GB5502		AF245297			
	MRL MF6799		AF373284			
<i>Chaunopycnis pustulata</i>	MRL GB6597		AF389190			
	MRL MF5368LR		AF373282			
<i>Cordyceps cylindrica</i>	CEM 1185	KJ878907	KJ878872	KJ878955		
<i>Cordyceps formosana</i>	TNM F13893	KJ878908		KJ878956	KJ878988	KJ878943
<i>Cordyceps gunnii</i>	OSC 76404	AF339572	AF339522	AY489616	AY489650	DQ522426
<i>Cordyceps irangiensis</i>	OSC 128579	EF469123	EF469076	EF469060	EF469089	EF469107
<i>Cordyceps nipponica</i>	BCC 18108	KF049608	KF049626	KF049681	KF049644	
<i>Cordyceps pleuricapitata</i>	NBRC 100745	KF049606	KF049624	KF049679	KF049642	KF049667
<i>Cordyceps pleuricapitata</i>	NBRC 100746	KF049607	KF049625	KF049680	KF049643	KF049668
<i>Cordyceps</i> sp.	EFCC 12075	KJ878909	KJ878873	KJ878957	KJ878989	
<i>Drechmeria coniospora</i>	CBS 596.92	AF106012				
<i>Elaphocordyceps capitata</i>	OSC 71233	AY489689	AY489721	AY489615	AY489649	DQ522421
<i>Elaphocordyceps fracta</i>	OSC 110990	DQ522545	DQ518759	DQ522328	DQ522373	DQ522425
<i>Elaphocordyceps japonica</i>	OSC 110991	DQ522547	DQ518761	DQ522330	DQ522375	DQ522428
<i>Elaphocordyceps longisegmentis</i>	OSC 110992		EF468816		EF468864	EF468919
<i>Elaphocordyceps ophioglossoides</i>	CBS 100239	KJ878910	KJ878874	KJ878958	KJ878990	KJ878944
	OSC 106405	AY489691	AY489723	AY489618	AY489652	DQ522429
<i>Elaphocordyceps subsessilis</i>	OSC 71235	EF469124	EF469077	EF469061	EF469090	EF469108
<i>Haptocillium balanoides</i>	CBS 250.82	AF339588	AF339539	DQ522342	DQ522388	DQ522442
<i>Haptocillium sinense</i>	CBS 567.95	AF339594	AF339545	DQ522343	DQ522389	DQ522443
<i>Haptocillium zeosporum</i>	CBS 335.8	AF339589	AF339540	EF469062	EF469091	EF469109
<i>Harposporium anguillulae</i>	ARSEF 5407		AY636080			
	ARSEF 5593		AY636081			
<i>Harposporium helicoides</i>	ARSEF 5354	AF339577	AF339527			
<i>Hirsutella crinalis</i>	TNS F18550	KJ878911	KJ878875	KJ878959		
<i>Hirsutella</i> sp.	OSC 128575	EF469126	EF469079	EF469064	EF469093	EF469110
<i>Hirsutella</i> sp.	NHJ 12525	EF469125	EF469078	EF469063	EF469092	EF469111
<i>Hymenostilbe aurantiaca</i>	OSC 128578	DQ522556	DQ518770	DQ522345	DQ522391	DQ522445
<i>Hymenostilbe muscaria</i>	OSC 151902	KJ878912	KJ878876		KJ878991	KJ878945
<i>Hymenostilbe odonatae</i>	TNS F18563		KJ878877		KJ878992	
	TNS F27117		KJ878878			
<i>Isaria takamizuensis</i>	NHJ 3582	EU369097	EU369034	EU369015		
<i>Isaria takamizusanensis</i>	NHJ 3497	EU369096	EU369033	EU369014	EU369053	EU369074
<i>Nomuraea atypicola</i>	RCEF 3833	KJ878913	KJ878879	KJ878960	KJ878993	
	OSC 151901	KJ878914	KJ878880	KJ878961	KJ878994	
	CBS 744.73	EF468987	EF468841	EF468786	EF468892	
<i>Ophiocordyceps acicularis</i>	OSC 110987	EF468950	EF468805	EF468744	EF468852	
	OSC 110988	EF468951	EF468804	EF468745	EF468853	
	OSC 128580	DQ522543	DQ518757	DQ522326	DQ522371	DQ522423
<i>Ophiocordyceps agriotidis</i>	ARSEF 5692	DQ522540	DQ518754	DQ522322	DQ522368	DQ522418
<i>Ophiocordyceps annulata</i>	CEM 303	KJ878915	KJ878881	KJ878962	KJ878995	
<i>Ophiocordyceps aphodii</i>	ARSEF 5498	DQ522541	DQ518755	DQ522323		DQ522419
<i>Ophiocordyceps brunneipunctata</i>	OSC 128576	DQ522542	DQ518756	DQ522324	DQ522369	DQ522420
<i>Ophiocordyceps clavata</i>	CEM 1762	KJ878916	KJ878882	KJ878963	KJ878996	
	CEM 1763		KJ878883	KJ878964	KJ878997	
	NBRC 106961	JN941727	JN941414		JN992461	
	NBRC 106962	JN941726	JN941415		JN992460	

Table 1. (Continued).

Species	Voucher Information	SSU	LSU	TEF	RPB1	RPB2
<i>Ophiocordyceps communis</i>	NHJ 12581	EF468973	EF468831	EF468775		EF468930
	NHJ 12582	EF468975	EF468830	EF468771		EF468926
<i>Ophiocordyceps curculionum</i>	OSC 151910	KJ878918	KJ878885		KJ878999	
<i>Ophiocordyceps dipterigena</i>	OSC 151911	KJ878919	KJ878886	KJ878966	KJ879000	
	OSC 151912	KJ878920	KJ878887	KJ878967	KJ879001	
<i>Ophiocordyceps elongata</i>	OSC 110989		EF468808	EF468748	EF468856	
<i>Ophiocordyceps entomorrhiza</i>	KEW 53484	EF468954	EF468809	EF468749	EF468857	EF468911
<i>Ophiocordyceps formicarum</i>	TNS F18565	KJ878921	KJ878888	KJ878968	KJ879002	KJ878946
<i>Ophiocordyceps forquignonii</i>	OSC 151908	KJ878922	KJ878889		KJ879003	KJ878947
<i>Ophiocordyceps gracilis</i>	EFCC 3101	EF468955	EF468810	EF468750	EF468858	EF468913
	EFCC 8572	EF468956	EF468811	EF468751	EF468859	EF468912
	OSC 151906	KJ878923	KJ878890	KJ878969		
<i>Ophiocordyceps heteropoda</i>	EFCC 10125	EF468957	EF468812	EF468752	EF468860	EF468914
	OSC 106404	AY489690	AY489722	AY489617	AY489651	
<i>Ophiocordyceps irangiensis</i>	OSC 128577	DQ522546	DQ518760	DQ522329	DQ522374	DQ522427
<i>Ophiocordyceps konnoana</i>	EFCC 7295	EF468958			EF468862	EF468915
<i>Ophiocordyceps konnoana</i>	EFCC 7315	EF468959		EF468753	EF468861	EF468916
<i>Ophiocordyceps lloydii</i>	OSC 151913	KJ878924	KJ878891	KJ878970	KJ879004	KJ878948
<i>Ophiocordyceps longissima</i>	EFCC 6814		EF468817	EF468757	EF468865	
	TNS F18448	KJ878925	KJ878892	KJ878971	KJ879005	
<i>Ophiocordyceps longissima</i>	HMAS_199600	KJ878926		KJ878972	KJ879006	KJ878949
<i>Ophiocordyceps melolonthae</i>	OSC 110993	DQ522548	DQ518762	DQ522331	DQ522376	
<i>Ophiocordyceps myrmecophila</i>	HMAS_199620	KJ878929	KJ878895	KJ878975	KJ879009	
	CEM 1710	KJ878927	KJ878893	KJ878973	KJ879007	
	TNS 27120	KJ878928	KJ878894	KJ878974	KJ879008	
	OSC 151903	KJ878930	KJ878896	KJ878976	KJ879010	
<i>Ophiocordyceps neovolkiana</i>	OSC 151903	KJ878930	KJ878896	KJ878976	KJ879010	
<i>Ophiocordyceps nigrella</i>	EFCC 9247	EF468963	EF468818	EF468758	EF468866	EF468920
<i>Ophiocordyceps nutans</i>	OSC 110994	DQ522549	DQ518763	DQ522333	DQ522378	
<i>Ophiocordyceps pruinosa</i>	NHJ 12994	EU369106	EU369041	EU369024	EU369063	EU369084
<i>Ophiocordyceps pulvinata</i>	TNS-F 30044	GU904208		GU904209	GU904210	
<i>Ophiocordyceps purpureostromata</i>	TNS F18430	KJ878931	KJ878897	KJ878977	KJ879011	
<i>Ophiocordyceps ravenelii</i>	OSC 110995	DQ522550	DQ518764	DQ522334	DQ522379	DQ522430
	OSC 151914	KJ878932		KJ878978	KJ879012	KJ878950
<i>Ophiocordyceps rhizoidea</i>	NHJ 12522	EF468970	EF468825	EF468764	EF468873	EF468923
	NHJ 12529	EF468969	EF468824	EF468765	EF468872	EF468922
<i>Ophiocordyceps ryogamiensis</i>	NBRC 101751	KF049614	KF049633	KF049688	KF049650	
<i>Ophiocordyceps sinensis</i>	EFCC 7287	EF468971	EF468827	EF468767	EF468874	EF468924
<i>Ophiocordyceps sobolifera</i>	KEW 78842	EF468972	EF468828		EF468875	EF468925
	TNS F18521	KJ878933	KJ878898	KJ878979	KJ879013	
<i>Ophiocordyceps</i> sp.	TNS F18495	KJ878937	KJ878901		KJ879017	
<i>Ophiocordyceps</i> sp.	OSC 110997	EF468976		EF468774	EF468879	EF468929
<i>Ophiocordyceps</i> sp.	OSC 151904	KJ878934	KJ878899	KJ878980	KJ879014	
<i>Ophiocordyceps</i> sp.	OSC 151905	KJ878935		KJ878981	KJ879015	KJ878951
<i>Ophiocordyceps</i> sp.	OSC 151909	KJ878936	KJ878900	KJ878982	KJ879016	KJ878952
<i>Ophiocordyceps sphecocephala</i>	OSC 110998	DQ522551	DQ518765	DQ522336	DQ522381	DQ522432
<i>Ophiocordyceps stylophora</i>	OSC 110999	EF468982	EF468837	EF468777	EF468882	EF468931
	OSC 111000	DQ522552	DQ518766	DQ522337	DQ522382	DQ522433
<i>Ophiocordyceps tricentri</i>	CEM 160	AB027330	AB027376			
<i>Ophiocordyceps unilateralis</i>	OSC 128574	DQ522554	DQ518768	DQ522339	DQ522385	DQ522436

Table 1. (Continued).

Species	Voucher Information	SSU	LSU	TEF	RPB1	RPB2
<i>Ophiocordyceps variabilis</i>	OSC 111003	EF468985	EF468839	EF468779	EF468885	EF468933
	ARSEF 5365	DQ522555	DQ518769	DQ522340	DQ522386	DQ522437
<i>Ophiocordyceps yakusimensis</i>	HMAS_199604	KJ878938	KJ878902		KJ879018	KJ878953
<i>Paecilomyces lilacinus</i>	ARSEF 2181	AF339583	AF339534	EF468790	EF468896	
	CBS 431.87	AY624188	EF468844	EF468791	EF468897	EF468940
	CBS 284.36	AY624189	AY624227	EF468792	EF468898	EF468941
<i>Podocrella harposporifera</i>	ARSEF 5472	AF339569	AF339519	DQ118747	DQ127238	
<i>Podonectria citrina</i>	TNS F18537		KJ878903	KJ878983		KJ878954
<i>Polycephalomyces cuboideus</i>	TNS F18487	KF049609	KF049628	KF049683		
<i>Polycephalomyces cuboideus</i>	NBRC 101740	KF049610	KF049629	KF049684	KF049646	
<i>Polycephalomyces formosus</i>	ARSEF 1424	KF049615	AY259544	DQ118754	DQ127245	KF049671
<i>Polycephalomyces nipponicus</i>	BCC 1881	KF049618	KF049636	KF049692		KF049674
	BCC 1682	KF049620	KF049638	KF049694		
	NHJ4286	KF049621	KF049639	KF049695	KF049654	KF049676
	BCC2325	KF049622	KF049640	KF049696	KF049655	KF049677
<i>Polycephalomyces paracuboideus</i>	NBRC 101742	KF049611	KF049630	KF049685	KF049647	KF049669
<i>Polycephalomyces prolificus</i>	TNS F18481	KF049612	KF049631	KF049686	KF049648	
	TNS F18547	KF0496613	KF049632	KF049687	KF049649	KF049670
<i>Polycephalomyces ramosopulvinatus</i>	SU-65		DQ118742	DQ118753	DQ127244	
	EFCC 5566		KF049627	KF049682	<i>KF049645</i>	
<i>Polycephalomyces</i> sp.	<i>JB07.08.16_08</i>	<i>KF049616</i>	<i>KF049635</i>	KF049690	<i>KF049652</i>	KF049672
<i>Polycephalomyces</i> sp.	<i>JB07.08.17_07b</i>	<i>KF049617</i>		KF049691	KF049653	KF049673
<i>Polycephalomyces</i> sp.	BBC 2637	KF049619	KF049637	KF049693		KF049675
<i>Polycephalomyces tomentosus</i>	BL4	KF049623	AY259545	KF049697	KF049656	KF049678
<i>Stilbella buquetii</i>	HMAS_199613	KJ878939	KJ878904	KJ878984	KJ879019	
	HMAS_199617	KJ878940	KJ878905	KJ878985	KJ879020	
<i>Tilachlidiopsis nigra</i>	TNS 16252	KJ878941	KJ878906	KJ878986		
	TNS 16250	KJ878942		KJ878987	KJ879021	
<i>Tolypocladium cylindrosporum</i>	NRRL 28025	AF049153	AF049173			

Table 2. Proposed list of generic names in *Ophiocordycipitaceae* to be protected and their competing synonyms. Names to be protected are in **bold** type, and names previously synonymized are in blue.

Proposed to protect	Proposed to suppress
<i>Ophiocordyceps</i> Petch, <i>Trans. Br. Mycol. Soc.</i> 16 : 74 (1931). Type: <i>O. blattae</i> Petch 1931.	<i>Sorospora</i> Sorokin <i>Zentbl. Bakt. ParasitKde.</i> , Abt. II 4 : 644 (1888). Type: <i>S. agrotidis</i> Sorokin 1888.
	<i>Hirsutella</i> Pat., <i>Revue Mycol.</i> 14 : 67 (1892). Type: <i>H. entomophila</i> Pat. 1892.
	<i>Didymobotryopsis</i> Henn., <i>Hedwigia</i> 41 : 149 (1902). Type: <i>D. parasitica</i> Henn. 1902.
	<i>Mahevia</i> Lagarde, <i>Archs Zool. Exp. Gen.</i> 56 : 292 (1917). Type: <i>M. guignardii</i> (Maheu) Lagarde 1917.
	<i>Synnematium</i> Speare, <i>Mycologia</i> 12 : 74 (1920). Type: <i>S. jonesii</i> Speare 1920.

Table 2. (Continued).

Proposed to protect	Proposed to suppress
	<i>Trichosterigma</i> Petch, <i>Trans. Br. Mycol. Soc.</i> 8 : 215 (1923). Type: <i>T. clavisporum</i> Petch 1923.
	<i>Didymobotrys</i> Clem. & Shear, <i>Gen. Fungi</i> : 228 (1931). Type: <i>D. parasitica</i> (Henn.) Clem. & Shear 1931.
	<i>Troglobiomyces</i> Pacioni, <i>Trans. Br. Mycol. Soc.</i> 74 : 244 (1980). Type: <i>T. guignardii</i> (Maheu) Pacioni 1980.
	<i>Hymenostilbe</i> Petch, <i>Naturalist (Hull)</i> , ser. 3, 1931 : 101 (1931). Type: <i>H. muscaria</i> Petch 1931.
	<i>Syngliocladium</i> Petch, <i>Trans. Br. Mycol. Soc.</i> 17 : 177 (1932). Type: <i>S. araneorum</i> Petch 1932.
	<i>Cordycepioideus</i> Stifler, <i>Mycologia</i> 33 : 83 (1941). Type: <i>C. bisporus</i> Stifler 1941.
	<i>Paraisaria</i> Samson & B.L. Brady, <i>Trans. Br. Mycol. Soc.</i> 81 : 285 (1983). Type: <i>P. dubia</i> (Delacr.) Samson & B.L. Brady 1983.
<i>Purpureocillium</i> Luangsa-ard et al., <i>FEMS Microbiol Lett</i> 321 : 144 (2011). Type: <i>P. lilacinum</i> (Thom) Luangsa-ard et al. 2011 (syn. <i>Penicillium lilacinum</i> Thom 1920).	
<i>Tolypocladium</i> W. Gams, <i>Persoonia</i> 6 : 185 (1971). Type: <i>T. inflatum</i> W. Gams 1971.	<i>Chaunopycnis</i> W. Gams, <i>Persoonia</i> 11 : 75 (1980). Type: <i>C. alba</i> W. Gams 1980. <i>Elaphocordyceps</i> G.H. Sung & Spatafora, <i>Stud. Mycol.</i> 57 : 36 (2007). Type: <i>E. ophioglossoides</i> (Ehrh. ex J.F. Gmel. : Fr.) G.H. Sung et al. 2007.
<i>Harposporium</i> Lohde, <i>Tagbl. Versamml. Ges. Deutsch. Naturf.</i> 47 : 206 (1874). Type: <i>H. anguillulae</i> Lohde 1874.	<i>Polyrhina</i> Sorokin, <i>Annlis Sci. Nat., Bot., sér 6, 4</i> : 65 (1876). Type: <i>P. multiformis</i> Sorokin 1876. <i>Podocrella</i> Seaver, <i>Mycologia</i> 20 : 57 (1928). Type: <i>P. poronioides</i> Seaver 1928. <i>Atricordyceps</i> Samuels, <i>N.Z. Jl. Bot.</i> 21 : 174 (1983). Type <i>A. harposporifera</i> Samuels 1983.
<i>Drechmeria</i> W. Gams & H.-B. Jansson, <i>Mycotaxon</i> 22 : 36 (1985). Type: <i>D. coniospora</i> (Drechsler) W. Gams & H.-B. Jansson 1985 (syn. <i>Meria coniospora</i> Drechsler 1941).	<i>Haptocillium</i> W. Gams & Zare, <i>Nova Hedwigia</i> 73 : 334 (2001). Type: <i>H. balanoides</i> (Drechsler) Zare & W. Gams 2001.
<i>Polycephalomyces</i> Kobayasi, <i>Sci. Rep. Tokyo Bunrika Daig., sect. B</i> 5 : 245 (1941). Type: <i>P. formosus</i> Kobayasi 1941.	<i>Blistum</i> B. Sutton, <i>Mycol. Pap.</i> 132 : 16 (1973). Type: <i>B. tomentosum</i> (Schrad.) B. Sutton 1973.