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# 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.

**Key words:**
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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, Leuchtmann *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 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 *Sorosporella*, 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 synnematous or mononematous on their arthropod hosts (Petch 1932, Hodge *et al.* 1998). *Sorosporella*, 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-1α (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 (Katoh *et al.* 2002, Katoh & 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 (Leuchtmann *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).

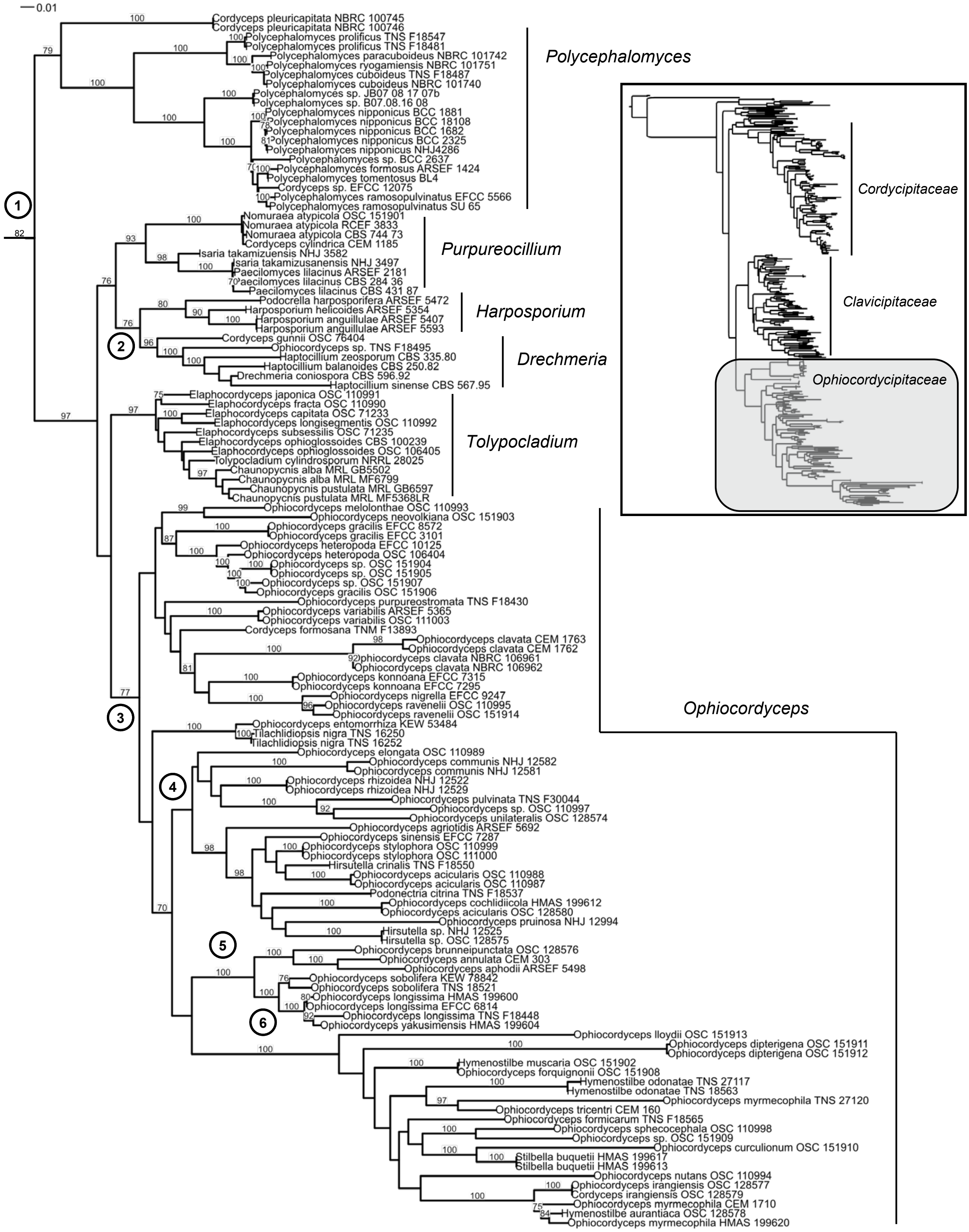

**Fig. 1.** ML tree of *Ophiocordycipitaceae* obtained using RAxML to analyze the concatenated five gene dataset (SSU, LSU, TEF, RPB1, and RPB2). Proposed genus level names to protect are delimited, but names of individual species have not been changed on the leaves of the tree, to demonstrate the diversity 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 *Sorosporella* is the oldest name for any members in this clade, there are only two described species, and Evans & Shah (2002) argued *Sorosporella* should be synonymized with *Synglioсladium* instead of being recognized as a an asexual morph, as *Synnematium* was previously treated with respect to *Hirsutella* (Evans & Samson 1982). We propose, therefore, to suppress the use of *Sorosporella* 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. cylindrosporum, 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 '*inegoënsis'*.

**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 '*michinokuënsis'*.

**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 '*jezoënsis'*.

**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 |
|---|---|---|---|---|---|---|
| *Chaunopycnis alba* | MRL GB5502 | | AF245297 | | | |
| | MRL MF6799 | | AF373284 | | | |
| *Chaunopycnis pustulata* | MRL GB6597 | | AF389190 | | | |
| | MRL MF5368LR | | AF373282 | | | |
| *Cordyceps cylindrica* | CEM 1185 | KJ878907 | KJ878872 | KJ878955 | | |
| *Cordyceps formosana* | TNM F13893 | KJ878908 | | KJ878956 | KJ878988 | KJ878943 |
| *Cordyceps gunnii* | OSC 76404 | AF339572 | AF339522 | AY489616 | AY489650 | DQ522426 |
| *Cordyceps irangiensis* | OSC 128579 | EF469123 | EF469076 | EF469060 | EF469089 | EF469107 |
| *Cordyceps nipponica* | BCC 18108 | KF049608 | KF049626 | KF049681 | KF049644 | |
| *Cordyceps pleuricapitata* | NBRC 100745 | KF049606 | KF049624 | KF049679 | KF049642 | KF049667 |
| *Cordyceps pleuricapitata* | NBRC 100746 | KF049607 | KF049625 | KF049680 | KF049643 | KF049668 |
| *Cordyceps* sp. | EFCC 12075 | KJ878909 | KJ878873 | KJ878957 | KJ878989 | |
| *Drechmeria coniospora* | CBS 596.92 | AF106012 | | | | |
| *Elaphocordyceps capitata* | OSC 71233 | AY489689 | AY489721 | AY489615 | AY489649 | DQ522421 |
| *Elaphocordyceps fracta* | OSC 110990 | DQ522545 | DQ518759 | DQ522328 | DQ522373 | DQ522425 |
| *Elaphocordyceps japonica* | OSC 110991 | DQ522547 | DQ518761 | DQ522330 | DQ522375 | DQ522428 |
| *Elaphocordyceps longisegmentis* | OSC 110992 | | EF468816 | | EF468864 | EF468919 |
| *Elaphocordyceps ophioglossoides* | CBS 100239 | KJ878910 | KJ878874 | KJ878958 | KJ878990 | KJ878944 |
| | OSC 106405 | AY489691 | AY489723 | AY489618 | AY489652 | DQ522429 |
| *Elaphocordyceps subsessilis* | OSC 71235 | EF469124 | EF469077 | EF469061 | EF469090 | EF469108 |
| *Haptocillium balanoides* | CBS 250.82 | AF339588 | AF339539 | DQ522342 | DQ522388 | DQ522442 |
| *Haptocillium sinense* | CBS 567.95 | AF339594 | AF339545 | DQ522343 | DQ522389 | DQ522443 |
| *Haptocillium zeosporum* | CBS 335.8 | AF339589 | AF339540 | EF469062 | EF469091 | EF469109 |
| *Harposporium anguillulae* | ARSEF 5407 | | AY636080 | | | |
| | ARSEF 5593 | | AY636081 | | | |
| *Harposporium helicoides* | ARSEF 5354 | AF339577 | AF339527 | | | |
| *Hirsutella crinalis* | TNS F18550 | KJ878911 | KJ878875 | KJ878959 | | |
| *Hirsutella* sp. | OSC 128575 | EF469126 | EF469079 | EF469064 | EF469093 | EF469110 |
| *Hirsutella* sp. | NHJ 12525 | EF469125 | EF469078 | EF469063 | EF469092 | EF469111 |
| *Hymenostilbe aurantiaca* | OSC 128578 | DQ522556 | DQ518770 | DQ522345 | DQ522391 | DQ522445 |
| *Hymenostilbe muscaria* | OSC 151902 | KJ878912 | KJ878876 | | KJ878991 | KJ878945 |
| *Hymenostilbe odonatae* | TNS F18563 | | KJ878877 | | KJ878992 | |
| | TNS F27117 | | KJ878878 | | | |
| *Isaria takamizuensis* | NHJ 3582 | EU369097 | EU369034 | EU369015 | | |
| *Isaria takamizusanensis* | NHJ 3497 | EU369096 | EU369033 | EU369014 | EU369053 | EU369074 |
| *Nomuraea atypicola* | RCEF 3833 | KJ878913 | KJ878879 | KJ878960 | KJ878993 | |
| | OSC 151901 | KJ878914 | KJ878880 | KJ878961 | KJ878994 | |
| | CBS 744.73 | EF468987 | EF468841 | EF468786 | EF468892 | |
| *Ophiocordyceps acicularis* | OSC 110987 | EF468950 | EF468805 | EF468744 | EF468852 | |
| | OSC 110988 | EF468951 | EF468804 | EF468745 | EF468853 | |
| | OSC 128580 | DQ522543 | DQ518757 | DQ522326 | DQ522371 | DQ522423 |
| *Ophiocordyceps agriotidis* | ARSEF 5692 | DQ522540 | DQ518754 | DQ522322 | DQ522368 | DQ522418 |
| *Ophiocordyceps annulata* | CEM 303 | KJ878915 | KJ878881 | KJ878962 | KJ878995 | |
| *Ophiocordyceps aphodii* | ARSEF 5498 | DQ522541 | DQ518755 | DQ522323 | | DQ522419 |
| *Ophiocordyceps brunneipunctata* | OSC 128576 | DQ522542 | DQ518756 | DQ522324 | DQ522369 | DQ522420 |
| *Ophiocordyceps clavata* | 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 |
|---|---|---|---|---|---|---|
| *Ophiocordyceps communis* | NHJ 12581 | EF468973 | EF468831 | EF468775 | | EF468930 |
| | NHJ 12582 | EF468975 | EF468830 | EF468771 | | EF468926 |
| *Ophiocordyceps curculionum* | OSC 151910 | KJ878918 | KJ878885 | | KJ878999 | |
| *Ophiocordyceps dipterigena* | OSC 151911 | KJ878919 | KJ878886 | KJ878966 | KJ879000 | |
| | OSC 151912 | KJ878920 | KJ878887 | KJ878967 | KJ879001 | |
| *Ophiocordyceps elongata* | OSC 110989 | | EF468808 | EF468748 | EF468856 | |
| *Ophiocordyceps entomorrhiza* | KEW 53484 | EF468954 | EF468809 | EF468749 | EF468857 | EF468911 |
| *Ophiocordyceps formicarum* | TNS F18565 | KJ878921 | KJ878888 | KJ878968 | KJ879002 | KJ878946 |
| *Ophiocordyceps forquignonii* | OSC 151908 | KJ878922 | KJ878889 | | KJ879003 | KJ878947 |
| *Ophiocordyceps gracilis* | EFCC 3101 | EF468955 | EF468810 | EF468750 | EF468858 | EF468913 |
| | EFCC 8572 | EF468956 | EF468811 | EF468751 | EF468859 | EF468912 |
| | OSC 151906 | KJ878923 | KJ878890 | KJ878969 | | |
| *Ophiocordyceps heteropoda* | EFCC 10125 | EF468957 | EF468812 | EF468752 | EF468860 | EF468914 |
| | OSC 106404 | AY489690 | AY489722 | AY489617 | AY489651 | |
| *Ophiocordyceps irangiensis* | OSC 128577 | DQ522546 | DQ518760 | DQ522329 | DQ522374 | DQ522427 |
| *Ophiocordyceps konnoana* | EFCC 7295 | EF468958 | | | EF468862 | EF468915 |
| *Ophiocordyceps konnoana* | EFCC 7315 | EF468959 | | EF468753 | EF468861 | EF468916 |
| *Ophiocordyceps lloydii* | OSC 151913 | KJ878924 | KJ878891 | KJ878970 | KJ879004 | KJ878948 |
| *Ophiocordyceps longissima* | EFCC 6814 | | EF468817 | EF468757 | EF468865 | |
| | TNS F18448 | KJ878925 | KJ878892 | KJ878971 | KJ879005 | |
| *Ophiocordyceps longissima* | HMAS_199600 | KJ878926 | | KJ878972 | KJ879006 | KJ878949 |
| *Ophiocordyceps melolonthae* | OSC 110993 | DQ522548 | DQ518762 | DQ522331 | DQ522376 | |
| *Ophiocordyceps myrmecophila* | HMAS_199620 | KJ878929 | KJ878895 | KJ878975 | KJ879009 | |
| | CEM 1710 | KJ878927 | KJ878893 | KJ878973 | KJ879007 | |
| | TNS 27120 | KJ878928 | KJ878894 | KJ878974 | KJ879008 | |
| *Ophiocordyceps neovolkiana* | OSC 151903 | KJ878930 | KJ878896 | KJ878976 | KJ879010 | |
| *Ophiocordyceps nigrella* | EFCC 9247 | EF468963 | EF468818 | EF468758 | EF468866 | EF468920 |
| *Ophiocordyceps nutans* | OSC 110994 | DQ522549 | DQ518763 | DQ522333 | DQ522378 | |
| *Ophiocordyceps pruinosa* | NHJ 12994 | EU369106 | EU369041 | EU369024 | EU369063 | EU369084 |
| *Ophiocordyceps pulvinata* | TNS-F 30044 | GU904208 | | GU904209 | GU904210 | |
| *Ophiocordyceps purpureostromata* | TNS F18430 | KJ878931 | KJ878897 | KJ878977 | KJ879011 | |
| *Ophiocordyceps ravenelii* | OSC 110995 | DQ522550 | DQ518764 | DQ522334 | DQ522379 | DQ522430 |
| | OSC 151914 | KJ878932 | | KJ878978 | KJ879012 | KJ878950 |
| *Ophiocordyceps rhizoidea* | NHJ 12522 | EF468970 | EF468825 | EF468764 | EF468873 | EF468923 |
| | NHJ 12529 | EF468969 | EF468824 | EF468765 | EF468872 | EF468922 |
| *Ophiocordyceps ryogamiensis* | NBRC 101751 | KF049614 | KF049633 | KF049688 | KF049650 | |
| *Ophiocordyceps sinensis* | EFCC 7287 | EF468971 | EF468827 | EF468767 | EF468874 | EF468924 |
| *Ophiocordyceps sobolifera* | KEW 78842 | EF468972 | EF468828 | | EF468875 | EF468925 |
| | TNS F18521 | KJ878933 | KJ878898 | KJ878979 | KJ879013 | |
| *Ophiocordyceps* sp. | TNS F18495 | KJ878937 | KJ878901 | | KJ879017 | |
| *Ophiocordyceps* sp. | OSC 110997 | EF468976 | | EF468774 | EF468879 | EF468929 |
| *Ophiocordyceps* sp. | OSC 151904 | KJ878934 | KJ878899 | KJ878980 | KJ879014 | |
| *Ophiocordyceps* sp. | OSC 151905 | KJ878935 | | KJ878981 | KJ879015 | KJ878951 |
| *Ophiocordyceps* sp. | OSC 151909 | KJ878936 | KJ878900 | KJ878982 | KJ879016 | KJ878952 |
| *Ophiocordyceps sphecocephala* | OSC 110998 | DQ522551 | DQ518765 | DQ522336 | DQ522381 | DQ522432 |
| *Ophiocordyceps stylophora* | OSC 110999 | EF468982 | EF468837 | EF468777 | EF468882 | EF468931 |
| | OSC 111000 | DQ522552 | DQ518766 | DQ522337 | DQ522382 | DQ522433 |
| *Ophiocordyceps tricentri* | CEM 160 | AB027330 | AB027376 | | | |
| *Ophiocordyceps unilateralis* | OSC 128574 | DQ522554 | DQ518768 | DQ522339 | DQ522385 | DQ522436 |

**Table 1.** (Continued).

| Species | Voucher Information | SSU | LSU | TEF | RPB1 | RPB2 |
|---|---|---|---|---|---|---|
| *Ophiocordyceps variabilis* | OSC 111003 | EF468985 | EF468839 | EF468779 | EF468885 | EF468933 |
| | ARSEF 5365 | DQ522555 | DQ518769 | DQ522340 | DQ522386 | DQ522437 |
| *Ophiocordyceps yakusimensis* | HMAS_199604 | KJ878938 | KJ878902 | | KJ879018 | KJ878953 |
| *Paecilomyces lilacinus* | ARSEF 2181 | AF339583 | AF339534 | EF468790 | EF468896 | |
| | CBS 431.87 | AY624188 | EF468844 | EF468791 | EF468897 | EF468940 |
| | CBS 284.36 | AY624189 | AY624227 | EF468792 | EF468898 | EF468941 |
| *Podocrella harposporifera* | ARSEF 5472 | AF339569 | AF339519 | DQ118747 | DQ127238 | |
| *Podonectria citrina* | TNS F18537 | | KJ878903 | KJ878983 | | KJ878954 |
| *Polycephalomyces cuboideus* | TNS F18487 | KF049609 | KF049628 | KF049683 | | |
| *Polycephalomyces cuboideus* | NBRC 101740 | KF049610 | KF049629 | KF049684 | KF049646 | |
| *Polycephalomyces formosus* | ARSEF 1424 | KF049615 | AY259544 | DQ118754 | DQ127245 | KF049671 |
| *Polycephalomyces nipponicus* | BCC 1881 | KF049618 | KF049636 | KF049692 | | KF049674 |
| | BCC 1682 | KF049620 | KF049638 | KF049694 | | |
| | NHJ4286 | KF049621 | KF049639 | KF049695 | KF049654 | KF049676 |
| | BCC2325 | KF049622 | KF049640 | KF049696 | KF049655 | KF049677 |
| *Polycephalomyces paracuboideus* | NBRC 101742 | KF049611 | KF049630 | KF049685 | KF049647 | KF049669 |
| *Polycephalomyces prolificus* | TNS F18481 | KF049612 | KF049631 | KF049686 | KF049648 | |
| | TNS F18547 | KF0496613 | KF049632 | KF049687 | KF049649 | KF049670 |
| *Polycephalomyces ramosopulvinatus* | SU-65 | | DQ118742 | DQ118753 | DQ127244 | |
| | EFCC 5566 | | KF049627 | KF049682 | *KF049645* | |
| *Polycephalomyces* sp. | *JB07.08.16_08* | *KF049616* | *KF049635* | KF049690 | *KF049652* | KF049672 |
| *Polycephalomyces sp.* | JB07.08.17_07b | *KF049617* | | KF049691 | KF049653 | KF049673 |
| *Polycephalomyces sp.* | BBC 2637 | KF049619 | KF049637 | KF049693 | | KF049675 |
| *Polycephalomyces tomentosus* | BL4 | KF049623 | AY259545 | KF049697 | KF049656 | KF049678 |
| *Stilbella buquetii* | HMAS_199613 | KJ878939 | KJ878904 | KJ878984 | KJ879019 | |
| | HMAS_199617 | KJ878940 | KJ878905 | KJ878985 | KJ879020 | |
| *Tilachlidiopsis nigra* | TNS 16252 | KJ878941 | KJ878906 | KJ878986 | | |
| | TNS 16250 | KJ878942 | | KJ878987 | KJ879021 | |
| *Tolypocladium cylindrosporum* | 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 |
|---|---|
| ***Ophiocordyceps*** Petch, *Trans. Br. Mycol. Soc.* **16**: 74 (1931).<br>*Type*: *O. blattae* Petch 1931. | *Sorosporella* Sorokin *Zentbl. Bakt. ParasitKde.*, Abt. II **4**: 644 (1888).<br>*Type*: *S. agrotidis* Sorokin 1888. |
| | *Hirsutella* Pat., *Revue Mycol.* **14**: 67 (1892).<br>*Type*: *H. entomophila* Pat. 1892. |
| | *Didymobotryopsis* Henn., *Hedwigia* **41**: 149 (1902).<br>*Type*: *D. parasitica* Henn. 1902. |
| | *Mahevia* Lagarde, *Archs Zool. Exp. Gen.* **56**: 292 (1917).<br>*Type*: *M. guignardii* (Maheu) Lagarde 1917. |
| | *Synnematium* Speare, *Mycologia* **12**: 74 (1920).<br>*Type*: *S. jonesii* Speare 1920. |

**Table 2.** (Continued).

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