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: arthropod-pathogens Article 59 new combinations nomenclature Ophiocordycipitaceae Tolypocladium

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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 offungus (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 Cordycyceps 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 Cordycyceps, but Sung et al. (2007) restored Ophiocordyceps to the rank of genus to include those Cordycyceps 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 Sorosporrella, the oldest name still in use for species in the clade, Hirustella, Hymenostilbe, Stilbella, Syngiocladium, and Paraisaria. Hirustella 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. sphecocosphala 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. Syngiocladium spp. often have laterally arising conidiophores similar in morphology to the hypocreacean asexual morph Gliocladium, and they may be either synnematous or mononematous on their arthropod hosts (Petch 1932, Hodge et al. 1998). Sorosporrella, a chlamydospore producing spore state, has been linked as a synasexual morph of Syngiocladium (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 Cordycyceps species to be described. Species in Elaphocordyceps are mostly parasites of the ectomycorrhizal truffle genus Elaphomyces (Ascomycota, Eurotales). 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 (Surva 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 conidigenous 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. atypica 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 atypica 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 Harposporum. One protozoan-infecting species of Drechmeria, D. harposporioide, produces crescent-shaped conidia similar to those of Harposporum (Barron & Szijarto 1982). Haptocilium 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 Ophiocordypitaceae, or if it was more closely related to Clavicipitaceae. Many morphological characters are shared between Ophiocordypitaceae 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 sporulating structures of Polycephalomyces often possess a wavy, tough, carbonaceous stipe which is a common morphology of Ophiocordypitaceae (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 Ophiocordypitaceae 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 *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 *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*, *Polycyphalomyces*, *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 (Shreshta *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 *Polycyphalomyces*, 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, *Elaphocordycopsis* and *Chaunopsycnis*. 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 *Elaphocordycopsis* species has been known for several years (Hodge *et al.* 1996), although where known most *Elaphocordycopsis* 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 *Elaphocordycopsis* (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 *Chaunopsycnis* 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 *Chaunopsycnis* 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 monophasic 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**: *Chaunopsycnis* W. Gams, *Persoonia* 11: 75 (1980).

*Elaphocordycopsis* 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.) TuU. & C. TuU., *Sel. Fung.* *Carpos.* 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 ‘*delicatistipitata*’.

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)

Synonym: *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 janicicum** (Lloyd) Quandt, Kepler & Spatafora, *comb. nov.*

*MycoBank* MB808705

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

Synonyms: *Elaphocordyceps janicica* (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).
**Ophiocordycipitaceae**

**Tolypocladium minazukiense** (Kobayasi & Shimizu) Quandt, Kepler & Spatafora, **comb. nov.**
MycoBank MB808857
Basionym: Cordyceps minazukiensis Kobayasi & Shimizu, Bull. Natn. Sci. Mus., Tokyo 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 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 paradoxo (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 rouxi 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 ‘szemaoëniss’.

**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).
**Toxopcalcadium 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 ‘valvatistipitata’.

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

**Toxopcalcadium 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. atypica* (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*, *Haptocillum*, 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 *Haptocillum*, and the isolate included in these analyses is nested within the *Haptocillum* isolates sampled. For this reason, we propose to protect *Drechmeria* over *Haptocillum*. 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. harpophoroides*, 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.

**Polycyphalomyces Kobayasi 1941**

This study is the first to have definitive ML support (MLBP=82) for the sister relationship between the *Polycyphalomyces* 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 *Polycyphalomyces* and related taxa must be moved into *Ophiocordycipitaceae*. We propose to accept *Polycyphalomyces* 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 *Polycyphalomyces* within the family. We have also formally revised the genus *Toxopcalcadium*, to reflect the nomenclature suggested by our results.

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| 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|
| Cordyceps gunnii              | OSC 76404           | AF339522|
|                               |                     | KJ878872|
| Cordyceps irangiensis        | OSC 128579          | EF469123|
|                               |                     | EF469076|
|                               |                     | EF469060|
|                               |                     | EF469089|
|                               |                     | EF469107|
| Cordyceps nipponica           | BCC 18108           | KF049626|
|                               |                     | KF049661|
| Cordyceps pleuricapitata      | NBRC 100745         | KF049606|
|                               |                     | KF049624|
| Cordyceps pleuricapitata      | NBRC 100746         | KF049607|
|                               |                     | KF049625|
| Cordyceps sp.                 | EFCC 12075          | KJ878909|
|                               |                     | KJ878873|
|                               |                     | KJ878957|
|                               |                     | KJ878989|
| Drechmeria coniospora         | CBS 596.92          | AF106012|
| Elaphocordyceps capitata      | OSC 71233           | AY489689|
|                               |                     | AY489721|
| Elaphocordyceps fracta        | OSC 110990          | DQ522545|
|                               |                     | DQ518759|
| Elaphocordyceps japonica      | OSC 110991          | DQ522547|
|                               |                     | DQ518761|
| Elaphocordyceps longisegments| OSC 110992          | EF468816|
| Elaphocordyceps ophioglossoides| CBS 10239       | KJ878910|
|                               |                     | KJ878874|
|                               |                     | KJ878958|
|                               |                     | KJ878990|
|                               |                     | KJ878944|
| Elaphocordyceps subsessilis   | OSC 71235           | EF469124|
|                               |                     | EF469077|
| Haptocladium balanoides       | CBS 250.82          | AF339588|
|                               |                     | AF339539|
| Haptocladium sinense          | CBS 567.95          | AF339594|
|                               |                     | AF339545|
| Haptocladium zeasporum        | CBS 335.8           | AF339589|
|                               |                     | AF339540|
| Harposporium anguillae        | ARSEF 5407          | KJ878977|
|                               |                     | KJ878991|
|                               |                     | KJ878945|
| Harposporium helicoides       | ARSEF 5354          | AF339577|
|                               |                     | AF339527|
| Hirsutella crinalis           | TNS F18550          | KJ878911|
|                               |                     | KJ878875|
|                               |                     | KJ878959|
| Hirsutella sp.                | OSC 128575          | EF469126|
|                               |                     | EF469079|
| Hirsutella sp.                | NHJ 12525           | EF469125|
|                               |                     | EF469078|
| Hymenostilbe aurantiaca      | OSC 128578          | DQ522556|
|                               |                     | DQ518770|
| Hymenostilbe muscaria         | OSC 151902          | KJ878912|
|                               |                     | KJ878786|
|                               |                     | KJ878991|
| Hymenostilbe odonatae        | TNS F18563          | KJ878877|
|                               |                     | KJ878992|
| Isaria takamizuensis          | NHJ 3582            | EU369097|
|                               |                     | EU369034|
| Isaria takamizusanensis       | NHJ 3497            | EU369096|
|                               |                     | EU369033|
| Nomuraea atypica              | RCEF 3833           | KJ878913|
|                               |                     | KJ878879|
|                               |                     | KJ878960|
|                               |                     | KJ878993|
| Ophiocordyceps acicularis     | OSC 110987          | EF468950|
|                               |                     | EF468805|
|                               |                     | EF468744|
|                               |                     | EF468852|
| Ophiocordyceps agriotidis     | OSC 128580          | DQ522543|
|                               |                     | DQ518757|
| Ophiocordyceps annulata       | CEM 303             | KJ878915|
|                               |                     | KJ878881|
| Ophiocordyceps aphidii        | ARSEF 5498          | DQ522541|
|                               |                     | DQ518755|
| Ophiocordyceps brunneipunctata| OSC 128576         | DQ522542|
|                               |                     | DQ518756|
| Ophiocordyceps clavata       | CEM 1762            | KJ878916|
|                               |                     | KJ878882|
|                               |                     | KJ878963|
|                               |                     | KJ878996|
|                               |                     | KJ878964|
|                               |                     | KJ878997|
|                               |                       | NBRC 106961  | JN941727  | JN941414  | JN992461  |
|                               |                       | NBRC 106962  | JN941726  | JN941415  | JN992460  |
| Species                        | Voucher Information | SSU     | LSU     | TEF     | RPB1   | RPB2   |
|-------------------------------|---------------------|---------|---------|---------|--------|--------|
| Ophiocordyceps communis       | NHU 12581           | EF468973| EF468831| EF468775|        |        |
|                               | NHU 12582           | EF468975| EF468830| EF468771|        |        |
| Ophiocordyceps curculonum     | OSC 151910          | KJ878918| KJ878885|         | KJ878999|        |
| Ophiocordyceps dipterigena    | OSC 151911          | KJ878919| KJ878886| KJ878966| KJ879000|        |
| Ophiocordyceps elongata       | OSC 110989          | EF468808| EF468748| EF468856|        |        |
| Ophiocordyceps entomorrhiza   | KEW 53484           | EF468954| EF468809| EF468749| EF468857|        |
| Ophiocordyceps formicarum     | TNS F18565          | KJ878921| KJ878888| KJ878968| KJ879002| KJ87946|
| Ophiocordyceps forquignonii   | OSC 151908          | KJ878922| KJ878889| KJ879003| KJ87947|        |
| Ophiocordyceps gracilis       | EFCC 8572           | EF468956| EF468811| EF468751| EF468859|        |
|                               | OSC 151906          | KJ878923| KJ878890| KJ878969|        |        |
| Ophiocordyceps heteropoda     | EFCC 10125          | EF468957| EF468812| EF468752| EF468860|        |
| Ophiocordyceps irangiensis    | OSC 128577          | DQ522546| DQ518760| DQ523239| DQ522374| DQ52247|
| Ophiocordyceps konnoana       | EFCC 7295           | EF468958|        |         |        |        |
| Ophiocordyceps konnoana       | EFCC 7315           | EF468959|        |         |        |        |
| Ophiocordyceps lloydii        | OSC 151913          | KJ878924| KJ878891| KJ878970| KJ879004| KJ87948|
| 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| DQ523331| DQ522376|        |
| Ophiocordyceps myrmecophila   | HMAS_199620         | KJ878929| KJ878895| KJ878975| KJ879009|        |
| Ophiocordyceps myrmecophila   | CEM 1710            | KJ878927| KJ878893| KJ878973| KJ879007|        |
| Ophiocordyceps neovolkiana    | OSC 151903          | KJ878930| KJ878896| KJ878976| KJ879010|        |
| Ophiocordyceps nigrella       | EFCC 9247           | EF468963| EF468818| EF468758| EF468866| EF468920|
| Ophiocordyceps nutans         | OSC 110994          | DQ522549| DQ518763| DQ523331| DQ522376|        |
| Ophiocordyceps pruinosa       | NHU 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| DQ523334| DQ522379| DQ522430|
| Ophiocordyceps rhizoidea      | NHU 12522           | EF468970| EF468825| EF468764| EF468873| EF468923|
| Ophiocordyceps ryogamiensis   | NBRG 110751         | KF049614| KF049633| KF049688| KF049650|        |
| Ophiocordyceps sinensis       | EFCC 7287           | EF468971| EF468827| EF468767| EF468874| EF468924|
| Ophiocordyceps sobolifera     | KEW 78842           | EF468972| EF468828| EF468875| EF468925|        |
| Ophiocordyceps sp.            | TNS F18521          | KJ878933| KJ878988| KJ878979| KJ879013|        |
| Ophiocordyceps sp.            | TNS F18495          | KJ878937| KJ878901| KJ879017|        |        |
| Ophiocordyceps sp.            | OSC 110997          | EF468976|         |         | EF468774| EF468879|
| Ophiocordyceps sp.            | OSC 151904          | KJ878934| KJ878999| KJ878960| KJ879014|        |
| Ophiocordyceps sp.            | OSC 151905          | KJ878935| KJ878981| KJ879015| KJ878951|        |
| Ophiocordyceps sp.            | OSC 151909          | KJ878936| KJ878900| KJ878982| KJ879016| KJ878952|
| Ophiocordyceps sp.            | OSC 110998          | DQ522551| DQ518765| DQ522336| DQ522381| DQ522432|
| Ophiocordyceps sp.            | OSC 110999          | EF468892| EF468837| EF468777| EF468882| EF468931|
| Ophiocordyceps sp.            | OSC 111000          | DQ522552| DQ518766| DQ522337| DQ522382| DQ522432|
| Ophiocordyceps sp.            | CEM 160             | AB027330| AB027376|        |        |        |
| Ophiocordyceps unilateralis    | OSC 128574          | DQ522554| DQ518768| DQ522339| DQ522385| DQ522436|
Table 1. (Continued).

| Species                          | Voucher Information | SSU          | LSU          | TEF          | RPB1        | RPB2        |
|----------------------------------|---------------------|--------------|--------------|--------------|-------------|-------------|
| *Ophiocordyces variabilis*       | OSC 111003          | EF468985     | EF468839     | EF468779     | EF468885    | EF468933    |
|                                  | ARSEF 5365          | DQ522555     | DQ518769     | DQ522340     | DQ522386    | DQ522437    |
| *Ophiocordyces yaksimensis*      | HMAS_199604         | KJ878938     | KJ878902     | KJ879018     | KJ879553    |             |
| *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     | DJ118747     | DJ127238    |             |
| *Podonectria citrina*            | TNS F18537          | KJ878903     | KJ878983     | KJ87954      |             |             |
| *Polycephalomyces cuboideus*     | TNS F18487          | KF049609     | KF049628     | KF049683     |             |             |
| *Polycephalomyces cuboideus*     | ARSEF 101740        | KF049610     | KF049629     | KF049684     | KF049646    |             |
| *Polycephalomyces formosus*      | BCC 1881            | KF049615     | AY259544     | DJ118754     | DJ127245    | KF049671    |
|                                  | BCC 1682            | KF049620     | KF049638     | KF049694     |             |             |
|                                  | NHJ4286             | KF049621     | KF049639     | KF049695     | KF049654    | KF049676    |
|                                  | BCC2325             | KF049622     | KF049640     | KF049696     | KF049655    | KF049677    |
|                                  |                    |              |              |              |             |             |
| *Polycephalomyces paracuboideus* | ARSEF 101742        | KF049611     | KF049630     | KF049685     | KF049647    | KF049669    |
| *Polycephalomyces prolificus*    | TNS F18481          | KF049612     | KF049631     | KF049686     | KF049648    |             |
|                                  | TNS F18547          | KF049613     | 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    |
|                                  | 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     | KJ879019     |             |             |
|                                  | HMAS_199617         | KJ878940     | KJ878905     | KJ878985     | KJ879020    |             |
|                                  | 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 |
|---------------------|----------------------|
| *Ophiocordyces* Petch, *Trans. Br. Mycol. Soc.* **16**: 74 (1931). Type: *O. blattae* Petch 1931. | *Sorosporella* Sorokin *Zentbl. Bakt. ParasitKde.*, Abt. II **4**: 644 (1888). Type: *S. agrotidis* Sorokin 1888. |
|                       | *Hirsutella* Pat., *Revue Mycol.* **14**: 67 (1892). Type: *H. entomophila* Pat. 1892. |
|                       | *Didymobotryopsis* Henn., *Hedwigia* **41**: 149 (1902). Type: *D. parasitica* Henn. 1902. |
|                       | *Mahevia* Lagarde, *Archs Zool. Exp. Gen.* **56**: 292 (1917). Type: *M. guignardii* (Maheu) Lagarde 1917. |
|                       | *Synnematium* Speare, *Mycologia* **12**: 74 (1920). Type: *S. jonesii* Speare 1920. |
Table 2. (Continued).

| Proposed to protect | Proposed to suppress |
|---------------------|----------------------|
| **Trichosterigma** Petch, *Trans. Br. Mycol. Soc.* **8**: 215 (1923). |
| **Type**: *T. clavisporum* Petch 1923. |
| **Didymobrytys** Clem. & Shear, *Gen. Fungi* **228** (1931). |
| **Type**: *D. parasitica* (Henn.) Clem. & Shear 1931. |
| **Troglobiomyces** Pacioni, *Trans. Br. Mycol. Soc.* **74**: 244 (1980). |
| **Type**: *T. guignardii* (Maheu) Pacioni 1980. |
| **Hymenostilbe** Petch, *Naturalist (Hull)*, ser. **3**, **101** (1931). |
| **Type**: *H. muscaria* Petch 1931. |
| **Syngliocladium** Petch, *Trans. Br. Mycol. Soc.* **17**: 177 (1932). |
| **Type**: *S. aranearum* Petch 1932. |
| **Cordycepioideus** Stifler, *Mycologia* **33**: 83 (1941). |
| **Type**: *C. bisporus* Stifler 1941. |
| **Paraisaria** Samson & B.L. Brady, *Trans. Br. Mycol. Soc.* **81**: 285 (1983). |
| **Type**: *P. dubia* (Delacr.) Samson & B.L. Brady 1983. |

**Purpureocillium** Luangsa-ard et al., *FEMS Microbiol Lett* **321**: 144 (2011).
*Type*: *P. lilacinum* (Thom) Luangsa-ard et al. 2011 (syn. *Penicillium lilacinum* Thom 1920).

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

**Chaunopycnis** W. Gams, *Persoonia* **11**: 75 (1980).
*Type*: *C. alba* W. Gams 1980.

**Elaphocordyceps** G.H. Sung & Spatafora, *Stud. Mycol.* **57**: 36 (2007).
*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).
*Type*: *H. anguillulae* Lohde 1874.

**Polyrhina** Sorokin, *Annls Sci. Nat.*, *Bot.*, *sér* **6**, **4**: 65 (1876).
*Type*: *P. multiformis* Sorokin 1876.

**Podocrella** Seaver, *Mycologia* **20**: 57 (1928).
*Type*: *P. poronioides* Seaver 1928.

**Atricordyceps** Samuels, *N.Z. Jl. Bot.* **21**: 174 (1983).
*Type*: *A. harposporifera* Samuels 1983.

**Drechmeria** W. Gams & H.-B. Jansson, *Mycotaxon* **22**: 36 (1985).
*Type*: *D. coniospora* (Drechsler) W. Gams & H.-B. Jansson 1985 (syn. *Meria coniospora* Drechsler 1941).

**Haptocillium** W. Gams & H.-B. Jansson, *Mycotaxon* **22**: 36 (1985).
*Type*: *H. balanoides* (Drechsler) Zare & W. Gams 2001.

**Blistum** B. Sutton, *Mycol. Pap.* **132**: 16 (1973).
*Type*: *B. tomentosum* (Schrad.) B. Sutton 1973.