

A phylogenetically-based nomenclature for *Cordycipitaceae* (*Hypocreales*)

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Abstract: The ending of dual nomenclatural systems for pleomorphic fungi in 2011 requires the reconciliation of competing names, ideally linked through culture based or molecular methods. The phylogenetic systematics of *Hypocreales* and its many genera have received extensive study in the last two decades, however resolution of competing names in *Cordycipitaceae* has not yet been addressed. Here we present a molecular phylogenetic investigation of *Cordycipitaceae* that enables identification of competing names in this family, and provides the basis upon which these names can be maintained or suppressed. The taxonomy presented here seeks to harmonize competing names by principles of priority, recognition of monophyletic groups, and the practical usage of affected taxa. In total, we propose maintaining nine generic names, *Akanthomyces*, *Ascopolyporus*, *Beauveria*, *Cordyceps*, *Engyodontium*, *Gibellula*, *Hyperdermium*, *Parengyodontium*, and *Simplicillium* and the rejection of eight generic names, *Evlachovaea*, *Granulomanus*, *Isaria*, *Lecanicillium*, *Microhilum*, *Phytocordyceps*, *Synsterigmatocystis*, and *Torrubiella*. Two new generic names, *Hevansia* and *Blackwellomyces*, and a new species, *Beauveria blattidicola*, are described. New combinations are also proposed in the genera *Akanthomyces*, *Beauveria*, *Blackwellomyces*, and *Hevansia*.

Key words:

Akanthomyces
Ascopolyporus
Beauveria
Blackwellomyces
Cordyceps
 Dual nomenclature
Engyodontium
Gibellula
Hevansia
Hyperdermium
Parengyodontium
Simplicillium

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INTRODUCTION

A molecular phylogenetic investigation of *Clavicipitaceae*, with an emphasis on *Cordyceps*, was conducted by Sung *et al.* (2007) and revealed that both *Clavicipitaceae* and *Cordyceps* were not monophyletic. Two additional families, *Cordycipitaceae* and *Ophiocordycipitaceae*, were recognized and species previously classified in *Cordyceps* were supported as members of all three families. *Clavicipitaceae* and *Ophiocordycipitaceae* collectively formed a monophyletic group, whereas *Cordycipitaceae*, defined by the phylogenetic position of the type species of *Cordyceps*, *C. militaris*, shared a more recent common ancestor with *Hypocreaceae*. The majority of sexually reproducing species

in *Cordyceps* s. str. produce stalked, erect stromatic ascomata that are fleshy in texture, but some species are characterized by reduced stipes or subiculate stromata. Stromata are frequently bright yellow to orange or red, but others are pallid to cream or white according to species.

In addition to *Cordyceps*, numerous genera for sexual morphs have been included in *Cordycipitaceae*, the most speciose and taxonomically problematic being *Torrubiella*. *Torrubiella* has traditionally been used to classify pathogens of spiders or less frequently scale insects that produce superficial perithecia, frequently on a subiculum. Work by Johnson *et al.* (2009) showed the genus to be polyphyletic with species of *Torrubiella* being placed in *Cordyceps* and

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Ophiocordyceps (*Ophiocordycipitaceae*) as well as the new genera *Conoideocrella* and *Orbiocrella* of *Clavicipitaceae*. *Torrubiella* is now restricted to *Cordycipitaceae* infecting spiders with most possessing asexual morphs that had been referred to as *Akanthomyces* or *Gibellula* (Johnson et al. 2009, Evans 2013). Other genera in *Cordycipitaceae* produce perithecia on a subiculum, including *Ascopolyporus* and *Hyperdermium*, but these differ from *Torrubiella* in being pathogens of scale insects (Bischoff et al. 2005). *Phytocordyceps* is a monotypic genus described for *P. ninchukispora*, which molecular data determined to be nested within *Cordyceps* (Sung et al. 2007), although, it is unusual for the genus with respect to host affiliation and ascospore morphology. The host is reported as a seed of *Beilschmiedia erythrophloia* (*Lauraceae*), although closely related *Cordyceps* species attack pupae of *Limacodidae*, which superficially resemble globose seeds. The ascospores feature swollen ends connected by a long, narrowed mid-section, a morphology referred to as bola-ascospores (Eriksson 1982) that are also present in *C. bifusispora* and *C. cf. pruinosa* (Sung et al. 2007).

Asexual morphs in *Cordycipitaceae* have been classified under many different names, and species of *Cordyceps* have been associated with a diversity of asexual reproductive morphologies. Many of these asexually typified genera have been demonstrated to be polyphyletic across *Hypocreales*. One of the oldest names for an asexually typified genus in *Cordycipitaceae* is *Isaria*. The use of *Isaria* has varied greatly over time and many associations outside of *Hypocreales* have been observed (Samson 1974, Luangsa-ard et al. 2004). The currently accepted concept of the genus was established by Hodge et al. (2005), who designated a drawing of *I. farinosa* by Holmskjöld from 1781 as the lectotype for the genus. This definition set arthropod-infecting species in *Hypocreales* apart from morphologically similar *Paecilomyces* in *Eurotiales*. Molecular data supported this distinction (Luangsa-ard et al. 2004), but also revealed a polyphyletic distribution of *Isaria* species in *Hypocreales* (Luangsa-ard et al. 2005). Taxonomic transfers for species with isarioid morphologies in the families *Clavicipitaceae* and *Ophiocordycipitaceae* have also been made in more inclusive investigations (Johnson et al. 2009, Luangsa-ard et al. 2011, Kepler et al. 2014, Quandt et al. 2014, Ban et al. 2015, Spatafora et al. 2015).

Within *Cordycipitaceae*, the asexually typified generic names *Lecanicillium* and *Simplicillium* were described for verticillium-like taxa. Species in *Lecanicillium* are distributed throughout *Cordycipitaceae* and do not form a single monophyletic clade (Sukarno et al. 2009). The type of *Lecanicillium* is *L. lecanii*, known as the asexual morph of *C. confragosa*, which was described as a *Torrubiella* based on its host association with scale insects and the production of superficial torrubielloid perithecia (Evans & Samson 1982). The asexual morph of *C. militaris* is also morphologically similar to *Lecanicillium* (Gams & Zare 2001). Relationships for species of *Lecanicillium* include affinities with isolates morphologically similar to *I. farinosa* and a unique clade of species characterized by *L. psalliotae* (Sung et al. 2001, 2007). *Simplicillium* identifies a clade of species that is sister to the remaining *Cordycipitaceae*; no known sexual form has been linked to the genus (Nonaka et al. 2013).

The morphology is that of slender, elongate, mostly solitary phialides producing singular or short chains of conidia (Zare & Gams 2001). These species are mostly pathogens of fungi, although occurrence on other substrates (e.g. air, soil, plants) is known (Nonaka et al. 2013).

Perhaps the best-known asexually typified generic name in *Cordycipitaceae* is *Beauveria*, due to its role in the development of the germ theory of disease and its long-standing use as a biocontrol agent against pest insects. Agostino Bassi demonstrated in 1834 that *B. bassiana* (a fungus that bears his name) was the cause of white muscardine disease of silkworm, which resulted in considerable loss to the silk industry in Europe (Yarrow 1958). This represented the first demonstration of pathogenic activity by a disease agent, predating Pasteur, who cited Bassi in his papers (Porter 1973). Today, the pathogenic ability of *B. bassiana* is intensely scrutinized in the effort to improve control of insect pests (Xiao et al. 2012). *Beauveria* is defined by the distinctive conidiogenous cells that elongate in a sympodial pattern to produce a zig-zag rachis-like structure. Molecular phylogenies support the monophyly of *Beauveria*, confirming the phylogenetic utility of this form of conidiogenesis, especially when combined with other characters (e.g., hydrophobic conidia, insect pathogenicity; Rehner et al. 2011). The genus is highly diverse, with many cryptic species, and links to several sexually typified species in *Cordyceps* (Rehner & Buckley 2005, Rehner et al. 2011). These include the moth pathogen *C. bassiana* (Huang et al. 2002), and the beetle pathogens *C. brongniartii* (Shimazu et al. 1988) and *C. scarabaeicola* (Shrestha et al. 2014a), as well as pathogens of grasshoppers, stick insects, and cockroaches from South America (Sanjuan et al. 2014), and crickets from Thailand (Ariyawansa et al. 2015).

Other asexually typified genera that produce conidia on a rachis-like conidiophore include *Evlachovaea*, *Engyodontium*, and *Parengyodontium*. A molecular investigation of *Evlachovaea* based on ITS and TEF data, including material from the ex-type strain of *E. kintrischica*, revealed a close association with some species placed in *Isaria* (Humber et al. 2013). They demonstrated this generic name was a later synonym of *Isaria*, but no formal transfer to the genus was made at that time. Likewise, molecular data have supported the separation of *Engyodontium* from *Beauveria*, and the classification of *P. album* as distinct from *Engyodontium* (Tsang et al. 2016). Finally, the monotypic genus *Microhilum* was described for the asexual morph of a *Cordyceps* (Yip & Rath 1989). It produces short conidiophores that give rise to conidium-producing denticles and is morphologically similar to *Beauveria* and *Isaria*; molecular data, however, place this species close to *C. militaris* and *C. kyusyuensis* (Sung et al. 2007).

Several asexually typified genera are associated with *Torrubiella*, the two most common being *Akanthomyces* and *Gibellula*. A revision of *Akanthomyces* by Mains (1950) included species forming hyaline conidia of various shapes on phialides covering a cylindrical synnema in a hymenium-like layer, with superficial similarity to species of *Hymenostilbe*. The type species of *Akanthomyces*, *A. aculeatus*, primarily infects *Lepidoptera*. *Cordyceps tuberculata* is linked to *A. pistillariiformis*, a pathogen of moths and a close relative of

A. aculeatus. *Gibellula* species are pathogens of spiders and produce synnemata with swollen conidiophores reminiscent of *Aspergillus*. Other minor asexual genera include *Granulomanus*, which is now considered to be a synonym of *Gibellula* (Humber & Rombach 1987), and *Pseudogibellula*, which is a synonym of *Ophiocordyceps* (Spatafora *et al.* 2015).

As summarized above, the taxonomic history of *Cordycipitaceae* is complex and involves numerous sexual and asexually typified names that have been used throughout *Hypocreales*. Here we present a phylogenetically informed resolution of competing generic names in *Cordycipitaceae* in order to determine the generic names to use since the end of dual nomenclature for different morphs of the same fungus in 2011 (McNeill *et al.* 2012). In making decisions on names, we sought to harmonize the competing interests among name priority, preferences of user communities, the number of name changes required, and recognition of monophyletic groups from molecular phylogenetic analyses. We also introduce new generic and species names where data support a straightforward taxonomic solution.

MATERIALS AND METHODS

This work employs the data used in name reconciliation for *Ophiocordycipitaceae* by Quandt *et al.* (2014), additional published sequences obtained from GenBank (Bischoff *et al.* 2005, Rehner *et al.* 2011, Humber *et al.* 2013, Sanjuan *et al.* 2014), and sequences determined as part of this work (Table 1). Phylogenetic analyses utilized data from five nuclear genes, including the small and large subunits of nuclear encoded ribosomal DNA genes (SSU and LSU), the protein coding genes translation elongation factor 1 alpha (TEF), and the largest (RPB1) and second largest (RPB2) subunits of RNA polymerase II, and representatives for the type species of sexual and asexual genera throughout the family (Table 1). After assembly of raw sequencing reads with CodonCode Aligner, version 2.0.6 (Dedham, MA) sequences were aligned with representative sequences from throughout *Hypocreales* as in Quandt *et al.* (2014) using MAFFT v.6 (Katoh *et al.* 2002, Katoh & Toh 2008). After alignment, gaps, introns and ambiguously aligned regions identified with Gblocks (Talavera & Castresana 2007) were removed using the editing capacity of Geneious v. 7.0.6 (Biomatters; available from <http://www.geneious.com>). Maximum likelihood analysis was performed with RAxML v. 8.2.8 employing a GTRGAMMA model of nucleotide substitution. The dataset was divided into eleven separate partitions, one for each ribosomal gene and one each for of the three codon positions in protein coding genes. The resulting phylogenetic framework serves as a guide to resolve conflicts between competing names for sexually and asexually typified generic names.

For description of new species, collections were rehydrated in sterilized water. Perithecia, asci, ascospores and part-spores were examined on a Leica DMRB compound microscope and Leica M28 stereomicroscope. *Methuen Handbook of Color* (Kornerup *et al.* 1984) was used for colour descriptions of stromata.

RESULTS

The overall topology recovered in this analysis agrees with that of previous works (Fig. 1; Sung *et al.* 2007, Johnson *et al.* 2009, Nonaka *et al.* 2013, Quandt *et al.* 2014). The family *Cordycipitaceae* is well supported, as are many of the internal nodes, and this phylogenetic hypothesis for the family supports the recognition of the genera *Akanthomyces*, *Ascoplyporus*, *Beauveria*, *Cordyceps*, *Engyodontium*, *Gibellula*, *Hyperdermium*, and *Simplicillium*. *Parengyodontium* was not sampled due to insufficient sequence data. Additionally, we describe two new genera, *Hevansia* and *Blackwellomyces*, to accommodate two clades of species without available generic names, and a new species of *Beauveria*, *B. blattidicola*, that infects cockroaches. We do not use *Evlachovaea*, *Isaria*, *Lecanicillium*, *Microhilum*, and *Torrubiella* and propose that they be rejected along with other lesser-known names (Table 2). There exist clades and lineages containing species named in *Cordyceps*, *Lecanicillium* and *Torrubiella* that are not members of the clades containing the type species of those genera; these are effectively treated as *incertae sedis*. Below we discuss the major genera of *Cordycipitaceae* for which sufficient sampling is available. In all cases, proposed genera are the least inclusive clades defined in the reference phylogeny as the terminal generic clade (Fig. 1).

TAXONOMY

***Akanthomyces* Lebert, Z. Wiss. Zool. 9: 449 (1858).**

Type: Akanthomyces aculeatus Lebert, Z. Wiss. Zool. 9: 449 (1858).

The genus *Akanthomyces* as proposed by Lebert (1858), including the type *A. aculeatus*, primarily infects *Lepidoptera* and forms a clade distinct from *Beauveria* and *Cordyceps*. It includes the moth pathogen *Cordyceps tuberculata*, which is linked to an asexual morph described as *A. pistillariiformis* (Samson & Evans 1974). Other fungi in this clade include *C. coccidioperitheciata* and *C. confragosa*, pathogens of spiders and scales insects, respectively, which produce torrubielloid perithecia (Kobayasi & Shimizu 1982). The production of superficial perithecia on a stipe distinguishes *C. coccidioperitheciata* from other sexual forms infecting spiders in *Cordycipitaceae*, which either lack a stipe or lack superficial perithecia if a stipe is present. *Cordyceps confragosa* was described by Mains (1949) in *Torrubiella*, and while the morphology is torrubielloid, *Akanthomyces* has taxonomic priority by date over *Torrubiella* (Boudier 1885). In addition, the sexual morph *C. confragosa* is linked to *Lecanicillium lecanii*, the type species of *Lecanicillium*, now considered a synonym of *Akanthomyces*, which has priority over *Lecanicillium* (Gams & Zare 2001). Chiriví-Salomón *et al.* (2015) also showed that *L. lecanii* (as *C. confragosa*) as well as some other species of *Lecanicillium*, namely *L. attenuatum*, *L. muscarium*, and *L. sabanense*, fall within *Akanthomyces*. *Akanthomyces* also includes asexually typified species names previously assigned to the genus *Isaria*, but not the type species, *I. farinosa*, which belongs

Table 1. Proposed list of generic names in *Cordycipitaceae* to be protected and their competing synonyms.

Proposed to protect	Proposed to reject
Akanthomyces Lebert in Z. Wiss. Zool. 9: 449. 1858. Typus: <i>Akanthomyces aculeatus</i> Lebert 1858.	(=) <i>Torrubiella</i> Boud. in Rev Mycol. (Toulouse) 7: 226. 1885. Typus: <i>T. aranica</i> Boud. 1885. (=) <i>Lecanicillium</i> W. Gams & Zare in Nova Hedwigia 72: 50. 2001. Typus: <i>L. lecanii</i> (Zimm.) Zare & W. Gams 2001, now regarded as <i>Akanthomyces lecanii</i> (Zimm.) Spatafora et al. 2017.
Ascopolyporus Möller in Bot. Mitt. Tropen 9: 300. 1901. Typus: <i>Ascopolyporus polychrous</i> Möller 1901.	
Beauveria Vuill. in Bull. Soc. Bot. France. 59: 40. 1912. Typus: <i>Beauveria bassiana</i> (Bals.-Criv.) Vuill. 1912 (<i>Botrytis bassiana</i> Bals.-Criv. 1835).	
Blackwellomyces Spatafora & Luangsa-ard in IMA Fungus 8: 345. 2017. Typus: <i>Blackwelliella cardinalis</i> (G.H. Sung & Spatafora) Spatafora & Luangsa-ard 2017 (<i>Cordyceps cardinalis</i> G.H. Sung & Spatafora 2004).	
Cordyceps Fr., Observ. Mycol. 2: 316 [cancellans]] 1818, nom. cons. Typus: <i>Cordyceps militaris</i> (L.) Fr. 1818 (<i>Clavaria militaris</i> L. 1753).	(=) <i>Isaria</i> Pers. in Neues Mag. Bot. 1: 121. 1794. Typus: <i>I. farinosa</i> (Holmsk.) Fr. 1832, now regarded as <i>Cordyceps farinosa</i> (Holmsk.) Kepler et al. 2017. (=) <i>Microhilum</i> H.Y. Yip & A.C. Rath in J. Invert. Path. 53: 361. 1989. Typus: <i>M. oncoperae</i> H.Y. Yip & A.C. Rath 1989, now regarded as <i>Cordyceps oncoperae</i> (H.Y. Yip & A.C. Rath) Kepler et al. 2017. (=) <i>Phytocordyceps</i> C.H. Su & H.H. Wang in Mycotaxon 26: 338. 1986. Typus: <i>P. ninchukispora</i> C.H. Su & H.H. Wang 1986, now regarded as <i>Cordyceps ninchukispora</i> (C.H. Su & H.H. Wang) G.H. Sung et al. 2007. (=) <i>Evlachovaea</i> Borisov & Tarasov in Mikol. Fitopatol. 33: 250. 1999. Typus: <i>E. kintrischica</i> B.A. Borisov & Tarasov 1999, now regarded as <i>Cordyceps kintrischica</i> (B.A. Borisov & Tarasov) Kepler et al. 2017.
Engyodontium de Hoog in Persoonia 10: 53. 1978. Typus: <i>Engyodontium parvisporum</i> (Petch) de Hoog 1978 (<i>Rhinotrichum parvispora</i> Petch 1932).	
Gibellula Cavara in Atti Ist. Bot. R. Univ. Pavia, ser. 2 3: 347. 1894. Typus: <i>Gibellula pulchra</i> Cavara 1894.	(=) <i>Synsterigmatocystis</i> Costantin in Bull. Soc. Mycol. France 4: 63. 1888. Typus: <i>S. arachnophila</i> Costantin ex Vuill. 1888, now regarded as <i>Gibellula arachnophila</i> (Ditmar) Vuill. 1910. (=) <i>Granulomanus</i> de Hoog & Samson in Persoonia 10: 70. 1978. Typus: <i>G. araneorum</i> (Petch) de Hoog & Samson 1978, basionym: <i>Cylindrophora araneorum</i> Petch 1944.
Hevansia Luangsa-ard, Hywel-Jones & Spatafora in IMA Fungus 8: 348. 2017. Typus: <i>Hevansia novoguineensis</i> (Samson & B.L. Brady) Luangsa-ard, Hywel-Jones & Spatafora 2017 (<i>Akanthomyces novoguineensis</i> Samson & B.L. Brady 1982).	
Hyperdermium J.F. White et al. in Mycologia 92: 910. 2000. Typus: <i>Hyperdermium caulium</i> (Berk. & M.A. Curtis) Chaverri & K.T. Hodge 2008 (<i>Corticium caulium</i> Berk. & M.A. Curtis 1854 [1853]).	
Parengyodontium C.C. Tsang et al. in Medical Mycology 54: 708. 2016. Typus: <i>Parengyodontium album</i> (Limber) C.C. Tsang et al. 2016 (<i>Tritirachium album</i> Limber 1940).	
Simplicillium W. Gams & Zare in Nova Hedwigia 73: 38. 2001. Typus: <i>Simplicillium lanosiniveum</i> (J.F.H. Beyma) Zare & W. Gams 2001 (<i>Phalosporium lanosiniveum</i> J.F.H. Beyma 1942).	

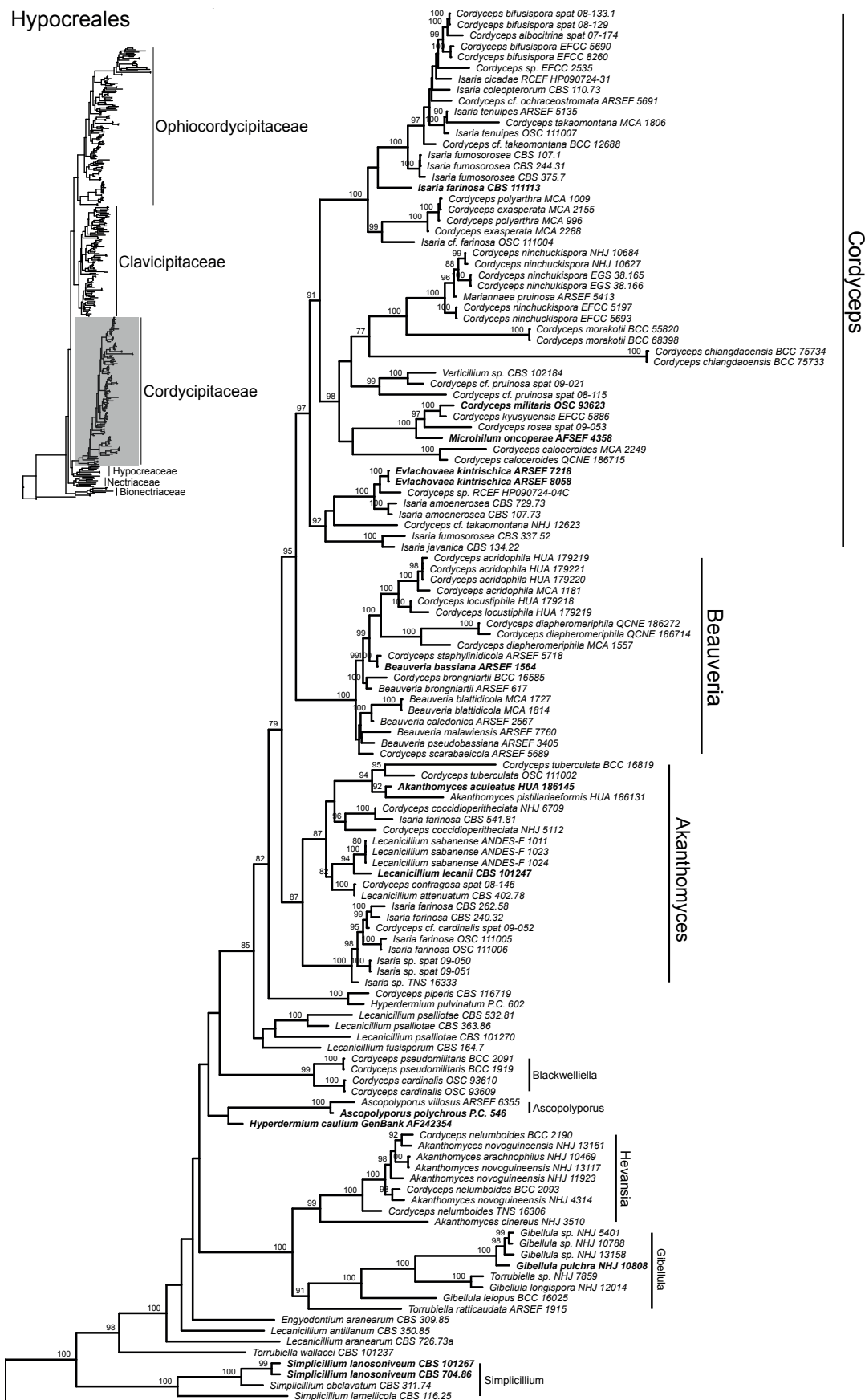


Fig. 1. RAxML tree of *Cordycipitaceae*. Dataset included 392 taxa and a concatenated alignment of 4569 bp from five nuclear genes (SSU, LSU, TEF, RPB1, and RPB2). Tips in bold represent examples of type species for their associated genera. Proposed genus level names to protect are delimited, but names of individual species have not been changed on the leaves of the tree, demonstrating diversity of taxa sampled. Values above branches are bootstrap proportions.

Table 2. Voucher information and Genbank numbers for samples appearing in Figure 1.

Species	Collection	nrSSU	nrLSU	TEF	RPB1	RPB2
<i>Akanthomyces aculeatus</i>	HUA 186145	MF416572	MF416520	MF416465		
<i>Akanthomyces arachnophilus</i>	NHJ 10469	EU369090	EU369031	EU369008	EU369047	
<i>Akanthomyces cinereus</i>	NHJ 3510	EU369091		EU369009	EU369048	EU369070
<i>Akanthomyces novoguineensis</i>	NHJ 13117	EU369092		EU369010	EU369049	EU369073
<i>Akanthomyces novoguineensis</i>	NHJ 13161	EU369093		EU369011	EU369050	
<i>Akanthomyces novoguineensis</i>	NHJ 4314	EU369094		EU369012	EU369051	EU369071
<i>Akanthomyces novoguineensis</i>	NHJ 11923	EU369095	EU369032	EU369013	EU369052	EU369072
<i>Akanthomyces pistillariaeformis</i>	HUA 186131	MF416573	MF416521	MF416466		
<i>Ascopolyporus polychrous</i>	P.C. 546		DQ118737	DQ118745	DQ127236	
<i>Ascopolyporus villosus</i>	ARSEF 6355		AY886544	DQ118750	DQ127241	
<i>Beauveria bassiana</i>	ARSEF 1564			HQ880974	HQ880833	HQ880905
<i>Beauveria blattidicola</i>	MCA 1727	MF416593	MF416539	MF416483	MF416640	
<i>Beauveria blattidicola</i>	MCA 1814	MF416594	MF416540	MF416484	MF416641	
<i>Beauveria brongniartii</i>	ARSEF 617			HQ880991	HQ880854	HQ880926
<i>Beauveria caledonica</i>	ARSEF 2567	AF339570	AF339520	EF469057	EF469086	
<i>Beauveria malawiensis</i>	ARSEF 7760			DQ376246	HQ880897	HQ880969
<i>Beauveria pseudobassiana</i>	ARSEF 3405			AY531931	HQ880864	HQ880936
<i>Cordyceps acridophila</i>	MCA 1181	MF416574	MF416522		MF416628	
<i>Cordyceps acridophila</i>	HUA 179220	JQ895527	JQ895536	JQ958614	JX003852	JX003842
<i>Cordyceps acridophila</i>	HUA 179219		JQ895541	JQ958613	JX003857	JX003841
<i>Cordyceps acridophila</i>	HUA 179221	JQ895526	JQ895537	JQ958615	JX003853	JX003843
<i>Cordyceps albocitrina</i>	spat 07-174	MF416575		MF416467	MF416629	
<i>Cordyceps bifusispora</i>	EFCC 5690	EF468952	EF468806	EF468746	EF468854	EF468909
<i>Cordyceps bifusispora</i>	EFCC 8260	EF468953	EF468807	EF468747	EF468855	EF468910
<i>Cordyceps bifusispora</i>	spat 08-129	MF416576	MF416523	MF416468	MF416630	
<i>Cordyceps bifusispora</i>	spat 08-133.1	MF416577	MF416524	MF416469	MF416631	MF416434
<i>Cordyceps brongniartii</i>	BCC 16585	JF415951	JF415967	JF416009	JN049885	JF415991
<i>Cordyceps caloceroides</i>	MCA 2249	MF416578	MF416525	MF416470	MF416632	
<i>Cordyceps caloceroides</i>	QCNE 186715	MF416579	MF416526			
<i>Cordyceps cardinalis</i>	OSC 93609	AY184973	AY184962	DQ522325	DQ522370	DQ522422
<i>Cordyceps cardinalis</i>	OSC 93610	AY184974	AY184963	EF469059	EF469088	EF469106
<i>Cordyceps cf. cardinalis</i>	spat 09-052	MF416580	MF416527	MF416471	MF416633	MF416435
<i>Cordyceps cf. ochraceostromata</i>	ARSEF 5691	EF468964	EF468819	EF468759	EF468867	EF468921
<i>Cordyceps cf. pruniosa</i>	spat 08-115	MF416586	MF416532	MF416476	MF416635	MF416439
<i>Cordyceps cf. pruniosa</i>	spat 09-021	MF416587	MF416533	MF416477	MF416636	
<i>Cordyceps cf. takaomontana</i>	NHJ 12623	EF468984	EF468838	EF468778	EF468884	EF468932
<i>Cordyceps cf. takaomontana</i>	BCC 12688	MF416599	MF416545	MF416489	MF416646	
<i>Cordyceps coccidioperitheciata</i>	NHJ 5112	EU369109	EU369043	EU369026	EU369066	
<i>Cordyceps coccidioperitheciata</i>	NHJ 6709	EU369110	EU369042	EU369025	EU369067	EU369086
<i>Cordyceps confragosa</i>	spat 08-146	MF416581	MF416528	MF416472	MF416634	MF416436
<i>Cordyceps diapheromeriphila</i>	MCA 1557	MF416582	MF416529			

Table 2. (Continued).

Species	Collection	nrSSU	nrLSU	TEF	RPB1	RPB2
<i>Cordyceps diapheromeriphila</i>	QCNE 186714	MF416601	MF416547	MF416491	MF416648	
<i>Cordyceps diapheromeriphila</i>	QCNE 186272	JQ895530	JQ895534	JQ958610	JX003848	
<i>Cordyceps exasperata</i>	MCA 2155	MF416596	MF416542	MF416486	MF416643	
<i>Cordyceps exasperata</i>	MCA 2288	MF416592	MF416538	MF416482	MF416639	
<i>Cordyceps kyusyuensis</i>	EFCC 5886	EF468960	EF468813	EF468754	EF468863	EF468917
<i>Cordyceps locustiphila</i>	HUA 179218	JQ895525	JQ895535	JQ958619	JX003846	JX003845
<i>Cordyceps locustiphila</i>	HUA 179219	JQ958598	JQ958597		JX003847	
<i>Cordyceps militaris</i>	OSC 93623	AY184977	AY184966	DQ522332	DQ522377	AY545732
<i>Cordyceps nelumboides</i>	BCC 2093	MF416583	MF416530	MF416473		MF416437
<i>Cordyceps nelumboides</i>	BCC 2190	MF416584	MF416531	MF416474		
<i>Cordyceps nelumboides</i>	TNS 16306	MF416585		MF416475		MF416438
<i>Cordyceps ninchuckispora</i>	EFCC 5197	EF468965	EF468820	EF468760	EF468868	
<i>Cordyceps ninchuckispora</i>	EFCC 5693	EF468966	EF468821	EF468762	EF468869	
<i>Cordyceps ninchuckispora</i>	NHJ 10627	EF468967	IEF468822	EF468763	EF468870	
<i>Cordyceps ninchuckispora</i>	NHJ 10684	EF468968	EF468823	EF468761	EF468871	
<i>Cordyceps ninchukispora</i>	EGS 38.165	EF468991	EF468846	EF468795	EF468900	
<i>Cordyceps ninchukispora</i>	EGS 38.166	EF468992	EF468847	EF468794	EF468901	
<i>Cordyceps piperis</i>	CBS 116719		AY466442	DQ118749	DQ127240	EU369083
<i>Cordyceps polyarthra</i>	MCA 996	MF416597	MF416543	MF416487	MF416644	
<i>Cordyceps polyarthra</i>	MCA 1009	MF416598	MF416544	MF416488	MF416645	
<i>Cordyceps pseudomilitaris</i>	BCC 1919	MF416588	MF416534	MF416478		MF416440
<i>Cordyceps pseudomilitaris</i>	BCC 2091	MF416589	MF416535	MF416479		MF416441
<i>Cordyceps rosea</i>	spat 09-053	MF416590	MF416536	MF416480	MF416637	MF416442
<i>Cordyceps scarabaeicola</i>	ARSEF 5689	AF339574	AF339524	DQ522335	DQ522380	DQ522431
<i>Cordyceps</i> sp.	EFCC 2535	EF468980	EF468835	EF468772		
<i>Cordyceps</i> sp.	RCEF HP090724-04C	MF416591	MF416537	MF416481	MF416638	MF416443
<i>Cordyceps staphylinidicola</i>	ARSEF 5718	EF468981	EF468836	EF468776	EF468881	
<i>Cordyceps takaomontana</i>	MCA 1806	MF416595	MF416541	MF416485	MF416642	
<i>Cordyceps tuberculata</i>	OSC 111002	DQ522553	DQ518767	DQ522338	DQ522384	DQ522435
<i>Cordyceps tuberculata</i>	BCC 16819	MF416600	MF416546	MF416490	MF416647	MF416444
<i>Engyodontium araneorum</i>	CBS 309.85	AF339576	AF339526	DQ522341	DQ522387	DQ522439
<i>Evlachovaea kintrischica</i>	ARSEF 7218			GU734751		
<i>Evlachovaea kintrischica</i>	ARSEF 8058			GU734750		
<i>Gibellula leiopus</i>	BCC 16025	MF416602	MF416548	MF416492	MF416649	
<i>Gibellula longispora</i>	NHJ 12014	EU369098		EU369017	EU369055	EU369075
<i>Gibellula pulchra</i>	NHJ 10808	EU369099	EU369035	EU369018	EU369056	EU369076
<i>Gibellula</i> sp.	NHJ 10788	EU369101	EU369036	EU369019	EU369058	EU369078
<i>Gibellula</i> sp.	NHJ 13158	EU369100	EU369037	EU369020	EU369057	EU369077
<i>Gibellula</i> sp.	NHJ 5401	EU369102			EU369059	EU369079
<i>Hyperdermium caulium</i>	GenBank AF242354		AF242354			
<i>Hyperdermium pulvinatum</i>	P.C. 602		DQ118738	DQ118746	DQ127237	
<i>Isaria amoenerosea</i>	CBS 107.73	AY526464	MF416550	MF416494	MF416651	MF416445
<i>Isaria amoenerosea</i>	CBS 729.73	MF416604	MF416551	MF416495	MF416652	MF416446
<i>Isaria</i> cf. <i>farinosa</i>	OSC 111004	EF468986	EF468840	EF468780	EF468886	
<i>Isaria cicadae</i>	RCEF HP090724-31	MF416605	MF416552	MF416496	MF416653	MF416447

Table 2. (Continued).

Species	Collection	nrSSU	nrLSU	TEF	RPB1	RPB2
<i>Isaria coleopterorum</i>	CBS 110.73	JF415965	JF415988	JF416028	JN049903	JF416006
<i>Isaria farinosa</i>	OSC 111005	DQ522558	DQ518772	DQ522348	DQ522394	
<i>Isaria farinosa</i>	OSC 111006	EF469127	EF469080	EF469065	EF469094	
<i>Isaria farinosa</i>	CBS 240.32	JF415958	JF415979	JF416019	JN049895	JF415999
<i>Isaria farinosa</i>	CBS 262.58	AB023943	AB080087	MF416497	MF416654	MF416448
<i>Isaria farinosa</i>	CBS 541.81	MF416606	MF416553	MF416498	MF416655	MF416449
<i>Isaria farinosa</i>	CBS 111113	AY526474	MF416554	MF416499	MF416656	MF416450
<i>Isaria fumosorosea</i>	CBS 337.52	MF416607	MF416555	MF416500	MF416657	MF416451
<i>Isaria fumosorosea</i>	CBS 375.70	AB083035	AB083035	MF416501	MF416658	MF416452
<i>Isaria fumosorosea</i>	CBS 107.10	MF416608	MF416556	MF416502	MF416659	MF416453
<i>Isaria fumosorosea</i>	CBS 244.31	MF416609	MF416557	MF416503	MF416660	MF416454
<i>Isaria javanica</i>	CBS 134.22	MF416610	MF416558	MF416504	MF416661	MF416455
<i>Isaria</i> sp.	TNS 16333	MF416611		MF416505	MF416662	MF416456
<i>Isaria</i> sp.	spat 09-050	MF416613	MF416559	MF416506	MF416663	MF416457
<i>Isaria</i> sp.	spat 09-051	MF416614	MF416560	MF416507	MF416664	MF416458
<i>Isaria tenuipes</i>	OSC 111007	DQ522559	DQ518773	DQ522349	DQ522395	DQ522449
<i>Isaria tenuipes</i>	ARSEF 5135	MF416612	JF415980	JF416020	JN049896	JF416000
<i>Lecanicillium antillanum</i>	CBS 350.85	AF339585	AF339536	DQ522350	DQ522396	DQ522450
<i>Lecanicillium aranearum</i>	CBS 726.73a	AF339586	AF339537	EF468781	EF468887	EF468934
<i>Lecanicillium attenuatum</i>	CBS 402.78	AF339614	AF339565	EF468782	EF468888	EF468935
<i>Lecanicillium fusisporum</i>	CBS 164.7	AF339598	AF339549	EF468783	EF468889	
<i>Lecanicillium lecanii</i>	CBS 101247	AF339604	AF339555	DQ522359	DQ522407	DQ522466
<i>Lecanicillium psalliotae</i>	CBS 532.81	AF339609	AF339560	EF469067	EF469096	EF469112
<i>Lecanicillium psalliotae</i>	CBS 101270	EF469128	EF469081	EF469066	EF469095	EF469113
<i>Lecanicillium psalliotae</i>	CBS 363.86	AF339608	AF339559	EF468784	EF468890	
<i>Mariannaea pruinosa</i>	ARSEF 5413	AY184979	AY184968	DQ522351	DQ522397	DQ522451
<i>Microhilum oncoperae</i>	AFSEF 4358	AF339581	AF339532	EF468785	EF468891	EF468936
<i>Simplicillium lamellicola</i>	CBS 116.25	AF339601	AF339552	DQ522356	DQ522404	DQ522462
<i>Simplicillium lanosoniveum</i>	CBS 101267	AF339603	AF339554	DQ522357	DQ522405	DQ522463
<i>Simplicillium lanosoniveum</i>	CBS 704.86	AF339602	AF339553	DQ522358	DQ522406	DQ522464
<i>Simplicillium obclavatum</i>	CBS 311.74	AF339567	AF339517	EF468798		
<i>Torrubiella ratticaudata</i>	ARSEF 1915	DQ522562	DQ518777	DQ522360	DQ522408	DQ522467
<i>Torrubiella</i> sp.	NHJ 7859	EU369107			EU369064	EU369085
<i>Torrubiella wallacei</i>	CBS 101237	AY184978	AY184967	EF469073	EF469102	EF469119
<i>Verticillium</i> sp.	CBS 102184	AF339613	AF339564	EF468803	EF468907	EF468948

in *Cordyceps*. In general, the host range for asexual and sexual forms of *Akanthomyces* are similar, although *L. attenuatum* (CBS 402.78) was cultured from leaf litter with no host reported. The morphological characters associated with *Akanthomyces* are also found in a clade of spider-pathogenic species sister to the *Gibellula* clade (see *Hevansia* below).

The type species of *Torrubiella*, *T. arancida*, known from a spider in France, was not available for inclusion in molecular phylogenetic analyses. However, several morphological characteristics of *T. arancida* suggest that it may belong in *Akanthomyces*. These include the superficial and separated arrangement of the perithecia and the lack of a subiculum in the type specimen as shown in Johnson *et al.* (2009). A number of sexual morphs now placed in *Akanthomyces* have torrubielloid ascomata, specifically *A. coccidioperitheciatus*

on spiders, *A. lecanii* on scale insects, and *A. tuberculata* on moths.

***Akanthomyces attenuatus* (Zare & W. Gams)**
 Spatafora, Kepler & B. Shrestha, **comb. nov.**

Mycobank MB820860

Basionym: *Lecanicillium attenuatum* Zare & W. Gams, *Nova Hedwigia* **73**: 19 (2001).

***Akanthomyces coccidioperitheciatus* (Kobayasi & Shimizu)**
 Spatafora, Kepler & B. Shrestha, **comb. nov.**

Mycobank MB820880

Basionym: *Cordyceps coccidioperitheciata* Kobayasi & Shimizu, *Bull. Natl. Sci. Mus. Tokyo*, **B 8**: 79 (1982).

Akanthomyces dipterigenus (Petch) Spatafora, Kepler, Zare & B. Shrestha, **comb. nov.**

MycoBank MB823235

Basionym: *Cephalosporium dipterigenum* Petch, *Naturalist* (Hull) **56**: 102 (1931).

Synonyms: *Cephalosporium longisporum* Petch, *Trans. Brit. Mycol. Soc.* **10**: 166 (1925).

Lecanicillium longisporum (Petch) Zare & W. Gams, *Nova Hedwigia* **73**: 16 (2001).

? *Acrostalagmus aphidum* Oudem., *Nederl. Kruidk. Arch.* **3**(2): 759 (1902) [no type collection found in L, only a drawing which does not allow a definite conclusion].

Non *Verticillium longisporum* (Stark) Karapappa *et al.*, *Mycol. Res.* **101**: 1293 (1997).

Non *Akanthomyces longisporus* B. Huang *et al.*, *Mycosystema* **19**: 172 (2000).

Akanthomyces lecanii (Zimm.) Spatafora, Kepler & B. Shrestha, **comb. nov.**

MycoBank MB820881

Basionym: *Cephalosporium lecanii* Zimm., *Teysmania* **9**: 241 (1899).

Synonyms: *Verticillium lecanii* (Zimm.) Viégas, *Revista Inst. Café Estado São Paulo* **14**: 754 (1939).

Lecanicillium lecanii (Zimm.) Zare & W. Gams, *Nova Hedwigia* **73**: 10 (2001).

Torrubiella confragosa Mains, *Mycologia* **41**: 305 (1949).

Cordyceps confragosa (Mains) G.H. Sung *et al.*, *Stud. Mycol.* **57**: 49 (2007).

Hirsutella confragosa Mains, *Mycologia* **41**: 303 (1949).

For further synonyms see Zare & Gams (2001).

Akanthomyces muscarius (Petch) Spatafora, Kepler & B. Shrestha, **comb. nov.**

MycoBank MB820861

Basionym: *Cephalosporium muscarium* Petch, *Naturalist* (Hull) **56**: 102 (1931).

Synonyms: *Lecanicillium muscarium* (Petch) Zare & W. Gams, *Nova Hedwigia* **73**: 13 (2001).

Cephalosporium aphidicola Petch, *Trans. Brit. Mycol. Soc.* **16**: 71 (1931).

Verticillium hemileiae Bouriquet, *Encycl. Mycol.* **12**: 155 (1946).

For further synonyms see Zare & Gams (2001).

Akanthomyces sabanensis (J.S. Chiriví-Salomón *et al.*) J.S. Chiriví-Salomón, T. Sanjuan & S. Restrepo, **comb. nov.**

MycoBank MB820862

Basionym: *Lecanicillium sabanense* J.S. Chiriví-Salomón *et al.*, *Phytotaxa* **234**: 68 (2015).

Akanthomyces tuberculatus (Lebert) Spatafora, Kepler & B. Shrestha, **comb. nov.**

MycoBank MB820863

Basionym: *Akrophyton tuberculatum* Lebert, *Z. Wiss. Zool.* **9**: 448 (1858).

Synonyms: *Cordyceps tuberculata* (Lebert) Maire, *Bull. Soc. Hist. Nat. Afrique N.* **8**: 165 (1917).

Isaria pistillariiformis Pat., *Bull. Soc. Mycol. Fr.* **9**: 163 (1893);

as "*pistillariaeformis*".

Insecticola pistillariiformis (Pat.) Mains, *Mycologia* **42**: 579 (1950); as "*pistillariaeformis*".

Akanthomyces pistillariiformis (Pat.) Samson & H.C. Evans, *Acta Bot. Neerl.* **23**: 29 (1974).

Ascopolyporus Möller, *Bot. Mitt. Tropen* **9**: 300 (1901).

Type: *Ascopolyporus polychrous* Möller, *Bot. Mitt. Tropen* **9**: 300 (1901).

Ascopolyporus is a genus containing seven species, represented in this study by the type *A. polychrous* and *A. villosus*. These two species are strongly supported as monophyletic, however their relationship to other taxa in *Cordycipitaceae* remains poorly resolved. Sexual or asexual morphologies have been observed in individual collections of *Ascopolyporus*, and they co-occur in some species (Bischoff *et al.* 2005). In the sexual form perithecia are produced in a dense hyphal mat directly on top of the scale insect host, and the appearance is similar to that of species in *Hypocrella* or *Moelleriella* in *Clavicipitaceae*. *Ascopolyporus* species produce multiseptate conidia, a feature also found in *Hyperdermium*. *Ascopolyporus* shares another characteristic with some species in *Hypocrella* in the apparent utilization of plant resources via the scale insect cadaver to attain sizes greatly in excess of the original host (Hywel-Jones & Samuels 1998, Bischoff *et al.* 2005, Chaverri *et al.* 2008).

Beauveria Vuill., *Bull. Soc. Bot. France* **59**: 40 (1912).

Type: *Beauveria bassiana* (Bals.-Criv.) Vuill., *Bull. Soc. Bot. France* **59**: 40 (1912).

The recognition of *Beauveria* as a genus separate from *Cordyceps* is a significant change for *Cordycipitaceae*; their respective type species are not congeneric. The morphological features that unite species of *Beauveria* have proved remarkably durable over time and no isolates described from other asexually typified genera are known in this clade. Direct links between species of *Beauveria* and cordyceps-like sexual morphs are well established from molecular data and culture-based experiments, including *B. bassiana* (Li *et al.* 2001, Huang *et al.* 2002), *B. brongniartii* (Shimizu *et al.* 1988), and *B. sungii* (Shrestha *et al.* 2014a). The host range for the asexual morphs is extensive, infecting many insect species across multiple orders (de Faria & Wraight 2007) as well as being isolated from soil and as foliar endophytes (Vega *et al.* 2009). The sexual morphs are known from *Coleoptera*, *Lepidoptera*, *Orthoptera*, and *Phasmatodea*, and here we also describe a new species from *Blattodea*, expanding the known host range of sexual morphs of *Beauveria*.

Beauveria acridophila (T. Sanjuan & Franco-Mol.) T. Sanjuan, B. Shrestha, Kepler & Spatafora, **comb. nov.**

MycoBank MB820883

Basionym: *Cordyceps acridophila* T. Sanjuan & Franco-Mol., *Mycologia* **106**: 268 (2014).

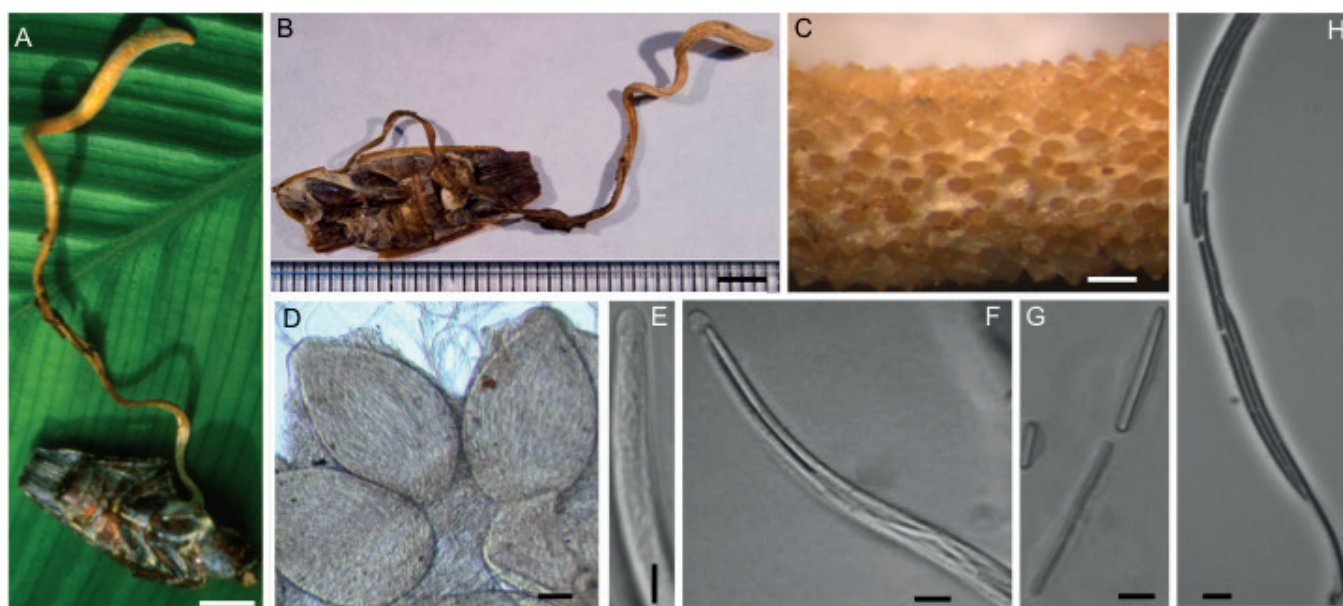


Fig. 2. *Beauveria blattidicola* (MCA1727 – holotype). **A.** Fresh stroma on cockroach. **B.** Dried stroma on cockroach. **C.** Stroma with partially immersed perithecia. **D.** Perithecia. **E.** Ascus showing prominent ascus cap. **F.** Ascus showing cylindrical ascospores. **G.** Part-spores. **H.** End of ascus showing ascus foot. Bars: A–B = 4 mm; C = 150 µm; D = 50 µm; E–H = 5 µm.

Beauveria bassiana (Bals.-Criv.) Vuill., *Bull. Soc. Bot. Fr.* **59**: 40 (1912).

Basionym: *Botrytis bassiana* Bals.-Criv., *Linnaea* **10**: 611 (1835).

Synonyms: *Spicaria bassiana* (Bals.-Criv.) Vuill., *Bull. Soc. Sc. Nancy*, ser. 3, **10**: 153 (1910).

Penicillium bassianum (Bals.-Criv.) Biourge, *Cellule* **33**: 101 (1923).

Cordyceps bassiana Z.Z. Li et al., *Chin. Sci. Bull.* **9**: 751 (2001).

Beauveria blattidicola M. Chen, Aime, T.W. Henkel & Spatafora, **sp. nov.** (Fig. 2)
MycoBank MB821050

Etymology: The species epithet refers to the fungus' occurrence on the host insect family *Blattidae*.

Diagnosis: Similar in host association to *Ophiocordyceps blattarioides* but differs in the yellow-orange fleshy stromata, long, sinuous stipe, and cylindrical to narrowly clavate fertile region with partially immersed perithecia.

Type: **Guyana**: *Region 8, Potaro-Siparuni*: Pakaraima Mountains, Upper Potaro River Basin, within a 4 km radius of Potaro base camp at 5°18'04.8"N, 59°54'40.4"W, 710–750 m elev.; on adult cockroach, 31 May, 2001, M.C. Aime MCA 1727 (BRG – holotype).

Description: *Stromata* solitary or paired, unbranched, arising from head or thorax of infected adult of cockroach, with fleshy texture, total length 50–60(–90) mm long; stalk 0.8–1.5 mm broad, light yellow (4A3–4A4); fertile area apical, cylindrical to narrowly clavate, 6–8 × 1.2–1.4 mm, yellowish orange (4A7–4A8). *Perithecia* partially immersed, darker concolorous, interspersed with white mycelial wefts, presented at right

angle to the surface of stroma, in longitudinal section oval to ovoid, 250–370 × 110–250 µm. *Asci* hyaline, cylindrical, 170–300 × 3–4 µm, with a prominent apical cap 3.0–4.0 µm diam. *Ascospores* filiform, nearly as long as the asci, smooth, hyaline, distinct irregularly multiseptate, not easily breaking into part-spores. *Part-spores* 6.0–23.0 × 1.0 µm, cylindrical with truncate ends.

Known distribution: Guyana.

Additional specimens examined: **Guyana**: *Region 8, Potaro-Siparuni*: Pakaraima Mountains, Upper Potaro River Basin, within a 4 km radius of Potaro base camp at 5°18'04.8"N, 59°54'40.4"W, 710–750 m elev., on adult cockroach adhered to leaf in litter, 12 June 2000, M.C. Aime MCA 1203 (PUL); on adult cockroach in leaf litter, 14 July 2000, T.W. Henkel TH 7645 (HSC); on adult cockroach, 25 May 2001, M.C. Aime MCA 1628 (PUL); on adult cockroach, 7 June 2001, M.C. Aime MCA 1814 (PUL); on adult cockroach in leaf litter, 24 July 2003, T.W. Henkel TH 8607 (HSC); on adult cockroach on mineral soil below leaf litter, 17 July 2009, T.W. Henkel TH 9049 (OSC); on adult cockroach, partially buried in litter, 27 May 2010, M.C. Aime & L. Williams MCA 4043 (PUL); on adult cockroach, 9 June 2012, M.C. Aime MCA 4883 (PUL).

GenBank: MCA1727 MF416593, MF416539, MF416483, MF416640; MCA1814 MF416594, MF416540, MF416484, MF416641

Commentary: Species of *Cordyceps* s. lat. infecting cockroaches have rarely been collected in nature. Only two cockroach-associated species are recorded in the literature: *Ophiocordyceps blattarioides* (Sanjuan et al. 2015) and *O. blattae* (Petch 1924, 1931), both classified in *Ophiocordycipitaceae*. The Neotropical *O. blattarioides* is associated with adult *Blattodea*, and is closely related to the morphologically similar adult *Orthoptera*-associated *O. amazonica* (Sanjuan et al. 2015).

Ophiocordyceps blattae was described originally from Sri Lanka (as *Cordyceps blattae*), but the species remains poorly known, as sequence data are lacking, and current taxonomic concepts are based entirely on the original description and drawings of Petch (1924). Based on the possession of ophio-ascospores and clavate asci with reduced apices, *O. blattae* is likely closely related to *O. unilateralis* (Petch 1931) and is the type of the genus *Ophiocordyceps* (Sung *et al.* 2007). *Beauveria blattidicola* is easily distinguished from both *O. blattarioides* and *O. blattae* by the combination of yellow to yellowish orange fleshy stromata, the long and sinuous stalk, cylindrical to narrowly clavate fertile region, and partially immersed perithecia typical of other sexual morphs of *Beauveria*. Molecular data also strongly support the placement of *B. blattidicola* in *Beauveria* (Fig. 1). While *B. blattidicola* cultures are currently unavailable, its phylogenetic placement predicts a *Beauveria*-type asexual morph.

Beauveria brongniartii (Sacc.) Petch, *Trans. Brit. Mycol. Soc.* **10**: 249 (1926).

Basionym: *Botrytis brongniartii* Sacc., *Syll. Fung.* **10**: 540 (1892).

Synonym: *Cordyceps brongniartii* Shimazu, *Trans. Mycol. Soc. Japan* **29**: 328 (1989).

Beauveria diapheromeriphila (T. Sanjuan & S. Restrepo) T. Sanjuan, B. Shrestha, Kepler & Spatafora, **comb. nov.**

MycoBank MB820882

Basionym: *Cordyceps diapheromeriphila* T. Sanjuan & S. Restrepo, *Mycologia* **106**: 270 (2014).

Beauveria locustiphila (Henn.) B. Shrestha, Kepler & Spatafora, **comb. nov.**

MycoBank MB820884

Basionym: *Cordyceps locustiphila* Henn., *Hedwigia* **43**: 246 (1904).

Beauveria scarabaeidicola (Kobayasi) S.A. Rehner & Kepler, **comb. nov.**

MycoBank MB820891

Basionym: *Cordyceps scarabaeidicola* Kobayasi, *Bull. Natl. Sci. Mus. Tokyo*, B **2**: 137 (1976); as "*scarabaeicola*".

Synonym: *Beauveria sungii* S.A. Rehner & R.A. Humber, *Mycologia* **103**: 1070 (2011).

Beauveria staphylinidicola (Kobayasi & Shimizu) B. Shrestha, Kepler & Spatafora, **comb. nov.**

MycoBank MB820895

Basionym: *Cordyceps staphylinidicola* Kobayasi & Shimizu, *Bull. Natl. Sci. Mus. Tokyo*, B **8**: 88 (1982); as "*staphylinidicola*".

Blackwellomyces Spatafora & Luangsa-ard, **gen. nov.**

MycoBank MB820864

Etymology: This genus is named for Meredith Blackwell and honours her invaluable contributions to our knowledge of insect-associated fungi.

Diagnosis: *Blackwellomyces* is the least inclusive genus-level clade that includes the species *B. cardinalis* and *B. pseudomilitaris*. *Blackwellomyces* is diagnosed by the unique characters of the ascospore, which have irregularly spaced septa and do not disarticulate into part-spores at maturity.

Type: *Blackwellomyces cardinalis* (G.H. Sung & Spatafora) Spatafora & Luangsa-ard 2017.

Description: *Sexual morph*: Stromata solitary or multiple, simple or branched. Stipe fleshy, orange to red, cylindrical to enlarging apically, 4–50 × 0.5–3.0 mm. Fertile area terminal, cylindrical, fusiform to clavate to irregularly shaped, 2–9 × 1–4 mm. *Perithecia* crowded, loosely embedded, ordinal in orientation, elliptical to fusiform to obclavate. *Asci* 8-spored, hyaline, cylindrical, possessing a prominent apex. *Ascospores* smooth, filiform, hyaline, irregularly multiseptate, not fragmenting into part-spores.

Asexual morph: Cultures moderately fast growing in PDA and may turn the media red. *Aerial mycelium* is whitish to whitish yellow and the reverse side of cultures is red or cream. *Conidiogenous cells* phialides, solitary or in whorls of 2 or 3, swollen at the base or slightly flask-shaped, wider near the base and tapering at the apex. *Conidia* hyaline, aseptate, ellipsoidal to elliptical, in some species produced in sympodially imbricate chains. *Asexual morphs* have been described as similar to species in *Clonostachys*, *Hirsutella*, *Isaria*, and *Mariannaea*.

Hosts: On larva of *Lepidoptera*.

Distribution: Southeastern USA, eastern China, Japan, Korea, and Thailand.

Commentary: The species placed here are supported as a distinct clade and separate from other genera of *Cordycipitaceae* based on the placement of their type species. We describe these taxa as *Blackwellomyces* on the basis of their phylogenetic novelty and irregularly septate ascospores that do not disarticulate into part-spores. This contrasts with other members of the family in which septation and disarticulation is common.

Blackwellomyces cardinalis (G.H. Sung & Spatafora) Spatafora & Luangsa-ard, **comb. nov.** MycoBank MB820865

Basionym: *Cordyceps cardinalis* G.H. Sung & Spatafora, *Mycologia* **96**: 660 (2004).

Blackwellomyces pseudomilitaris (Hywel-Jones & Sivichai) Spatafora & Luangsa-ard, **comb. nov.** MycoBank MB820866

Basionym: *Cordyceps pseudomilitaris* Hywel-Jones & Sivichai, *Mycol. Res.* **98**: 940 (1994).

Cordyceps Fr., *Observ. Mycol.* **2**: 316 [cancellans] (1818), nom. cons.

Type: *Cordyceps militaris* (L.) Fr., *Observ. Mycol.* **2**: 317 [cancellans] (1818).

In this analysis, many species of *Cordyceps*, including the type, are resolved as a well-supported clade interspersed with genera described originally for asexual morphs, including *Evlachovaea*, *Isaria*, and *Microhilum* (Fig. 1). Additionally, our analysis indicates this core *Cordyceps* is not monophyletic with *C. cardinalis* and *C. pseudomilitaris*, a result consistent with Sung et al. (2007); the latter two species are proposed in the new genus *Blackwellomyces* here (see above). Within the core *Cordyceps* clade, internal relationships are generally well-supported, giving rise to a phylogenetic structure that roughly corresponds to stromatal colour (red to orange vs. white to yellow). A thorough review of the taxonomic history of *Cordyceps* was provided by Shrestha et al. (2014b), who concluded that *Cordyceps* is the oldest accepted generic name in this clade and is typified by a sexual morph. Based on the cylindrical shape of the stroma, pre-Linnaean literature of the 17th and early 18th century had recorded *C. militaris*, the type species of *Cordyceps*, under the old but obsolete generic names *Fungus* and *Fungoides* (Shrestha et al. 2014b). The species was transferred to *Clavaria* by Linnaeus (1753). *Clavaria militaris* was then transferred to the ascomycete genus *Sphaeria* (now rejected in favour of *Hypoxylon*), a classification that was followed until the early 19th century (Shrestha et al. 2014b). The genus *Cordyceps* was established (Fries 1818, Link 1833) and over the years was circumscribed to include pathogens of more than 12 insect orders and the fungal genera *Elaphomyces* and *Claviceps* (Kobayasi 1941, Mains 1958, Sung et al. 2007, Kepler et al. 2012, Araújo & Hughes 2016, Shrestha et al. 2016). This generic concept of *Cordyceps* stood for approximately 200 years until the polyphyletic nature of *Cordyceps* as it had been understood by Kobayasi and Mains was revealed (Sung et al. (2007).

Three monotypic generic names are now considered to be synonyms of *Cordyceps*. Our data confirmed the findings of Humber et al. (2013) who demonstrated that the type species of the monotypic *Evlachovaea*, *E. kintrischica*, is a synonym of *Isaria* (see below). Similarly, the type species of *Microhilum*, *M. oncoperae*, known to have a *Cordyceps* sexual morph, was nested within *Cordyceps*, as is the type species of *Phytocordyceps*, *P. ninchukispora*.

The generic name *Isaria* is the oldest available name for the entire group of taxa considered here, including *Cordyceps*. However, the concept of *Isaria* has a long and convoluted history, with many changes of status and differences of opinion in how the name should be applied (e.g. Hodge et al. 2005, Gams et al. 2005). Petch (1934) concluded the name was too confusing to use and suggested it be applied to a subgenus of *Spicaria*. However, Hodge et al. (2005) lectotypified *Isaria sensu* Fries using an illustration of *I. farinosa* that appeared in the original description of this species as *Ramaria farinosa* (Holmskjöld 1781). Gams et al. (2005) proposed the use of *Isaria* for *Paecilomyces* sect. *Isarioidea*, now also regarded as a synonym of *Cordyceps*. Entomogenous species morphologically similar to *Isaria* can be found distributed throughout *Hypocreales* (Luangsa-ard et al. 2004), and here are shown to be polyphyletic within *Cordycipitaceae*. The ex-epitype isolate of *I. farinosa* (CBS 111113, Gams et al. 2005) is here determined to belong within *Cordyceps*. We therefore propose the rejection of *Isaria* in

favour of *Cordyceps* owing to the confusion surrounding the application of *Isaria*. Additionally, rejecting *Cordyceps* would be disruptive to a large user community while the name *Isaria* is not as widely used. Species of *Isaria* are herein integrated into the monophyletic application of *Cordyceps*. The diversity of species infecting cicada nymphs complicates the transfer of *I. cicadae*, and will be addressed in a subsequent paper focused on the group.

Cordyceps amoene-rosea* (Henn.) Kepler, B. Shrestha & Spatafora, *comb. nov.

MycoBank MB820975

Basionym: *Isaria amoene-rosea* Henn., *Hedwigia* **41**: 66 (1902).

Synonym: *Paecilomyces amoeneroseus* (Henn.) Samson, *Stud. Mycol.* **6**: 37 (1974).

Cordyceps cateniannulata* (Z.Q. Liang) Kepler, B. Shrestha & Spatafora, *comb. nov.

MycoBank MB820976

Basionym: *Paecilomyces cateniannulatus* Z.Q. Liang, *Acta Phytopathol. Sin.* **11**: 10 (1981).

Synonym: *Isaria cateniannulata* (Z.Q. Liang) Samson & Hywel-Jones, *Mycol. Res.* **109**: 588 (2005).

Cordyceps cateniobliqua* (Z.Q. Liang) Kepler, B. Shrestha & Spatafora, *comb. nov.

MycoBank MB820977

Basionym: *Paecilomyces cateniobliquus* Z.Q. Liang, *Acta Phytopathol. Sin.* **11**: 9 (1981).

Synonym: *Isaria cateniobliqua* (Z.Q. Liang) Samson & Hywel-Jones, *Mycol. Res.* **109**: 588 (2005).

Cordyceps coleopterorum* (Samson & H.C. Evans) Kepler, B. Shrestha & Spatafora, *comb. nov.

MycoBank MB820978

Basionym: *Paecilomyces coleopterorum* Samson & H.C. Evans, *Stud. Mycol.* **6**: 47 (1974).

Synonym: *Isaria coleopterorum* (Samson & H.C. Evans) Samson & Hywel-Jones, *Mycol. Res.* **109**: 588 (2005); as “*coleoptera*”.

Cordyceps farinosa* (Holmsk.) Kepler, B. Shrestha & Spatafora, *comb. nov.

MycoBank MB820979

Basionym: *Ramaria farinosa* Holmsk., *K. Danske Vidensk. Selsks. Skr., Nye Samling* **1**: 279 (1781).

Synonyms: *Clavaria farinosa* (Holmsk.) Dicks., *Fasc. Pl. Crypt. Brit.* **2**: 25 (1790).

Isaria farinosa (Holmsk.) Fr., *Syst. Mycol.* **3**: 271 (1832); nom. sanct.

Corynoides farinosa (Holmsk.) Gray, *Nat. Arr. Brit. Pl.* **1**: 654 (1821).

Spicaria farinosa (Holmsk.) Vuill., *Bull. Soc. Mycol. France* **27**: 76 (1911).

Penicillium farinosum (Holmsk.) Biourge, *Cellule* **33**: 102 (1923).

Paecilomyces farinosus (Holmsk.) A.H.S. Br. & G. Sm., *Trans. Brit. Mycol. Soc.* **40**: 50 (1957).

Cordyceps fumosorosea (Wize) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820980

Basionym: *Isaria fumosorosea* Wize, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math. Nat.*: 721 (1905) ["1904"].

Synonyms: *Spicaria fumosorosea* (Wize) Vassiljevski, *Morbi Plant.* **18**:146 (1929).

Paecilomyces fumosoroseus (Wize) A.H.S. Br. & G. Sm., *Trans. Brit. Mycol. Soc.* **40**: 67 (1957).

Cordyceps ghanensis (Samson & H.C. Evans) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820981

Basionym: *Paecilomyces ghanensis* Samson & H.C. Evans, *Stud. Mycol.* **6**: 46 (1974).

Synonym: *Isaria ghanensis* (Samson & H.C. Evans) Samson & Hywel-Jones, *Mycol. Res.* **109**: 588 (2005).

Cordyceps javanica (Frieder. & Bally) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820982

Basionym: *Spicaria javanica* Frieder. & Bally, *Meded. Koffiebessenboeboek-Fonds* **6**: 146 (1923).

Synonyms: *Paecilomyces javanicus* (Frieder. & Bally) A.H.S. Br. & G. Sm., *Trans. Brit. Mycol. Soc.* **40**: 65 (1957).

Isaria javanica (Frieder. & Bally) Samson & Hywel-Jones, *Mycol. Res.* **109**: 588 (2005).

Cordyceps kintrischica (B.A. Borisov & Tarasov) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820983

Basionym: *Evlachovaea kintrischica* B.A. Borisov & Tarasov, *Mikol. Fitopatol.* **33**: 250 (1999).

Cordyceps locusticola (Z.Q. Liang *et al.*) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820984

Basionym: *Isaria locusticola* Z.Q. Liang *et al.*, *Mycotaxon* **105**: 31 (2008).

Cordyceps oncoperae (H.Y. Yip & A.C. Rath) P.J. Wright, *J. Invert. Path.* **64**: 146 (1994).

MycoBank MB363549

Basionym: *Microhilum oncoperae* H.Y. Yip & A.C. Rath, *J. Invert. Path.* **53**: 362 (1989).

Cordyceps poprawskii (Cabanillas *et al.*) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820985

Basionym: *Isaria poprawskii* Cabanillas *et al.*, *Mycoscience* **54**: 162 (2013).

Cordyceps tenuipes (Peck) Kepler, B. Shrestha & Spatafora, **comb. nov.**

MycoBank MB820986

Basionym: *Isaria tenuipes* Peck, *Ann. Rep. N.Y. St. Mus. Nat. Hist.* **31**: 44 (1879).

Synonyms: *Paecilomyces tenuipes* (Peck) Samson, *Stud. Mycol.* **6**: 49 (1974).

Cordyceps takaomontana Yakush. & Kumaz., *Sci. Rep. Tokyo Bunrika Daig.*, B **5**: 108 (1941).

Engyodontium de Hoog, *Persoonia* **10**: 53 (1978).

Type: *Engyodontium parvisporum* (Petch) de Hoog, *Persoonia* **10**: 53 (1978).

Engyodontium was erected by de Hoog (1978) to accommodate the type species, *E. parvisporum*, and *E. album*, the latter species was formerly classified in *Beauveria*, and most recently placed in *Parengyodontium* (see below). Gams *et al.* (1984) added four more species. The genus is restricted here to species with cobweb-like colonies that produce dense clusters of denticles on elongated rachides. Conidia are hyaline and globose to subglobose. No sexual reproductive morph has been linked to *Engyodontium*. Molecular phylogenetic analyses based on *E. araneum* support the distinction from *Beauveria*, but additional study of the type species is required. Species are isolated from soil and arthropod cadavers, and as opportunistic cutaneous and subcutaneous infections of animals including humans.

Gibellula Cava, *Atti Ist. Bot. R. Univ. Pavia*, 2 ser. **3**: 347 (1894).

Type: *Gibellula pulchra* Cava, *Atti Ist. Bot. Univ. Lab. Crittog. Pavia* **3**: 347 (1894).

The genus *Gibellula* is recognized here for spider-pathogenic fungi that produce primarily synnematus, aspergillus-like conidiophores with terminal vesicles, which give rise to phialides produced on metulae. Molecular phylogenies place all sampled *Gibellula* species in a single clade along with *Torrubiella*-like sexual morphs. *Torrubiella* has been shown to be polyphyletic, including astipitate taxa throughout *Cordycipitaceae* and *Hypocreales*. The status of *Torrubiella* is complicated further by the uncertain phylogenetic placement of the type species, *T. aranicida*. The original description indicated an asexual morphology that more closely approximates *Lecanicillium* or *Simplicillium*. Further, the production of scattered perithecia directly from the host, rather than aggregated on a subiculate pad, do not suggest inclusion of *Gibellula* in *Torrubiella*. Rather, the genus *Torrubiella* is regarded as a synonym of *Akanthomyces* here based on the perithecial arrangement and lack of a subiculum in the type specimen (discussed under *Akanthomyces*). The genus *Granulomanus*, based on *G. araneum* which is linked to the sexually typified *T. albolanata*, was regarded as a synonym of *Gibellula* by Humber & Rombach (1987), but no molecular data exist to confirm or refute this suggestion.

Gibellula arachnophila (Ditmar) Vuill., *Bull. Séanc. Soc. Sci. Nancy, sér. 3* **11**: 156 (1910).

Basionym: *Isaria arachnophila* Ditmar, in Sturm, *Deutschl. Fl.*, 3 Abt. (Pilze Deutschl.) **1**(4): tab. 55 (1817).

Synonyms: *Hymenostilbe arachnophila* (Ditmar) Petch, *Naturalist* (Hull) **56**: 249 (1931).

Synsterigmatocystis arachnophila Costantin ex Vuill., *Bull. Soc. Mycol. France* **27**: 81 (1911).

Gibellula arachnophila f. *macropus* Vuill., *Bull. Soc. Mycol. France* **36**: 41 (1920).

Torrubiella arachnophila f. *alba* Kobayasi & Shimizu, *Kew Bull.* **31**: 561 (1977).

Cordyceps arachnophila J.R. Johnst., *Bull. Puerto Rico Insula Exp. Sta.* **10**: 23 (1915).

Torrubiella arachnophila (J.R. Johnst.) Mains, *Mycologia* **42**: 316 (1950).

Gibellula araneorum P. Syd., *Just's Bot. Jahresber.* **57**: 321 (1922).

Synonym: *Torrubiella gibellulae* Petch, *Ann. Mycol.* **30**: 391 (1932).

Gibellula clavata Samson & H.C. Evans, *Mycologia* **84**: 306 (1992).

Synonym: *Torrubiella clavata* Samson & H.C. Evans, *Mycologia* **84**: 306 (1992).

Gibellula dabieshanensis B. Huang et al., *Mycosystema* **17**: 110 (1998).

Synonym: *Torrubiella dabieshanensis* B. Huang et al., *Mycosystema* **17**: 110 (1998).

Gibellula dimorpha Tzean et al., *Mycol. Res.* **102**: 1350 (1998).

Synonym: *Torrubiella dimorpha* Tzean et al., *Mycol. Res.* **102**: 1350 (1998).

Gibellula globosa Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo*, B **8**: 45 (1982).

Synonym: *Torrubiella globosa* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo*, B **8**: 45 (1982).

Gibellula globosostipitata Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo*, B **8**: 49 (1982).

Basionym: *Torrubiella globosostipitata* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo*, B **8**: 49 (1982).

Gibellula leiopus (Vuill. ex Maubl.) Mains, *Mycologia* **42**: 313 (1950).

Basionym: *Gibellula arachnophila* f. *leiopus* Vuill. ex Maubl., *Bull. Soc. Mycol. France* **36**: 42 (1920).

Torrubiella arachnophila var. *leiopus* Mains, *Mycologia* **42**: 318 (1950).

Torrubiella leiopus (Mains) Kobayasi & Shimizu, *Kew Bull.* **31**: 564 (1977); as "*pleiopus*".

Gibellula pulchra Cavara, *Atti Ist. bot. R. Univ. Pavia*, 2 sér. **3**: 347 (1894).

Synonyms: *Torrubiella arachnophila* var. *pulchra* Mains, *Mycologia* **42**: 316 (1950).

Torrubiella pulchra (Mains) Koval, *Klavitsipital'nye Griby SSSR*: 71 (1984).

Hevansia Luangsa-ard, Hywel-Jones & Spatafora, *gen. nov.*

Mycobank MB820885

Etymology: This genus is named for Harry C Evans and honours his invaluable contributions to our knowledge of insect associated fungi.

Diagnosis: *Hevansia* is the least inclusive genus-level clade that includes *H. novoguineensis* and *H. nelumboides*. *Hevansia* is diagnosed by the immersed perithecia, an *Akanthomyces*-like asexual morph, and parasitism on spiders.

Type: *Hevansia novoguineensis* (Samson & B.L. Brady) Luangsa-ard et al. 2017 (see below)

Description: *Sexual morph:* Stroma arising from dorsal abdomen, stipe 1–2 mm, fertile part ca 1 mm, white to cream, or in astipitate perithecial cushions surrounding host abdomen or sides of legs. *Perithecia* immersed, crowded at stipe apex or in cushions, few (<5) to numerous (30+), narrowly ovoid or sickle-shaped. *Asci* 8-spored, ascospores filiform, hyaline, whole, or disarticulating into part-spores.

Asexual morph: Stroma white, cream-yellow, brown or grey mycelium completely covering host. Synnemata erect, simple or branched, solitary to numerous, cylindrical to clavate, cream to ash-grey or brownish white. In some species 2–4 prominent synnemata up to 6 mm long interspersed with numerous tiny synnemata scattered over host. *Phialides* in a monolayer, sparsely scattered or crowded, on a basal cell or arising from lateral cells, usually single, occasionally two or three on lateral basal cell, smooth-walled, cylindrical, globose, obovoid, obpyriform or ellipsoid, terminating in short but distinct neck or tapering into a long neck. *Conidia* catenate, usually one-celled, smooth-walled, hyaline, clavate, cylindrical, cymbiform, fusiform to narrowly obclavate. *Colony* on PDA white front, reverse cream, orange to pale red, some species with pale wine-red pigment on the agar.

Hosts: On spiders on the underside of leaves of forest plants.

Distribution: Primarily in tropical regions globally, although specimens are known from temperate regions.

Commentary: A biphyletic split is observed among the astipitate species previously considered in *Torrubiella* with asexual morphs in *Gibellula* forming a clade of species pathogenic on spiders. Another clade includes species on spiders in the tropics, many of which were previously considered members of *Akanthomyces*. These species constitute the new genus *Hevansia* described here. Placement of the spider pathogen *C. nelumboides* in this genus demonstrates the diverse morphology of *Hevansia* species, as *C. nelumboides* produces perithecia in a disc sitting atop a well-formed stipe.

Hevansia arachnophila (Petch) Luangsa-ard, Hywel-Jones & Spatafora, *comb. nov.*

Mycobank MB820886

Basionym: *Trichosterigma arachnophilum* Petch, *Trans. Brit. Mycol. Soc.* **8**: 215 (1923); as "*arachnophila*".

Synonyms: *Hirsutella arachnophila* (Petch) Petch, *Trans. Brit. Mycol. Soc.* **9**: 93 (1923).

Akanthomyces arachnophilus (Petch) Samson & H.C. Evans, *Acta Bot. Neerl.* **23**: 33 (1974).

Torrubiella flava Petch, *Trans. Brit. Mycol. Soc.* **9**: 127 (1923).

Hevansia cinerea (Hywel-Jones) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820887

Basionym: *Akanthomyces cinereus* Hywel-Jones, *Mycol. Res.* **100**: 1068 (1996).

Hevansia koratensis (Hywel-Jones) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820888

Basionym: *Akanthomyces koratensis* Hywel-Jones, *Mycol. Res.* **100**: 1067 (1996).

Hevansia longispora (B. Huang *et al.*) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820889

Basionym: *Akanthomyces longisporus* B. Huang *et al.*, *Mycosystema* **19**: 172 (2000).

Hevansia nelumboides (Kobayasi & Shimizu) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820890

Basionym: *Cordyceps nelumboides* Kobayasi & Shimizu, *Kew Bull.* **31**: 557 (1977).

Hevansia novoguineensis (Samson & B.L. Brady) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820892

Basionym: *Akanthomyces novoguineensis* Samson & B.L. Brady, *Trans. Brit. Mycol. Soc.* **79**: 571 (1982).

Hevansia ovolongata (L.S. Hsieh *et al.*) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820893

Basionym: *Akanthomyces ovalongatus* L.S. Hsieh *et al.*, *Mycologia* **89**: 321 (1997).

Hevansia websteri (Hywel-Jones) Luangsa-ard, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB820894

Basionym: *Akanthomyces websteri* Hywel-Jones, *Mycol. Res.* **100**: 1068 (1996).

Hyperdermium J.F. White *et al.*, *Mycologia* **92**: 910 (2000).

Type: *Hyperdermium caulium* (Berk. & M.A. Curtis) Chaverri & K.T. Hodge, *Stud. Mycol.* **60**: 63 (2008) [syn. *H. bertonii* (Speg.) J.F. White *et al.*, *Mycologia* **92**: 910 (2000)].

Hyperdermium was erected by Sullivan *et al.* (2000) for *Epichloë bertonii* and *H. pulvinatum*, which parasitize scale insects in the tropics. Stromata are flattened or pulvinate and vary in colour from white to orange. Perithecia are immersed to sub-immersed with asci and ascospores characteristic of *Cordycipitaceae*, but are unique in producing multiseptate conidia. *Hyperdermium bertonii*, the type species of the

genus, was found to have an earlier epithet, so the name was corrected to *H. caulium* by Chaverri *et al.* (2008). In these analyses *H. caulium*, with *C. piperis*, is placed in an unresolved position.

Parengyodontium C.C. Tsang *et al.*, *Med. Mycol.* **54**: 708 (2016).

Type: *Parengyodontium album* (Limber) C.C. Tsang *et al.*, *Med. Mycol.* **54**: 709 (2016).

Based on molecular phylogenetic analyses, *Parengyodontium* was erected by Tsang *et al.* (2016) to recognize *Engyodontium album* as a distinct taxon relative to *E. parvisporum*. To date it is a monotypic genus.

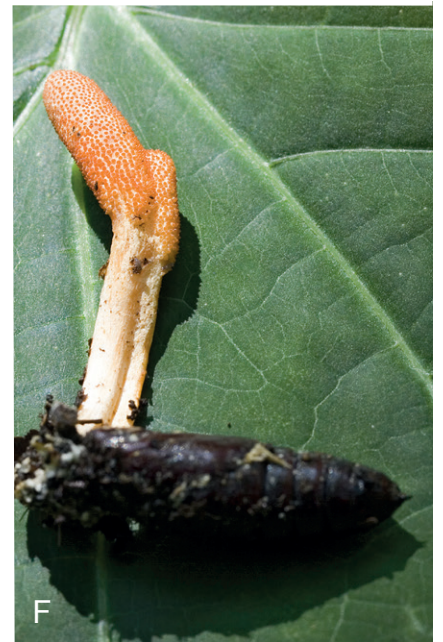
Simplicillium W. Gams & Zare, *Nova Hedwigia* **73**: 38 (2001).

Type: *Simplicillium lanosiniveum* (J.F.H. Beyma) Zare & W. Gams, *Nova Hedwigia* **73**: 39 (2001).

Simplicillium includes species isolated from other fungi and soil environments (Zare & Gams 2001, Nonaka *et al.* 2013). Current phylogenetic analyses resolve *Simplicillium* as the earliest diverging lineage in *Cordycipitaceae* (Fig. 1). *Simplicillium* species are morphologically reduced, producing conidia on the tips of long, slender, solitary phialides. No sexual forms have been associated with *Simplicillium*.

CONCLUSIONS

In this paper we used a multigene phylogeny (Fig. 1) to guide a taxonomic revision of *Cordycipitaceae* in compliance with changes to Art. 9 of the ICN to no longer permit the separate naming of fungal morphs (McNeill *et al.* 2012). The resulting analysis provides the basis for recognition of 11 genera in *Cordycipitaceae* regardless of life-stage or the associated morphological differences (Fig. 3). The generic name *Cordyceps* is retained, and we sought to circumscribe that genus in the most inclusive way possible. The ex-epitype isolate of the type of *Isaria*, *I. farinosa*, is nested within *Cordyceps*, yet we recommend the rejection of *Isaria*, to avoid further splitting of *Cordyceps*. Here, *Beauveria* includes the traditional species known from asexual morphs, but also several taxa previously described for sexual morphs in *Cordyceps* and a new sexually typified species described here. Our approach allows continuity for the use of names of taxa important for biocontrol and historical concepts of diversity for the group. We propose to use the name *Gibellula* for a clade of spider pathogens, rather than *Torrubiella*. This decision is based on morphology of the type species, *T. arancida*, which includes superficial perithecia produced in a scattered manner, and not on a subiculum, and an asexual morph described as more similar to *Akanthomyces* than *Gibellula*. *Akanthomyces* has priority over *Torrubiella*, although we cannot discount a phylogenetic affinity of *Torrubiella* to *T. wallacei* or *Simplicillium*. Therefore, we recommend the rejection of *Torrubiella* against *Akanthomyces*. Finally, the use of *Lecanicillium* is resolved.



The type, *L. lecanii*, is nested within *Akanthomyces*, which has priority over *Lecanicillium*. We classify several species of *Lecanicillium* in *Akanthomyces*. *Lecanicillium psalliotae* and *L. fusisporum* do not show a strong affinity with other species previously placed in *Lecanicillium* nor with any other clade in *Cordycipitaceae*, so these species cannot yet be placed in any named genera.

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Fig. 3. Representative taxa for *Cordycipitaceae*. **A.** *Isaria* sp. CEM 1729). **B.** *Torrubiella arachnophila* (rmk 12-001). **C.** *Cordyceps bifusispora* (CEM 1615). **D.** *Cordyceps confragosa* (CEM 1633). **E.** *Isaria tenuipes* (CEM 1032). **F.** *Cordyceps militaris* (CEM 740). **G.** *Cordyceps rosea* (CEM 1734). **H.** *Cordyceps cf. cardinalis* (CEM 1733). **I.** *Cordyceps takaomontana* with co-occurring *I. tenuipes* (CEM 1954). **J.** *Cordyceps nelumboides* (TNS 16306). Images not to scale.

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