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, Ascopolyphorus, Beauveria, Cordyceps, Engyodontium, Gibellula, Hyperdermium, Parengyodontium, and Simplicillium and the rejection of eight generic names, Evlachovaea, Granulomanus, Isaria, Lecanicillium, Microhilum, Phytocordyceps, Synsterigmatocystis, and Torrubia. Two new generic names, Hevansia and Blackwellomyces, and a new species, Beauveria blattidiocila, are described. New combinations are also proposed in the genera Akanthomyces, Beauveria, Blackwellomyces, and Hevansia.

Key words: Akanthomyces Ascopolyphorus Beauveria Blackwellomyces Cordyceps Dual nomenclature Engyodontium Gibellula Hevansia Hyperdermium Parengyodontium Simplicillium

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 Cordycipitaceae were not monophyletic. Two additional families, Cordycipitaceae and Ophiocordycipitaceae, were recognized and species previously classified in Cordycipitaceae 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 Torrubia. Torrubia 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 Torrubia being placed in Cordyceps and...
Ophiocordyceps (Ophiocordycipitaceae) as well as the new genera Conoideocrella and Orbiocrella of Clavicipitaceae. Torrubiola is now restricted to Cordycipitaceae producing spores 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 Ascopoly porous and Hyperdermium, but these differ from Torrubiola 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 Cordycps (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 erythroploia (Luangsa-ard et al. 2007). 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 conidigenous 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., hyalophoric conidia, insect pathogenicity; Rehner et al. 2011). The genus is highly diverse, with many cryptic species, and links to several sexually typified species in Cordycps (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 Eulachovaea, Engyodontium, and Parengyodontium. A molecular investigation of Eulachovaea 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 Cordycps (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. kyusuensis (Sung et al. 2007).

Several asexually typified genera are associated with Torrubiola, 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. Cordycps 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 Ophiocordyceps 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 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, Ascopolyergus, Beauveria, Cordyceps, Engyodontium, Gibellula, Hyperdermium, and Simplicillium. Parengrindontium 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. biatildicola, 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. pistillariformis (Samson & Evans 1974). Other fungi in this clade include C. coccidioperithecata and C. confarosa, pathogens of spiders and scales insects, respectively, which produce torrubiolliid perithecia (Kobayasi & Shimizu 1982). The production of superficial perithecia on a stipe distinguishes C. coccidioperithecata from other sexual forms infecting spiders in Cordycipitaceae, which either lack a stipe or lack superficial perithecia if a stipe is present. Cordycepstragosa was described by Mains (1949) in Torrubiella, and while the morphology is torrubiollioid, Akanthomyces has taxonomic priority by date over Torrubiella (Boudier 1885). In addition, the sexual morph C. confarosa is linked to Lecanicillium lecanii, the type species of Lecanicillium, now considered a synonym of Akanthomyces, which has priority over Lecanicillium (Gams & Zare 2001). Chirivi-Salomón et al. (2015) also showed that L. lecanii (as C. confarosa) 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. | (=) *Torrubiella* Boud. in Rev Mycol. (Toulouse) 7: 226. 1885. |
| Typus: *Akanthomyces aculeatus* Lebert 1858.             | Typus: *T. aranicida* Boud. 1885.                       |
|                                                          | (=) *Lecanicillium* W. Gams & Zare in Nova Hedwigia 72: 50. 2001. |
|                                                          | Typus: *L. lecanii* (Zimm.) Zare & W. Gams 2001, now regarded as *Akanthomyces lecanii* (Zimm.) Spatafora et al. 2017. |
| **Ascopolyposum** Möller in Bot. Mitt. Tropen 9: 300. 1901. |                                                         |
| Typus: *Ascopolyposum polychrous* Möller 1901.           |                                                         |
| **Beauveria** Vuill. in Bull. Soc. Bot. France. 59: 40. 1912. |                                                         |
| Typus: *Beauveria bassiana* (Bals.-Criv.) Vuill. 1912 (Botrytis bassiana Bals.-Criv. 1835). |                                                         |
| **Blackwellomyces** Spatafora & Luangsa-ard in IMA Fungus 8: 345. 2017. |                                                         |
| Typus: *Blackwelliella cardinalis* (G.H. Sung & Spatafora) Spatafora & Luangsa-ard 2017 (Cordyceps cardinalis G.H. Sung & Spatafora 2004) |                                                         |
| **Cordyceps** Fr., Observ. Mycol. 2: 316 [cancellans]] 1818, nom. cons. | (=) *Isaria* Pers. in Neues Mag. Bot. 1: 121. 1794. |
| Typus: *Cordyceps militaris* (L.) Fr. 1818 (Clavaria militaris L.1753). | Typus: *I. farinosa* (Holmsk.) Fr. 1832, now regarded as *Cordyceps farinosa* (Holmsk.) Kepler et al. 2017. |
|                                                          | (=) *Microhilum* H.Y. Yip & A.C. Rath in J. Invert. Path. 53: 361. 1989. |
|                                                          | Typus: *M. oncope aerae* H.Y. Yip & A.C. Rath 1989, now regarded as *Cordyceps oncope aerae* (H.Y. Yip & A.C. Rath) Kepler et al. 2017. |
|                                                          | (=) *Phytocordyceps* C.H. Su & H.H. Wang in Mycotaxon 26: 338. 1986. |
|                                                          | Typus: *P. ninchukispora* C.H. Su & H.H. Wang 1986. now regarded as *Cordyceps ninchukispora* (C.H. Su & H.H. Wang) G.H. Sung et al. 2007. |
|                                                          | (=) *Evlachovaea* Borisov & Tarasov in Mikol. Fitopatol. 33: 250. 1999. |
|                                                          | Typus: *E. kintrischica* B.A. Borisov & Tarasov 1999, now regarded as *Cordyceps kintrischica* (B.A. Borisov & Tarasov) Kepler et al. 2017. |
| **Engyodontium** de Hoog in Persoonia 10: 53. 1978. |                                                          |
| Typus: *Engyodontium parvisporum* (Petch) de Hoog 1978 (Rhinotrichum parvispora Petch 1932). |                                                          |
| **Gibellula** Cavara in Atti Ist. Bot. R. Univ. Pavia, ser. 2 3: 347. 1894. | (=) *Synsterigmatocystis* Costantin in Bull. Soc. Mycol. France 4: 63. 1888. |
| Typus: *Gibellula pulchra* Cavara 1894. | Typus: *S. arachnophila* Costantin ex Vuill. 1888, now regarded as *Gibellula arachnophila* (Ditm) Vuill. 1910. |
|                                                          | (=) *Granulomanus* de Hoog & Samson in Persoonia 10: 70. 1978. |
|                                                          | Typus: *G. aranearum* (Petch) de Hoog & Samson 1978, basionym: *Cylindrophora aranearum* Petch 1944. |
| **Hevansia** Luangsa-ard, Hywel-Jones & Spatafora in IMA Fungus 8: 348. 2017. |                                                          |
| Typus: *Hevansia novoguineensis* (Samson & B.L. Brady) Luangsa-ard, Hywel-Jones & Spatafora 2017 (*Akanthomyces novoguineensis* Samson & B.L. Brady 1982). |                                                          |
| **Hyperdermium** J.F. White et al. in Mycologia 92: 910. 2000. |                                                          |
| Typus: *Hyperdermium caulium* (Berk. & M.A. Curtis) Chaverri & K.T. Hodge 2008 (Corticium caulium Berk. & M.A. Curtis 1853 [1854]). |                                                          |
| **Parengyodontium** C.C. Tsang et al. in Medical Mycology 54: 708. 2016. |                                                          |
| Typus: *Parengyodontium album* (Limber) C.C. Tsang et al. 2016 (Tritirachium album Limber 1940). |                                                          |
| **Simplicillium** W. Gams & Zare in Nova Hedwigia 73: 38. 2001. |                                                          |
| Typus: *Simplicillium lanosiniveum* (J.F.H. Beyma) Zare & W. Gams 2001 (Phalosporium lanosoniveum J.F.H. Beyma 1942). |                                                          |
Phylogeny and nomenclature of Cordycipitaceae

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       |
|------------------------------|------------|---------------|---------------|----------|------------|------------|
| Akanthomyces aculeatus       | HUA 186145 | MF416572      | MF416520      | MF41645  |            |            |
| Akanthomyces arachnophilus   | NHJ 10469  | EU369090      | EU369031      | EU36908  | EU369047   |            |
| Akanthomyces cinereus        | NHJ 3510   | EU369091      | EU369009      | EU369048 | EU369070   |            |
| Akanthomyces novoguineensis  | NHJ 13117  | EU369092      | EU369010      | EU369049 | EU369073   |            |
| Akanthomyces novoguineensis  | NHJ 13161  | EU369093      | EU369011      | EU369050 |            |            |
| Akanthomyces novoguineensis  | NHJ 4314   | EU369094      | EU369012      | EU369051 | EU369071   |            |
| Akanthomyces novoguineensis  | NHJ 11923  | EU369095      | EU369013      | EU369052 | EU369072   |            |
| Akanthomyces pistillariaeformis | HUA 186131 | MF416573     | MF416521      | MF41646  |            |            |
| Ascoscylops polychaetus      | P.C. 546   | DQ118737      | DQ118745      | DQ127236 |            |            |
| Ascoscylops polychaetus      | ARSEF 6355 | AY886544      | DQ118750      | DQ127241 |            |            |
| Beauveria bassiana           | ARSEF 1564 |              |              |          |            |            |
| Beauveria blattidicola       | MCA 172    | MF416593      | MF416539      | MF41648  | MF416640   | MF416464   |
| Beauveria blattidicola       | MCA 1814   | MF416594      | MF416540      | MF41648  | MF416641   |            |
| Beauveria brongniarii        | ARSEF 617  |              |              |          |            |            |
| Beauveria caledonica         | ARSEF 2567 | AF339570      | AF339520      | EF46905  | EF469086   |            |
| Beauveria malawiensis        | ARSEF 7760 |              |              |          |            |            |
| Beauveria pseudobassiana     | ARSEF 3405 | AY531931      |              | HQ88096  | HQ880969   | HQ880936   |
| Cordyceps acridophila        | MCA 1181   | MF416574      | MF416522      | MF41662  |            |            |
| Cordyceps acridophila        | HUA 179220 | JQ989527      | JQ989536      | JQ98614  | JX003852   | JX003842   |
| Cordyceps acridophila        | HUA 179219 | JQ989541      | JQ985613      | JX00385  | JX003841   |            |
| Cordyceps acridophila        | HUA 179221 | JQ989526      | JQ958615      | JX00385  | JX003843   |            |
| Cordyceps albocinctin        | spat 07-174 | MF416575      |              | MF41646  | MF416629   |            |
| Cordyceps bifusispora        | EFCC 5690  | EF468952      | EF468806      | EF46874  | EF468854   | EF468909   |
| Cordyceps bifusispora        | EFCC 8260  | EF468953      | EF468807      | EF46874  | EF468855   | EF468910   |
| Cordyceps bifusispora        | spat 08-129 | MF416576      | MF416523      | MF41663  | MF416630   |            |
| Cordyceps bifusispora        | spat 08-133,1 | MF416577 | MF416524      | MF41649  | MF416631   | MF416434   |
| Cordyceps brongniarii        | BCC 16858  | JF415951      | JF415967      | JF16009  | JN049885   | JF15991    |
| Cordyceps caloceroides       | MCA 2249   | MF416578      | MF416525      | MF41647  | MF416632   |            |
| Cordyceps caloceroides       | QCNE 18671 5 | MF416579 | MF416526      |            |            |            |
| Cordyceps cardinalis         | OSC 93609  | AY184973      | AY184962      | DQ52235  | DQ522370   | DQ52242    |
| Cordyceps cardinalis         | OSC 93610  | AY184974      | AY184963      | EF46905  | EF469088   | EF469106   |
| Cordyceps cf. cardinalis     | spat 09-052 | MF416580      | MF416527      | MF41647  | MF416633   | MF416435   |
| Cordyceps cf. ochraceostromata | ARSEF 5691 | EF468964      | EF468819      | EF46875  | EF468867   | EF468921   |
| Cordyceps cf. pruniosa       | spat 08-115 | MF416586      | MF416532      | MF41647  | MF416635   | MF416439   |
| Cordyceps cf. pruniosa       | spat 09-021 | MF416587      | MF416533      | MF41647  | MF416636   | MF41639    |
| Cordyceps cf. takaomontiana  | NHJ 12623  | EF468984      | EF468838      | EF46877  | EF468884   | EF468932   |
| Cordyceps cf. takaomontiana  | BCC 12688  | MF416599      | MF416545      | MF41648  | MF416646   |            |
| Cordyceps coccidoperitheciata | NHJ 5112   | EU369109      | EU369043      | EU36902  | EU369066   |            |
| Cordyceps coccidoperitheciata | NHJ 6709   | EU369110      | EU369042      | EU369025 | EU369067   | EU369086   |
| Cordyceps confragosa         | spat 08-146 | MF416581      | MF416528      | MF41647  | MF416634   | MF416436   |
| Cordyceps diapheromeriphipha  | MCA 1557   | MF416582      | MF416529      |            |            |            |
Table 2. (Continued).

| Species                    | Collection | nrSSU   | nrLSU   | TEF       | RPB1       | RPB2       |
|----------------------------|------------|---------|---------|-----------|------------|------------|
| Cordyceps diapheromeriphila| QCNE 186714| MF416601| MF416547| MF416491  | MF416648   |            |
| Cordyceps diapheromeriphila| QCNE 186272| JQ985530| JQ985534| JQ958610  | JX003848   |            |
| Cordyceps exasperata        | MCA 2155   | MF416596| MF416542| MF416486  | MF416643   |            |
| Cordyceps exasperata        | MCA 2288   | MF416592| MF416538| MF416482  | MF416639   |            |
| Cordyceps kyusyuensis       | EFCC 5886  | EF468960| EF468813| EF468754  | EF468863   | EF468917   |
| Cordyceps locustiphila      | HUA 179218 | JQ985525| JQ985535| JQ958619  | JX003846   | JX003845   |
| Cordyceps locustiphila      | HUA 179219 | JQ958598| JQ958597|           |            |            |
| Cordyceps militaris         | OSC 93623  | AY184977| AY184966| DQ522332  | DQ522377   | AY545732   |
| Cordyceps nelumboides       | BCC 2190   | MF416583| MF416530| MF416473  | MF416437   |            |
| Cordyceps nelumboides       | TNS 16306  | MF416585| MF416475| MF416475  | MF416438   |            |
| Cordyceps ninchukispora     | EFCC 5197  | EF468965| EF468820| EF468760  | EF468868   |            |
| Cordyceps ninchukispora     | EFCC 5693  | EF468966| EF468821| EF468762  | EF468869   |            |
| Cordyceps ninchukispora     | NHJ 10627  | IEF468967| IEF468822| IEF468870 | IEF468870  |            |
| Cordyceps ninchukispora     | NHJ 10684  | EF468968| EF468823| EF468761  | EF468871   |            |
| Cordyceps ninchukispora     | EGS 38.165 | EF468991| EF468846| EF468795  | EF468900   |            |
| Cordyceps ninchukispora     | EGS 38.166 | EF468992| EF468847| EF468794  | EF468901   |            |
| Cordyceps piperis           | CBS 116719 | AY66442 | DQ118749| DQ127240  | EU369083   |            |
| Cordyceps polyarthra        | MCA 996    | MF416597| MF416543| MF416487  | MF416644   |            |
| Cordyceps polyarthra        | MCA 1009   | MF416598| MF416544| MF416488  | MF416645   |            |
| Cordyceps pseudomilitaris   | BCC 1919   | MF416588| MF416534| MF416478  | MF416440   |            |
| Cordyceps pseudomilitaris   | BCC 2091   | MF416589| MF416535| MF416479  | MF416441   |            |
| Cordyceps rosea             | spat 09-053| MF416590| MF416536| MF416480  | MF416637   | MF416442   |
| Cordyceps scarabaeicola     | ARSEF 5689 | AF339574| AF339524| DQ522335  | DQ522380   | DQ522431   |
| Cordyceps sp.               | EFCC 2535  | EF468980| EF468835| EF468772   |            |            |
| Cordyceps sp.               | RCEF HP090724-04C | MF416591| MF416537| MF416481  | MF416638   | MF416443   |
| Cordyceps staphylindicola   | ARSEF 5718 | EF468981| EF468836| EF468776  | EF468881   |            |
| Cordyceps takaomontana      | MCA 1806   | MF416595| MF416541| MF416485  | MF416642   |            |
| Cordyceps tuberculata       | OSC 111002 | DQ522553| DQ518767| DQ522338  | DQ522384   | DQ522435   |
| Cordyceps tuberculata       | BCC 16819  | MF416600| MF416546| MF416490  | MF416647   | MF416444   |
| Engyodontium aranearum      | CBS 309.85 | AF339576| AF339526| DQ522341  | DQ522380   | DQ522439   |
| Evlavochaeva kirschina      | ARSEF 7218 | GU734751|          |            |            |            |
| Evlavochaeva kirschina      | ARSEF 8058 | GU734750|          |            |            |            |
| Gibellula leipus            | BCC 16025  | MF416602| MF416548| MF416492  | MF416649   |            |
| Gibellula longispora        | NHJ 12014  | EU369099| EU369017| EU369055  | EU369075   |            |
| Gibellula pulchra           | NHJ 10808  | EU369099| EU369035| EU369018  | EU369056   | EU369076   |
| Gibellula sp.               | NHJ 10788  | EU369101| EU369036| EU369019  | EU369058   | EU369078   |
| Gibellula sp.               | NHJ 13158  | EU369100| EU369037| EU369020  | EU369057   | EU369077   |
| Gibellula sp.               | NHJ 5401   | EU369102| EU369059| EU369059  | EU369079   |            |
| Hyperdermium caulium        | GenBank    | AF242354|          |            |            |            |
| Hyperdermium pulvinatum     | P.C. 602   | DQ118738| DQ118746| DQ127237  |            |            |
| Isaria amoenerosea          | CBS 107.73 | AY526464| MF416550| MF416494  | MF416651   | MF416445   |
| Isaria amoenerosea          | CBS 729.73 | MF416604| MF416551| MF416495  | MF416652   | MF416446   |
| Isaria cf. farinosa         | OSC 111004 | EF468986| EF468840| EF468780  | EF468886   |            |
| Isaria cicadae              | RCEF HP090724-31 | MF416605| MF416552| MF416496  | MF416653   | MF416447   |
### Table 2. (Continued).

| Species              | Collection | nrSSU        | nrLSU        | TEF         | RPB1       | RPB2       |
|----------------------|------------|--------------|--------------|-------------|------------|------------|
| Isaria coleopterorum | CBS 110.73 | JF415965     | JF415988     | JF416028    | JN049903   | JF416006   |
| Isaria farinosa      | OSC 11005  | DG522558     | DG518772     | DG522348    | DG522394   |            |
| Isaria farinosa      | OSC 11106  | EF469127     | EF469080     | EF469065    | EF469094   |            |
| Isaria farinosa      | CBS 240.32 | JF415958     | JF415979     | JF416019    | JN049895   | JF415999   |
| Isaria farinosa      | CBS 262.58 | AB082394     | AB080087     | MF416497    | MF416564   | MF416448   |
| Isaria farinosa      | CBS 541.81 | MF416606     | MF416553     | MF416498    | MF416555   | MF416449   |
| Isaria farinosa      | CBS 111113 | AY526474     | MF416554     | MF416499    | MF416566   | MF416545   |
| Isaria fumosorosea   | CBS 337.52 | MF416607     | MF416555     | MF416500    | MF416557   | MF416451   |
| Isaria fumosorosea   | CBS 375.70 | DQ522558     | DQ522348     | DQ522395    | DQ522449   |            |
| Isaria fumosorosea   | CBS 107.10 | DQ522350     | DQ522396     | DQ522450    |            |            |
| Isaria fumosorosea   | CBS 244.31 | AB080305     | AB080303     | AB080305    | MF416501   | EF469887   | EF469394   |
| Isaria fumosorosea   | CBS 262.58 | DQ522350     | DQ522396     | DQ522450    |            |            |
| Isaria javanica      | CBS 134.22 | AY526474     | MF416554     | MF416502    | MF416560   | MF416545   |
| Isaria sp.           | TNS 16333  | MF416616     | MF416505     | MF416662    | MF416546   |            |
| Isaria sp.           | spat 09-050| MF416613     | MF416559     | MF416563    | MF416547   |            |
| Isaria sp.           | spat 09-051| MF416614     | MF416560     | MF416564    | MF416548   |            |
| Isaria tenuepis      | OSC 11106  | DG522559     | DG518772     | DG522349    | DG522395   | DG522449   |
| Isaria tenuepis      | ARSEF 5135 | MF416612     | MF416506     | MF416505    | MF416662   | MF416546   |
| Lecanicillium antillanum | CBS 350.85 | AF339585     | AF339536     | DG522350    | DG522396   | DG522450   |
| Lecanicillium aranearum | CBS 726.73a | AF339586     | AF339537     | EF468781    | EF468878   | EF468394   |
| Lecanicillium attenuatum | CBS 402.78 | AF339614     | AF339565     | EF468782    | EF468888   | EF468935   |
| Lecanicillium fusisorum | CBS 164.7  | AF339598     | AF339549     | EF468783    | EF468889   |            |
| Lecanicillium lecanii | CBS 101247 | AF339604     | AF339555     | DQ522359    | DQ522407   | DQ522468   |
| Lecanicillium psalliota | CBS 532.81 | AF339609     | AF339560     | EF469067    | EF469096   | EF469112   |
| Lecanicillium psalliota | CBS 101270 | EF469128     | EF469081     | EF469066    | EF469095   | EF469113   |
| Lecanicillium psalliota | CBS 363.86 | AF339608     | AF339559     | EF468784    | EF468890   |            |
| Mariannaea pruinosa  | ARSEF 5413 | AY184979     | AY184968     | DQ522351    | DQ522397   | DQ522451   |
| Microhilitum oncoperae | AFSEF 4358 | AF339581     | AF339532     | EF468785    | EF468891   | EF468936   |
| Simplicillium lamellicola | CBS 116.25 | AF339601     | AF339552     | DQ522356    | DQ522404   | DQ522462   |
| Simplicillium lanosoniveum | CBS 101267 | AF339603     | AF339554     | DQ522357    | DQ522405   | DQ522463   |
| Simplicillium lanosoniveum | CBS 704.86 | AF339602     | AF339553     | DQ522358    | DQ522406   | DQ522464   |
| Simplicillium obclavatum | CBS 311.74 | AF339567     | AF339517     | EF468798    |            |            |
| Torrubiella ratticaudata | ARSEF 1915 | DQ522562     | DQ518777     | DQ522360    | DQ522408   | DQ522467   |
| Torrubiella wallacei  | NHU 7859   | EU369107     | EU369064     | EU369085    |            |            |
| Verticillium 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. aranicida*, known from a spider in France, was not available for inclusion in molecular phylogenetic analyses. However, several morphological characteristics of *T. aranicida* 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 coccidiopertheciata Kobayasi & Shimizu, *Bull. Natl. Sci. Mus. Tokyo, B* 8: 79 (1982).
Akanthomyces dipterigenus (Petch) Spatafora, Kepler, Zare & B. Shrestha, *comb. nov.*
MycoBank MB8223235

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

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

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

*Akanthomyces muscarium* (Petch) Spatafora, Kepler & B. Shrestha, *comb. nov.*
MycoBank MB820861

*Basionym:* Cephalosporium muscarium Petch, *Teysmannia* **9:** 241 (1899).

*Synonyms:* Verticillium muscarium (Petch) Viégas, *Revue Inst. Café Este São Paulo* **14:** 754 (1939).

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

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

*Cordycipitaceae* 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 lecanii (Zimm.) Spatafora, Kepler & B. Shrestha, *comb. nov.*
MycoBank MB820862

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

*Synonyms:* Verticillium lecanii (Zimm.) Zare & W. Gams, *Nova Hedwigia* **73:** 13 (2001).

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

*Verticillium hemileiae* Bourquiæt, *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:* Lecanicipitum 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:* Cordycipitaceae tuberculata (Lebert) Maires, *Bull. Soc. Hist. Nat. Afrique N.* **8:** 165 (1917).

*Isaria pistillariformis* Pat., *Bull. Soc. Mycol. Fr.* **9:** 163 (1893); as "pistillariaiformis".

Insecticolia pistillariformis (Pat.) Mains, *Mycologia* **42:** 579 (1950); as "pistillariaiformis".

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

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

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

Ascopolyporus is a genus containing seven species, represented in this study by the type *A. polychronus* 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 *Hypocrellales* or *Moelleriella* in *Clavicipitaceae*. Ascopolyrupor species produce multisepate conidia, a feature also found in *Hyperdermium*. Ascopolyporus shares another characteristic with some species in *Hypocrellales* 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 *Cordycipitaceae* 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 *Cordycipitaceae* share another characteristic 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 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 *Phasmadoidea*, 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:* Cordycipitaceae acridophila T. Sanjuan & Franco-Mol., *Mycologia* **106:** 268 (2014).
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 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 “staphylinidaecola”.

Blackwellomyces Spatafora & Luangs-aard, 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 & Luangs-aard 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. Ascii 8-spored, hyaline, cylindrical, possessing a prominent apex. Ascospores smooth, filiform, hyaline, irregularly multisepitate, 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 & Luangs-aard, comb. nov. MycoBank MB820865
Basionym: Cordyceps cardinalis G.H. Sung & Spatafora, Mycologia 96: 660 (2004).

Blackwellomyces pseudomilitaris (Hywel-Jones & Sivichai) Spatafora & Luangs-aard, comb. nov. MycoBank MB820866
Basionym: Cordyceps pseudomilitaris Hywel-Jones & Sivichai, Mycol. Res. 98: 940 (1994).

Cordyceps Fr., Observ. Mycol. 2: 316 [cancellars] (1818), nom. cons.
Type: Cordyceps militaris (L.) Fr., Observ. Mycol. 2: 317 [cancellars] (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 Evlachovaeae, 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, Entomophora, Isaria (see below). Similarly, the type species 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 Evlachovaeae, E. kirnitschicha, 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 (Holmskjold 1781). Gams et al. (2005) proposed the use of Isaria for Paecilomyces sect. Isariaeoidae, now also regarded as a synonym of Cordyceps. Entomogenous species morphologically similar to Isaria can be found distributed throughout Hypocreales (Luangsara-ard et al. 2004), and here are shown to be polyphyletic within Cordycipitaceae. The ex-epitope 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 Hann., 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 "coleopterora".

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: Cliaria 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: Spica 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: Spica javanica Frieder. & Bally, Meded. Koffiebessenboebok-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 takamontana 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. aranearum 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 Cavara, Atti Ist. Bot. R. Univ. Pavia, 2 ser. 3: 347 (1894).
Type: Gibellula pulchra Cavara, Atti Ist. Bot. Univ. Lab. Crittog. Pavia 3: 347 (1894).

The genus Gibellula is recognized here for spider-pathogenic fungi that produce primarily synnematous, 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 Cordycepiaceae 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 Lecanicularia or Simplicillium. Further, the production of scattered perithecia directly from the host, rather than aggregated on a subiculum 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. aranearum 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).
Cordycps arachnophila J.R. Johnst., Bull. Puerto Rico Insula Exp. Sta. 10: 23 (1915).
Torrubiella arachnophila (J.R. Johnst.) Mains, Mycologia 42: 316 (1950).

Gibellula aranearum 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., Mycosestema 17: 110 (1998).
Synonym: Torrubiella dabieshanensis B. Huang et al., Mycosistema 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.
Hevansia arachnophila (Petch) Luangsa-ard, 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 desdicarting 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).

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

Type: Hyperdermium caulium (Limber) C.C. Tsang et al., Med. Mycol. 54: 708 (2016).

Based on molecular phylogenetic analyses, Hyperdermium 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 lanosinum (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. aranicida, 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 *Lecanicillum*. We classify several species of *Lecanicillum* in *Akanthomyces*. *Lecanicillum psalliota* and *L. fusisporum* do not show a strong affinity with other species previously placed in *Lecanicillum* 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 confroagosa* (CEM 1633). E. *Isaria tenuepis* (CEM 1032). F. *Cordyceps militaris* (CEM 740). G. *Cordyceps rosea* (CEM 1734). H. *Cordyceps cf. cardinallis* (CEM 1733). I. *Cordyceps takaomontana* with co-occurring *I. tenuepis* (CEM 1954). J. *Cordyceps relumboides* (TNS 16306). Images not to scale.
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