

Phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi

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Abstract: *Cordyceps*, comprising over 400 species, was historically classified in the *Clavicipitaceae*, based on cylindrical asci, thickened ascus apices and filiform ascospores, which often disarticulate into part-spores. *Cordyceps* was characterized by the production of well-developed often stipitate stromata and an ecology as a pathogen of arthropods and *Elaphomyces* with infrageneric classifications emphasizing arrangement of perithecia, ascospore morphology and host affiliation. To refine the classification of *Cordyceps* and the *Clavicipitaceae*, the phylogenetic relationships of 162 taxa were estimated based on analyses consisting of five to seven loci, including the nuclear ribosomal small and large subunits (*nrSSU* and *nrLSU*), the elongation factor 1 α (*tef1*), the largest and the second largest subunits of RNA polymerase II (*rpb1* and *rpb2*), β -tubulin (*tub*), and mitochondrial ATP6 (*atp6*). Our results strongly support the existence of three clavicipitaceous clades and reject the monophyly of both *Cordyceps* and *Clavicipitaceae*. Most diagnostic characters used in current classifications of *Cordyceps* (e.g., arrangement of perithecia, ascospore fragmentation, etc.) were not supported as being phylogenetically informative; the characters that were most consistent with the phylogeny were texture, pigmentation and morphology of stromata. Therefore, we revise the taxonomy of *Cordyceps* and the *Clavicipitaceae* to be consistent with the multi-gene phylogeny. The family *Cordycipitaceae* is validated based on the type of *Cordyceps*, *C. militaris*, and includes most *Cordyceps* species that possess brightly coloured, fleshy stromata. The new family *Ophiocordycipitaceae* is proposed based on *Ophiocordyceps* Petch, which we emend. The majority of species in this family produce darkly pigmented, tough to pliant stromata that often possess aperithecial apices. The new genus *Elaphocordyceps* is proposed for a subclade of the *Ophiocordycipitaceae*, which includes all species of *Cordyceps* that parasitize the fungal genus *Elaphomyces* and some closely related species that parasitize arthropods. The family *Clavicipitaceae* s. s. is emended and includes the core clade of grass symbionts (e.g., *Balansia*, *Claviceps*, *Epichloë*, etc.), and the entomopathogenic genus *Hypocrella* and relatives. In addition, the new genus *Metacordyceps* is proposed for *Cordyceps* species that are closely related to the grass symbionts in the *Clavicipitaceae* s. s. *Metacordyceps* includes teleomorphs linked to *Metarhizium* and other closely related anamorphs. Two new species are described, and lists of accepted names for species in *Cordyceps*, *Elaphocordyceps*, *Metacordyceps* and *Ophiocordyceps* are provided.

Taxonomic novelties: **New family:** *Ophiocordycipitaceae* G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. **New genera:** *Elaphocordyceps* G.H. Sung & Spatafora, *Metacordyceps* G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora. **New species:** *Metacordyceps yongmunensis* G.H. Sung, J.M. Sung & Spatafora; *Ophiocordyceps communis* Hywel-Jones & Samson. **New combinations:** *Cordyceps confragosa* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *C. ninchukispora* (C.H. Su & H.-H. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora; ***Elaphocordyceps capitata*** (Holmsk.) G.H. Sung, J.M. Sung & Spatafora, *E. delicatistipitata* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *E. fracta* (Mains) G.H. Sung, J.M. Sung & Spatafora, *E. inegoënsis* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *E. intermedia* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, *E. japonica* (Lloyd) G.H. Sung, J.M. Sung & Spatafora, *E. jezoënsis* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, *E. longisegmentis* (Ginns) G.H. Sung, J.M. Sung & Spatafora, *E. minazukiensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *E. miomoteana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *E. ophioglossoides* (Ehrh.) G.H. Sung, J.M. Sung & Spatafora, *E. paradoxo* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *E. ramosa* (Teng) G.H. Sung, J.M. Sung & Spatafora, *E. rouxii* (Cand.) G.H. Sung, J.M. Sung & Spatafora, *E. subsessilis* (Petch) G.H. Sung, J.M. Sung & Spatafora, *E. szemaoënsis* (M. Zang) G.H. Sung, J.M. Sung & Spatafora, *E. tenuispora* (Mains) G.H. Sung, J.M. Sung & Spatafora, *E. toriharamontana* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *E. valliformis* (Mains) G.H. Sung, J.M. Sung & Spatafora, *E. valvatistipitata* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, *E. virens* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora; **infraspecific:** *E. intermedia* f. *ichinokuënsis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, *E. ophioglossoides* f. *alba* (Kobayasi & Shimizu ex Y.J. Yao) G.H. Sung, J.M. Sung & Spatafora, *E. ophioglossoides* f. *cuboides* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora; ***Metacordyceps brittlebankisoides*** (Z.Y. Liu, Z.Q. Liang, Whalley, Y.J. Yao & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *M. campsosterni* (W.M. Zhang & T. H. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *M. chlamydosporia* (H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *M. liangshanensis* (M. Zang, D. Liu & R. Hu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *M. taii* (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora; ***Ophiocordyceps agriotidis*** (A. Kawam.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ainictos* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. amazonica* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. aphodii* (Mathieson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. appendiculata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. arachneicola* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. arbuscula* (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. armeniaca* (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. asyuënsis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. aurantia* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. australis* (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. barnesii* (Thwaites) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. bicephala* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. bispora* (Stiffler) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. brunneipunctata* (Hywel-Jones) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cantharelloides* (Samson & H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. carabidicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cicadidicola* (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. clavata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. coccidiicola* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. coccigena* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cochliidicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. corallomyces* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. crassisporea* (M. Zang, D. R. Yang & C.D. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. crinalis* (Ellis ex Lloyd) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cucumispora* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. curculionum* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cusu* (Pat.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cylindrostromata* (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. dayiensis* (Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. dermapterigena* (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones &

Spatafora, *O. dipterigena* (Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. discoideicapitata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ditmarii* (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. dovei* (Rodway) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. elateridicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. elongata* (Petch) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. elongatiperitheciata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. elongatistromata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. emeiensis* (A.Y. Liu & Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. engleriana* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. entomorrhiza* (Dicks.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. evdodgeorgiae* (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. falcata* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. falcatooides* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. fasciculatistromata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ferruginosa* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. filliformis* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. formicarum* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. forquignonii* (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. furcicaudata* (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. gansuensis* (K. Zhang, C. Wang & M. Yan) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. geniculata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. gentilis* (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. glaziovii* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. goniophora* (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. gracilioides* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. gracilis* (Grev.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. heteropoda* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. hiugensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. huberiana* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. humbertii* (C.P. Robin) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. insignis* (Cooke & Ravenel) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. irangiensis* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. japonensis* (Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. jiangxiensis* (Z.Q. Liang, A.Y. Liu & Y.C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. jinggangshanensis* (Z.Q. Liang, A.Y. Liu & Y.C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. kangdingensis* (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. kniphofioides* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. koningsbergeri* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. konnoana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. lachnopoda* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. larvarum* (Westwood) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. lloydii* (H.S. Fawc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. longissima* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. lutea* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. melolonthae* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. michiganensis* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. minutissima* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. monticola* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. mrciensis* (J.C. Jung, Z.Q. Liang, Soyong & K.D. Hyde) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. multiaxialis* (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. myrmecophila* (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. neovolkiiana* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. nepalensis* (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. nigra* (Samson, H.C. Evans & Hoekstra) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. nigrella* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. nigripes* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. nutans* (Pat.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. obtusa* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. octospora* (M. Blackwell & Gilb) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. odonatae* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. osuzumontana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ouwensii* (Höhn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. owariensis* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. oxycephala* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. pentatoma* (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. petchii* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. proliferans* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. pseudolloydii* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. pseudolongissima* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. purpureostromata* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ravenelii* (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. robertsii* (Hook.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. rubiginosiperitheciata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. rubripunctata* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. ryogamiensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. salebrosa* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. scottiana* (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. selkirkii* (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. sichuanensis* (Z.Q. Liang & B. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. sinensis* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. smithii* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. sobolifera* (Hill ex Watson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. sphecocephala* (Klotzsch ex Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. stipitata* (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. stylophora* (Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. subflavida* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. superficialis* (Peck) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. takaoensis* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. taylorii* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. thyrsoides* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. tricentri* (Yasuda) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. uchiyamae* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. variabilis* (Petch) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. voeltzkowii* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. volkiana* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. wuyishanensis* (Z.Q. Liang, A.Y. Liu & J.Z. Huang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. yakusimensis* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. zhangjiensis* (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora; infraspecific: *O. amazonica* var. *neoamazonica* (Kobayasi & Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. cucumispora* var. *dolichoderi* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. kniphofioides* var. *dolichoderi* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. kniphofioides* var. *ponerinarum* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. lloydii* var. *binata* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. melolonthae* var. *rickii* (Lloyd) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. owariensis* f. *viridescens* (Uchiyama & Udagawa) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. purpureostromata* f. *recurvata* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, *O. superficialis* f. *crustacea* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora; **Pochochia parasitica** (G.L. Barron) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora.

Key words: *Clavicipitaceae*, *Cordyceps*, *Cordycipitaceae*, *Elaphocordyceps*, *Metacordyceps*, multigene phylogeny, *Ophiocordyceps*, *Ophiocordycipitaceae*.

INTRODUCTION

Cordyceps Fr. is the most diverse genus in the family *Clavicipitaceae* in terms of number of species and host range (Kobayasi 1941, 1982, Mains 1957, 1958). There are estimated to be more than 400 species (Mains 1958, Kobayasi 1982, Stensrud *et al.* 2005) although this is

expected to be an underestimation of the extant global diversity (Hawksworth & Rossman 1997). Its host range is broad, ranging from ten orders of arthropods to the truffle-like genus *Elaphomyces*, although most species are restricted to a single host species or a set of closely related host species (Kobayasi 1941, 1982, Mains 1957, 1958). The distribution is cosmopolitan, including

all terrestrial regions except Antarctica, with the height of known species diversity occurring in subtropical and tropical regions, especially East and Southeast Asia (Kobayasi 1941, 1982, Samson *et al.* 1988). The genus is generally included in the family *Clavicipitaceae*, based on its cylindrical asci, thickened ascus apices, and filiform ascospores that often disarticulate into part-spores (Mains 1958, Kobayasi 1982, Rossman *et al.* 1999, Hywel-Jones 2002). *Cordyceps* is characterized and distinguished from other genera of the family by its production of superficial to completely immersed perithecia on stipitate and often clavate to capitate stromata and its ecology as a pathogen of arthropods and the fungal genus *Elaphomyces* (Kobayasi 1941, Mains 1957, 1958, Kobayasi & Shimizu 1960, Rogerson 1970).

Modern infrageneric classifications of *Cordyceps* have been based primarily on the taxonomic studies of Kobayasi (1941, 1982) and Mains (1958) (but see Masee 1895). Kobayasi (1941, 1982) recognized three subgenera (*C. subg. Cordyceps*, *C. subg. Ophiocordyceps*, and *C. subg. Neocordyceps*), emphasizing arrangement of perithecia and morphology of asci, ascospores and part-spores. Species of *C. subg. Cordyceps* (type *C. militaris*) were characterized by the production of either immersed or superficial perithecia produced at approximately right angles (ordinal) to the surface of the stroma and ascospores that disarticulate into part-spores at maturity. *Cordyceps subg. Ophiocordyceps* (Petch) Kobayasi (type *C. blattae* Petch) was distinguished by the production of whole ascospores that do not disarticulate into part-spores and, in some species, asci lacking pronounced apical hemispheric caps. *Cordyceps subg. Neocordyceps* Kobayasi (type *C. sphecocephala* (Klotzsch ex Berk.) Berk. & M.A. Curtis) was characterized by perithecia immersed at oblique angles in the clava region of the stroma and ascospores that disarticulate into part-spores upon maturity.

Mains (1958) expanded the infrageneric classification with a different emphasis on diagnostic characters and recognized two additional subgenera, *C. subg. Racemella* (Ces.) Sacc. and *C. subg. Cryptocordyceps* Mains. *Cordyceps subg. Racemella* (type *C. memorabilis* (Ces.) Sacc.) included species that produce superficial perithecia and asci with hemispheric to short cylindrical caps. *Cordyceps subg. Cryptocordyceps* (type *C. ravenelii* Berk. & M.A. Curtis) was diagnosed by the production of brown, partly immersed to superficial perithecia in a palisade-like layer at more or less right angles to the surface of the stroma. Kobayasi and Mains also differed in their treatments of *C. subg. Ophiocordyceps* and *C. subg. Neocordyceps*. In contrast to Kobayasi (1941), who essentially adopted the diagnosis of Petch (1931) but at the rank of subgenus, Mains (1958) placed only *C. blattae* and *C. peltata* Wakef. in *C. subg. Ophiocordyceps* based on their lack of a thickened ascus apex, thus deemphasizing the importance of ascospore disarticulation at the subgeneric level. Furthermore, Mains (1958) did not recognize *C. subg. Neocordyceps*, rather he included species with oblique

perithecia in *C. subg. Cordyceps* sect. *Cremastocarpon* subsect. *Entomogenae*. Currently, the subgenera *C. subg. Cordyceps*, *C. subg. Ophiocordyceps*, and *C. subg. Neocordyceps sensu Kobayasi* (1941) have been arguably the most widely used infrageneric taxa of *Cordyceps* (Zang & Kinjo 1998, Artjariyasripong *et al.* 2001, Hywel-Jones 2002, Sung & Spatafora 2004, Stensrud *et al.* 2005) with the relatively recent addition of *C. subg. Bolacordyceps* O.E. Erikss., which is characterized by the production of bola-ascospores (Eriksson 1986). Although this ascospore form has been likened to the South American bola or the East Asian ninchuk (martial arts weapon), the overall form is best likened to that of a skipping rope. The two handles of the skipping rope are two terminal sets of four cells. The 'rope' is a slender hyphal thread, which appears to lack cytoplasm or, at most, has relic quantities.

In addition to the morphological characters discussed above, host affiliation has played an important role in the classification of *Cordyceps* (Masee 1895, Kobayasi 1982). *Cordyceps* species that parasitize the truffle genus *Elaphomyces* have been recognized as a unique taxon. The genus *Cordylia* Fr. (1818) was once assigned for the mycogenous *Cordyceps* species (Masee 1895) although it is a homonym of *Cordylia* Pers. 1807. Kobayasi (1941, 1982) also recognized the mycogenous *Cordyceps* species as taxonomic units (e.g., *C. subg. Cordyceps* sect. *Cystocarpon* subsect. *Eucystocarpon* ser. *Mycogenae*) and emphasized the utility of host affiliations in delimiting closely related species of arthropod pathogens. Mains (1958) adopted Kobayasi's treatment of the parasites of *Elaphomyces*, but questioned whether morphologically similar species on different insect hosts (e.g., *C. irangiensis* Moureau and *C. sphecocephala* attacking ants and wasps, respectively) are conspecific. The applicability of hosts as a taxonomic character is complicated, however, due to the difficulty in identifying immature hosts (e.g., larvae and pupae) and insufficient host identification for many herbarium collections.

Several phylogenetic studies employing ribosomal DNA (Artjariyasripong *et al.* 2001, Sung *et al.* 2001, Stensrud *et al.* 2005) have been conducted to test and refine the classification of *Cordyceps*. Such studies were restricted by both limited taxon sampling and the inadequate resolution power of ribosomal DNA, resulting in limited conclusions regarding systematics of the genus. Recent phylogenetic studies (Spatafora *et al.* 2007, Sung *et al.* 2007) based on multiple independent loci provided a greater level of resolution and support, and revealed that neither *Cordyceps* nor the family *Clavicipitaceae* is monophyletic. Three monophyletic groups of the clavicipitaceous fungi were recognized, all of which include species of *Cordyceps*. These results reject the current infrafamilial classification (Diehl 1950) and indicate that the phylogenetic diversity of *Cordyceps* is representative of the entire family *Clavicipitaceae* (Spatafora *et al.* 2007, Sung *et al.* 2007). Therefore, a new classification of *Cordyceps* and the *Clavicipitaceae* is necessary to reflect the current hypotheses of phylogenetic relationships and to be predictive in nature.

Here, we conducted the most extensive multi-gene phylogenetic analyses to provide a basis for the phylogenetic classification of *Cordyceps* and the clavicipitaceous fungi. The main objectives of this study are to 1) reassess the morphological traits used in the current classifications of *Cordyceps* in the context of phylogeny, 2) investigate the taxonomic utility of the anamorphic forms in classification of *Cordyceps* and better understand the teleomorph–anamorph connections, and 3) revise the classification of *Cordyceps* and *Clavicipitaceae* to be consistent with phylogenetic relationships.

MATERIALS AND METHODS

Taxon and character sampling

A total of 162 taxa were sampled from *Clavicipitaceae* and other families of *Hypocreales* with *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk (*Glomerellaceae*) and *Verticillium dahliae* Kleb. (*Plectosphaerellaceae*) included as outgroups (Table 1). DNA extractions from cultures or herbarium specimens were conducted using a FastDNA kit (Qbiogene) following the manufacturer's instruction, with minor modifications. Polymerase chain and sequencing reactions were performed as previously described (Sung *et al.* 2007). DNA sequence data unique to this study were determined from five genes, including the nuclear ribosomal small and large subunits (*nrSSU* and *nrLSU*), the elongation factor 1 α (*tef1*), and the largest and second largest subunits of RNA polymerase II (*rpb1* and *rpb2*). These sequences were combined with data from 91 taxa, which were obtained from Sung *et al.* (2007). Information pertaining to voucher numbers concerning the sequences is provided in Table 1.

Sequence alignment and phylogenetic analyses

Sequences were edited using SeqEd 1.0.3 (Applied Biosystems Inc.) and contigs were assembled using CodonCode Aligner 1.4 (CodonCode Inc.). Sequences of each gene partition were initially aligned with Clustal W 1.64 (Thompson *et al.* 1994) and appended to an existing alignment (Sung *et al.* 2007). This initial alignment was manually edited as necessary in MacClade 4.0 (Maddison & Maddison 2000). All five gene regions sampled in this study were concatenated into a single, combined data set (162-taxon 5-gene data set) with ambiguously aligned regions excluded from phylogenetic analyses. Sequences from two additional gene regions, β -tubulin (*tub*) and mitochondrial ATP6 (*atp6*), from Sung *et al.* (2007) were also combined with the 162-taxon 5-gene data set to generate a supermatrix of 162-taxon 7-gene data set.

In order to detect incongruence among the five individual gene regions sampled in this study, bootstrap proportions were used for each individual data set with the 107 taxa that was complete for all five genes (Table 1). Bootstrap proportions (BP) were determined in a maximum-parsimony framework using the program PAUP* 4.0b10 (Swofford 2002). Only parsimony-

informative characters were used with the following search options: 100 replicates of random sequence addition, TBR branch swapping, and MulTrees OFF. The incongruence was assumed to be significant if two different relationships for the same set of taxa were both supported with greater than 70 % bootstrap proportions by different genes (Mason-Gamer & Kellogg 1996, Wiens 1998). Previous studies revealed that *tub* was double copy in some clavicipitaceous species (Spatafora *et al.* 2007), and Sung *et al.* (2007) also showed that while *atp6* possessed conflicting data for a limited number of taxa, the conflict was localized and the locus simultaneously provided increased level of support for other nodes. Thus, although we focused our sampling and analyses of the five aforementioned loci, we also conducted phylogenetic supermatrix analyses with *tub* and *atp6* (162-taxon 7-gene) to detect any increased nodal support provided by those two loci.

Maximum parsimony (MP) analyses were conducted on the 162-taxon 5-gene and the 162-taxon 7-gene data set (Table 1, Fig. 3). All characters were equally weighted and unordered. MP analyses were performed using only parsimony-informative characters with the following settings: 100 replicates of random sequence addition, TBR branch swapping, and MulTrees ON. Phylogenetic confidence was assessed by nonparametric bootstrapping (Felsenstein 1985). A total of 200 bootstrap replicates were used to calculate bootstrap proportions; bootstrapping used the same search options with five replicates of random sequence addition per bootstrap replicate.

Maximum likelihood (ML) analyses were performed with RAxML-VI-HPC v2.2. using a GTRCAT model of evolution with 25 rate categories (Stamatakis *et al.* 2005). The model was separately applied to each of the eleven partitions, which consisted of *nrSSU*, *nrLSU* and the nine codon positions of three protein-coding genes (*tef1*, *rpb1*, and *rpb2*). Nodal support was assessed with nonparametric bootstrapping using 200 replicates. Bayesian Metropolis coupled Markov chain Monte Carlo (B-MCMCMC) analyses were performed on combined datasets using MrBayes 3.0b4 (Huelsenbeck & Ronquist 2001). In estimating the likelihood of each tree, we used the general time-reversible model, with invariant sites and gamma distribution (GTR+I+ Γ) and employed the model separately for each partition. In an initial analysis, a B-MCMCMC analysis with five million generations and four chains was conducted in order to test the convergence of log-likelihood. Trees were sampled every 100 generations, for a total of 50,000 trees. For a second analysis, five independent Bayesian runs with two million generations and random starting trees were conducted to reconfirm log-likelihood convergence and mixing of chains.

In addition to the analyses with 162-taxon 5-gene data set, a series of analyses were conducted in MP, ML, and Bayesian frameworks with different taxon samplings (107- and 152-taxon 5-gene data sets) to address the potential topological effects of missing data. Previous phylogenetic and simulation studies demonstrated that the phylogenetic analyses are often not negatively

affected if less than 50 % characters are missing for each taxon in the phylogenetic analyses (Wiens 2003, Phylippe *et al.* 2004). In this study, we assumed that the phylogenetic analysis is not confounded if the taxa were complete for at least three out of five gene partitions. Therefore, ten taxa (Table 1) in the 162-taxon 5-gene data set that were complete for only two gene partitions were excluded to generate the 152-taxon 5-gene data set. A 107-taxon 5-gene data set that does not contain any missing data in gene partitions was also prepared to compare the phylogenetic relationships between 107-taxon and 152-taxon 5-gene analyses. MP, ML, and Bayesian analyses based on the 162-taxon 5-gene data set (Figs 1–2) showed that the *C. sphecocephala* clade is characterized by long-branch lengths relative to the rest of the clavicipitaceous fungi. To address the impact of the *C. sphecocephala* clade on the phylogenetic resolution, we excluded all members of the *C. sphecocephala* clade from the 152-taxon 5-gene data set and constructed a 147-taxon 5-gene data set.

RESULTS

Sequence alignment

The combined 162-taxon 5-gene dataset consisted of 4927 base pairs of sequence data (*nrSSU* 1102 bp, *nrLSU* 954 bp, *tef1* 1020 bp, *rpb1* 803 bp, *rpb2* 1048 bp). As a result of excluding ambiguously aligned regions, the final alignment comprised 4600 base pairs (*nrSSU* 1088 bp, *nrLSU* 767 bp, *tef1* 1020 bp, *rpb1* 677 bp, *rpb2* 1048 bp), 1882 of which were parsimony-informative (*nrSSU* 233 bp, *nrLSU* 220 bp, *tef1* 466 bp, *rpb1* 382 bp, *rpb2* 581 bp). A total of 107 taxa were complete for all five genes and the number of complete taxa for each gene was as follows: *nrSSU* 158 taxa, *nrLSU* 157 taxa, *tef1* 149 taxa, *rpb1* 143 taxa, *rpb2* 122 taxa (Table 1).

Phylogenetic analyses

The reciprocal comparisons of 70 % bootstrap trees from individual data sets of the 162-taxon 5-gene dataset did not reveal any significantly supported contradictory nodes (data not shown). These results were interpreted as indicating that no strong incongruence existed among the individual data sets that would be indicative of different phylogenetic gene histories (e.g., lineage sorting or horizontal gene transfer). As a result, all five individual data sets were combined in simultaneous analyses.

MP analyses of the 162-taxon 5-gene data set resulted in 156 equally parsimonious trees. These trees were 21,323 steps with a consistency index (CI) of 0.1598 and a retention index (RI) of 0.6131. One of 156 equally parsimonious trees is shown in Fig. 1. Nodes that collapse in the strict consensus tree are denoted with asterisks. ML analyses of the 162-taxon 5-gene data set resulted in a tree with a log-likelihood ($-\ln$) of 92019.95. In the Bayesian analyses, the five-million generation analysis converged on the log-likelihood (harmonic mean = $-\ln$ 99561.22)

at approximately around 250,000 generations. The results from five of two-million generation analyses also showed a convergence on the log-likelihood at approximately 250,000 generations and the topologies were identical. As a result, the 3,000 trees from the first 300,000 generations were deleted from the five million generation analysis to generate a 50 % majority-rule consensus tree.

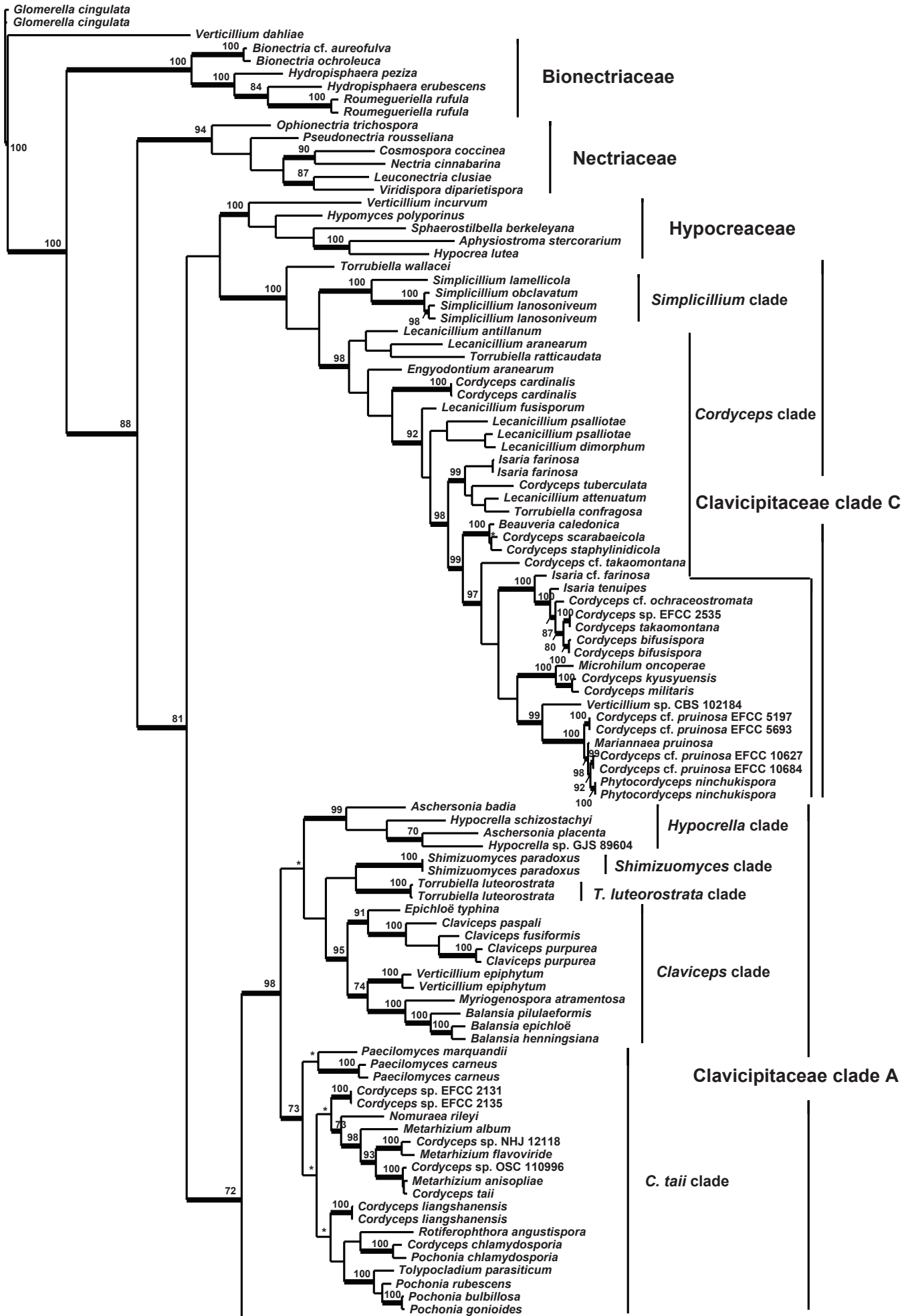
A 50 % majority consensus tree (Fig. 2) was generated from the 5 million generation analysis. Since the topology of ML analyses (tree not shown) was nearly identical to that of the Bayesian consensus tree of Fig. 2, the bootstrap proportions of ML analyses are provided above the corresponding nodes in Fig. 2. Previous studies have shown that in interpreting the supports of the phylogenetic estimates of relationships, the posterior probability tends to overestimate the phylogenetic confidence (Doaudy *et al.* 2003, Lutzoni *et al.* 2004, Reeb *et al.* 2004). As a result, the posterior probabilities were used as a supplementary indicator to bootstrap proportions. In this study, nodes were considered strongly supported when supported by both bootstrap proportions (BP \geq 70 %) and posterior probabilities (PP \geq 0.95) (Lutzoni *et al.* 2004).

Phylogenetic relationships of the clavicipitaceous fungi

All MP, ML, and Bayesian analyses of the five-gene 162-taxon 5-gene data set recognized three well-supported clades of clavicipitaceous fungi (Figs 1–2), designated here as *Clavicipitaceae* clades A, B, and C (Figs 1–2), following the convention of the previous phylogenetic studies (Spatafora *et al.* 2007, Sung *et al.* 2007). These clades were statistically well supported by the bootstrap proportions of the MP (MP-BP) and ML (ML-BP) analyses and posterior probabilities (PP) of the Bayesian analyses (clade A: MP-BP = 98 %, ML-BP = 99 %, PP = 1.00; clade B: MP-BP = 93 %, ML-BP = 98 %, PP = 1.00; clade C: MP-BP = 100 %, ML-BP = 100 %, PP = 1.00). A sister-group relationship between clades A and B was also strongly supported (MP-BP = 72 %, ML-BP = 90 %, PP = 1.00). The monophyletic group of clade C and *Hypocreaceae* was moderately to strongly supported (MP-BP = 63 %, ML-BP = 92 %, PP = 1.00).

***Clavicipitaceae* clade A** comprised five statistically well-supported subclades (Figs 1–2, 4). These were labelled in Figs 1, 2, and 4 as the *C. taii* clade (MP-BP = 73 %, ML-BP = 78 %, PP = 1.00), the *Claviceps* clade (MP-BP = 95 %, ML-BP = 98 %, PP = 1.00), the *Hypocrella* clade (MP-BP = 99 %, ML-BP = 99 %, PP = 1.00), the *Shimizuomyces* clade (MP-BP = 100 %, ML-BP = 100 %, PP = 1.00), and the *Torrubiella luteorostrata* clade (MP-BP = 100 %, ML-BP = 100 %, PP = 1.00). As indicated previously by Sung *et al.* (2007), internal relationships among these five subclades were not strongly supported in MP and ML analyses (Figs 1–2, 4).

***Clavicipitaceae* clade B** consisted of five major subclades designated as the *C. gunnii*, *C. ophioglossoides*, *C. sphecocephala*, *C. unilateralis*, and *Pa. lilacinus* clades (Figs 1–2, 6). Nearly all of



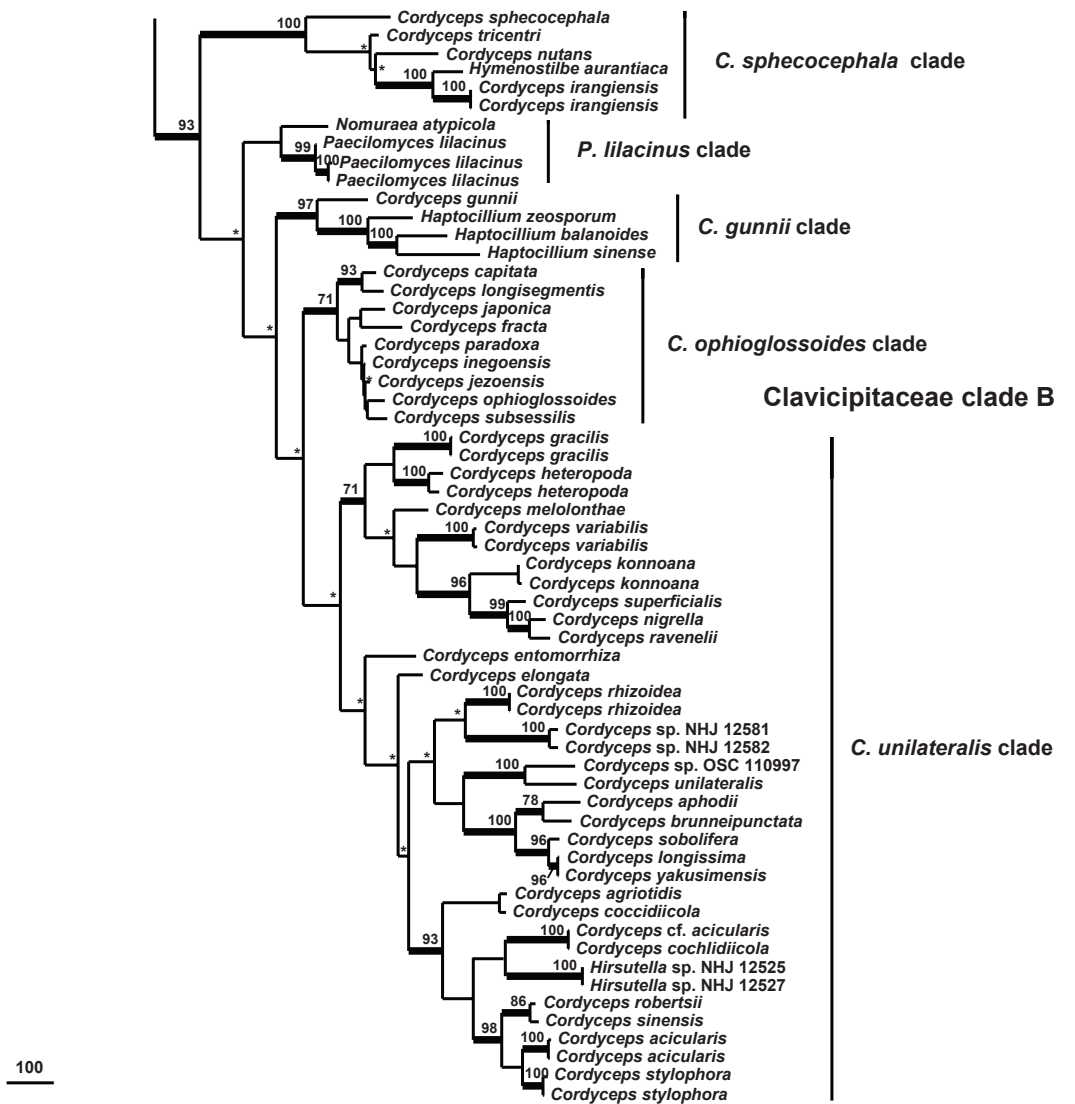
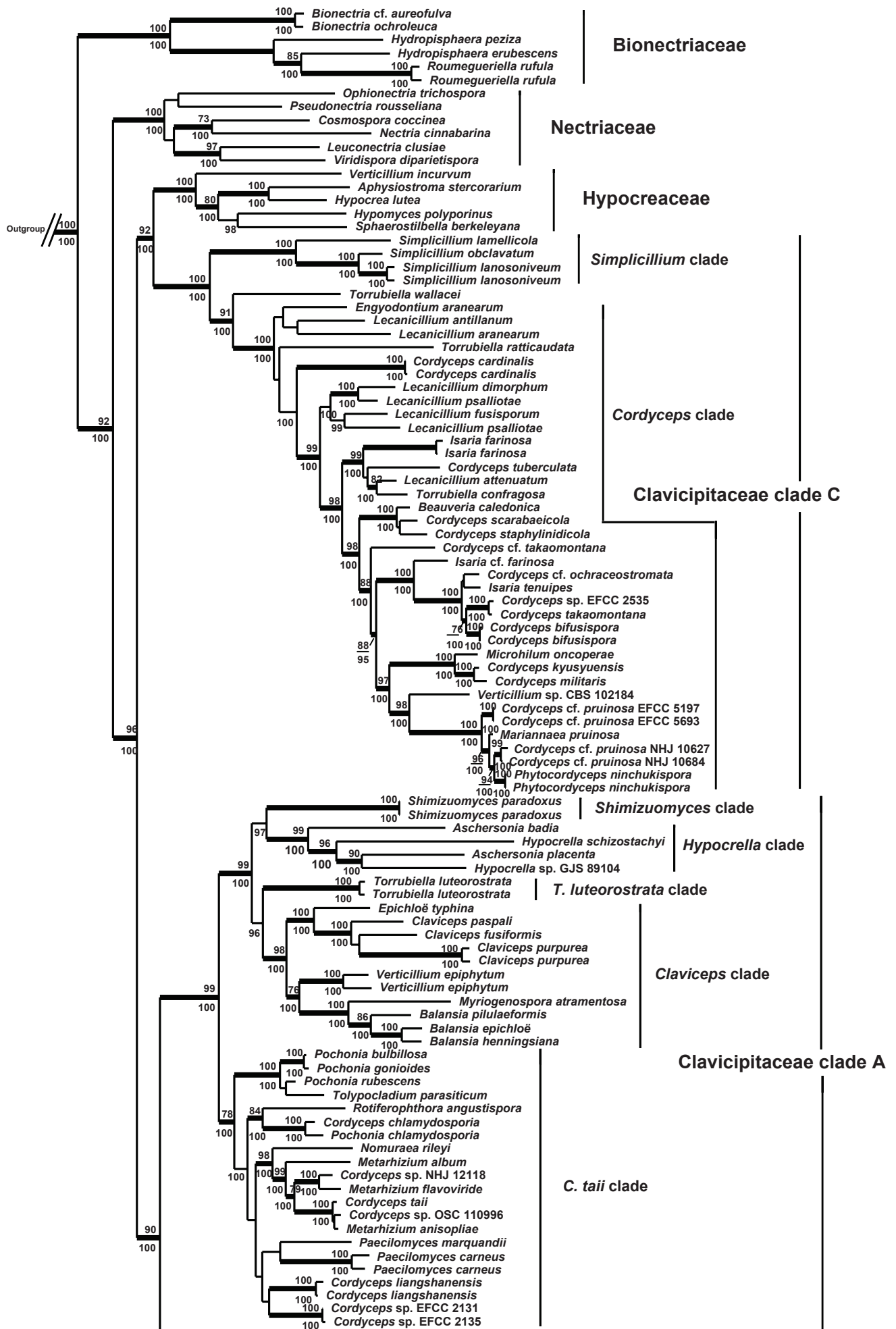


Fig. 1. Continued.

the subclades in clade B were strongly supported by bootstrap proportions and posterior probabilities (*C. gunnii* clade: MP-BP = 97 %, ML-BP = 100 %, PP = 1.00; *C. ophioglossoides* clade: MP-BP = 71 %, ML-BP = 88 %, PP = 1.00; *C. sphecocephala* clade: MP-BP = 100 %, ML-BP = 100 %, PP = 1.00, *Pa. lilacinus* clade: MP-BP = 64 %, ML-BP = 76 %, PP = 1.00). It should be noted, however, that the *C. unilateralis* subclade was not resolved in the MP analyses (Fig. 1). This lack of resolution was due to the instability of the *C. sphecocephala* clade, which is characterized by long-branch lengths relative to the rest of the clavicipitaceous fungi. Multiple placements of the *C. sphecocephala* subclade, ranging from a basal lineage of the *Clavicipitaceae* clade B to a terminal clade nested within the *C. unilateralis* subclade, were present among the most parsimonious trees (data not shown). Our ML and Bayesian results (Fig. 3) indicate that the *C. sphecocephala* subclade is either a sister-

group of the *C. unilateralis* subclade (107-taxon 5-gene data set) or in the terminal group of the *C. unilateralis* subclade (152-taxon 5-gene data set). In MP, ML, and Bayesian analyses with a supermatrix of 162-taxon 7-gene data set (Fig. 3), the *C. sphecocephala* subclade was placed as a terminal group of the *C. unilateralis* subclade with strong support (MP-BP = 89 %, ML-BP = 94 %, PP = 1.00) as seen in the previous analyses (Sung *et al.* 2007). In the light of long-branch attraction problems associated with the MP analyses (Fig. 1), we use the Bayesian tree (Fig. 2) to further discuss the relationships in clade B and we conclude that the *C. sphecocephala* subclade was best included as a member of the *C. unilateralis* subclade (Figs 2, 6). In interpreting the *C. unilateralis* subclade in terms of statistical support, we used the bootstrap proportions and posterior probabilities (MP-BP = 88 %, ML-BP = 88 %, PP = 1.00) based on the results of 147-taxon 5-gene data set (Fig. 3).

Fig. 1 (Page 10/11). Phylogenetic relationships among 162 taxa in the *Clavicipitaceae* and other families in the *Hypocreales*. One of 156 equally parsimonious trees is shown based on maximum parsimony analyses with combined data set of five genes (i.e., *nrSSU*, *nrLSU*, *tef1*, *rpb1* & *rpb2*). Bootstrap proportions (MP-BP) of ≥ 70 % are provided above corresponding nodes and in a thicker line. Internodes that are collapsed in strict consensus tree are marked with an asterisk (*).



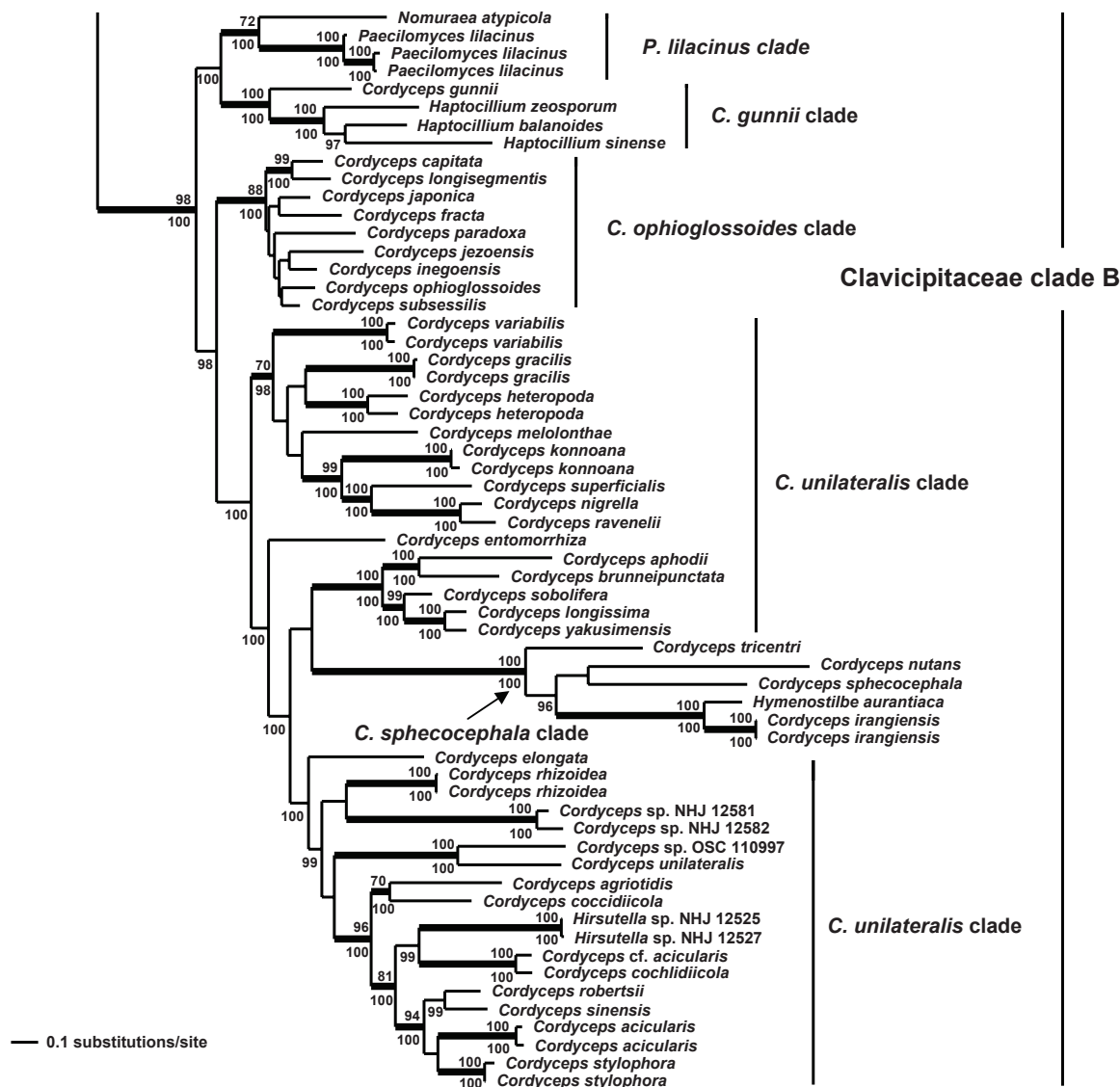


Fig. 2. Continued.

Clavicipitaceae clade C comprised two well-supported subclades (Figs 1–2, 8). The *Simplicillium* subclade (MP-BP = 100 %, ML-BP = 100 %, PP = 1.00) consisted of isolates of the anamorph genus *Simplicillium*, most of which were isolated as parasites of other fungi. The *Cordyceps* subclade (MP-BP = 98 %, ML-BP = 100 %, PP = 1.00) included numerous species of *Torrubiella* and species of *Cordyceps* that produce pallid to brightly coloured stromata with ascospore morphologies ranging from whole ascospores to part-spores to bola-ascospores according to species. Importantly, the *Clavicipitaceae* clade C included *C. militaris* and represents the core *Cordyceps* clade. The remaining species, *Torrubiella wallacei* H.C. Evans, was also a member of the *Cordyceps* clade with strong support (ML-BP = 91 %, PP = 1.00) in ML and Bayesian analyses (Figs 2, 8), but could not be confidently assigned to either subclade in MP analyses (Fig. 1).

DISCUSSION

Phylogenetic implications on the systematics of the genus *Cordyceps*

The present and previous phylogenetic analyses (Spatafora *et al.* 2007, Sung *et al.* 2007) have revealed that species in the *Clavicipitaceae* form three strongly supported monophyletic groups based on combined data sets of six or seven genes (the genes analyzed herein with and without *atp6*). Although more taxa were used in our study, these results were consistent with the previous studies, recognizing three monophyletic groups designated as *Clavicipitaceae* clades A–C (Figs 1–2). In addition, our results also support the paraphyly of the *Clavicipitaceae* as defined by the monophyly of *Clavicipitaceae* clade C and *Hypocreaceae* (Figs 1–2). Although the paraphyly of the *Clavicipitaceae* (clade C

Fig. 2 (Page 12/13). Phylogenetic relationships among 162 taxa in the *Clavicipitaceae* and other families in the *Hypocreales*. A 50 % majority consensus tree is shown based on Bayesian analyses with combined data set of five genes (i.e., *nrSSU*, *nrLSU*, *tef1*, *rpb1* & *rpb2*). Outgroups (*Glomerella cingulata* and *Verticillium dahliae*) are not shown. Posterior probabilities (PP) of ≥ 0.95 are provided in percentage below corresponding nodes. Bootstrap proportions (ML-BP) are obtained in maximum likelihood analyses and shown above corresponding nodes for ≥ 70 %. Internodes that are supported with both bootstrap proportions (ML-BP ≥ 70 %) and posterior probabilities (PP ≥ 0.95) are considered strongly supported and drawn in a thicker line.

+ *Hypocreaceae*) was moderately supported (MP-BP = 63 %) in the 162-taxon 5-gene MP analyses (Fig. 1), it was strongly supported (ML-BP = 92 %, PP = 1.00) in the ML and Bayesian analyses (Fig. 2) and more robustly addressed in the previous MP analyses, which investigated localized conflicts among gene partitions and compared bootstrap proportions among alternative sampling strategies (Sung et al. 2007).

The phylogenetic hypothesis presented here contradicts current infrafamilial classification of the *Clavicipitaceae*. Diehl (1950) proposed three subfamilies, *Oomyceitoideae*, *Clavicipitoideae*, and *Cordycipitoideae*, based on the development of stromata, anamorphic characters and host affiliations. However, these three subfamilies do not coincide with the three clades of the *Clavicipitaceae* inferred in the present

analyses (Figs 1–2). *Clavicipitaceae* clade A includes members of all three subfamilies (e.g., *Claviceps* of *Clavicipitoideae*, *Cordyceps* of *Cordycipitoideae*, and *Hypocrella* of *Oomyceitoideae*), whereas the remaining clades only comprise members of *Cordycipitoideae* (e.g., *Cordyceps* and *Torrubiella*). Importantly, all three major clades include members of *Cordyceps*, indicating that *Cordyceps*, like *Clavicipitaceae*, is not monophyletic (Figs 1–2). As a result, the three recognized well-supported clades (clades A–C) of the clavicipitaceous fungi represent a robust phylogenetic framework for the taxonomic revision of *Cordyceps* and the *Clavicipitaceae*.

In the current infrageneric classification of the genus, *Cordyceps* comprises four subgenera (*C. subg. Bolacordyceps*, *C. subg. Cordyceps*, *C. subg.*

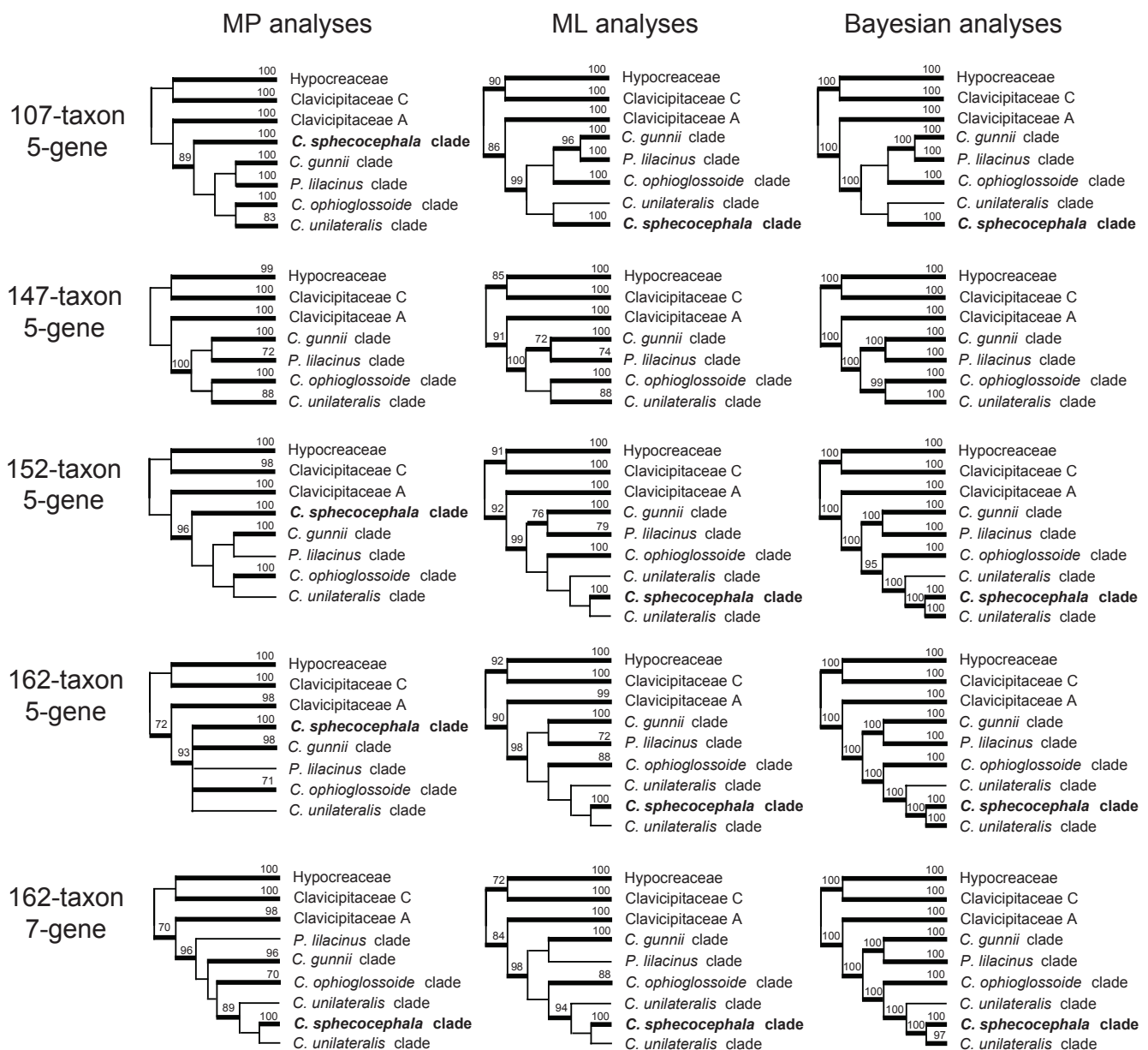


Fig. 3. Schematic diagrams of phylogenetic relationships from MP, ML, and Bayesian analyses that differ in character or taxon sampling. In addition to 162-taxon 5-gene and 7-gene data sets, 107-taxon and 152-taxon 5-gene data sets were generated with taxa complete for five genes (i.e., *nrSSU*, *nrLSU*, *tef1*, *rpb1* and *rpb2*) and at least three genes, respectively. To address the impact of *C. sphecocephala* clade to nodal support of *C. unilateralis* clade in Fig. 1, a 147-taxon 5-gene data set was constructed after members of *C. sphecocephala* clade were excluded. Bootstrap proportions (BP ≥ 70 %) or posterior probabilities (PP ≥ 0.95 in percentage) are shown above corresponding nodes and in a thicker line.

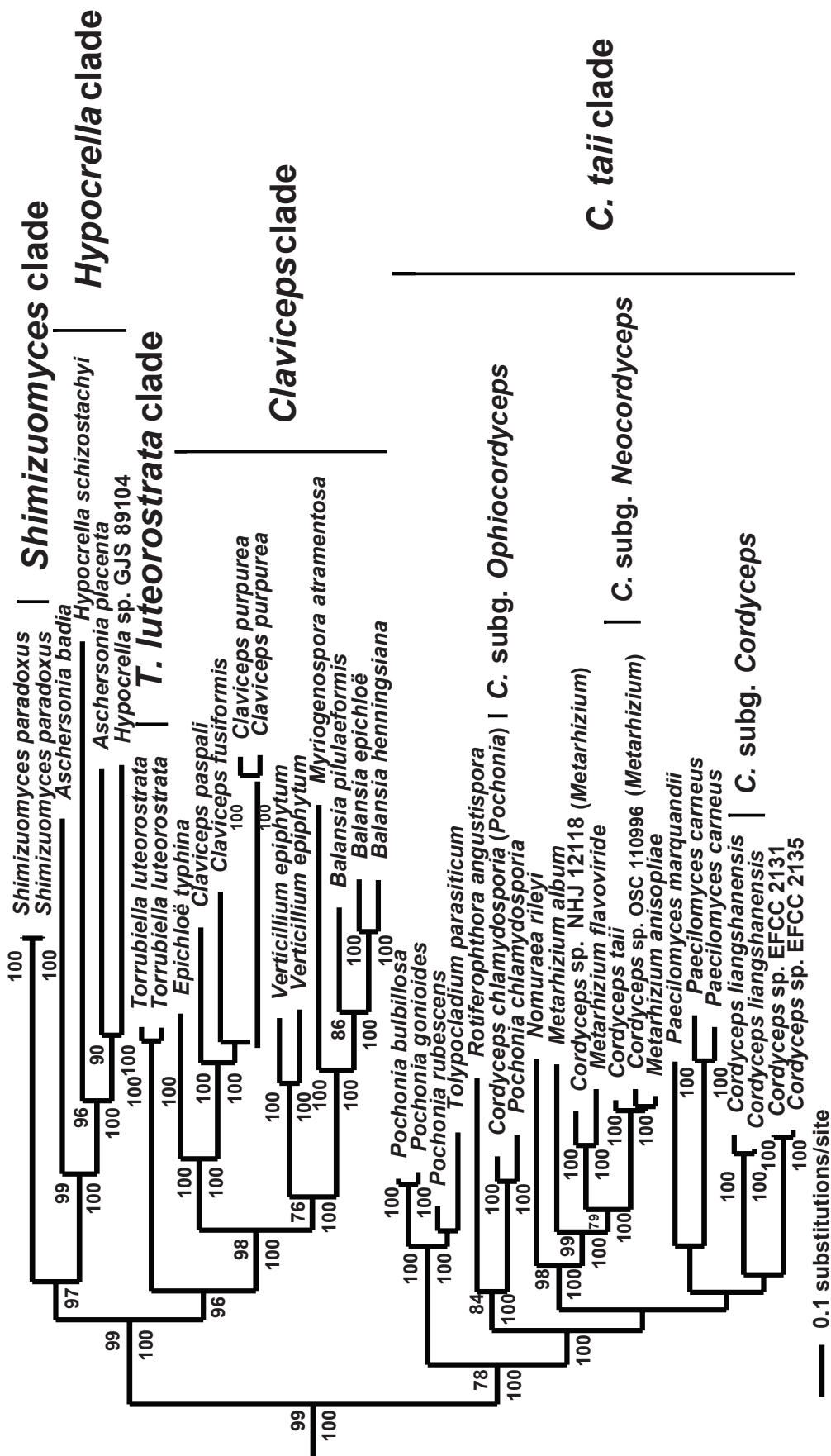


Fig. 4. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade A, to emphasize relationships within the clade. Respective subgenera of *Cordyceps* species in current classification are provided to the right of species. Known anamorphic genera of *Cordyceps* species are in parentheses. Tree description is the same as in Fig. 2.

Neocordyceps, and *C.* subg. *Ophiocordyceps*) based on ascospore morphology and arrangement of the perithecia in the stromata (Kobayasi 1941, 1982, Eriksson 1986). However, most of these characters are not consistent with the new phylogenetic hypothesis and are not diagnostic of monophyletic taxa (e.g., subgenera and genera) (Figs 1–2). For example, Kobayasi (1941, 1982) emphasized ascospore morphology and the lack of ascospore disarticulation into part-spores to delimit *C.* subg. *Ophiocordyceps* from the other subgenera. Species with non-disarticulating ascospores, however, are included in all three major clades (*C. acicularis* Ravenel of clade B, *C. cardinalis* G.H. Sung & Spatafora of clade C, and *Cordyceps* sp. EFCC 2131 and 2135 of clade A described below as *Metacordyceps yongmunensis*) (Figs 1–2), indicating that non-disarticulating ascospores are not phylogenetically informative at this level (Figs 1–2). Therefore, a reassessment of diagnostic characters, in the previous and current classifications of *Cordyceps*, is necessary for the three major clades to provide a basis for taxonomic revisions of *Cordyceps* and the *Clavicipitaceae*.

Species in *Clavicipitaceae* clade A

Clavicipitaceae clade A comprises five well-supported subclades (Fig. 4). All known species of *Cordyceps* in the clade are included in the *C. taii* clade. Species of *Cordyceps* in the clade possess partially or completely immersed perithecia on clavate to cylindrical fertile parts of the stromata (Zang *et al.* 1982, Liang *et al.* 1991, Zare *et al.* 2001). They produce ascospores that either disarticulate or remain intact at maturity and include species that possess ordinal and obliquely embedded perithecia. In the current classification, clade A includes species of *Cordyceps* that were formerly classified in

three subgenera of *Cordyceps*. *Cordyceps liangshanensis* M. Zang, D. Liu & R. Hu forms ordinal perithecia and possess disarticulating ascospores, consistent with *C.* subg. *Cordyceps* (Kobayasi 1982, Zang *et al.* 1982). *Cordyceps chlamydosporia* H.C. Evans possesses nondisarticulating ascospores, consistent with *C.* subg. *Ophiocordyceps* (Zare *et al.* 2001). *Cordyceps taii* Z.Q. Liang & A.Y. Liu, a known teleomorph species linked to the anamorph genus *Metarhizium* Sorokin, produces disarticulating ascospores and obliquely embedded perithecia in the stromata, a trait used to recognize *C.* subg. *Neocordyceps* (Liang *et al.* 1991). Importantly, *Cordyceps* sp. EFCC 2131 and 2135 (described below as *Metacordyceps yongmunensis*) produce non-disarticulating ascospores and obliquely embedded perithecia in the stromata, characters inconsistent with any of the subgenera in the current classification.

These results suggest that ascospore morphology and arrangement of perithecia are not phylogenetically informative in recognizing either the *C. taii* clade, or higher clades of clavicipitaceous fungi. Rather, they are more useful at species level classification. For example, our phylogenetic analyses revealed that *C. taii* is closely related to *C. brittlebankisoides* Z. Y. Liu, Z.Q. Liang, Whalley, Y.J. Yao & A.Y. Liu, the purported teleomorph of *M. flavoviride* (Huang *et al.* 2005). Although these species are similar to each other in macromorphology (e.g., greenish clavate stromata), they differ in the arrangement of the perithecia. *C. brittlebankisoides* possesses perithecia that are ordinally placed in the stromata, whereas *C. taii* has obliquely embedded perithecia. These results therefore suggest that arrangement of the perithecia in the stromata is useful in delimiting these closely related species in the *C. taii* clade (Fig. 4).

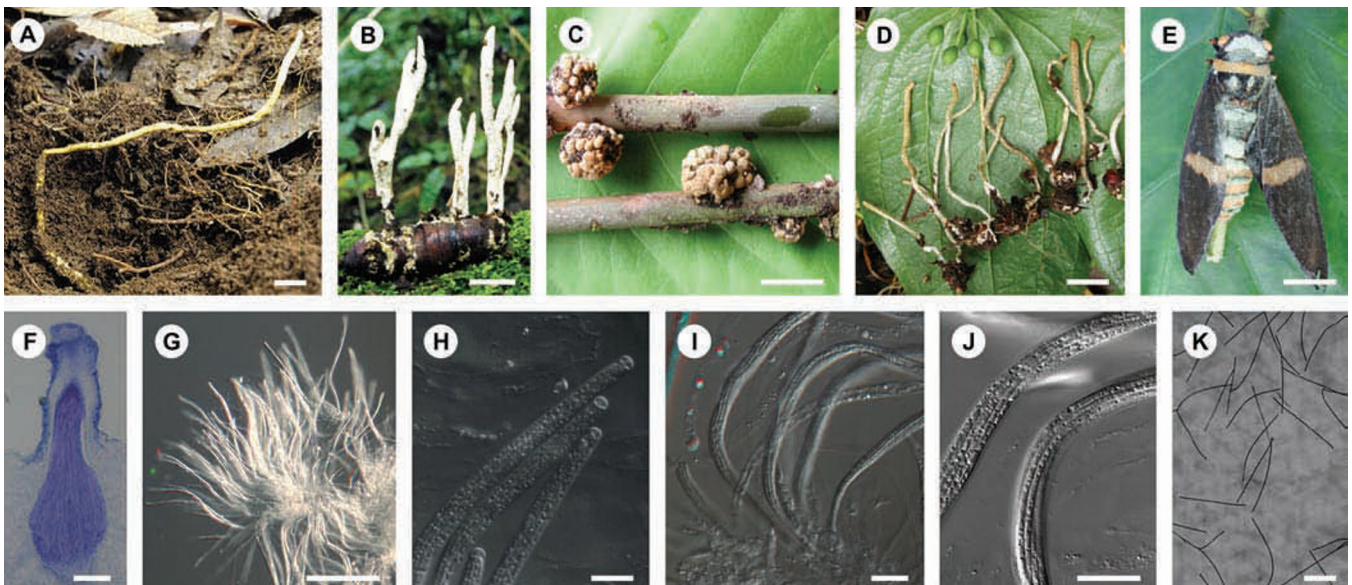


Fig. 5. A–E. Representative species of *Cordyceps* and its allies in *Clavicipitaceae* clade A. F–K. Morphology of *Cordyceps* sp. (described here as *Metacordyceps yongmunensis* sp. nov. below). A. *C. liangshanensis* on lepidopteran larva, EFCC 1452. B. *Cordyceps* sp. on lepidopteran pupa, EFCC 12285. C. *Hypocrella schizostachyi* on scale insect (Hemiptera). D. *Shimizuomyces paradoxus* on seed of plant (*Smilax sieboldii*: Smilacaceae). E. *Metarhizium* sp. on adult of cicada. F. Section of perithecium, EFCC 2131. G. Asci and fascicle, EFCC 2131. H. Asci showing prominent ascus cap, EFCC 2131. I. Asci showing ascus foot, EFCC 2131. J. Ascospores showing indistinct septation, EFCC 2131. K. Discharged intact ascospores on SDAY agar, EFCC 2131. Scale bars: A–E = 10 mm, F = 200 μ m, G = 100 μ m, H–J = 10 μ m, K = 100 μ m.

Species in *Clavicipitaceae* clade B

Species of *Cordyceps* in *Clavicipitaceae* clade B possess disarticulating or non-disarticulating ascospores and produce superficial to completely immersed perithecia that are ordinally or obliquely inserted in the stromata. As with the *Cordyceps* species of clade A, this clade also includes members of the former *C.* subg. *Cordyceps* (e.g., *C. ophioglossoides* (Ehrh.) Link and *C. variabilis* Petch), *C.* subg. *Ophiocordyceps* (e.g., *C. acicularis* and *C. unilateralis* (Tul. & C. Tul.) Sacc.), and *C.* subg. *Neocordyceps* (e.g., *C. nutans* Pat. and *C. sphecocephala*). The majority of *Cordyceps* species in this clade produce wiry to pliant or fibrous stromata that typically are completely or partially darkly pigmented and parasitize subterranean or wood-inhabiting hosts, which are buried in soil or embedded in decaying wood. Exceptions to this morphology and ecology do exist, however; for example, *C. melolonthae* (Tul. & C. Tul.) Sacc. is pigmented bright yellow but stains darkly upon handling, and members of the *C. sphecocephala* clade parasitize adult insects.

Clade B consists of five subclades. All subclades include either species of *Cordyceps* or anamorphs with potential links to *Cordyceps* (e.g., *Nomuraea atypicola* (Yasuda) Samson linked to *C. cylindrica* Petch) (Fig. 6, Evans & Samson 1987). The well-resolved tree in the present study (Fig. 6) provides the basis to characterize three of the five subclades of clade B. Due to insufficient taxon sampling, it is not possible to characterize the members of the *Cordyceps* species in the *C. gunnii* and *Pa. lilacinus* subclades. In the light of this, we focus on the remaining three subclades that include sufficient numbers of *Cordyceps* species.

The *C. ophioglossoides* subclade primarily consists of *Cordyceps* species that parasitize species of the genus *Elaphomyces* (e.g., *C. ophioglossoides* and *C. capitata* (Holmsk.) Link) and the nymphs of cicadas (e.g., *C. inegoënsis* Kobayasi and *C. paradoxa* Kobayasi) buried in soil (Kobayasi 1939, Mains 1957, Kobayasi & Shimizu 1960, 1963). Species in this subclade produce partially or completely immersed perithecia, in clavate to capitate fertile parts of stromata that are darkly pigmented with olivaceous tints (Kobayasi & Shimizu 1960, 1963). Because they produce disarticulating ascospores and ordinal perithecia, all known species of this clade are classified in *C.* subg. *Cordyceps*.

Cordyceps subsessilis Petch is unique to the *C. ophioglossoides* subclade (Fig. 6). It produces perithecia on white or pallid reduced stromata, arising from a rhizomorph-like structure from scarabaeid beetle larvae (Hodge *et al.* 1996). It is the only member of the subclade that parasitizes beetles embedded in decaying wood (Hodge *et al.* 1996). Therefore, *C. subsessilis* differs greatly in ecology and morphology of its stromata from most other taxa in the *C. ophioglossoides* clade, but it possesses several characters shared by its close relative, *C. ophioglossoides* (Kobayasi & Shimizu 1960, Hodge *et al.* 1996). Both species grow axenically on simple media, produce verticilliate anamorphs (*C. subsessilis* has a *Tolypocladium* anamorph, whereas *C. ophioglossoides* has verticillium-like conidiophores),

possess nearly identical part-spore morphologies, and produce stromata that are connected to their hosts via rhizomorph-like structures. In contrast, *C. capitata*/*C. longisegmentis* have not successfully been grown in culture, they are attached directly to the host, and an anamorph is unknown.

The *C. ophioglossoides* subclade (Fig. 6) also includes parasites of subterranean cicada nymphs (e.g., *C. inegoënsis* and *C. paradoxa*), which are grouped with their close relatives (e.g., *C. jezoënsis* S. Imai and *C. ophioglossoides*) that parasitize subterranean truffles of *Elaphomyces*. Despite low support of inter-species relationships within the *C. ophioglossoides* subclade due to short branch lengths, *C. paradoxa* and *C. inegoënsis* are morphologically more similar to *C. jezoënsis* and *C. ophioglossoides* than to any other members of the clade. These taxa produce clavate fertile parts of the stromata rather than capitate stromata like other members of the clade (e.g., *C. capitata* and *C. fracta* Mains). Many of these species (e.g., *C. jezoënsis* and *C. paradoxa*) are also known to connect to their hosts via rhizomorph-like structures (Kobayasi & Shimizu 1960, 1963), supporting a close phylogenetic relationship.

The *C. unilateralis* subclade includes the most morphologically diverse assemblages of *Cordyceps* species (Fig. 6). Most of the species in the clade parasitize larval, pupal or nymph stages of arthropods (Kobayasi 1941, Mains 1958). Species of this clade produce superficial to completely immersed perithecia on the stromata with morphologies ranging from capitate to clavate to filiform (Kobayasi 1941, Mains 1958). They typically possess tough, pliant, or fibrous stromata that are entirely or partially darkly pigmented, although some exceptions (e.g., *C. melolonthae* and *C. variabilis*) do exist, which produce brightly pigmented stromata (Mains 1958). Many species in the clade (e.g., *C. brunneipunctata* Hywel-Jones, *C. stylophora* Berk. & Broome, and *C. unilateralis*) are also differentiated by aperithecial stromatal apices while the production of perithecia occurs in subterminal regions of the stroma.

Similar to *Cordyceps* species in clade A, the *C. unilateralis* subclade includes species that produce disarticulating or non-disarticulating (intact) ascospores. For example, some species in the *C. unilateralis* subclade (e.g., *C. sinensis* (Berk.) Sacc. and *C. unilateralis*) were formerly classified in *C.* subg. *Ophiocordyceps*. But these species are interspersed among other species (e.g., *C. agriotidis* A. Kawam. and *C. robertsii* (Hook.) Berk.) that are classified in *C.* subg. *Cordyceps*. This indicates that, while ascospore morphology is useful in delimiting closely related *Cordyceps* species and uniting others in species complexes, it is not diagnostic of the *C. unilateralis* subclade itself (Fig. 6).

Most members of *C.* subg. *Neocordyceps*, as classically treated by Kobayasi (1941, 1982) and others (e.g., Artjariyasripong *et al.* 2001, Stensrud *et al.* 2005), form a monophyletic group labelled as the *C. sphecocephala* subclade within the *C. unilateralis* group (Fig. 6). The majority of species in the *C. sphecocephala* subclade produce long, thin, pliant, brightly coloured (or dark marasmioid in a few species) stromata,

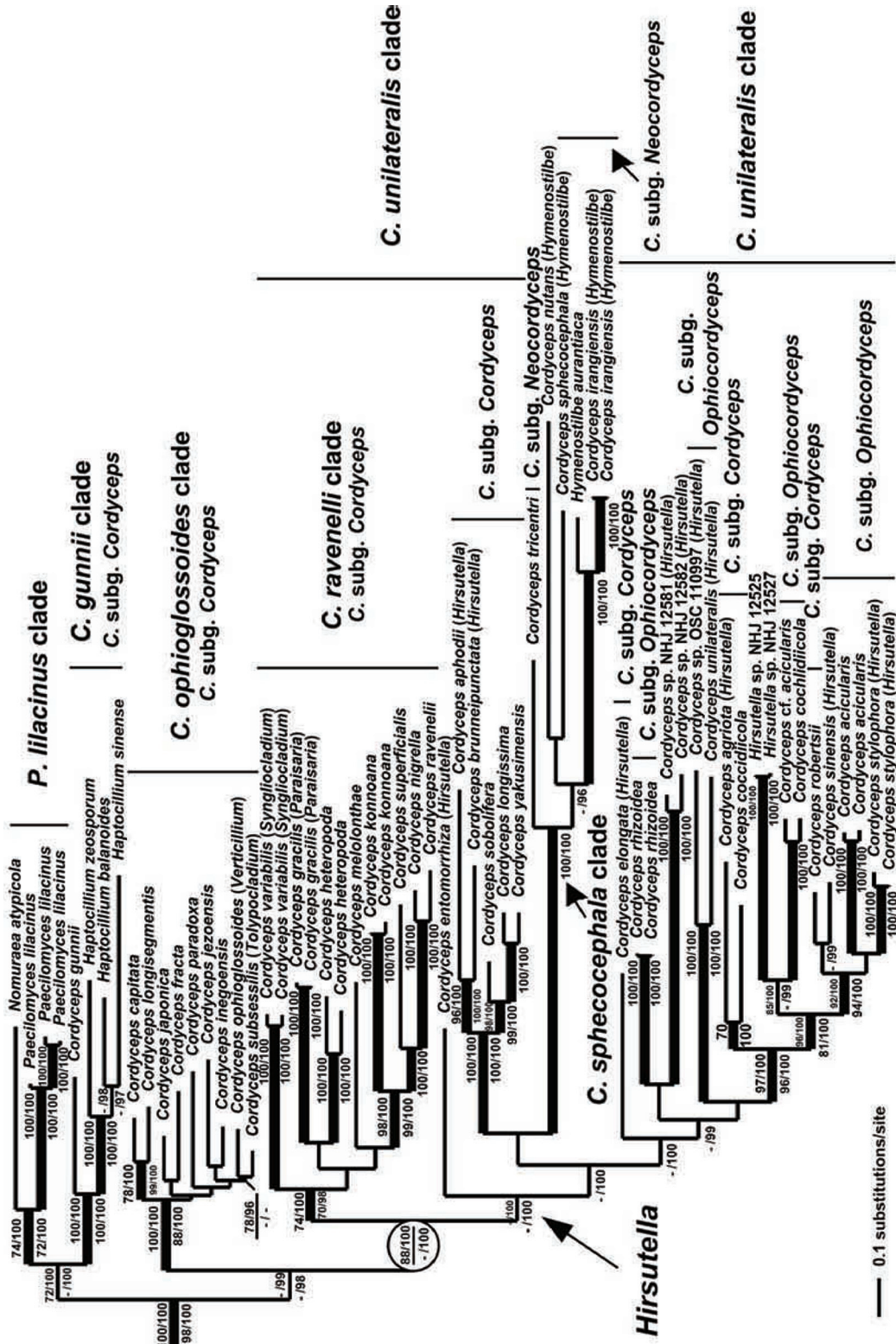


Fig. 6. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade B, to emphasize relationships within the clade. Respective subgenera of *Cordyceps* species in current classification are provided to the right or below of species. Known anamorphic genera of *Cordyceps* species are in parentheses. Numbers above corresponding nodes are bootstrap proportions of ML analyses (before the backslash) and posterior probabilities (after the backslash) from 147-taxon 5-gene data set in Fig. 3. Numbers below corresponding nodes are bootstrap proportions of ML analyses (before the backslash) and posterior probabilities (after the backslash) from 162-taxon 5-gene data set in Fig. 2. Bootstrap proportions of $\geq 70\%$ or posterior probabilities of ≥ 0.95 (in percentage) are shown in corresponding nodes. Internodes in a thicker line are supported by the bootstrap proportions and posterior probabilities from either 147-taxon or 162-taxon 5-gene data sets. Numbers in a circle correspond to intermode that is informative for placing the *C. sphecocephala* clade.

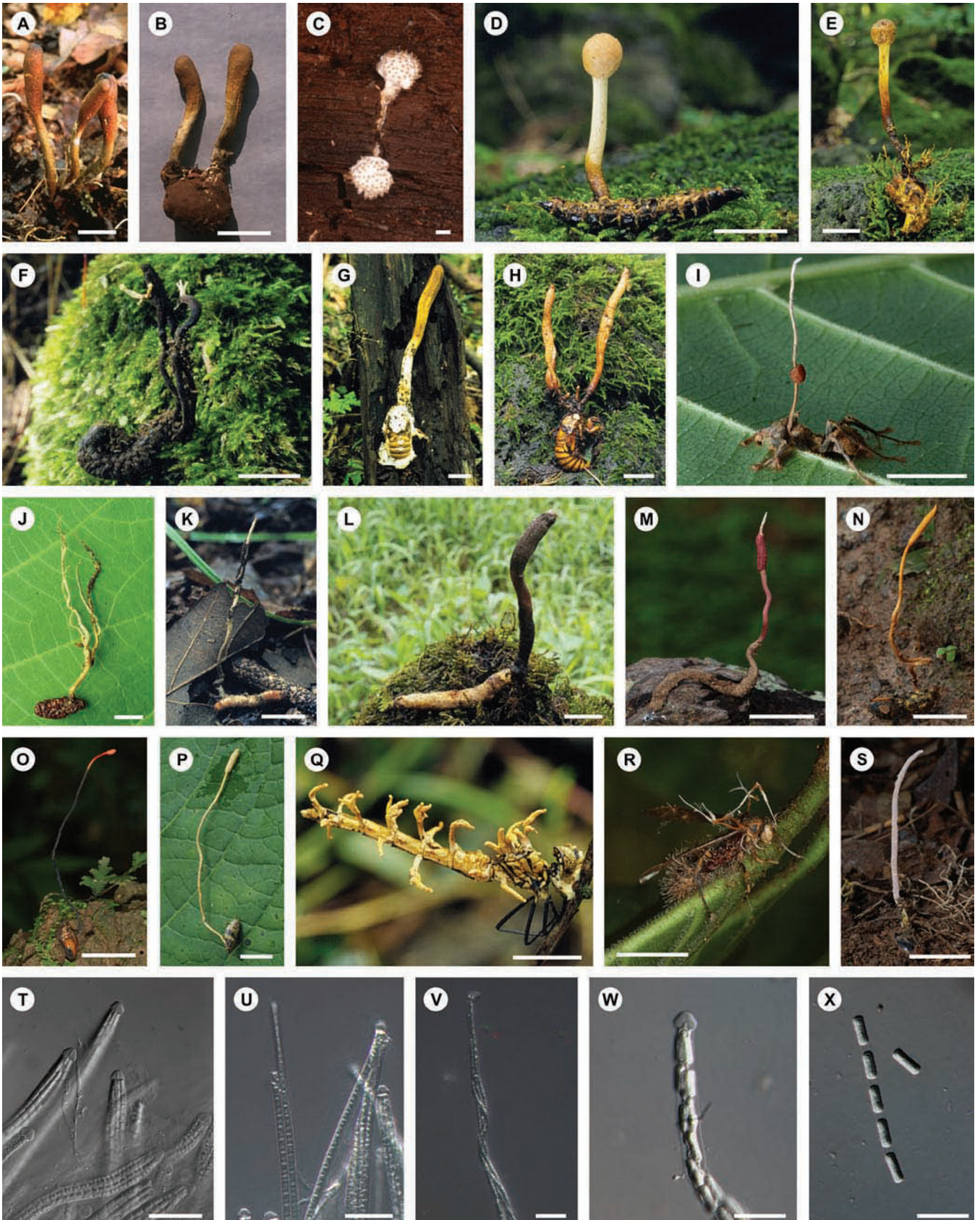


Fig. 7. A–S. Representative species of *Cordyceps* and its allies in *Clavicipitaceae* clade B. **T–X.** Ascus and ascospore of *Cordyceps* species in this clade. **A.** *C. ophioglossoides* on truffle (*Elaphomyces* sp.: *Eurotiomycetes*). **B.** *C. japonica* on truffle (*Elaphomyces muricatus*: *Eurotiomycetes*), OSC 110991. **C.** *C. subsessilis* on scarabaeid beetle in decaying wood (Coleoptera), OSC 128581. **D.** *C. gracilis* on lepidopteran larva, EFCC 10121. **E.** *C. heteropoda* on nymph of cicada (Hemiptera), EFCC 7768. **F.** *C. nigrella* on coleopteran larva, EFCC 3438. **G.** *C. sobolifera* on nymph of cicada (Hemiptera), EFCC 10125. **H.** *C. longissima* on nymph of cicada (Hemiptera), EFCC 8576. **I.** *C. unilateralis* on ant (Hymenoptera). **J.** *C. cochliodicola* on lepidopteran larva, EFCC 377. **K.** *C. agriotidis* on coleopteran larva, EFCC 5274. **L.** *C. sinensis* on larva of *Hepialus* sp. (Lepidoptera), EFCC 3248. **M.** *C. brunneipunctata* on coleopteran larva. **N.** *C. sphecocephala* on wasp (Hymenoptera). **O.** *C. nutans* on stink bug (Hemiptera). **P.** *C. tricentri* on adult of *Tricentrus* sp. (Hemiptera), EFCC 1001; bar = 10 mm. **Q.** *Hymenostilbe odonatae* on adult of dragonfly (Odonata), EFCC 12459; bar = 10 mm. **R.** *Hirsutella* sp. on wasp (Hymenoptera). **S.** *Paecilomyces lilacinus*. **T.** *C. robertsii*, ascus with disarticulating ascospores, MICH 28746. **U.** *C. acicularis*, ascus and nondisarticulating ascospores, OSC 110987. **V.** *C. paludosa*, non-disarticulating ascospores, MICH 14366. **W.** *C. variabilis*, disarticulated part-spores in ascus, and **X.** Part-spores, OSC 128581. Scale bars: A–B = 10 mm, C = 1 mm, D–H = 10 mm, I = 5 mm, J–S = 10 mm, T–X = 10 μ m.

which terminate in clavate to elongated fertile parts, and possess ascospores that disarticulate into sixty-four part-spores (Kobayasi 1941, 1982, Hywel-Jones 2002). Species in this clade produce perithecia, which are partially or completely immersed in the stromata at strongly oblique angles (Kobayasi 1941, 1982, Mains 1958, Hywel-Jones 1996). This clade is one of the best characterized by its morphology (obliquely embedded perithecia in a well-defined clava) and its ecology of parasitizing adult stages of insects.

Species in *Clavicipitaceae* clade C

Clavicipitaceae clade C includes *C. militaris*, the type species of the genus *Cordyceps* (Fig. 8). Most *Cordyceps* species in this clade are currently classified in *C.* subg. *Cordyceps* (Kobayasi 1941, 1982). This clade also contains the members of the former *C.* subg. *Ophiocordyceps* and *C.* subg. *Bolacordyceps*, resulting in *C.* subg. *Cordyceps* being paraphyletic within clade C (Eriksson 1982, Hywel-Jones 1994, Sung & Spatafora 2004). Species of *Cordyceps* in this clade produce three ascospore types, including disarticulating ascospores (e.g., *C. militaris*), intact ascospores (e.g., *C. cardinalis* and *C. pseudomilitaris* Hywel-Jones & Sivichai), and bola-ascospores (e.g., *C. bifusispora* O.E. Erikss.). Of particular note, this clade includes *Phytocordyceps ninchukispora* C.H. Su & H.-H. Wang in the unispecific genus *Phytocordyceps* C.H. Su & H.-H. Wang. The genus *Phytocordyceps* was originally described based on bola-ascospores and its host affiliation as a pathogen of *Beilschmiedia erythrophloia* Hayata (*Lauraceae*) plant seeds (Su & Wang 1986). Morphologically, this species is most similar to *C. bifusispora* in that it produces bola-ascospores typical of *C.* subg. *Bolacordyceps*. However, the phylogenetic analyses in this study reveal that species producing bola-ascospores (e.g., *C. bifusispora* and *P. ninchukispora*) do not form a monophyletic group (Fig. 8). Rather, they are interspersed among other *Cordyceps* species possessing disarticulating ascospores, most notably *C. militaris*.

Species of *Cordyceps* in clade C produce superficial to partially immersed perithecia on fleshy stromata that are pallid to brightly pigmented. This is in contrast to *Cordyceps* species in clade B, which produce darkly pigmented, wiry to pliant or fibrous stromata. This suggests that pigmentation and texture of stromata may be phylogenetically informative at a higher level of classification. It should be noted, however, that some *Cordyceps* species in clade C are morphologically similar to distantly related *Cordyceps* species (e.g., *C. melolonthae* and *C. variabilis*) in stromatal pigmentation. Although these characters are useful in recognizing *Cordyceps* species of clade C, the utility of these characters for any future infrageneric classification is probably limited (Fig. 8). For example, *C. militaris* is macroscopically similar to *C. cardinalis* and *C. pseudomilitaris*. All three species produce orangish to red-coloured and fleshy stromata; however, these species differ in ascospore and anamorph morphology (Sung & Spatafora 2004). Furthermore, *C. militaris* is

known as exhibiting considerable variability in stroma morphology (Sung & Spatafora 2004). Potentially conspecific species, such as *C. roseostromata* Kobayasi & Shimizu and *C. kyusyuënsis* A. Kawam., differ in stroma morphology, but are closely related to *C. militaris* and possess identical ascospore and ascus morphologies (Fig. 8, Hywel-Jones 1994, Sung & Spatafora 2004).

The variation in ascospore morphology of *Clavicipitaceae* clade C combined with old descriptions and unavailable type material complicates species identification for many taxa, as is the case for much of *Cordyceps*. For example, this study reveals a close relationship between the anamorphic species, *Mariannaea pruinosa* Z.Q. Liang from China, *C.* cf. *pruinosa* from Korea and Thailand, and *Phytocordyceps ninchukispora* from Taiwan (Fig. 8). The teleomorph of *M. pruinosa* is *C. pruinosa* Petch, which was originally described as producing disarticulating ascospores and reddish orange stromata, parasitizing lepidopteran cocoons (Petch 1924, Kobayasi 1941, Liang 1991). Although the isolate of *M. pruinosa* was obtained from ascospores (Liang 1991), the morphology of the ascospores was not well characterized. The species was identified primarily based on its host affiliation and macroscopic characters. In our study, *C.* cf. *pruinosa* EFCC 5197 and N.H.J. 10627 were collected from the same host family (Lepidoptera, Limacodidae) in Korea and Thailand. They are also closely related and produce reddish orange stromata (Fig. 8) and bola-ascospores and not the typical *C.* subg. *Cordyceps* part-spores. It should be noted, however, that Petch did not provide any drawings or images of ascospores and it is possible that the terminal cells of bola-ascospores could easily be interpreted as part-spores. Thus, at this time we use the name *C. pruinosa* for the Chinese, Korean and Thai collections and, if further attempts fail to locate type material for *C. pruinosa*, one of these may have to be designated a neotype. The *C. pruinosa* collections are closely related to and morphologically indistinguishable from *P. ninchukispora* with the exception of host affiliation, suggesting the possibility of host misidentification in the original description of *P. ninchukispora*. Because the tree topology of the *C. pruinosa*/*P. ninchukispora* complex is indicative of greater phylogenetic species diversity, i.e., the Korean, Thai, and Taiwanese material may represent unique phylogenetic species (Fig. 8), we retain the use of both names until more detailed sampling and analyses have been conducted.

Clavicipitaceae clade C not only includes members of *Cordyceps* but also species of the genus *Torrubiella*, which generally parasitize spiders and scale insects (Kobayasi & Shimizu 1982). The genus *Torrubiella* is morphologically characterized by the production of superficial perithecia on a mycelial subiculum that partially or completely surrounds the host (Kobayasi & Shimizu 1982, Humber & Rombach 1987). Species of *Torrubiella* also produce disarticulating (e.g., *T. ratticaudata* Humber & Rombach) and intact (e.g., *T. wallacei*) ascospores. Among species of *Cordyceps*, *C. tuberculata* (Lebert) Maire, a pathogen of adult

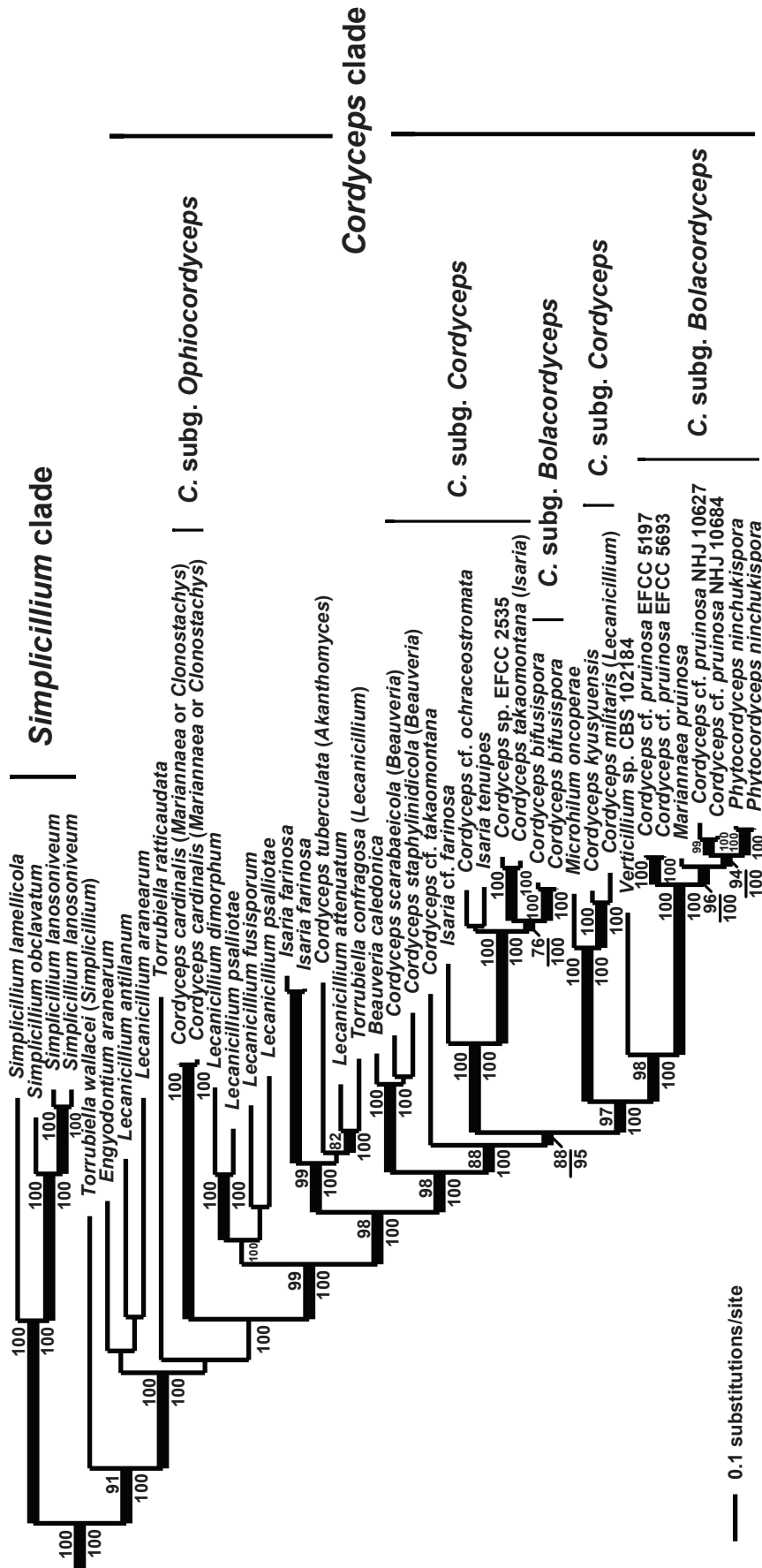


Fig. 8. Enlargement of Bayesian consensus tree in Fig. 2, showing Clavicipitaceae clade C, to emphasize relationships within the clade. Respective subgenera of *Cordyceps* species in previous classification are provided to the right of the species. Known anamorphic genera of *Cordyceps* species are in parentheses. Tree description is the same as in Fig. 2.

Lepidoptera, has been considered an intermediate species between *Torrubiella* and *Cordyceps* (Humber & Rombach 1987, Kobayasi 1941, Mains 1958). Phylogenetic analyses in this study indicate that the members of *Torrubiella* do not form a monophyletic group within clade C and are interspersed among species of *Cordyceps*. This suggests that the stipitate stromata of *Cordyceps* have been gained or lost several times during the evolution of these fungi. Currently, more than 50 species of *Torrubiella* have been described and the members of genus *Torrubiella* are clearly undersampled in this study (Kobayasi & Shimizu 1982).

In summary, the characters of ascospore morphology and the arrangement of perithecia used in the current classification of the genus *Cordyceps* are not congruent with the three higher clades inferred in these analyses. These characters are likely to prove useful, however, in lower level classifications, such as the delimitation of closely related species and species complexes. The characters most congruent with the three higher clades of clavicipitaceous fungi are texture, pigmentation and morphology of the stromata, but with exceptions. Although we have divided *Cordyceps* species into three major clades, it is difficult to characterize *Cordyceps* species within the *Clavicipitaceae* clade A due to the relatively few teleomorph species that are part of this clade (see key on p. 54). They tend to produce green to white stromata, often with lilac tints, but additional sampling is needed to more definitively characterize the teleomorphs of these species. However, the majority of species within clades B and C are morphologically and/or ecologically distinct (Figs 1–2).

The majority of *Cordyceps* species in clade B are characterized by darkly pigmented, wiry, pliant or fibrous stromata. The dominant form of parasitism exhibited by these species is on subterranean or wood-inhabiting hosts, buried in soil or embedded in decaying wood, such as larval and pupal stages of arthropods. In contrast, *Cordyceps* species of clade C have brightly pigmented and fleshy stromata and parasitize their hosts in relatively more accessible environments, such as leaf litter, moss, or the uppermost soil layer. Exceptions to these morphological and ecological traits are found in some *Cordyceps* species in clade B. *Cordyceps melolonthae*, for example, produces brightly-coloured stromata, although it bruises dark upon handling and its hosts are the larvae of cockchafers or June beetles buried in soil (Mains 1958). *Cordyceps unilateralis* parasitizes adult ants, but is darkly pigmented with a wiry stroma and subterminal production of perithecia, and members of the *C. sphecocephala* clade are at least partially brightly pigmented and are restricted to adult stages of insects. These findings suggest that the traits described above are not universally informative, but collectively useful in characterizing *Cordyceps* species within clade B. That is, there have been gains, losses, and diversifications of most if not all traits during the evolution of these fungi, but general trends in character state evolution are evident.

The taxonomic utility of anamorphic forms in classification of *Cordyceps*

The genus *Cordyceps* is characterized by a diverse assemblage of more than 25 anamorph genera (e.g., *Beauveria* Vuill., *Hirsutella* Pat., *Hymenostilbe* Petch, *Isaria* Fr., *Lecanicillium* W. Gams & Zare, *Metarhizium*, and *Tolypocladium* W. Gams) (Kobayasi 1982, Samson *et al.* 1988, Gams & Zare 2003, Hodge 2003). The anamorph genera of *Cordyceps* are hyphomycetes with conidiogenous cells that are hyaline to brightly coloured and produce conidia in dry chains or slimy drops (Samson *et al.* 1988). Some anamorph genera (e.g., *Hymenostilbe*) are known as a useful diagnostic character in recognizing monophyletic groups of *Cordyceps* species (Artjariyasripong *et al.* 2001, Kobayasi 1941, 1982), while other anamorph morphologies and genera are placed in more than one clade of the *Clavicipitaceae*. Therefore, the distribution of anamorphic forms is discussed to evaluate their phylogenetic utility in characterizing the three clades of *Cordyceps* and *Clavicipitaceae* and to better understand teleomorph–anamorph connections.

Anamorphs of *Clavicipitaceae* clade A

Clavicipitaceae clade A includes isolates of the anamorph genera *Aschersonia* Mont., *Metarhizium*, *Nomuraea* Maublanc, *Pochonia* Bat. & O.M. Fonseca, *Paecilomyces s. l.*, *Rotiferophthora* G.L. Barron, *Tolypocladium* W. Gams, and verticillium-like (Fig. 4). *Nomuraea*, *Paecilomyces*, and *Tolypocladium* are found in other clades of *Clavicipitaceae* (Figs 1–2). Significantly, *Verticillium s. s.* is known from the *Plectosphaerellaceae*, which is closely related with the *Glomerellaceae* in the Sordariomycetidae (Zare *et al.* 2007). *Paecilomyces s. s.* is in the *Eurotiales* (*Eurotiomycetidae*), but species of *Paecilomyces s. l.* are also present elsewhere in the *Hypocreales* (Luangsa-ard *et al.* 2004). In contrast, the anamorph genera *Aschersonia*, *Metarhizium*, *Pochonia* and *Rotiferophthora* are restricted to clade A (Figs 1–2).

Anamorph taxa of the *C. taii* subclade include *Nomuraea rileyi* (Farl.) Samson, *Paecilomyces carneus* (Duché & R. Heim) A.H.S. Brown & G. Smith and *Pa. marquandii* (Masse) S. Hughes, *Pochonia*, *Tolypocladium parasiticum*, and *Metarhizium* (Fig. 4). The genera *Nomuraea*, *Pochonia* and *Tolypocladium* are not monophyletic, although *Pochonia* is restricted to clade A. *Nomuraea rileyi* and *Metarhizium* are entomogenous; *Pa. carneus* is a common soil fungus considered a weak insect pathogen, while *Pa. marquandii*, *Pochonia* and *T. parasiticum* are also common soil fungi and can be parasitic on nematodes. *Metarhizium* is the only monophyletic anamorph genus of clade A (Fig. 4). The conidiogenous cells in the genus *Metarhizium* are cylindrical to clavate without a neck and produced in candelabrum-like or palisade-like fashion (Rombach *et al.* 1986, Driver *et al.* 2000, Evans 2003). The genus is most similar to *Nomuraea* and differs in the compact conidiophores that form a hymenial layer (Evans 2003). *Nomuraea rileyi* groups with species of *Metarhizium*, while *N. atypicola* (Yasuda) Samson belongs to the *Pa. lilacinus* clade

in clade B. Interestingly, *N. rileyi* produces greenish-coloured conidia, as do species of *Metarhizium* in the *C. taii* subclade, while *N. atypicola* possesses lavender-coloured conidia similar to those of *Pa. lilacinus* (Coyle *et al.* 1990, Hywel-Jones & Sivichai 1995, Evans 2003). Currently, three teleomorphic species of *Metarhizium* (*C. brittlebankisoides*, *C. campsosterni*, and *C. taii*) have been reported (Liang *et al.* 1991, Liu *et al.* 2001, Zhang *et al.* 2004). The species *M. taii* was described with its teleomorph species, *C. taii* (Liang *et al.* 1991) and recently synonymized with *M. anisopliae* var. *majus* (Huang *et al.* 2005). *Cordyceps brittlebankisoides* was once also considered to have the anamorph *M. anisopliae* var. *Omajus* (Liu *et al.* 2001), but it is likened to *M. flavoviride* (Huang *et al.* 2005). In general, *Metarhizium* species show extensive variation in size and colour of conidia (Driver *et al.* 2000, Evans 2003) and more intensive sampling of anamorphs and teleomorphs is needed for this group.

The genus *Tolypocladium* is characterized by producing single or whorled (verticillate) conidiogenous cells (phialides), which are flask-shaped with enlarged bases that taper into a needle-like neck usually bent from the axis of the phialides (Gams 1971, Bissett 1983). The type of the genus *Tolypocladium*, *T. inflatum* W. Gams, is linked to the teleomorph *C. subsessilis* (Hodge *et al.* 1996, Gams & Zare 2003). *Tolypocladium inflatum* is placed in clade B and is distantly related to *T. parasiticum* in the *C. taii* clade. *Tolypocladium parasiticum* was described from the rotifer host *Adineta* and described with underwater conidiation (Barron 1980). Morphologically, *T. parasiticum* differs from other species of *Tolypocladium*, as it is the only member of the genus that produces chlamydospores *in vivo* (Barron 1980) and in culture (Bissett 1983, Zare *et al.* 2001, Gams & Zare 2003). In a recent treatment of *Verticillium* sect. *Prostrata* W. Gams, the genus *Pochonia* was also reclassified based on production of dictyochlamydospores or at least swollen hyphal cells (Gams & Zare 2001, Zare *et al.* 2001), supporting the close phylogenetic relationship of *T. parasiticum* and *Pochonia* species demonstrated in this study (Fig. 4). Hence, *T. parasiticum* is transferred to *Pochonia* below, rendering the remaining species in *Tolypocladium* monophyletic. *Paecilomyces marquandii* also produces infrequent chlamydospores in culture, as does the anamorph of *Metacordyceps yongmunensis* sp. nov. (discussed below). As suggested by Barron & Onions (1966), the presence of chlamydospores can be a taxonomically informative character.

The genus *Aschersonia* is a monophyletic lineage labelled as *Hypocrella* subclade (Fig. 4). The genus *Aschersonia* is characterized by its pycnidial or acervular conidiomata with hymenial phialides and its ecology of parasitizing only the nymphs of scale insects and whiteflies (Petch 1921, Hywel-Jones & Evans 1993). The teleomorphs of *Aschersonia* have long been linked to the species of *Hypocrella* and more than 25 species have been reported (Petch 1921, Mains 1959). While this study does not focus on sampling of *Hypocrella* and *Aschersonia*, these findings corroborate that the unique morphology of *Aschersonia* is phylogenetically

informative and diagnostic of a monophyletic group of clavicipitaceous fungi (Fig. 4).

Anamorphs of Clavicipitaceae clade B

Clavicipitaceae clade B includes several anamorph genera including *Haptocillium* W. Gams & Zare, *Hirsutella*, *Hymenostilbe* and *Tolypocladium* (Fig. 6). Several of the anamorphic forms in the clade are phylogenetically informative. *Hirsutella* and *Hymenostilbe* occur dominantly in the *C. unilateralis* subclade.

Hirsutella is characterized by its typical basally-subulate phialides, narrowing into one (usually) or more (occasionally) very slender needle-like necks, on synnemata or mononematous mycelium (Hodge 1998, Gams & Zare 2003). *Hirsutella* species normally produce a few (<5) conidia in mucus and the phialides are not usually bent in their needle-like necks such as in the genus *Tolypocladium*, but also single conidia as in *Hi. thompsonii* F.E. Fisher. Not all *Cordyceps* species in the *C. unilateralis* subclade are connected to *Hirsutella* anamorphs. Some are connected to *Paecilomyces* s. l., *Paraisaria* Samson & B.L. Brady, and *Syngliocladium* Petch, whereas anamorphic forms are not known for many of the *Cordyceps* species, especially in the *C. ravenelii* subclade (e.g., *C. heteropoda* Kobayasi). However, most *Cordyceps* species in the rest of the *C. unilateralis* subclade have been linked to *Hirsutella* anamorphs (Fig. 6). These results suggest that *Hirsutella* anamorphs are phylogenetically informative for at least part of the *C. unilateralis* subclade or possibly symplesiomorphic for the *C. unilateralis* subclade as a whole.

The taxonomic utility of *Hirsutella* anamorphs is exemplified by the teleomorph–anamorph connection of the genus *Cordycepioideus* Stiffler, a termite pathogen, which does not have typical ascospore and ascus morphologies of clavicipitaceous fungi (Blackwell & Gilbertson 1984, Suh *et al.* 1998). It possesses thick-walled multiseptate ellipsoid ascospores and its asci lack the thickened ascus tip characteristic of most clavicipitaceous fungi (Blackwell & Gilbertson 1984, Ochiel *et al.* 1997). The anamorph of *Cordycepioideus bisporus* Stiffler is a synnematus *Hirsutella* that is either conspecific with or closely related to *Hi. thompsonii* (Ochiel *et al.* 1997, Suh *et al.* 1998, Sung *et al.* 2001). Although *Cordycepioideus bisporus* differs greatly from other members of the *C. unilateralis* subclade in its teleomorphic characters, molecular data strongly support it as a member of the *C. unilateralis* subclade, a finding consistent with its *Hirsutella* anamorph. It should be noted that species of *Cordyceps* outside of clade B have been described with atypical *Hirsutella* anamorphs (e.g., *C. pseudomilitaris*), but upon further investigation were more accurately characterized in other anamorph genera (e.g., *Simplicillium* W. Gams & Zare).

The *C. unilateralis* clade includes the members of the *C. sphecocephala* subclade, which possess a *Hymenostilbe* anamorph. The genus *Hymenostilbe* usually produces cylindrical to clavate conidiogenous cells, which are produced in a more or less dense

palisade in synnemata (Samson *et al.* 1988). It is differentiated from closely related genera (e.g., *Akanthomyces* Lebert and *Hirsutella*) by its polyblastic conidiogenous cells, which holoblastically produce single conidia on short denticles or scars (Samson *et al.* 1988, Hywel-Jones 1996). The results from the present study indicate that *Hymenostilbe* anamorphs may be derived from within *Hirsutella* (Fig. 6). The close phylogenetic relationship between *Hirsutella* and *Hymenostilbe* anamorphs is exemplified by the morphologically intermediate synnematous *Hirsutella/Hymenostilbe* species. For example, *Hy. lecaniicola* (Jaap) Mains, the anamorph of *C. clavulata* (Schwein.) Ellis & Everh. (Hodge 1998), was previously classified in *Hirsutella* although it possesses extensively polyphialidic conidiogenous cells in a discontinuous layer (Mains 1950, 1958, Samson & Evans 1975, Hodge 1998). In addition, some *Hirsutella* species (e.g., *Hi. rubripunctata* Samson, H.C. Evans & Hoekstra) produce only a single conidium without a mucous sheath on denticles of extensively polyphialidic conidiogenous cells. Therefore, the modes of asexual reproduction in *Hirsutella* and *Hymenostilbe* may overlap to some extent and additional work is necessary to address the relationships between the two genera (Hodge 1998, Gams & Zare 2003).

In addition to the *C. unilateralis* subclade, the remaining three subclades contain *Haptocillium*, *Tolypocladium* and verticillium-like anamorphs. The genus *Haptocillium* was reclassified from the former *Verticillium* sect. *Prostrata* primarily based on its adhesive conidia and its ability to parasitize free-living nematodes (Zare & Gams 2001b). This study shows that the genus is a monophyletic group in the *C. gunnii* subclade (Fig. 6). However, the teleomorph–anamorph connection has not been established for any of the species in the clade or its close relative, *C. gunnii*, and thus its taxonomic utility remains unclear. The *C. ophioglossoides* and *Pa. lilacinus* subclades include anamorphic forms of *Paecilomyces* s. l., *Nomu-raea*, *Tolypocladium*, and verticillium-like, all of which are polyphyletic as previously discussed (Figs 1–2; Oborník *et al.* 2001, Luangsa-ard *et al.* 2004, 2005). Several teleomorph–anamorph connections have been reported for *Cordyceps* species in the *C. ophioglossoides* and *Pa. lilacinus* subclades although their taxonomic utility is limited. *Cordyceps subsessilis* is known to be the teleomorph of *Tolypocladium inflatum* (Hodge *et al.* 1996) and *C. ophioglossoides* produces a verticillium-like anamorph (Gams 1971). In the *Pa. lilacinus* subclade, *N. atypicola* is linked to *C. cylindrica* (Evans & Samson 1987, Hywel-Jones & Sivichai 1995).

Anamorphs of Clavicipitaceae clade C

The anamorph genera sampled that are members of clade C include *Beauveria*, *Isaria*, *Lecanicillium*, *Microhilum* H.Y. Yip & A.C. Rath, and *Simplicillium*. Species of *Lecanicillium* and *Simplicillium* were previously placed in *Verticillium* sect. *Prostrata* and recently reclassified based on the phylogenetic studies of Sung *et al.* (2001) and Zare & Gams (2001a, b). The genus *Lecanicillium* is characterized by producing

slender aculeate phialides that are produced singly or in whorls and usually arise from prostrate aerial hyphae (Zare & Gams 2001a). Conidia are mostly produced at the tip of phialides and attached in heads or fascicles (Zare & Gams 2001a). The morphological delimitation of *Simplicillium* from *Lecanicillium* is difficult although the species of *Simplicillium* tend to produce phialides that more or less arise singly from prostrate aerial hyphae (Zare & Gams 2001a). This study shows again that the species of *Lecanicillium* form a paraphyletic group, as species of other well-delimited anamorphic genera (e.g., *Beauveria*, *Engyodontium* G.S. de Hoog, and *Isaria*) are interspersed among species of *Lecanicillium* (Fig. 8).

Some *Lecanicillium* species are known to be anamorphic forms of *Cordyceps* and *Torrubiella* (Petch 1932, Evans & Samson 1982, Zare & Gams 2001a). For example, *C. militaris* produces a *Lecanicillium* anamorph in culture (Zare & Gams 2001a) and the anamorph of *Torrubiella alba* Petch is *L. aranearum* (Petch) Zare & W. Gams (Petch 1932). The type species of *Lecanicillium* is *L. lecanii* (Zimm.) Zare & W. Gams, which is connected to the teleomorph *T. confragosa* Mains, a pathogen of scale insects (Evans & Samson 1982), which we transfer here to *Cordyceps*. In addition to *Lecanicillium* anamorphs, other genera (e.g., *Akanthomyces*, *Gibellula* Cavara, *Hirsutella*, *Paecilomyces* (*Isaria*), and *Simplicillium*) have also been linked to *Torrubiella* (Kobayasi & Shimizu 1982, Samson *et al.* 1988, 1989, Zare & Gams 2001a).

Clavicipitaceae clade C also includes the species of *Isaria*, the generic name of which has been conserved with *I. farinosa* (Holmsk.) Fr. as the type, for some of the clavicipitaceous *Paecilomyces* species (Gams *et al.* 2005, Luangsa-ard *et al.* 2005). The genus *Paecilomyces* was a diverse genus, with molecular studies indicating its polyphyletic status (Oborník *et al.* 2001, Luangsa-ard *et al.* 2004, 2005). The type species, *Pa. variotii* Bainier, belongs to the order *Eurotiales* (*Ascomycota*) and is distantly related to the clavicipitaceous *Paecilomyces* species that were previously classified in *Paecilomyces* sect. *Isarioidea* (Samson 1974, Luangsa-ard *et al.* 2004). The previous taxonomy of *Paecilomyces* was primarily based on the monographic study by Samson (1974), which included approximately 22 species in *Paecilomyces* sect. *Isarioidea*. In a recent molecular study, Luangsa-ard *et al.* (2005) demonstrated that species in *Paecilomyces* sect. *Isarioidea* are subdivided into four monophyletic groups, three of which are statistically supported. As a result, eleven species of *Paecilomyces* sect. *Isarioidea* were reclassified in *Isaria* (e.g., *I. fumosorosea* Wize, *I. javanica* (Frieder. & Bally) Samson & Hywel-Jones and *I. tenuipes* Peck) (Luangsa-ard *et al.* 2005). The present study indicates that the four isolates of *Isaria* do not form a monophyletic group in clade C, as they are interspersed among other anamorphic forms in the clade. Thus, the taxonomic utility of *Isaria* anamorph is limited to clade C, as seen with *Lecanicillium* and *Simplicillium* anamorphs. Furthermore, few connections have been made between teleomorphs of the *Clavicipitaceae* and species of *Isaria*. Kobayasi

(1941) reported that the anamorph of *C. takaomontana* Yakush. & Kumaz. is *Isaria japonica* Yasuda, which Samson (1974) synonymized with *Pa. tenuipes* (= *I. tenuipes*). *Isaria farinosa* is the anamorph of *C. memorabilis* (Pacioni & Frizzi 1978), but was once mistakenly linked to *C. militaris* (Petch 1936). *Isaria farinosa* was also connected to two *Torrubiella* species, *T. gonylepticida* (A. Möller) Petch and *T. pulvinata* Mains. The anamorph of the latter was reported as *Spicaria pulvinata* Mains, and Petch described the conidial state of *T. gonylepticida* as *Spicaria longipes* Petch, two *Spicaria* species that Samson (1974) synonymized with *Paecilomyces farinosus* (= *I. farinosa*). Although *T. gonylepticida* was originally described in combination with *Cordyceps*, Petch (1937) transferred the species to its current combination and redescribed the species. *Isaria farinosa* has been reported to occur on six insect orders (Lepidoptera, Coleoptera, Hemiptera, Homoptera, Diptera, and Hymenoptera) and also on spiders (Araneae). The simplicity and plasticity in the morphology of most *Isaria* species make it difficult to set boundaries among and between sister-taxa and the search for better markers in species delimitation must be a goal for further studies.

The closely related species, *C. scarabaeicola* Kobayasi and *C. staphylinidicola* Kobayasi & Shimizu produce *Beauveria* anamorphs (Fig. 8; Sung 1996), and *C. bassiana* Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan and *C. brongniartii* Shimazu are known as teleomorphs of *B. bassiana* (Bals.) Vuill. and *B. brongniartii* (Sacc.) Petch, respectively (Shimazu *et al.* 1988, Li *et al.* 2001). The genus *Beauveria* is morphologically well-characterized by producing basally-inflated conidiogenous cells that sympodially produce conidia on divergent denticles (MacLeod 1954, de Hoog 1972). *Beauveria* has a cosmopolitan distribution with quite a broad host range (Mugnai *et al.* 1989, Evans 2003, Rehner & Buckley 2005). A recent molecular study (Rehner & Buckley 2005) that included 87 isolates of five *Beauveria* species (*B. amorpha* (Höhn.) Samson & H.C. Evans, *B. bassiana*, *B. brongniartii*, *B. caledonica* Bissett & Widden, and *B. vermiconia* de Hoog & V. Rao) demonstrated that the genus is monophyletic and one of the more phylogenetically-informative anamorphs of clade C.

In fungal systematics, the naming of anamorphic forms is allowed for Phyla Ascomycota and Basidiomycota by Article 59 of the International Code of Botanical Nomenclature (McNeill *et al.* 2006) and multiple names exist for the same organisms of teleomorphic and anamorphic taxa. Recently, molecular phylogenetics has played an important role in integrating teleomorphic and anamorphic forms in a unified classification system in the clavicipitaceous fungi (Reynolds & Taylor 1993, Sung *et al.* 2001, Luangsa-ard *et al.* 2005). In such efforts, *Verticillium* sect. *Prostrata* and *Paecilomyces* sect. *Isarioidea* have recently been reclassified into several anamorphic genera (e.g., *Haptocillium*, *Isaria*, *Lecanicillium*, *Pochonia*, *Rotiferophthora*, and *Simplicillium*) to be consistent with the current hypotheses of relationships (Zare & Gams 2001a, Zare *et al.* 2001, Luangsa-ard *et al.* 2005). The phylogeny

presented here further improves our understanding of the teleomorph–anamorph connections in *Cordyceps* and implies that several anamorphic genera (e.g., *Beauveria*, *Hirsutella*, *Hymenostilbe*, and *Metarhizium*) are more restricted in their phylogenetic distribution and therefore phylogenetically informative in characterizing *Cordyceps* species (Figs 4, 6, 8).

TAXONOMIC REVISION

The present phylogenetic analyses reveal three strongly supported monophyletic groups (i.e., *Clavicipitaceae* clades A, B, and C) of clavicipitaceous fungi (Figs 1–2), a result consistent with studies involving fewer taxa (Spatafora *et al.* 2007, Sung *et al.* 2007). In reviewing the diagnostic characters used in previous classification schemes, most characters are not consistent with the phylogeny presented here. Therefore, the phylogenetic relationships of *Cordyceps* and the related clavicipitaceous fungi provide the evidence for rejecting most of the previous classifications of *Cordyceps* and *Clavicipitaceae* (Kobayasi 1941, 1982, Diehl 1950, Mains 1958). Here, we propose a new phylogenetic classification for *Cordyceps* and *Clavicipitaceae* as follows (Fig. 10).

Clavicipitaceae Clade A

Clavicipitaceae clade A is a well-supported monophyletic group that represents the *Clavicipitaceae* s. s. (MP-BP = 98 %, ML-BP = 99 %, PP = 1.00 in Figs 1–2, 10). The name *Clavicipitaceae* was first used in 1901 by Earle for the former *Hypocreaceae* subfam. *Clavicipiteae* Lindau (Earle 1901). However, Earle (1901) used it without description and without reference to its basionym. The name was then invalidly used by subsequent workers, such as Nannfeldt (1932) and Diehl (1950), until it was validated by Rogerson (1970) as confirmed by Eriksson & Hawksworth (1985). Although *Clavicipitaceae* is well characterized by cylindrical asci, thickened ascus apices, and filiform ascospores that tend to disarticulate at maturity as in the original description, we restrict the application of *Clavicipitaceae* s. s. to the members of *Clavicipitaceae* clade A because of the non-monophyly of *Clavicipitaceae* s. l. (Fig. 10). These findings suggest that the character states of cylindrical asci and filiform ascospores that disarticulate at maturity are plesiomorphic for the *Clavicipitaceae* s. l./*Hypocreaceae* clade. Importantly, the *Hypocreaceae* also possesses cylindrical asci and while its ascospores are subglobose to fusiform and easily distinguished from those of *Clavicipitaceae* s. l., they show a similarly high frequency of disarticulation (Rogerson 1970, Rossman *et al.* 1999).

The family *Clavicipitaceae* s. s. includes the grass-associated genera *Balansia* Speg., *Claviceps*, *Epichloë* (Fr.) Tul. & C. Tul., and *Myriogenospora* G.F. Atk., which were classified in *Clavicipitaceae* subfam. *Clavicipitoideae* sensu Diehl 1950 (Fig. 10). Recent molecular studies show that *Aciculosporium* I. Miyake, *Atkinsonella* Diehl, *Heteroëpichloë* E. Tanaka, C.

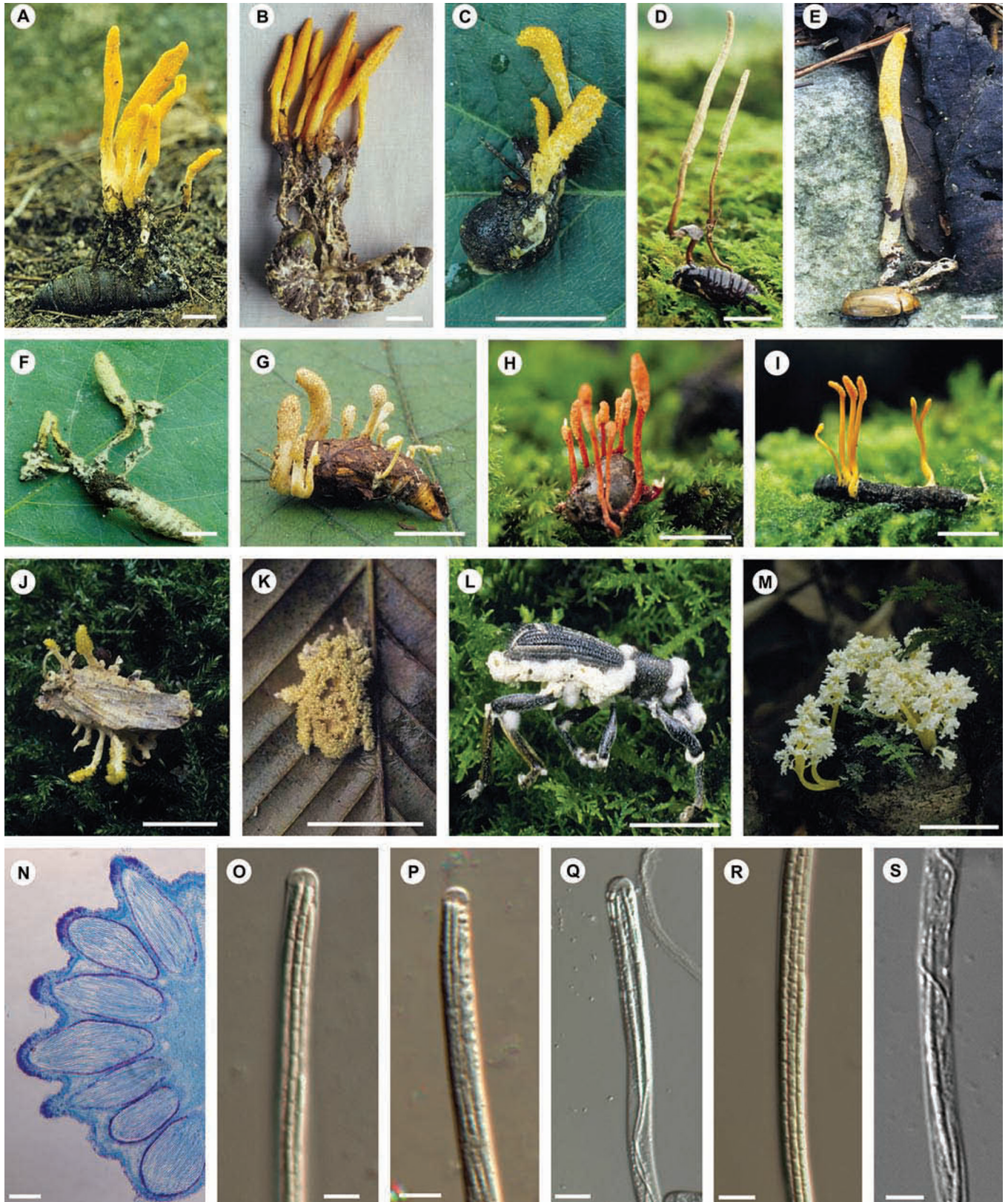


Fig. 9. A–M. Representative species of *Cordyceps* and its allies in *Clavicipitaceae* clade C. N–S. Perithecia, asci, and ascospores. **A.** *C. militaris* on lepidopteran pupa, EFCC 5192. **B.** *C. kysuyuensis* on lepidopteran larva, EFCC 10985. **C.** *C. chichibuensis* on coleopteran pupa, EFCC 422. **D.** *C. cf. ochraceostromata* on lepidopteran larva, EFCC 11846. **E.** *C. scarabaeicola* on scarabaeid beetle (Coleoptera), EFCC 5014. **F.** *C. staphylinidicola* on coleopteran larva, EFCC 783. **G.** *C. bifusispora* on lepidopteran pupa, EFCC 2626. **H.** *C. cf. pruinosa* on lepidopteran pupa (Limacodidae), EFCC 11756. **I.** *C. cardinalis* on lepidopteran larva, EFCC 12212. **J.** *C. tuberculata* on adult of moth (Lepidoptera), EFCC 2067. **K.** *Torrubiella* sp. on spider (Arachnida), EFCC 10882. **L.** *Beauveria* sp. on adult of beetle (Coleoptera), EFCC 1357. **M.** *Isaria tenuipes* on lepidopteran pupa, EFCC 1497. **N.** *C. cardinalis*, section of perithecia in stroma, OSC 93609. **O.** *C. militaris*, ascus with disarticulating ascospores, OSC 93623. **P.** *C. cardinalis*, ascus with nondisarticulating ascospores, OSC 93609. **Q.** *C. cf. pruinosa*, fusiform terminal parts of ascospores in ascus, EFCC 7481. **R.** *C. militaris*, multiseptated ascospores in ascus, OSC 93623. **S.** *C. cf. pruinosa*, thread-like structures connecting fusiform terminal parts of ascospores, EFCC 7481. Scale bars: A–M = 10 mm, N = 100 μm, O–S = 5 μm.

Tanaka, Gafur & Tsuda, *Neoclaviceps* J.F. White, Bills, S.C. Alderman & Spatafora, and *Parepichloë* J.F. White & P.V. Reddy are also members of this clade, thus supporting their classification in the *Clavicipitaceae* s. s. (White & Reddy 1998, Sullivan *et al.* 2001, Tanaka *et al.* 2002). *Clavicipitaceae* s. s. also includes the plant-associated *Shimizuoomyces paradoxus* Kobayasi, which occurs on seeds of *Smilax* (*Smilacaceae*). In addition to plant-associated fungi, *Clavicipitaceae* s. s. contains four arthropod-associated lineages. Three of the four arthropod-associated lineages are characterized as pathogens of scale insects, including *Hypocrella* (pathogens of scale insects and white flies; Hywel-Jones & Evans 1993, Hywel-Jones & Samuels 1998), *Regiocrella* P. Chaverri & K.T. Hodge (pathogen of scale insects; Chaverri *et al.* 2006), and *Torrubiella luteoestrata* Zimm. (pathogen of scale insects; Hywel-Jones 1993). The fourth lineage is described here as *Metacordyceps*; it comprises former species of *Cordyceps* and their related anamorphs and as a genus displays relatively broad arthropod host associations.

CLAVICIPITACEAE (Lindau) Earle ex Rogerson, *Mycologia* 62 : 900. 1970, emend. G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

Stromata or subiculum darkly or brightly coloured, fleshy or tough. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci cylindrical with thickened ascus apex. Ascospores usually cylindrical and multiseptate, disarticulating into part-spores or non-disarticulating.

Type: Claviceps Tul., *Ann. Sci. Nat. Bot.*, Sér. 3, 20: 43. 1853.

Teleomorphic genera: Aciculosporium, Atkinsonella, Balansia, Claviceps, Epichloë, Heteroepichloë, Hypocrella, Metacordyceps gen. nov., *Myriogenospora, Neoclaviceps, Parepichloë, Regiocrella, Shimizuoomyces.*

Anamorphic genera: Aschersonia, Ephelis Fr., *Metarhizium, Neotyphodium* A.E. Glenn, C.W. Bacon & Hanlin, *Nomuraea*, paecilomyces-like, *Pochonia, Sphacelia* Lév., verticillium-like.

METACORDYCEPS G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **gen. nov.** MycoBank MB504182.

Stromata solitaria vel nonnulla aggregata, simplicia vel ramosa. Stipes carnosus vel tenax, albidus, viridi-luteus vel viridulus, cylindricus vel sursum dilatatus. Pars fertilis cylindrica vel clavata. Perithecia partim vel omnino in stromate immersa, perpendicularia vel oblique inserta. Asci cylindrici, apice inspissato. Ascosporae cylindricae, multiseptatae, in cellulas diffrangentes vel maturae integrae remanentes.

Stromata solitary or several, simple or branched. Stipe fleshy or tough, whitish, greenish yellow to greenish, cylindrical to enlarging in fertile part. Fertile part cylindrical to clavate. Perithecia partially or completely immersed in stromata, ordinal or oblique in arrangement. Asci cylindrical with thickened ascus apex. Ascospores

cylindrical, multiseptate, disarticulating into part-spores or remaining intact at maturity.

Type: Cordyceps taii Z.Q. Liang & A.Y. Liu

Etymology: Greek *meta* = behind, a genus close to *Cordyceps* (and suggesting relationship to *Metarhizium*).

Anamorphic genera: Metarhizium, Nomuraea, paecilomyces-like, Pochonia.

Commentary: The genus *Metacordyceps* is proposed for species of *Cordyceps* s. l. in the *Clavicipitaceae* s. s. based on the phylogenetic placement of *C. taii* (Figs 1–2, 10). The genus is applied to the *C. taii* clade, which is strongly supported (MP-BP = 73 %, ML-BP = 78 %, PP = 1.00 in Figs 1–2, 10). Among the members of the clade, the best-known taxon is the anamorphic genus *Metarhizium*, because of its importance in biological control (Samson *et al.* 1988, Evans 2003). Currently, three species of *Cordyceps* (viz., *C. brittlebankisoides*, *C. campsosterni*, and *C. taii*) are known as teleomorphs of *Metarhizium* (Liang *et al.* 1991, Liu *et al.* 2001, Zhang *et al.* 2004). The genus name *Metacordyceps* is here used to emphasize that the clade includes the species of *Cordyceps* s. l. that produce *Metarhizium* anamorphs although other species of *Cordyceps* (e.g., *C. chlamydosporia*) in the clade are not connected to *Metarhizium* anamorphs.

Metacordyceps yongmunensis G.H. Sung, J.M. Sung & Spatafora, **sp. nov.** MycoBank MB504183. Figs 5B, 5F-K, 11A-G.

Anamorph: pochonia-like.

Stromata nonnulla vel raro singula, clavata, simplicia vel saepius ramosa, in chrysalidibus Lepidopterarum. Pars fertilis alba vel dilute lutea, a stipite haud distincta. Perithecia sparsa vel dense aggregata, partim immersa, brunneo-lutea, dilute brunnea vel aurantio-brunnea, oblique inserta, fusiformia vel clavata, 550–800 × 450–500 µm. Asci 8-sporei, hyalini, cylindrici, 205–360 × 5–7 µm, apice conspicue inspissato. Ascosporae filiformes, hyalinae, inconspicue multiseptatae, haud fragmentatae, 180–345 × 1 µm. Anamorphe *Pochoniae* similis.

Stromata several or rarely solitary, clavate, simple or more usually branched, on pupa of Lepidoptera. Fertile area white to pale yellow, not differentiated from stipe. Perithecia scattered or crowded, loosely immersed, brownish yellow, pale brown to orangish brown, oblique in arrangement, fusiform to clavate, 550–800 × 450–500 µm. Asci 8-spored, hyaline, cylindrical, 205–360 × 5–7 µm, possessing a prominent apical cap. Ascospores filiform, hyaline, multiseptate with indistinct septation, not fragmenting into part-spores, 180–345 × 1 µm. Conidiophores erect, produced in prostrate aerial hyphae. Phialides hyaline, solitary, awl-shaped, 20–28 × 2–2.2 µm. Conidia hyaline, elliptical to oblong, in slimy heads, 2–3.5 × 1.5–2.4 µm. Chlamydospores present.

Etymology: *Yongmunensis* in reference to the known locality of the first record of the species being Mt. Yongmun, Republic of Korea.

Table 1. Taxa used in molecular phylogenetic analyses. (^{AUT} Authentic material, ^T ex-type culture).

Species	Voucher Info. ¹	Host/Substratum	GenBank Accession Number						
			nrSSU	nrLSU	tef1	rpb1	rpb2	tub	atp6
<i>Aphysiostroma stercorarium</i>	ATCC 62321 ^T	Cow dung	AF543769	AF543792	AF543782	AY489633	EF469103	EF469132	AY489566
<i>Aschersonia badia</i>	BCC 8105	Scale insect (Hemiptera)	DQ522573	DQ518752	DQ522317	DQ522363	DQ522411	DQ522472	EF468996
<i>Aschersonia placenta</i>	BCC 7869	Scale insect (Hemiptera)	EF469121	EF469074	EF469056	EF469085	EF469104	EF469133	EF468998
<i>Balansia epichloë</i>	A.E.G. 96-15a	Poaceae	EF468949		EF468743	EF468851	EF468908		
<i>Balansia henningiana</i>	GAM 16112	<i>Panicum</i> sp. (Poaceae)	AY545723	AY545727	AY489610	AY489643	DQ522413	DQ522474	AY489576
<i>Balansia pilulaeformis</i>	A.E.G. 94-2	Poaceae	AF543764	AF543788	DQ522319	DQ522365	DQ522414	DQ522475	EF468999
<i>Beauveria caledonica</i>	ARSEF 2567 ^T	Soil	AF339570	AF339520	EF469057	EF469086		EF469134	EF469000
<i>Bionectria cf. aureofulva</i>	G.J.S. 71-328	Bark	DQ862044	DQ862027	DQ862029		DQ862013	EF469135	EF469001
<i>Bionectria ochroleuca</i>	CBS 114056		AY489684	AY489716	AY489611		DQ522415	DQ522476	EF469002
<i>Claviceps fusiformis</i>	ATCC 26019	Poaceae	DQ522538	U17402	DQ522320	DQ522366		DQ522477	
<i>Claviceps paspali</i>	ATCC 13892	Poaceae	U32401	U47826	DQ522321	DQ522367	DQ522416	DQ522478	
<i>Claviceps purpurea</i>	GAM 12885	<i>Dactylis glomerata</i> (Poaceae)	AF543765	AF543789	AF543778	AY489648	DQ522417	DQ522479	
<i>Claviceps purpurea</i>	S.A. cp11	Poaceae	EF469122	EF469075	EF469058	EF469087	EF469105	EF469136	
<i>Cordyceps acicularis</i>	OSC 110987	Coleopteran larva	EF468950	EF468805	EF468744	EF468852			
<i>Cordyceps acicularis</i>	OSC 110988	Coleopteran larva	EF468951	EF468804	EF468745	EF468853			
<i>Cordyceps cf. acicularis</i>	OSC 128580	Coleoptera	DQ522543	DQ518757	DQ522326	DQ522371	DQ522423	DQ522485	EF469003
<i>Cordyceps agriotidis</i>	ARSEF 5692	Coleoptera	DQ522540	DQ518754	DQ522322	DQ522368	DQ522418	DQ522480	EF469004
<i>Cordyceps aphodii</i>	ARSEF 5498 ^T	<i>Aphodius hewitti</i> (Coleoptera)	DQ522541	DQ518755	DQ522323		DQ522419	DQ522481	EF469005
<i>Cordyceps bifusispora</i>	EFCC 5690	Lepidopteran pupa	EF468952	EF468806	EF468746	EF468854	EF468909		
<i>Cordyceps bifusispora</i>	EFCC 8260	Lepidopteran pupa	EF468953	EF468807	EF468747	EF468855	EF468910		
<i>Cordyceps brunneipunctata</i>	OSC 128576 ^{AUT}	Coleoptera	DQ522542	DQ518756	DQ522324	DQ522369	DQ522420	DQ522482	
<i>Cordyceps capitata</i>	OSC 71233	<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)	AY489689	AY489721	AY489615	AY489649	DQ522421	DQ522483	AY489581
<i>Cordyceps cardinalis</i>	CBS 113411 ^T	Lepidopteran larva	AY184973	AY184962	DQ522325	DQ522370	DQ522422	DQ522484	EF469006
<i>Cordyceps cardinalis</i>	CBS 113412 ^{AUT}	Lepidopteran larva	AY184974	AY184963	EF469059	EF469088	EF469106	EF469137	EF469007
<i>Cordyceps chlamydosporia</i>	CBS 101244 ^{AUT}	Egg of slug (Diplopoda)	DQ522544	DQ518758	DQ522327	DQ522372	DQ522424	DQ522486	EF469008
<i>Cordyceps coccidiicola</i>	AB031195	Scale Insect (Hemiptera)	AB031195	AB031196					
<i>Cordyceps cochlidicola</i>	AB027331	Lepidopteran pupa	AB027331	AB027377					
<i>Cordyceps elongata</i>	OSC 110989	Lepidopteran larva		EF468808	EF468748	EF468856			
<i>Cordyceps entomorrhiza</i>	KEW 53484	Coleopteran larva	EF468954	EF468809	EF468749	EF468857	EF468911		

Species	Voucher Info. ¹	Host/Substratum	GenBank Accession Number						
			nrSSU	nrLSU	tef1	rpb1	rpb2	tub	atp6
<i>Cordyceps fracta</i>	OSC 110990	<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)	DQ522545	DQ518759	DQ522328	DQ522373	DQ522425	DQ522487	EF469009
<i>Cordyceps gracilis</i>	EFCC 3101	Lepidopteran larva	EF468955	EF468810	EF468750	EF468858	EF468913		
<i>Cordyceps gracilis</i>	EFCC 8572	Lepidopteran larva	EF468956	EF468811	EF468751	EF468859	EF468912		
<i>Cordyceps gunnii</i>	OSC 76404	Lepidopteran larva	AF339572	AF339522	AY489616	AY489650	DQ522426	DQ522488	AY489582
<i>Cordyceps heteropoda</i>	EFCC 10125	Nymph of cicada (Hemiptera)	EF468957	EF468812	EF468752	EF468860	EF468914		
<i>Cordyceps heteropoda</i>	OSC 106404	Nymph of cicada (Hemiptera)	AY489690	AY489722	AY489617	AY489651			
<i>Cordyceps inegoënsis</i>		Nymph of cicada (Hemiptera)	AB027322	AB027368					
<i>Cordyceps irangiensis</i>	OSC 128577	Ant (Hymenoptera)	DQ522546	DQ518760	DQ522329	DQ522374	DQ522427	DQ522489	
<i>Cordyceps irangiensis</i>	OSC 128579	Ant (Hymenoptera)	EF469123	EF469076	EF469060	EF469089	EF469107	EF469138	
<i>Cordyceps japonica</i>	OSC 110991	<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)	DQ522547	DQ518761	DQ522330	DQ522375	DQ522428	DQ522490	EF469010
<i>Cordyceps jezoënsis</i>		<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)	AB027320	AB027365					
<i>Cordyceps konnoana</i>	EFCC 7295	Coleopteran larva	EF468958			EF468862	EF468915		
<i>Cordyceps konnoana</i>	EFCC 7315	Coleopteran larva	EF468959			EF468753	EF468861	EF468916	
<i>Cordyceps kyusyuënsis</i>	EFCC 5886	Lepidopteran pupa	EF468960	EF468813	EF468754	EF468863	EF468917		
<i>Cordyceps liangshanensis</i>	EFCC 1452	Lepidopteran pupa	EF468962	EF468815	EF468756				
<i>Cordyceps liangshanensis</i>	EFCC 1523	Lepidopteran pupa	EF468961	EF468814	EF468755		EF468918		
<i>Cordyceps longisegmentis</i>	OSC 110992	<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)		EF468816		EF468864	EF468919		
<i>Cordyceps longissima</i>	EFCC 6814	Nymph of cicada (Hemiptera)		EF468817	EF468757	EF468865			
<i>Cordyceps melolonthae</i>	OSC 110993	Scarabaeid larva (Coleoptera)	DQ522548	DQ518762	DQ522331	DQ522376	DQ522491	EF469011	
<i>Cordyceps militaris</i>	OSC 93623	Lepidopteran pupa	AY184977	AY184966	DQ522332	DQ522377	AY545732	DQ522492	EF469012
<i>Cordyceps nigrella</i>	EFCC 9247	Lepidopteran larva	EF468963	EF468818	EF468758	EF468866	EF468920		
<i>Cordyceps nutans</i>	OSC 110994	Stink bug (Hemiptera)	DQ522549	DQ518763	DQ522333	DQ522378		DQ522493	
<i>Cordyceps</i> cf. <i>ochraceostromata</i>	ARSEF 5691	Lepidoptera	EF468964	EF468819	EF468759	EF468867	EF468921		
<i>Cordyceps ophioglossoides</i>	OSC 106405	<i>Elaphomyces</i> sp. (<i>Eurotiomycetes</i>)	AY489691	AY489723	AY489618	AY489652	DQ522429	DQ522494	AY489583
<i>Cordyceps paradoxa</i>		Nymph of cicada (Hemiptera)	AB027323	AB027369					
<i>Cordyceps</i> cf. <i>pruinosa</i>	EFCC 5197	limacodid pupa (Lepidoptera)	EF468965	EF468820	EF468760	EF468868			
<i>Cordyceps</i> cf. <i>pruinosa</i>	EFCC 5693	limacodid pupa (Lepidoptera)	EF468966	EF468821	EF468762	EF468869			
<i>Cordyceps</i> cf. <i>pruinosa</i>	N.H.J. 10627	limacodid pupa (Lepidoptera)	EF468967	EF468822	EF468763	EF468870			

30 Table 1. Continued.

Species	Voucher Info. ¹	Host/Substratum	GenBank Accession Number								
			nrSSU	nrLSU	tef1	rpb1	rpb2	tub	atp6		
<i>Cordyceps cf. pruinosa</i>	N.H.J. 10684	Limacodid pupa (Lepidoptera)	EF468968	EF468823	EF468761	EF468871					
<i>Cordyceps ravenelii</i>	OSC 110995	Coleopteran larva	DQ522550	DQ518764	DQ522334	DQ522379	DQ522430	DQ522495			
<i>Cordyceps rhizoidea</i>	N.H.J. 12522	Termite (Isoptera)	EF468970	EF468825	EF468764	EF468873	EF468923				
<i>Cordyceps rhizoidea</i>	N.H.J. 12529	Termite (Isoptera)	EF468969	EF468824	EF468765	EF468872	EF468922				
<i>Cordyceps robertsii</i>	KEW 27083	Lepidoptera		EF468826	EF468766						
<i>Cordyceps scarabaeicola</i>	ARSEF 5689	Scarabaeid adult (Coleoptera)	AF339574	AF339524	DQ522335	DQ522380	DQ522431	DQ522496	EF469013		
<i>Cordyceps sinensis</i>	EFCC 7287	Lepidopteran pupa	EF468971	EF468827	EF468767	EF468874	EF468924				
<i>Cordyceps sobolifera</i>	KEW 78842	Nymph of cicada (Hemiptera)	EF468972	EF468828	EF468875	EF468925					
<i>Cordyceps sphecocephala</i>	OSC 110998	Wasp (Hymenoptera)	DQ522551	DQ518765	DQ522336	DQ522381	DQ522432				EF469014
<i>Cordyceps staphylinidicola</i>	ARSEF 5718	Staphylinid pupa (Coleoptera)	EF468981	EF468836	EF468776	EF468881					
<i>Cordyceps stylophora</i>	OSC 110999	Coleopteran larva	EF468982	EF468837	EF468777	EF468882	EF468931				
<i>Cordyceps stylophora</i>	OSC 111000	Eliaterid larva (Coleoptera)	DQ522552	DQ518766	DQ522337	DQ522382	DQ522433	DQ522497			
<i>Cordyceps subsessilis</i>	OSC 71235	Scarabaeid larva (Coleoptera)	EF469124	EF469077		EF469090	EF469108	EF469139	EF469015		
<i>Cordyceps superficialis</i>	MICH 36253	Coleopteran larva	EF468983			EF468883					
<i>Cordyceps taii</i>	ARSEF 5714	Lepidoptera	AF543763	AF543787	AF543775	DQ522383	DQ522434	DQ522498	EF469016		
<i>Cordyceps takaomontana</i>		Lepidoptera	AB044631	AB044637							
<i>Cordyceps cf. takaomontana</i>	N.H.J. 12623	Lepidoptera	EF468984	EF468838	EF468778	EF468884	EF468932				
<i>Cordyceps tricenri</i>		Spittlebug (Hemiptera)	AB027330	AB027376							
<i>Cordyceps tuberculata</i>	OSC 111002	Lepidoptera	DQ522553	DQ518767	DQ522338	DQ522384	DQ522435	DQ522499	EF469017		
<i>Cordyceps unilateralis</i>	OSC 128574	Ant (Hymenoptera)	DQ522554	DQ518768	DQ522339	DQ522385	DQ522436				
<i>Cordyceps variabilis</i>	ARSEF 5365	Dipteran larva	DQ522555	DQ518769	DQ522340	DQ522386	DQ522437	DQ522500	EF469018		
<i>Cordyceps variabilis</i>	OSC 111003	Dipteran larva	EF468985	EF468839	EF468779	EF468885	EF468933				
<i>Cordyceps yakusimensis</i>		Nymph of cicada (Hemiptera)	AB044632	AB044633							
<i>Cordyceps</i> sp.	EFCC 2131	Lepidopteran pupa	EF468977	EF468833	EF468770	EF468876					
<i>Cordyceps</i> sp.	EFCC 2135	Lepidopteran pupa	EF468979	EF468834	EF468769	EF468877					
<i>Cordyceps</i> sp.	EFCC 2535	Coleoptera	EF468980	EF468835	EF468772						
<i>Cordyceps</i> sp.	N.H.J. 12118	Lepidoptera	EF468978	EF468829	EF468768	EF468878	EF468927				
<i>Cordyceps</i> sp.	N.H.J. 12581	Termite (Isoptera)	EF468973	EF468831	EF468775		EF468930				
<i>Cordyceps</i> sp.	N.H.J. 12582	Termite (Isoptera)	EF468975	EF468830	EF468771		EF468926				

Species	Voucher Info. ¹	Host/Substratum	GenBank Accession Number							
			nrSSU	nrLSU	tefl	rpb1	rpb2	tub	atp6	
<i>Cordyceps</i> sp.	OSC 110996	Lepidoptera	EF468974	EF468832	EF468773	EF468880	EF468928			
<i>Cordyceps</i> sp.	OSC 110997	Ant (Hymenoptera)	EF468976		EF468774	EF468879	EF468929			
<i>Cosmospora coccinea</i>	CBS 114050	<i>Inonotus nodulosus</i> (Hymenomycetes)	AY489702	AY489734	AY489629	AY489667	DQ522438	DQ522501	AY489596	
<i>Engyodontium aranearium</i>	CBS 309.85	spider (Arachnida)	AF339576	AF339526	DQ522341	DQ522387	DQ522439	DQ522502	EF469019	
<i>Epichloë typhina</i>	ATCC 56429	<i>Festuca rubra</i> (Poaceae)	U32405	U17396	AF543777	AY489653	DQ522440	DQ522503	AY489584	
<i>Glomerella cingulata</i>	CBS 114054	<i>Fragaria</i> sp. (Rosaceae)	AF543762	AF543786	AF543773	AY489659	DQ522441	DQ522504	AY489590	
<i>Glomerella cingulata</i>	F.A.U. 513	<i>Fragaria</i> sp. (Rosaceae)	U48427	U48428	AF543772	DQ858454	DQ858455	EF469140	EF469020	
<i>Haptocillium balanoides</i>	CBS 250.82	Nematode	AF339588	AF339539	DQ522342	DQ522388	DQ522442	DQ522505	EF469021	
<i>Haptocillium sinense</i>	CBS 567.95 ^T	Nematode	AF339594	AF339545	DQ522343	DQ522389	DQ522443	DQ522506	EF469022	
<i>Haptocillium zeosporum</i>	CBS 335.80	Nematode	AF339589	AF339540	EF469062	EF469091	EF469109	EF469141	EF469023	
<i>Hirsutiella</i> sp.	N.H.J. 12525	Hemipteran adult	EF469125	EF469078	EF469063	EF469092	EF469111	EF469142		
<i>Hirsutiella</i> sp.	OSC 128575	Hemipteran adult	EF469126	EF469079	EF469064	EF469093	EF469110	EF469143		
<i>Hydropisphaera erubescens</i>	ATCC 36093	<i>Cordylone banksii</i> (Laxmanniaceae)	AY545722	AY545726	DQ522344	DQ522390	AY545731	DQ522535	EF469024	
<i>Hydropisphaera peziza</i>	CBS 102038	On bark	AY489698	AY489730	AY489625	AY489661	DQ522444	DQ522507	AY489591	
<i>Hymenostilbe aurantiaca</i>	OSC 128578	Ant (Hymenoptera)	DQ522556	DQ518770	DQ522345	DQ522391	DQ522445	DQ522508		
<i>Hypocrea lutea</i>	ATCC 208838	On decorticated conifer wood	AF543768	AF543791	AF543781	AY489662	DQ522446	DQ522509	AY489592	
<i>Hypocrella schizostachyi</i>	BCC 14123	Scale insect (Hemiptera)	DQ522557	DQ518771	DQ522346	DQ522392	DQ522447	DQ522510	EF469025	
<i>Hypocrella</i> sp.	G.J.S. 89-104	Scale insect (Hemiptera)	U32409	U47832	DQ522347	DQ522393	DQ522448	DQ522511	EF469026	
<i>Hypomyces polyorinus</i>	ATCC 76479	<i>Trametes versicolor</i> (Hymenomycetes)	AF543771	AF543793	AF543784	AY489663			AY489593	
<i>Isaria cf. farinosa</i>	OSC 111004	Lepidopteran pupa	EF468986	EF468840	EF468780	EF468886				
<i>Isaria farinosa</i>	OSC 111005	Lepidopteran pupa	DQ522558	DQ518772	DQ522348	DQ522394		DQ522512	EF469028	
<i>Isaria farinosa</i>	OSC 111006	Lepidopteran pupa	EF469127	EF469080	EF469065	EF469094		EF469144	EF469027	
<i>Isaria tenuipes</i>	OSC 111007	Lepidopteran pupa	DQ522559	DQ518773	DQ522349	DQ522395	DQ522449	DQ522513	EF469029	
<i>Lecanicillium antillarum</i>	CBS 350.85 ^T	Agaric (Hymenomycetes)	AF339585	AF339536	DQ522350	DQ522396	DQ522450	DQ522514	EF469030	
<i>Lecanicillium aranearium</i>	CBS 726.73a	Spider (Arachnida)	AF339586	AF339537	EF468781	EF468887	EF468934			
<i>Lecanicillium attenuatum</i>	CBS 402.78	Leaf litter of <i>Acer saccharum</i>	AF339614	AF339565	EF468782	EF468888	EF468935			
<i>Lecanicillium dimorphum</i>	CBS 363.86 ^T	<i>Agaricus bisporus</i> (Hymenomycetes)	AF339608	AF339559	EF468784	EF468890				
<i>Lecanicillium fusisporum</i>	CBS 164.70 ^T	<i>Coltricia perennis</i> (Hymenomycetes)	AF339598	AF339549	EF468783	EF468889				
<i>Lecanicillium psalliotae</i>	CBS 101270	Soil	EF469128	EF469081	EF469066	EF469095	EF469113	EF469146	EF469031	
<i>Lecanicillium psalliotae</i>	CBS 532.81	Soil	AF339609	AF339560	EF469067	EF469096	EF469112	EF469145	EF469032	
<i>Leuconectria clusiae</i>	ATCC 22228 ^T	Soil	AY489700	AY489732	AY489627	AY489664	EF469114	EF469147	AY489595	
<i>Mariannaea pruinosa</i>	ARSEF 5413 ^{AUT}	<i>Iragoides fasciata</i> (Lepidoptera)	AY184979	AY184968	DQ522351	DQ522397	DQ522451	DQ522515	EF469033	
<i>Metarhizium album</i>	ARSEF 2082	<i>Cofana spectra</i> (Hemiptera)	DQ522560	DQ518775	DQ522352	DQ522398	DQ522452	DQ522516	EF469034	

32
Table 1. Continued.

Species	Voucher Info. ¹	Host/Substratum	nrSSU	nrLSU	tef1	GenBank Accession Number					
						rpb1	rpb2	tub	atp6		
<i>Metarhizium anisopliae</i>	ARSEF 3145	<i>Oryctes rhinoceros</i> (Coleoptera)	AF339579	AF339530	AF543774	DQ522399	DQ522453	DQ522536	EF469035		
<i>Metarhizium flavoviride</i>	ARSEF 2037 ^T	<i>Nilaparvata lugens</i> (Hemiptera)	AF339580	AF339531	DQ522353	DQ522400	DQ522454	DQ522517	EF469036		
<i>Microhilum oncoperae</i>	AFSEF 4358 ^{AUT}	<i>Oncopera intricata</i> (Lepidoptera)	AF339581	AF339532	EF468785	EF468891	EF468936				
<i>Myriogenospora atramentosa</i>	A.E.G. 96-32	<i>Andropogon virginicus</i> (Poaceae)	AY489701	AY489733	AY489628	AY489665	DQ522455	DQ522518			
<i>Nectria cinnabarina</i>	CBS 114055	<i>Betula</i> sp. (Betulaceae)	U32412	U00748	AF543785	AY489666	DQ522456	DQ522519	EF469037		
<i>Nomuraea typicola</i>	CBS 744.73	Spider (Arachnida)	EF468987	EF468841	EF468786	EF468892					
<i>Nomuraea rileyi</i>	CBS 806.71	Lepidoptera	AY624205	AY624250	EF468787	EF468893	EF468937				
<i>Ophionectria trichospora</i>	CBS 109876	On liana	AF543766	AF543790	AF543779	AY489669	DQ522457	DQ522520	EF469039		
<i>Paecilomyces carneus</i>	CBS 239.32 ^T	Sand dune	EF468988	EF468843	EF468789	EF468894	EF468938				
<i>Paecilomyces carneus</i>	CBS 399.59	Soil	EF468989	EF468842	EF468788	EF468895	EF468939				
<i>Paecilomyces cinus</i>	ARSEF 2181	<i>Meloidogynesp.</i> (Nematoda)	AF339534	EF468790	EF468896						
<i>Paecilomyces lilacinus</i>	CBS 284.36 ^T	Soil	AY624189	AY624227	EF468792	EF468898	EF468941				
<i>Paecilomyces lilacinus</i>	CBS 431.87	<i>Meloidogynesp.</i> (Nematoda)	AY624188	EF468844	EF468791	EF468897	EF468940				
<i>Paecilomyces marquandii</i>	CBS 182.27 ^T	Soil	EF468990	EF468845	EF468793	EF468899	EF468942				
<i>Phytocordyceps ninchukispora</i>	E.G.S. 38.165 ^{AUT}	<i>Beilschmiedia erythrophloia</i> (Lauraceae)	EF468991	EF468846	EF468795	EF468900					
<i>Phytocordyceps ninchukispora</i>	E.G.S. 38.166 ^{AUT}	<i>Beilschmiedia erythrophloia</i> (Lauraceae)	EF468992	EF468847	EF468794	EF468901					
<i>Pochonia bulbilosa</i>	CBS 145.70 ^T	Root of <i>Picea abies</i>	AF339591	AF339542	EF468796	EF468902	EF468943				
<i>Pochonia chlamydosporia</i>	CBS 504.66 ^T	Nematode	AF339593	AF339544	EF469069	EF469098	EF469120	EF469149	EF469040		
<i>Pochonia gonioides</i>	CBS 891.72	Nematode	AF339599	AF339550	DQ522354	DQ522401	DQ522458	DQ522521	EF469041		
<i>Pochonia rubescens</i>	CBS 464.88 ^T	<i>Heterodera avenae</i> (Nematoda)	AF339615	AF339566	EF468797	EF468903	EF468944				
<i>Pseudonectria rousselliana</i>	CBS 114049	<i>Buxus sempervirens</i> (Buxaceae)	AF543767	U17416	AF543780	AY489670	DQ522459	DQ522522	AY489598		
<i>Rotiferophthora angustispora</i>	CBS 101437	Rotifer (Rotifera)	AF339584	AF339535	AF543776	DQ522402	DQ522460	DQ522523	EF469042		
<i>Roumegueriella rufula</i>	CBS 346.85	<i>Globodera rostochiensis</i> (Nematoda)	DQ522561	DQ518776	DQ522355	DQ522403	DQ522461	DQ522524	EF469043		
<i>Roumegueriella rufula</i>	G.J.S. 91-164	<i>Globodera rostochiensis</i> (Nematoda)	EF469129	EF469082	EF469070	EF469099	EF469116	EF469150	EF469044		
<i>Shimizuomyces paradoxus</i>	EFCC 6279	<i>Smilax sieboldii</i> (Smilacaceae)	EF469131	EF469084	EF469071	EF469100	EF469117	EF469151	EF469046		
<i>Shimizuomyces paradoxus</i>	EFCC 6564	<i>Smilax sieboldii</i> (Smilacaceae)	EF469130	EF469083	EF469072	EF469101	EF469118	EF469152	EF469045		
<i>Simplicillium lamellicola</i>	CBS 116.25 ^T	<i>Agaricus bisporus</i> (Hymenomycetes)	AF339601	AF339552	DQ522356	DQ522404	DQ522462	DQ522525	EF469047		
<i>Simplicillium lanosoniveum</i>	CBS 101267	<i>Hemileia vastatrix</i> (Uredinales)	AF339603	AF339554	DQ522357	DQ522405	DQ522463	DQ522526	EF469048		
<i>Simplicillium lanosoniveum</i>	CBS 704.86	<i>Hemileia vastatrix</i> (Uredinales)	AF339602	AF339553	DQ522358	DQ522406	DQ522464	DQ522527	EF469049		
<i>Simplicillium obclavatum</i>	CBS 311.74 ^T	Air above sugarcane field	AF339567	AF339517	EF468798						
<i>Sphaerostilbella berkeleyana</i>	CBS 102308	Polypore (Hymenomycetes)	AF543770	U00756	AF543783	AY489671	DQ522465	DQ522528	EF469050		

Species	Voucher Info. ¹	Host/Substratum	GenBank Accession Number						
			nrSSU	nrLSU	tef1	rpb1	rpb2	tub	atp6
<i>Tolypocladium parasiticum</i>	ARSEF 3436 ^{AUT}	Bdelloid rotifer (Rotifera)	EF468993	EF468848	EF468799	EF468904	EF468945		
<i>Torrubiella confregosa</i>	CBS 101247	<i>Coccus viridis</i> (Hemiptera)	AF339604	AF339555	DQ522359	DQ522407	DQ522466	DQ522529	EF469051
<i>Torrubiella luteoestrata</i>	N.H.J. 11343	Scale insect (Hemiptera)	EF468995	EF468850	EF468801	EF468906			
<i>Torrubiella luteoestrata</i>	N.H.J. 12516	Scale insect (Hemiptera)	EF468994	EF468849	EF468800	EF468905	EF468946		
<i>Torrubiella ratticaudata</i>	ARSEF 1915 ^{AUT}	Spider (Arachnida)	DQ522562	DQ518777	DQ522360	DQ522408	DQ522467	DQ522530	EF469052
<i>Torrubiella wallacei</i>	CBS 101237 ^T	Lepidoptera	AY184978	AY184967	EF469073	EF469102	EF469119	EF469153	
<i>Verticillium dahliae</i>	ATCC 16535	<i>Crataegus crus-galli</i> (Rosaceae)	AY489705	AY489737	AY489632	AY489673	DQ522468	DQ522531	AY489600
<i>Verticillium epiphytium</i>	CBS 154.61 ^T	<i>Hemileia vastatrix</i> (Uredinales)	AF339596	AF339547	EF468802	EF468947			
<i>Verticillium epiphytium</i>	CBS 384.81	<i>Hemileia vastatrix</i> (Uredinales)	AF339596	AF339547	DQ522361	DQ522409	DQ522469	DQ522532	EF469053
<i>Verticillium incurvum</i>	CBS 460.88 ^T	<i>Ganoderma lipsiense</i> (Hymenomycetes)	AF339600	AF339551	DQ522362	DQ522410	DQ522470	DQ522533	EF469054
<i>Verticillium</i> sp.	CBS 102184	Spider (Arachnida)	AF339613	AF339564	EF468803	EF468907	EF468948		
<i>Viridispora diparietispora</i>	CBS 102797	<i>Crataegus crus-galli</i> (Rosaceae)	AY489703	AY489735	AY489630	AY489668	DQ522471	DQ522534	EF469055

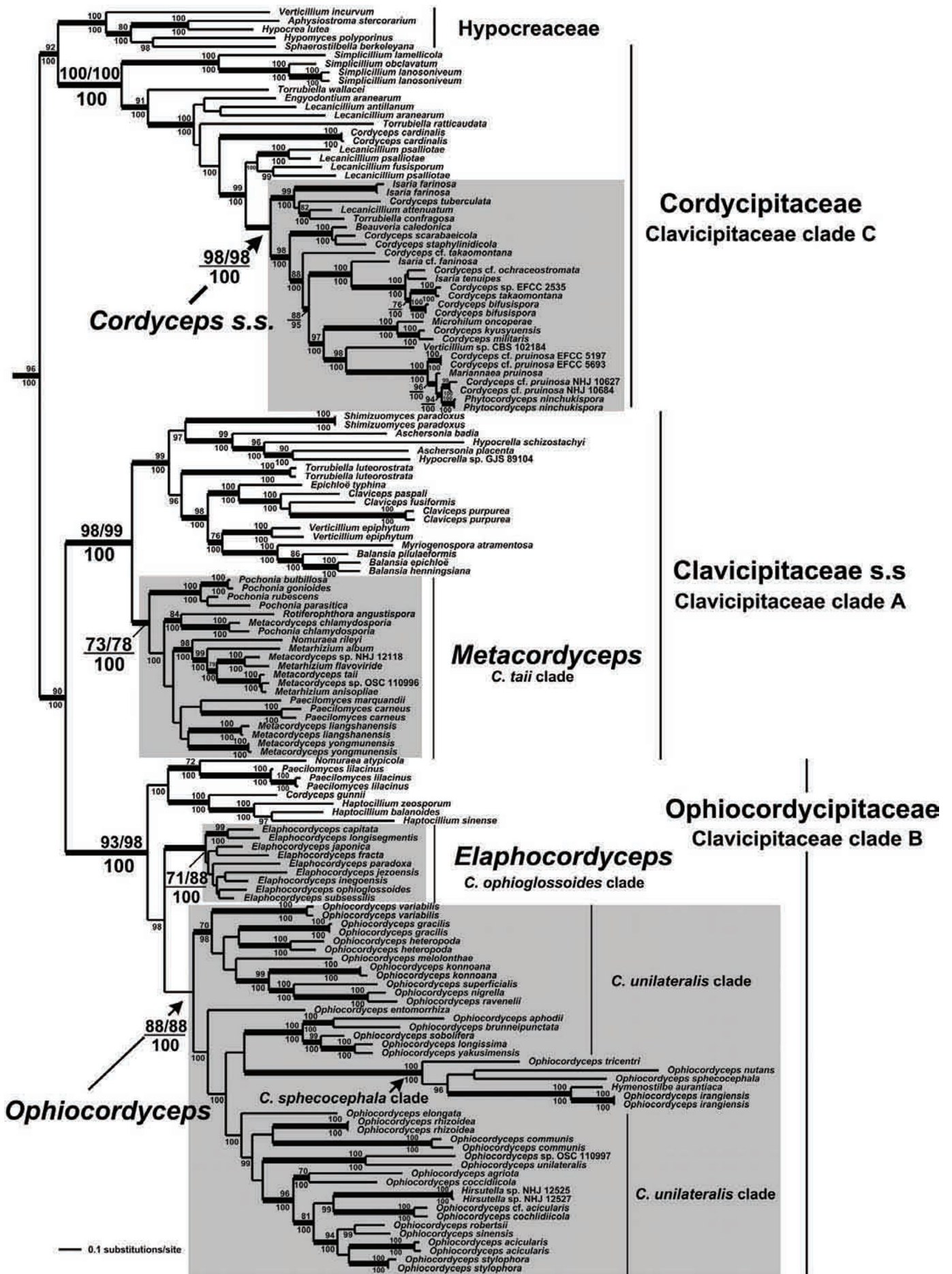
¹A.E.G., A. E. Glenn personal collection; ARSEF, USDA-ARS Collection of Entomopathogenic Fungal cultures, Ithaca, NY; ATCC, American Type Culture Collections, Manassas, VA; BCC, BIOTEC Culture Collection, Klong Luang, Thailand; CBS, Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; EFCC, Entomopathogenic Fungal Culture Collection, Chuncheon, Korea; F.A.U., F. A. Uecker personal collection; E.G.S., E. G. Simmons personal collection; GAM, Julian H. Miller Mycological Herbarium Athens, GA; G.J.S., G. J. Samuels personal collection; KEW, mycology collection of Royal Botanical Garden, KEW, Surrey, UK; MICH, University of Michigan Herbarium, Ann Arbor, MI; N.H.J., Nigel Hywel-Jones personal collection; OSC, Oregon State University Herbarium, Corvallis, OR; S.A., S. Alderman personal collection.

Known distribution: Republic of Korea.

Specimens examined: Mt. Yongmun, Gyunggi Province, **Republic of Korea**: 13 June 1998, EFCC 2131 (**holotype**); 13 June 1998, EFCC 2134; 13 June 1998, EFCC 2135; 30 June 1999, EFCC 3379; 30 June 1999, EFCC 3380; 29 Aug. 1999, EFCC 4342; 8 Aug. 1999, EFCC 4343; 8 June 2000, EFCC 4951; 30 June 2004, EFCC 12287; 30 June 2004, EFCC 12288; 30 June 2004, EFCC 12291; 8 Aug. 2004, EFCC 12467. Mt. Chiak, Kangwon Province, Republic of Korea: 8 Aug. 2000, EFCC 5750. Bukbang-myun, Kangwon Province, Republic of Korea: 21 June 2002, EFCC 8808. Living culture in EFCC.

Commentary: Most specimens of *M. yongmunensis* possess several stromata (up to 10), on a large pupa of Lepidoptera deeply buried in soil (Fig. 5B). Stroma of the species is typically branched in a dichotomous way at its basal or upper regions (Fig. 5B). Perithecia are usually obliquely inserted in the stromata with a few exceptions that are ordinally arranged, i.e. at right angles to the surface of the stromata (Fig. 5B). While some perithecia are characterized by an acute narrowing of the perithecium at the ostiole, producing a narrow terminal end (Fig. 5F), others are not significantly narrowed (Fig. 11B). In the asci the ascospores are arranged parallel for their entire length and almost reach the ascus foot, suggesting that ascospores are of approximately the same length as the asci (Figs 5I, 11A). Unlike the distinct septation of ascospores as seen in *C. militaris* (Fig. 9O), the septa of the ascospores are indistinct and discharged ascospores do not disarticulate into part-spores (Figs 5K, 11A).

In the anamorph of *M. yongmunensis*, cultures derived from ascospores are moderately fast growing in SDAY (Sabouraud-dextrose-yeast extract agar) and the colonies reach 25–35 mm diam at 25 °C in 10 d. Colonies are slightly cottony without zonation and white with a green margin, remaining greenish brown at the reverse side of the cultures. Conidiophores are erect and produced in prostrate aerial hyphae. Phialides are solitary, not in whorls, broader at the base and tapering towards the end, measuring 20–28 × 2.0–2.2 µm (Fig. 11C). Conidia are in slimy heads (with usually 2 or 3 conidia) and ellipsoidal to oblong, measuring 2–3.5 × 1.5–2.4 µm (Fig. 11C). In submerged areas of the cultures, chlamydospores are developed in chains or reduced to intercalary swollen structures (Figs 11E–G). The anamorph of *M. yongmunensis* is best classified as pochonia-like because of its subulate phialides and production of chlamydospores, although verticillium-like whorls of phialides were not observed (Zare *et al.* 2001). In *Metacordyceps*, *M. yongmunensis* is most similar to *M. chlamydosporia* (= *C. chlamydosporia*) in the shape of perithecia and its anamorph. Both species produce brownish perithecia that possess long terminal ends in white or pale yellow stromata (Zare *et al.* 2001). The anamorph of *M. chlamydosporia* is identical with the type of *Pochonia*. Thus the production of chlamydospores can be informative for recognizing some species of *Metacordyceps*.



Accepted names and new combinations for *Metacordyceps*

The following taxa are accepted species of *Metacordyceps* based on their inclusion in molecular phylogenies presented herein¹ (see Table 1) or morphological descriptions matching the characters described above². The known anamorph connection is provided for the species of *Metacordyceps*.

²*Metacordyceps brittlebankisoides* (ZuoY. Liu, Z.Q. Liang, Whalley, Y.-J. Yao & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504184.

≡ *Cordyceps brittlebankisoides* ZuoY. Liu, Z.Q. Liang, Whalley, Y.-J. Yao & A.Y. Liu, J. Invert. Pathol. 78: 179. 2001.

Anamorph: *Metarhizium*

²*Metacordyceps campsosterni* (W.M. Zhang & T.H. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504185

≡ *Cordyceps campsosterni* W.M. Zhang & T.H. Li, Fungal Diversity 17: 240. 2004. [as *C. 'campsosterna'*].

Anamorph: *Metarhizium*

¹*Metacordyceps chlamydosporia* (H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504186.

≡ *Cordyceps chlamydosporia* H.C. Evans, in Zare *et al.*, Nova Hedwigia 73: 59. 2001.

Anamorph: *Pochonia chlamydosporia* (Goddard) Zare & W. Gams

¹*Metacordyceps liangshanensis* (M. Zang, D. Liu & R. Hu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504187.

≡ *Cordyceps liangshanensis* M. Zang, D. Liu & R. Hu, Acta Bot. Yunnanica 4: 174. 1982.

¹*Metacordyceps taii* (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones, Spatafora, **comb. nov.** MycoBank MB504188.

≡ *Cordyceps taii* Z.Q. Liang & A.Y. Liu, Acta Mycol. Sin. 10: 257. 1991.

Anamorph: *Metarhizium anisopliae* var. *anisopliae* (Metschn.) Sorokin

¹*Metacordyceps yongmunensis* G.H. Sung, J.M. Sung, Spatafora, **sp. nov.**, see p. 27.

Anamorph: pochonia-like

New combinations for anamorphs associated with *Metacordyceps*

T. parasiticum is transferred to the genus *Pochonia* based on molecular phylogenies presented herein¹.

¹*Pochonia parasitica* (G.L. Barron) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504189.

≡ *Tolypocladium parasiticum* G.L. Barron, Canad. J. Bot. 58: 439. 1980.

CLAVICIPITACEAE Clade B

Clavicipitaceae clade B is strongly supported (MP-BP = 93 %, ML-BP = 98 %, PP = 1.00 in Figs 1–2, 10) and the family *Ophiocordycipitaceae* is proposed for it with the type genus *Ophiocordyceps* Petch. Most species of the *Ophiocordycipitaceae* produce darkly pigmented stromata that are pliant to wiry, or fibrous to tough in texture. Ecologically, many species of the family are known as pathogens of subterranean or wood-inhabiting hosts, buried in soil or embedded in decaying wood. Notable exceptions do exist to these traits with brightly coloured species that may or may not attack adult stages of hosts and occur in exposed habitats.

OPHIOCORDYCIPIITACEAE G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **fam. nov.** MycoBank MB504190.

Stromata vel subiculum fusca vel raro laete colorata, tenacia, fibrosa vel flexibilia, raro carnosae, saepe ostiolis peritheciis prominentibus, summa saepe peritheciis carentia. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem vel oblique inserta. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae in cellulas diffrangentes vel integrae remanentes.

Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous to pliant, rarely fleshy, often with aperithecial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci usually cylindrical with thickened ascus apex. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating.

Type: *Ophiocordyceps* Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

Teleomorphic genera: *Elaphocordyceps*, *Ophiocordyceps*

Anamorphic genera: *Haptocillium*, *Harposporium* Lohde, *Hirsutella*, *Hymenostilbe*, paecilomyces-like, *Paraisaria*, *Syngliocladium*, *Tolypocladium*, verticillium-like.

Fig. 10 (Page 34). New classification of *Cordyceps* and clavicipitaceous fungi based on Bayesian consensus tree in Fig. 2. Portions of *Bionectriaceae* and *Nectriaceae* are not shown. Tree description is the same as in Fig. 2. For internodes that are related with nomenclatural changes, bootstrap proportions of MP analyses (MP-BP) in Fig. 1 are shown above corresponding nodes before the backslash. Bootstrap proportions of ML analyses (ML-BP) and posterior probabilities (PP) in Fig. 2 are shown above internodes after backslash and below internodes, respectively. For the corresponding internode of *Ophiocordyceps*, bootstrap proportions (MP-BP & ML-BP) and posterior probabilities (PP) were obtained from analyses based on the 147-taxon 5-gene data set in Fig. 3. Portions of the tree in grey rectangular boxes indicate nomenclatural changes of *Cordyceps*.

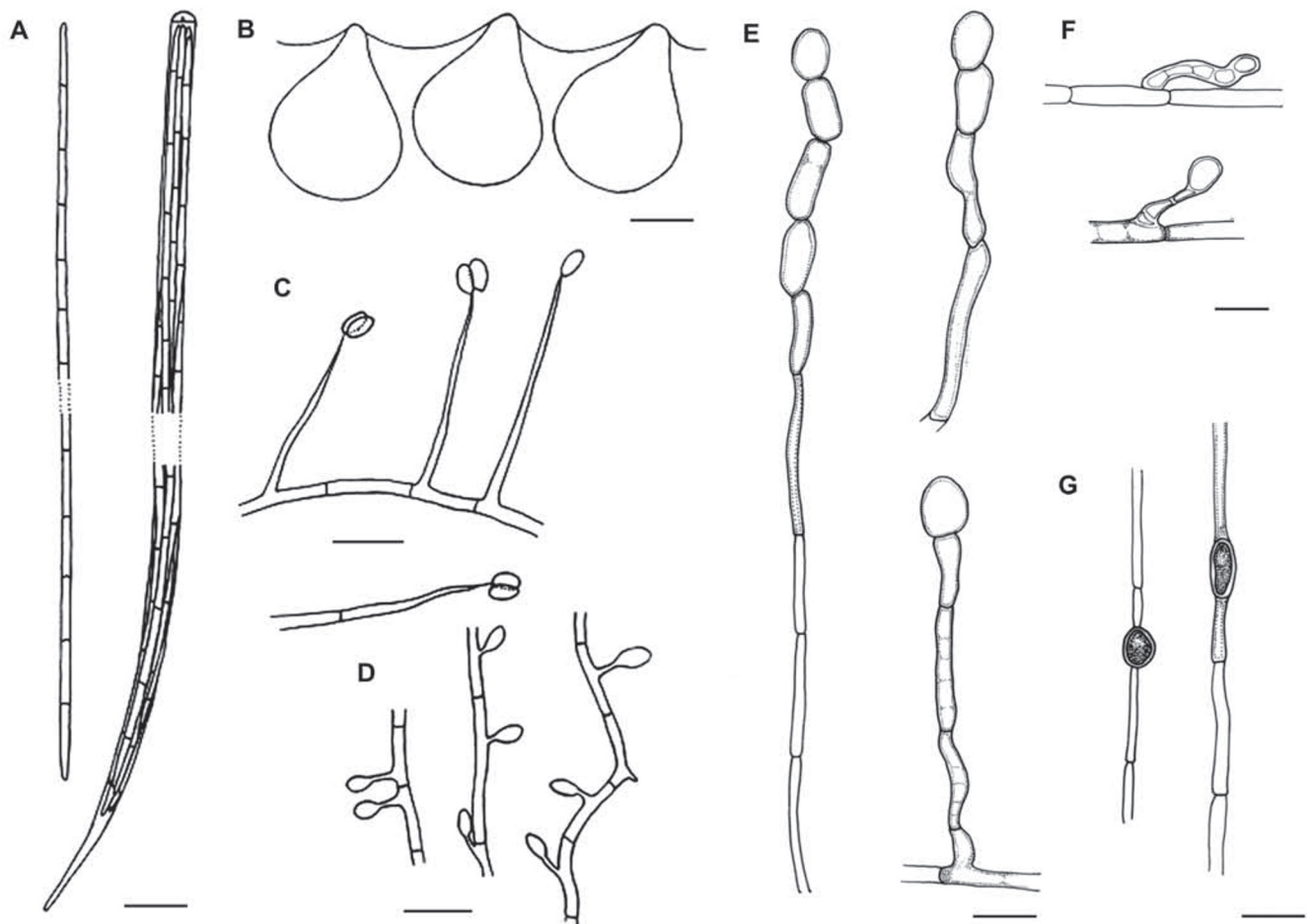


Fig. 11. A–B. Line drawings of morphology of *Metacordyceps yongmunensis*. C–G. Line drawings of pochonina-like anamorph of *M. yongmunensis*. A. Non-disarticulating ascospore and ascus. B. Oblique arrangement of perithecia in stroma. C. Conidia and phialides. D. Developing conidia germinated from ascospore. E. Chlamydospores submerged in SDAY agar. F. Developing chlamydospores submerged in SDAY agar. G. Intercalary swollen hyphae. Scale bars: A, C–G = 10 μ m, B = 200 μ m.

ELAPHOCORDYCEPS G.H. Sung & Spatafora,
gen. nov. MycoBank MB504191.

Stromata singula vel nonnulla aggregata, simplicia vel ramosa. Stipes fibrosus vel tenax, raro carnosus, obscure brunneus vel olivaceo-viridulus, raro albidus, cylindricus vel sursum dilatatus. Stromata hospite insidentia vel rhizomorpha eo conjuncta. Pars fertilis clavata vel capitata, raro indistincta. Perithecia partim vel omnino in stromate immersa, perpendicularia ad superficiem. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae in cellulas diffragentes. Anamorphe *Verticillii* similis vel absens.

Stromata solitary to several, simple or branched. Stipe fibrous to tough, rarely fleshy, dark brownish to greenish with olivaceous tint, rarely whitish, cylindrical to enlarging in the fertile part. Stroma connected directly to the host or indirectly through rhizomorph-like structures. Fertile part clavate to capitate, rarely undifferentiated. Perithecia partially or completely immersed in stromata, ordinal in arrangement. Asci cylindrical with thickened ascus apex. Ascospores cylindrical, multiseptate, disarticulating into part-spores.

Type: *Cordyceps ophioglossoides* (Ehrh.) Link

Etymology: Greek *elaphe* = deer, from the host fungus, *Elaphomyces*.

Commentary: The *C. ophioglossoides* clade is strongly supported (MP-BP = 71 %, ML-BP = 88 %, PP = 100 in Figs 1–2, 10) and includes species of *Cordyceps* s. l. that parasitize the truffle-like genus *Elaphomyces* and cicada nymphs (e.g., *C. inegoënsis* and *C. paradoxa*) and beetles (e.g., *C. subsessilis*) (Figs 6, 10). Currently, 22 species are anticipated to be included in the *C. ophioglossoides* clade, of which more than 18 species are known as parasites of *Elaphomyces* (Mains 1957, Kobayasi & Shimizu 1960, 1963). The host affiliation of *Elaphomyces* parasites has long been recognized as a diagnostic character in *Cordyceps* classification (Masseé 1895, Kobayasi 1941, 1982, Mains 1957, 1958). The oldest applicable genus name is *Cordylia* Fr. 1818 (Masseé 1895). However, it cannot be applied to the *C. ophioglossoides* clade because it is a homonym of *Cordylia* Pers. 1807 (Mains 1958), which is also homonym of *Cordyla* Lour. 1790 (*Leguminosae*). Therefore, the genus *Elaphocordyceps* is proposed based on the phylogenetic placement of *C. ophioglossoides* and applied to the well-supported *C. ophioglossoides* clade. Although *C. subsessilis* is morphologically and ecologically distinct, the genus is well recognized by its dominant ecology as being pathogens of *Elaphomyces* and cicadas. The darkly pigmented, fibrous stromata with more or less

olivaceous tint are also good diagnostic characters for recognizing the species of *Elaphocordyceps*.

Anamorphic genera: *Tolypocladium*, verticillium-like.

Accepted names and new combinations for *Elaphocordyceps*

The following taxa are accepted species of *Elaphocordyceps* based on their inclusion in molecular phylogenies presented herein¹ (see Table 1) or morphological descriptions matching the characters described above². Where known we provide anamorph connection for the species of *Elaphocordyceps*.

¹*Elaphocordyceps capitata* (Holmsk.) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504192.

≡ *Sphaeria capitata* Holmsk., Beata Ruris Otia Fungis Danicis 1: 38. 1790 : Fries, Syst. Mycol. 2: 324, 1823.

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

≡ *Cordyceps capitata* (Holmsk. : Fr.) Link., Handbuch zur Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse 3: 347. 1833.

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

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

= *Sphaeria agariciformis* Bolt., Hist. Fung. Halifax, p. 130. 1789.

≡ *Cordyceps agariciformis* (Bolt.) Seaver, North Amer. Fl. 3: 33. 1910.

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

Anamorph unknown, not growing in culture.

²*Elaphocordyceps delicatistipitata* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504193.

≡ *Cordyceps delicatistipitata* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 5: 79. 1960 (as *C. 'delicatostipitata'*).

¹*Elaphocordyceps fracta* (Mains) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504194.

≡ *Cordyceps fracta* Mains, Bull. Torrey Bot. Club 84: 250. 1957.

¹*Elaphocordyceps inegoënsis* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504195.

≡ *Cordyceps inegoënsis* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 292. 1963.

²*Elaphocordyceps intermedia* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504196.

≡ *Cordyceps intermedia* S. Imai, Proc. Imp. Acad. Tokyo 10: 677. 1934.

²*Elaphocordyceps intermedia* f. *michinokuënsis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504197.

≡ *Cordyceps intermedia* f. *michinokuënsis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 116. 1982.

¹*Elaphocordyceps japonica* (Lloyd) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504198.

≡ *Cordyceps japonica* Lloyd, Mycol. Writ. 6: 913. 1920.

= *Cordyceps umemurae* S. Imai, Trans. Sapporo Nat. Hist. Soc. 11: 32. 1929 (as *C. 'umemurai'*).

¹*Elaphocordyceps jezoënsis* (S. Imai) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504199.

≡ *Cordyceps jezoënsis* S. Imai, Trans. Sapporo Nat. Hist. Soc. 11: 33. 1929.

¹*Elaphocordyceps longisegmentis* (Ginns) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504200.

≡ *Cordyceps longisegmentis* Ginns, Mycologia 80: 219. 1988.

²*Elaphocordyceps minazukiensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504201.

≡ *Cordyceps minazukiensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 117. 1982.

²*Elaphocordyceps miomoteana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504202.

≡ *Cordyceps miomoteana* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 118. 1982.

¹*Elaphocordyceps ophioglossoides* (Ehrh. : Fr.) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504203.

≡ *Sphaeria ophioglossoides* Ehrh., in Pers., Comment de Fung. Clavaef. p. 12. 1797 : Fries, Syst. Mycol. 2: 324. 1823.

≡ *Torrubia ophioglossoides* (Ehrh. : Fr.) Tul., Sel. Fung. Carpol. 3: 20. 1865.

≡ *Cordyceps ophioglossoides* (Ehrh. : Fr.) Link, Handbuch zur Erkennung der nutzbarsten und am häufigsten vorkommenden Gewächse 3: 347. 1833.

Anamorph: verticillium-like

²*Elaphocordyceps ophioglossoides* f. *alba* (Kobayasi & Shimizu ex Y.J. Yao) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504204.

≡ *Cordyceps ophioglossoides* f. *alba* Kobayasi & Shimizu ex Y.J. Yao, in Yao, Li, Pegler & Spooner, Acta. Mycol. Sin. 14: 257. 1995.

²*Elaphocordyceps ophioglossoides* f. *cuboides* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504205.

≡ *Cordyceps ophioglossoides* f. *cuboides* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 5: 77. 1960.

¹*Elaphocordyceps paradoxa* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504206.

≡ *Cordyceps paradoxa* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 156. 1939.

²*Elaphocordyceps ramosa* (Teng) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504207.

≡ *Cordyceps ramosa* Teng, Sinensia 7: 810. 1936.

²*Elaphocordyceps rouxii* (Cand.) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504208.

≡ *Cordyceps rouxii* Cand., Mycotaxon 4: 544. 1976.

¹*Elaphocordyceps subsessilis* (Petch) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504209.

≡ *Cordyceps subsessilis* Petch, Trans. Brit. Mycol. Soc. 21: 39. 1937.

= *Cordyceps facis* Kobayasi & Shimizu, Trans. Mycol. Soc. Japan 23: 361. 1982.

Anamorph: *Tolypocladium inflatum* W. Gams

²*Elaphocordyceps szemaoënsis* (M. Zang) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504210.

≡ *Cordyceps szemaoënsis* M. Zang, Acta Bot. Yunnanica 23: 295. 2001.

²*Elaphocordyceps tenuispora* (Mains) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504211.

≡ *Cordyceps tenuispora* Mains, Bull. Torrey Bot. Club 84: 247. 1957.

²*Elaphocordyceps toriharamontana* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504212.

≡ *Cordyceps toriharamontana* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 305. 1963.

²*Elaphocordyceps valliformis* (Mains) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504213.

≡ *Cordyceps valliformis* Mains, Bull. Torrey Bot. Club 84: 250. 1957.

²*Elaphocordyceps valvatistipitata* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504214.

≡ *Cordyceps valvatistipitata* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 5: 81. 1960 (as *C. volvatostipitata*).

²*Elaphocordyceps virens* (Kobayasi) G.H. Sung, J.M. Sung & Spatafora, **comb. nov.** MycoBank MB504215

≡ *Cordyceps virens* Kobayasi, J. Jap. Bot. 58: 222. 1983.

OPHIOCORDYCEPS Petch, Trans. Brit. Mycol. Soc. 16: 73. 1931 **emend.** G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= *Cordycepioideus* Stiffler, Mycologia 33: 83. 1941.

Stromata or subiculum darkly pigmented or rarely brightly coloured, tough, fibrous, pliant to wiry, rarely fleshy, often with aperithelial apices or lateral pads. Perithecia superficial to completely immersed, ordinal or oblique in arrangement. Asci hyaline, cylindrical, usually with thickened ascus apex, rarely fusoid to ellipsoid. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating.

Type: Cordyceps blattae Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.

Anamorphic genera: Hirsutella, Hymenostilbe, Paraisaria, Syngliocladium.

Commentary: The *C. unilateralis* clade is strongly supported (MP-BP = 88 %, ML-BP = 88 %, PP = 1.00 in Figs 3, 10) and includes the species of *Ophiocordyceps* (e.g., *C. acicularis* and *C. unilateralis*) (Petch 1931, 1933). The genus *Ophiocordyceps* was proposed

by Petch (1931, 1933) for species of *Cordyceps* that produce non-disarticulating ascospores. The genus was not accepted by subsequent workers who reclassified the species of *Ophiocordyceps* as *Cordyceps* subg. *Ophiocordyceps* (Kobayasi 1941) or in multiple subgenera of *Cordyceps* (Mains 1958). The type of *Ophiocordyceps* Petch is *O. blattae* (= *C. blattae*), but it was not available for this taxonomic treatment. According to the morphological description, it fits in the present generic concept. Because *O. unilateralis* is a well-known species that was included in the original publication of *Ophiocordyceps* (Petch 1931) and because additional *Ophiocordyceps* species (e.g., *O. acicularis*) are members of this clade, we apply the name *Ophiocordyceps* based on the placement of *O. unilateralis*. The genus *Ophiocordyceps* includes the most morphologically diverse group of the species of *Cordyceps* s. l. including the members of *C.* subg. *Neocordyceps* (Figs 6, 10). For most of the species in *Ophiocordyceps*, the stromata are fibrous to tough or wiry to pliant in texture and darkly pigmented in at least some part of the stroma. The genus includes many species of *Cordyceps* s. l. that produce perithecia in subterminal regions of the stromata resulting in aperithelial apices. Of particular note, *Ophiocordyceps* is characterized by the dominant occurrence of *Hirsutella* and *Hymenostilbe* anamorphs (Fig. 6). Although the genus *Cordycepioideus* possesses thick-walled multiseptate ellipsoid ascospores and its asci lack the thickened ascus tip of most clavicipitaceous fungi (Blackwell & Gilbertson 1984, Ochiel *et al.* 1997), this study indicates that the genus *Cordycepioideus* can be merged with *Ophiocordyceps* according to its placement in molecular analyses and because of the *Hirsutella* anamorph (Fig. 10, Ochiel *et al.* 1997, Suh *et al.* 1998).

Ophiocordyceps communis Hywel-Jones & Samson, **sp. nov.** MycoBank MB504216. Figs 12A–G.

Anamorph: *hirsutella/hymenostilbe*-like.

Stromata ex duabus (tribus) termitis adultis oriunda, mycelio albo circumdata, filiformia; 50–100 mm sub superficie stramenti oriunda, 300–600 µm lata, albido-grisea, 70–130 mm super stramentum emergentia, 600–1000 µm lata, cuius 30–40 mm pars inferior hyphis sterilibus dematiaceis (luteo-brunneis) tomentosa; pars superior, ca 90 mm longa, fertilis, levis, griseo-brunnea vel grisea, conidia in strato griseo ferens et perithecia dense aggregata. Perithecia superficialia, subterminalia, 285–675 × 195–390 µm. Asci apice conspicue inspissato, 8-spori, filiformes, 215–250 × 15 µm. Ascosporae integrae, crassitunicatae, dilute pigmentatae, (100–)120–150(–180) × 5–6 µm. Cellulae conidiogenae hymenium hyalinum formantes, cylindricae, 10–14 × 2.7–3.3 µm, unum (raro duos) denticulos fertiles apicales ferentes. Blastoconidia hyalina, amygdaliformia, 8–9 × 2.5–3 µm. Anamorphe *Hirsutellae* vel *Hymenostilbe* similis.

Hosts two (rarely three) adult termites surrounded by loose, coarse white mycelium. Stromata filiform, 50–100 mm below ground, 300–600 µm wide, whitish-grey; 70–130 mm emerging above leaf litter, 600–1000 µm wide; lower 30–40 mm of above-ground portion usually hirsute with sterile, dematiaceous (yellow-brown) hairs becoming smooth, silver-brown to grey along terminal

fertile (anamorph) part of ca 90 mm. Perithecia superficial subterminal; emerging through grey anamorph, tightly packed around the stipe, 285–675 × 195–390 µm. Asci with stout cap, 8-spored, filiform, 215–250 × 15 µm. Ascospores whole, stout, lightly pigmented (100–)120–150(–180) × 5–6 µm. Conidiogenous cells in a palisade, hyaline, cylindrical, 10–14 × 2.7–3.3 µm, solitary (rarely two), prominent, terminal denticle. Conidia hyaline, almond-shaped, 7–9 × 2.5–3 µm.

Etymology: refers to the communal nature of the stromata, i.e. the fact that 500–1000 *Cordyceps* stromata can be found in a small area (20 × 20 metres).

Type: Holotype: N.H.J. 10673, isotypes: N.H.J. 10674, N.H.J. 10675, N.H.J. 10676, N.H.J. 10677, all on termites; coll. R. Nasit; Khao Yai National Park, Gong Giao Nature Trail; 13 June 2000.

Commentary: Most collections of *O. communis* were from Khao Yai National Park with the type locality (Gong Giao Nature Trail) regularly having epizootics containing (in any one season) several hundred stromata over a 20 × 20 metre area. A few other collections were from Khao Soi Dao Wildlife Sanctuary (N.H.J. 6422 and N.H.J. 6452) and Sam Lan National Park (N.H.J. 6332). All collections of the species were from adult termites. Although surveys were made over an eighteen-year period from the far north of Thailand to the far south and from sea level to over 2500 metres, *O. communis* is only known from these three sites in central Thailand below 800 metres elevation.

In any year there appeared to be a single ‘flush’ with *O. communis* first appearing at the start of the rainy season in May/June. The earliest collections were made in May (10 May 1994: N.H.J. 3687, N.H.J. 3681 and N.H.J. 3683, Heo Sawat Waterfall; 23 May 1996; N.H.J. 6330, Gong Giao Nature Trail). In the first 2–3 weeks after appearance, the stromata appeared slender and acicular with the lower part having a shiny silken appearance and the terminal part dull greyish. The terminal grey region consisted of a palisade of tightly packed conidiogenous cells with typically a stout elongate denticle, giving rise to a single conidium.

This anamorph is intermediate between a typical *Hirsutella* (e.g., *Hi. formicarum*, *Hi. citriformis*, and *Hi. saussurei*) and a typical *Hymenostilbe* (e.g., *Hy. dipterigena* – closer to the latter) (Figs 12F–G). The palisade of crowded conidiogenous cells is indicative of *Hymenostilbe* rather than *Hirsutella*, where conidiogenous cells are sparse and mostly immature at any given time (Fig. 12F). The denticulate nature of the conidiogenous cell also is indicative of *Hymenostilbe*. However, in all specimens examined to date there is no evidence of multiple denticles (five or more) usually associated with *Hymenostilbe*; only a few conidiogenous cells were seen with two denticles (Figs 12F–G).

The anamorph of *O. communis* is closest to *Hy. ventricosa* Hywel-Jones (Hywel-Jones 1995). That species infects cockroaches and is found attached to the under side of leaves. As with the anamorph of *O. communis*, *Hy. ventricosa* produces conidiogenous

cells with only a single terminal stout denticle. Conidia of *Hy. ventricosa* have a pronounced point and are not typical of the clavate shape usually associated with *Hymenostilbe*. Similarly, the conidia of the *O. communis* anamorph are also fattened naviculate, appearing similar to those of *Hy. ventricosa* but without the processed tip.

The perithecia erupt through the dull greyish anamorph spike appearing first as longitudinal splits in the palisade of conidiogenous cells at the base of the anamorph spike. Each develops as a superficial perithecium, but they become crowded and give the overall appearance of a brown subterminal fertile region (Kobayasi 1941; Figs 12A–B). The ascus shape and the form of the ascus cap comes close to Kobayasi’s Figs 12C–D (Kobayasi 1941) being typical of species in the *C. unilateralis* clade (with *Hirsutella* as an anamorph). Mature perithecia eject pigmented, whole ascospores (Fig. 12E) and often the ostiole becomes blocked with these half-emerged ascospores.

Only a few species of *Cordyceps sensu* Kobayasi and Mains have been reported from termites. Currently accepted species include *O. koningsbergeri* (= *C. koningsbergeri* Penz. & Sacc.), which is known only from the type locality (Java, Indonesia) (Kobayasi 1941), and *C. termitophila* Kobayasi & Shimizu which is known from Japan and Taiwan (Kobayasi & Shimizu 1976, 1978). Penzig & Saccardo (1904) found *O. koningsbergeri* to be similar to *O. myrmecophila* in that it had a terminal, globose head with immersed perithecia. In this feature alone it differs significantly from *O. communis* with its subterminal and superficial perithecia. However, as with *O. communis*, Penzig & Saccardo (1904) described whole ascospores of *O. koningsbergeri*, which were 150 × 1 µm compared with 120–150 × 5–6 µm for *O. communis*. *Cordyceps termitophila* differs from *O. communis* in having a ‘pale rosy-grey’ stroma, much smaller perithecia (280–320 × 175–190 µm for *C. termitophila* versus 285–675 × 195–390 µm for *O. communis*) and smaller ascospores (100–125 × 3 µm).

Accepted names and new combinations for *Ophiocordyceps*

The following taxa are accepted species of *Ophiocordyceps* based on their inclusion in molecular phylogenies presented herein¹ or morphological descriptions matching the characters described above². Where known, the anamorph connection is provided for the species of *Ophiocordyceps*.

¹*Ophiocordyceps acicularis* (Ravenel) Petch, Trans. Brit. Mycol. Soc. 18: 60. 1933.

= *Cordyceps acicularis* Ravenel, J. Linn. Soc. 1: 158. 1857.
= *Cordyceps caroliniensis* Berk. & Ravenel, Fungi Carolina 4: 29. 1855.

Anamorph: *Hirsutella*

¹*Ophiocordyceps agriotidis* (A. Kawam.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504217.

- ≡ *Cordyceps agriotidis* A. Kawam., Icon. Jap. Fungi 8: 837. 1955. [as *C. 'agriota'*]
Anamorph: *Hirsutella*
- ²*Ophiocordyceps ainictos* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504218.
≡ *Cordyceps ainictos* A. Möller, Phycomyceten u. Ascomyceten, p. 226. 1901.
Anamorph: *Hirsutella*
- ²*Ophiocordyceps amazonica* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504219.
≡ *Cordyceps amazonica* Henn., Hedwigia 43: 247. 1904.
- ²*Ophiocordyceps amazonica* var. *neoamazonica* (Kobayasi & Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504220.
≡ *Cordyceps amazonica* var. *neoamazonica* Kobayasi & Hara, J. Jap. Bot. 57: 17. 1982.
- ¹*Ophiocordyceps aphodii* (Mathieson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504221.
≡ *Cordyceps aphodii* Mathieson, Trans. Brit. Mycol. Soc. 32: 134. 1949.
Anamorph: *Hirsutella*
- ²*Ophiocordyceps appendiculata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504222.
≡ *Cordyceps appendiculata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 6. 1983.
- ²*Ophiocordyceps arachneicola* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504223.
≡ *Cordyceps arachneicola* Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 123. 1941.
- ²*Ophiocordyceps arbuscula* (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504225
≡ *Cordyceps arbuscula* Teng, Sinensia 7: 812. 1936.
- ²*Ophiocordyceps armeniaca* (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504226.
≡ *Cordyceps armeniaca* Berk. & M.A. Curtis, J. Linn. Soc. 1: 158. 1857.
- ²*Ophiocordyceps asyuënsis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504227.
≡ *Cordyceps asyuënsis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 138. 1980.
- ²*Ophiocordyceps aurantia* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504228.
≡ *Cordyceps aurantia* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 125. 1980.
- ²*Ophiocordyceps australis* (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504229.
≡ *Cordyceps unilateralis* var. *australis* Speg., Anales Soc. Ci. Argent. 12: 215. 1881.
≡ *Cordyceps australis* (Speg.) Speg., Syll. Fung. 2: 571. 1883.
- ²*Ophiocordyceps barnesii* (Thwaites) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504230.
≡ *Cordyceps barnesii* Thwaites, J. Linn. Soc. 14: 110. 1875.
≡ *Torrubia barnesii* (Thwaites) Ces., Atti Accad. Sci. Fis. Mat., Napoli 8: 14. 1879.
- ²*Ophiocordyceps bicephala* (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504231.
≡ *Cordyceps bicephala* Berk., J. Bot. (Hooker) 8: 278. 1856.
- ²*Ophiocordyceps bispora* (Stiffler) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504232.
≡ *Cordycepioideus bisporus* Stiffler, Mycologia 33: 85. 1941.
Anamorph: *Hirsutella*
- ²*Ophiocordyceps blattae* (Petch) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.
≡ *Cordyceps blattae* Petch, Trans. Brit. Mycol. Soc. 10: 35. 1924.
- ¹*Ophiocordyceps brunneipunctata* (Hywel-Jones) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504233.
≡ *Cordyceps brunneipunctata* Hywel-Jones, Mycol. Res. 99: 1195. 1995. [as *C. 'brunneapunctata'*]
Anamorph: *Hirsutella*
- ²*Ophiocordyceps caloceroides* (Berk. & M.A. Curtis) Petch, Trans. Brit. Mycol. Soc. 18: 63. 1933.
≡ *Cordyceps caloceroides* Berk. & M.A. Curtis, J. Linn. Soc. 10: 375. 1868.
= *Cordyceps wittii* Henn., Bot. Jahrb. Syst. 23: 539. 1897.
- ²*Ophiocordyceps cantharelloides* (Samson & H.C. Evans) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504234.
≡ *Cordyceps cantharelloides* Samson & H.C. Evans, Proc. Indian Acad. Sci., Pl. Sci. 94: 312. 1985.
- ²*Ophiocordyceps carabidicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504235.
≡ *Cordyceps carabidicola* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 85. 1980. [as *C. 'carabidicola'*]
- ²*Ophiocordyceps cicadicola* (Teng) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504236.
≡ *Cordyceps cicadicola* Teng, Sinensia 6: 191. 1935.
- ²*Ophiocordyceps clavata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504237.
≡ *Cordyceps clavata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 140. 1980.
- ²*Ophiocordyceps clavulata* (Schwein.) Petch, Trans. Brit. Mycol. Soc. 18: 53. 1933.
≡ *Sphaeria clavulata* Schwein., Trans. Amer. Philos. Soc. New Ser. 4, 188. 1832.

≡ *Xylaria clavulata* (Schwein.) Berk. & M. A. Curtis, J. Linn. Soc. 10: 380. 1868.
 ≡ *Torrubia clavulata* (Schwein.) Peck, Ann. Rep. N. Y. State Mus. 28: 70. 1876.
 ≡ *Cordyceps clavulata* (Schwein.) Ellis & Everh., North Amer. Pyrenom. p. 61. 1892.

= *Cordyceps pistillariiformis* Berk. & Broome, Ann. Mag. Nat. Hist. Ser. 3, 7: 451. 1861 [as *C. pistillariaeformis*].

≡ *Torrubia pistillariiformis* (Berk. & Broome) Cooke, Handb. Brit. Fungi 2: 771. 1871.

Anamorph: *Hymenostilbe lecaniicola* (Jaap) Mains

¹*Ophiocordyceps coccidiicola* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504238.

≡ *Cordyceps coccidiicola* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 57. 1978.

²*Ophiocordyceps coccigena* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504239.

≡ *Torrubia coccigena* Tul. & C. Tul., Sel. Fung. Carpol. 3: 19. 1865.

≡ *Cordyceps coccigena* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.

²*Ophiocordyceps cochliidicola* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504240.

≡ *Cordyceps cochliidicola* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 128. 1980.

¹*Ophiocordyceps communis* Hywel-Jones & Samson, **sp. nov.**, see above.

Anamorph: hirsutella/hymenostilbe-like

²*Ophiocordyceps corallomyces* (A. Möller) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504241.

≡ *Cordyceps corallomyces* A. Möller, Phycomycceten u. Ascomyceten, p. 217. 1901.

²*Ophiocordyceps crassispora* (M. Zang, D.R. Yang & C.D. Li) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504242.

≡ *Cordyceps crassispora* M. Zang, D.R. Yang & C.D. Li, Mycotaxon 37: 58. 1990.

²*Ophiocordyceps crinalis* (Ellis ex Lloyd) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504243.

≡ *Cordyceps crinalis* Ellis ex Lloyd, Mycol. Writ. 6: 912. 1920.

²*Ophiocordyceps cucumispora* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504244.

≡ *Cordyceps cucumispora* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 442. 1982.

Anamorph: *Hirsutella ovalispora* H.C. Evans & Samson

²*Ophiocordyceps cucumispora* var. *dolichoderi* (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504245.

≡ *Cordyceps cucumispora* var. *dolichoderi* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 79: 445. 1982.

Anamorph: *Hirsutella ovalispora* var. *dolichoderi* H.C. Evans & Samson

²*Ophiocordyceps curculionum* (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504246.

≡ *Torrubia curculionum* Tul. & C. Tul., Sel. Fung. Carpol. 3: 20. 1865.

≡ *Cordyceps curculionum* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.

≡ *Cordyceps bicephala* subsp. *curculionum* (Tul. & C. Tul.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 50. 1949.

Anamorph: *Hymenostilbe*

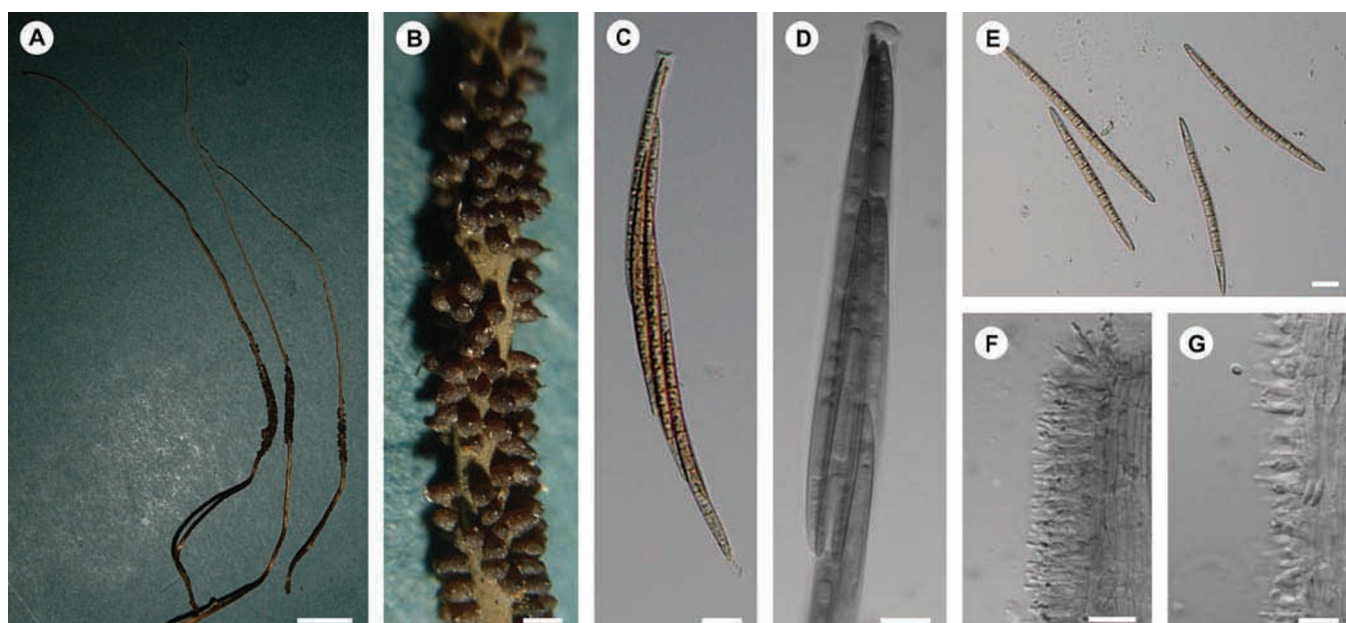


Fig. 12. A–G. Morphology of *Ophiocordyceps communis*. A. Stromata, bar = 10 mm. B. Arrangement of perithecia. C. Ascus with ascospores. D. Ascus and ascus apex. E. Non-disarticulating ascospores. F. Conidiophores (*Hymenostilbe/Hirsutella* anamorph). G. Denticles of phialide (*Hymenostilbe/Hirsutella* anamorph). Scale bars: A, C–G = 10 µm, B = 500 µm.

- ²***Ophiocordyceps cylindrostromata*** (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504247.
 ≡ *Cordyceps cylindrostromata* Z.Q. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 97. 2003.
- ²***Ophiocordyceps dayiensis*** (Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504248
 ≡ *Cordyceps dayiensis* Z.Q. Liang, Fungal Diversity 12: 131. 2003.
- ²***Ophiocordyceps dermapterigena*** (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504249.
 ≡ *Cordyceps dermapterigena* Z.Q. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 96. 2003 (as *C. 'dermapteoigena'*).
- ²***Ophiocordyceps dipterigena*** (Berk. & Broome) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504250.
 ≡ *Cordyceps dipterigena* Berk. & Broome, J. Linn. Soc. 14: 111. 1875.
 = *Cordyceps muscicola* A. Möller, Phycomycten u. Ascomyceten, p. 221. 1901.
 = *Cordyceps surinamensis* Henn., Hedwigia 41: 169. 1902.
 = *Cordyceps oumensis* Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 309. 1909.
 = *Cordyceps ouwensii* Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 309. 1909.
 = *Cordyceps thwaitesii* Lloyd, Mycol. Writ. 6: 1060. 1921.
 = *Cordyceps opposita* Syd., Bot. Jahrb. Syst. 57: 325. 1922.
 Anamorph: *Hymenostilbe dipterigena* Petch
- ²***Ophiocordyceps discoideicapitata*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504251.
 ≡ *Cordyceps discoideicapitata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 85. 1982 (as *C. 'discoideocapitata'*).
- ²***Ophiocordyceps ditmarii*** (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504252.
 ≡ *Cordyceps ditmarii* Quél., Bull. Soc. Bot. France 24: 330. 1877. [as *C. ditmari*]
 Anamorph: *Hymenostilbe*
- ²***Ophiocordyceps dovei*** (Rodway) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504253.
 ≡ *Cordyceps dovei* Rodway, Paper Proc. Roy. Soc. Tasmania for 1898–1899, p. 101. 1900.
 = *Cordyceps aemonae* Lloyd, Mycol. Notes 62: 932. 1920.
 Anamorph: hirsutella-like
- ²***Ophiocordyceps elateridicola*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504255.
 ≡ *Cordyceps elateridicola* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 4. 1983.
- ²***Ophiocordyceps elongata*** (Petch) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504256.
 ≡ *Cordyceps elongata* Petch, Trans. Brit. Mycol. Soc. 21: 47. 1937.
 Anamorph: *Hirsutella*
- ²***Ophiocordyceps elongatiperitheciata*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504257.
 ≡ *Cordyceps elongatiperitheciata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 126. 1980 (as *C. 'elongatoperitheciata'*).
- ²***Ophiocordyceps elongatistromata*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504258.
 ≡ *Cordyceps elongatistromata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 12. 1983 (as *C. 'elongatostromata'*).
- ²***Ophiocordyceps emeiensis*** (A.Y. Liu & Z.Q. Liang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504259.
 ≡ *Cordyceps emeiensis* A.Y. Liu & Z.Q. Liang, Mycosystema 16: 139. 1997.
- ²***Ophiocordyceps engleriana*** (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504260.
 ≡ *Cordyceps engleriana* Henn., Bot. Jahrb. Syst. 23: 538. 1897.
 Anamorph: *Hymenostilbe*
- ¹***Ophiocordyceps entomorrhiza*** (Dicks.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504261.
 ≡ *Sphaeria entomorrhiza* Dicks., Plant. Crypt. Brit., Fasc. 1: 22. 1785.
 ≡ *Cordyceps entomorrhiza* (Dicks.) Fr., Obs. Mycol. 2: 317. 1818.
 ≡ *Torrubia entomorrhiza* (Dicks.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 13. 1865.
 = *Torrubia cinerea* Tul. & C. Tul., Sel. Fung. Carpol. 3: 14. 1865.
 ≡ *Cordyceps cinerea* (Tul. & C. Tul.) Sacc., Michelia 1: 320. 1879.
 = *Cordyceps carabi* Quél., Comp. Rend. Assoc. Franç. Avancem. Sci. 26: 452. 1898.
 Anamorph: *Hirsutella eleutheratorum* (Nees) Petch
- ²***Ophiocordyceps evdodgeorgiae*** (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504262.
 ≡ *Cordyceps evdodgeorgiae* Koval, Bot. Mater. Otd. Sporov. Rast. 14: 160. 1961.
- ²***Ophiocordyceps falcata*** (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504263.
 ≡ *Cordyceps falcata* Berk., J. Bot. (Hooker) 6: 211. 1854 [Decad. Fung. No. 479].
 Anamorph: *Stilbella*
- ²***Ophiocordyceps falcatooides*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504264.
 ≡ *Cordyceps falcatooides* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 91. 1980.
- ²***Ophiocordyceps fasciculatistromata*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504265.
 ≡ *Cordyceps fasciculatistromata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 83. 1982 (as *C. 'fasciculatostromata'*).

- ²*Ophiocordyceps ferruginosa* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504266.
 ≡ *Cordyceps ferruginosa* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 139. 1980.
- ²*Ophiocordyceps filiformis* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504267.
 ≡ *Cordyceps filiformis* Moureau, Mém. Inst. Roy. Colon. Belge 7: 14. 1949.
- ²*Ophiocordyceps formicarum* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504268
 ≡ *Cordyceps formicarum* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 286. 1939.
 Anamorph: *Hymenostilbe*
- ²*Ophiocordyceps forquignonii* (Quél.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504269.
 ≡ *Cordyceps forquignonii* Quél., 16th Suppl. Champ. Jura et Vosges, p. 6. 1887.
 Anamorph: *Hymenostilbe muscarium* Petch
- ²*Ophiocordyceps furcicaudata* (Z.Q. Liang, A.Y. Liu & M.H. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504270.
 ≡ *Cordyceps furcicaudata* Z.Q. Liang, A.Y. Liu & M.H. Liu, Fungal Diversity 14: 95. 2003 (as *C. furcicaudata*).
- ²*Ophiocordyceps gansuënsis* (K. Zhang, C. Wang & M. Yan) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504271.
 ≡ *Cordyceps gansuënsis* K. Zhang, C. Wang & M. Yan, Trans. Mycol. Soc. Japan 30: 295. 1989.
- ²*Ophiocordyceps geniculata* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504272.
 ≡ *Cordyceps geniculata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 85. 1980.
- ²*Ophiocordyceps gentilis* (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504273.
 ≡ *Torrubia gentilis* Ces., Atti Accad. Sci. Fis. Mat., Napoli, 8: 14. 1879.
 ≡ *Cordyceps gentilis* (Ces.) Sacc., Syll. Fung. 2: 569. 1883.
- ²*Ophiocordyceps glaziovii* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504274.
 ≡ *Cordyceps glaziovii* Henn., Naturw. Wochenschr. 6: 318. 1896.
- ²*Ophiocordyceps goniophora* (Speg.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504275.
 ≡ *Cordyceps goniophora* Speg., Bol. Acad. Nac. Ci. Córdoba 11: 307. 1889.
- ²*Ophiocordyceps gracilioides* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504276.
 ≡ *Cordyceps gracilioides* Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 140. 1941.
 Anamorph: paecilomyces-like
- ¹*Ophiocordyceps gracilis* (Grev.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504277.
 ≡ *Xylaria gracilis* Grev., Scot. Crypt. Fl. 2. t. 86. 1824.
 ≡ *Cordyceps gracilis* (Grev.) Durieu & Mont., Fl. Algérie Crypt. 1: 449. 1846.
 = *Cordyceps mawleyi* Westwood, Gard. Chron. Ser. 3, 9: 553. 1891.
 Anamorph: *Paraisaria dubia* (Delacr.) Samson & B.L. Brady
- ²*Ophiocordyceps gryllotalpae* Petch, Trans. Brit. Mycol. Soc. 25: 255. 1941.
 ≡ *Cordyceps gryllotalpae* Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku 5: 70. 1942 [non Lloyd 1924].
 ≡ *Cordyceps koreana* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 8. 1981.
- ¹*Ophiocordyceps heteropoda* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504278.
 ≡ *Cordyceps heteropoda* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 158. 1939.
- ²*Ophiocordyceps hiugensis* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504279.
 ≡ *Cordyceps hiugensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 3. 1983.
- ²*Ophiocordyceps huberiana* (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504280.
 ≡ *Cordyceps huberiana* Henn., Hedwigia 48: 105. 1909.
- ²*Ophiocordyceps humbertii* (C.P. Robin) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504281.
 ≡ *Cordyceps humbertii* C.P. Robin, in Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865 (as *C. humbertii*).
 Anamorph: *Hirsutella saussurei* (Cooke) Speare
- ²*Ophiocordyceps insignis* (Cooke & Ravenel) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504282.
 ≡ *Cordyceps insignis* Cooke & Ravenel, Grevillea 12: 38. 1883.
- ¹*Ophiocordyceps irangiensis* (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504283.
 ≡ *Cordyceps irangiensis* Moureau, Lejeunia, Mém. 15: 33. 1961.
 Anamorph: *Hymenostilbe*
- ²*Ophiocordyceps japonensis* (Hara) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504284.
 ≡ *Cordyceps japonensis* Hara, Bot. Mag. Tokyo 28: 351. 1914.
- ²*Ophiocordyceps jiangxiensis* (Z.Q. Liang, A.Y. Liu & Yong C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504285.

- ≡ *Cordyceps jiangxiensis* Z.Q. Liang, A.Y. Liu & Yong C. Jiang, *Mycosystema* 20: 306. 2001.
- ²***Ophiocordyceps jinggangshanensis*** (Z.Q. Liang, A.Y. Liu & Yong C. Jiang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504286.
≡ *Cordyceps jinggangshanensis* Z.Q. Liang, A.Y. Liu & Yong C. Jiang, *Mycosystema* 20: 307. 2001.
- ²***Ophiocordyceps kangdingensis*** (M. Zang & N. Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504287.
≡ *Cordyceps kangdingensis* M. Zang & N. Kinjo, *Mycotaxon* 66: 221. 1998.
- ²***Ophiocordyceps kniphofioides*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504288.
≡ *Cordyceps kniphofioides* H.C. Evans & Samson, *Trans. Brit. Mycol. Soc.* 79: 434. 1982.
Anamorph: *Hirsutella stilbelliformis* H.C. Evans & Samson
- ²***Ophiocordyceps kniphofioides* var. *dolichoderi*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504289.
≡ *Cordyceps kniphofioides* var. *dolichoderi* H.C. Evans & Samson, *Trans. Brit. Mycol. Soc.* 79: 437. 1982.
Anamorph: *Hirsutella stilbelliformis* var. *dolichoderi* H.C. Evans & Samson
- ²***Ophiocordyceps kniphofioides* var. *monacidis*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504290.
≡ *Cordyceps kniphofioides* var. *monacidis* H.C. Evans & Samson, *Trans. Brit. Mycol. Soc.* 79: 439. 1982.
Anamorph: *Hirsutella stilbelliformis* var. *monacidis* H.C. Evans & Samson
- ²***Ophiocordyceps kniphofioides* var. *ponerinarum*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504291.
≡ *Cordyceps kniphofioides* var. *ponerinarum* H.C. Evans & Samson, *Trans. Brit. Mycol. Soc.* 79: 441. 1982.
Anamorph: *Hirsutella stilbelliformis* var. *ponerinarum* H.C. Evans & Samson
- ²***Ophiocordyceps koningsbergeri*** (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504292.
≡ *Cordyceps koningsbergeri* Penz. & Sacc., *Malpighia* 11: 522. 1897.
- ¹***Ophiocordyceps konnoana*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504293.
≡ *Cordyceps konnoana* Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo*, Ser. B, 6: 84. 1980.
- ²***Ophiocordyceps lachnopoda*** (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504295.
≡ *Cordyceps lachnopoda* Penz. & Sacc., *Malpighia* 11: 521. 1897.
- ²***Ophiocordyceps larvarum*** (Westwood) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504397.
≡ *Sphaeria larvarum* Westwood, *Proc. Entomol. Soc. Lond.* 2: 6. 1836.
≡ *Cordyceps larvarum* (Westwood) Olliff, *Gaz. New South Wales* 6: 410. 1895.
= *Cordyceps huegelii* Corda, *Icon. Fung.* 4: 44. 1840.
- ²***Ophiocordyceps lloydii*** (H.S. Fawc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504296.
≡ *Cordyceps lloydii* H.S. Fawc., *Ann. Mag. Nat. Hist.*, Ser. 5, 18: 317. 1886.
= *Cordyceps sheeringii* Masee, *Ann. Bot.* 5: 510. 1890.
= *Cordyceps subdiscoidea* Henn., *Hedwigia* 41: 168. 1902.
Anamorph: *Hymenostilbe formicarum* Petch
- ²***Ophiocordyceps lloydii* var. *binata*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504297.
≡ *Cordyceps lloydii* var. *binata* H.C. Evans & Samson, *Trans. Brit. Mycol. Soc.* 82: 133. 18: 316. 1984.
- ¹***Ophiocordyceps longissima*** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504298.
≡ *Cordyceps longissima* Kobayasi, *Bull. Natn. Sci. Mus. Tokyo* 6: 300. 1963.
- ²***Ophiocordyceps lutea*** (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504299.
≡ *Cordyceps lutea* Moureau, *Mém. Inst. Roy. Colon. Belge* 7: 41. 1949.
Anamorph: *Hymenostilbe sulphurea* Samson & H.C. Evans
- ²***Ophiocordyceps macularis*** Mains, *Proc. Amer. Philos. Soc.* 74: 269. 1934.
≡ *Cordyceps macularis* (Mains) Mains, *Pap. Michigan Acad. Sci.* 25: 82. 1940.
- ¹***Ophiocordyceps melolonthae*** (Tul. & C. Tul.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504300.
≡ *Torrubia melolonthae* Tul. & C. Tul., *Sel. Fung. Carpol.* 3: 12. 1865.
≡ *Cordyceps melolonthae* (Tul. & C. Tul.) Sacc., *Michelia* 1: 320. 1879.
- ²***Ophiocordyceps melolonthae* var. *rickii*** (Lloyd) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504301.
≡ *Cordyceps rickii* Lloyd, *Mycol. Writ.* 6: 914. 1920.
≡ *Cordyceps melolonthae* var. *rickii* (Lloyd) Mains, *Mycologia* 50: 198. 1958.
- ²***Ophiocordyceps michiganensis*** (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504302.
≡ *Cordyceps michiganensis* Mains, *Proc. Amer. Philos. Soc.* 74: 266. 1934.

- ²*Ophiocordyceps minutissima* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504303.
 ≡ *Cordyceps minutissima* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 77. 1980.
- ²*Ophiocordyceps monticola* (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504304.
 ≡ *Cordyceps monticola* Mains, Mycologia 32: 310. 1940.
- ²*Ophiocordyceps mrciensis* (Aung, J.C. Kang, Z.Q.Liang, Soyong & K.D. Hyde) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504305.
 ≡ *Cordyceps mrciensis* Aung, J.C. Kang, Z.Q.Liang, Soyong & K.D. Hyde, Mycotaxon 97: 236. 2006.
- ²*Ophiocordyceps multiaxialis* (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504306.
 ≡ *Cordyceps multiaxialis* M. Zang & Kinjo, Mycotaxon 66: 224. 1998.
- ²*Ophiocordyceps myrmecophila* (Ces.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504307.
 ≡ *Cordyceps myrmecophila* Ces., Bot. Zeitung 4: 877. 1846.
 ≡ *Torrubia myrmecophila* (Ces.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.
 Anamorph: *Hymenostilbe*
- ²*Ophiocordyceps neovolkiana* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504308.
 ≡ *Cordyceps neovolkiana* Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 169. 1941.
 Anamorph: *Hirsutella neo-volkiana* Kobayasi
- ²*Ophiocordyceps nepalensis* (M. Zang & Kinjo) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504309.
 ≡ *Cordyceps nepalensis* M. Zang & Kinjo, Mycotaxon 66: 224. 1998.
- ²*Ophiocordyceps nigra* (Samson, H.C. Evans & E.S. Hoekstra) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504310.
 ≡ *Cordyceps nigra* Samson, H.C. Evans & E.S. Hoekstra, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 85: 596. 1982.
- ¹*Ophiocordyceps nigrella* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504311.
 ≡ *Cordyceps nigrella* Kobayasi & Shimizu, Icon. Veg. Wasps and Plant Worms p. 145. 1983.
 ≡ *Cordyceps nigra* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo 9(1): 13. 1983 [non Samson *et al.* 1982]
- ²*Ophiocordyceps nigripes* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504312.
 ≡ *Cordyceps nigripes* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 116. 1982 (as *C. 'nigripoda'*).
- ¹*Ophiocordyceps nutans* (Pat.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504313.
 ≡ *Cordyceps nutans* Pat., Bull. Soc. Mycol. France 3: 127. 1887.
 ≡ *Cordyceps bicephala* subsp. *nutans* (Pat.) Moureau, Mém. Inst. Roy. Colon. Belge 7: 47. 1949.
 Anamorph: *Hymenostilbe nutans* Samson & H.C. Evans
- ²*Ophiocordyceps obtusa* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504314.
 ≡ *Cordyceps obtusa* Penz. & Sacc., Malpighia 11: 523. 1897.
- ²*Ophiocordyceps octospora* (M. Blackwell & Gilb.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504315.
 ≡ *Cordycepioideus octosporus* M. Blackwell & Gilb., Mycologia 73: 358. 1981.
 Anamorph: *Hirsutella*
- ²*Ophiocordyceps odonatae* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504316.
 ≡ *Cordyceps odonatae* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 7: 6. 1981.
 Anamorph: *Hymenostilbe odonatae* Kobayasi
- ²*Ophiocordyceps osuzumontana* (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504317.
 ≡ *Cordyceps osuzumontana* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 77. 1980.
- ²*Ophiocordyceps owariensis* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504318.
 ≡ *Cordyceps owariensis* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 166. 1939.
- ²*Ophiocordyceps owariensis* f. *viridescens* (Uchiyama & Udagawa) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504319.
 ≡ *Cordyceps owariensis* f. *viridescens* Uchiyama & Udagawa, Mycoscience 43: 136. 2002.
 Anamorph: *Nomuraea owariensis* Uchiyama & Udagawa
- ²*Ophiocordyceps oxycephala* (Penz. & Sacc.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504320.
 ≡ *Cordyceps oxycephala* Penz. & Sacc., Malpighia 11: 521. 1897.
 ≡ *Cordyceps sphecocephala* f. *oxycephala* (Penz. & Sacc.) Kobayasi, Trans. Mycol. Soc. Japan 23: 361. 1982.
 Anamorph: *Hymenostilbe*
- ²*Ophiocordyceps paludosa* Mains, Proc. Amer. Philos. Soc. 74: 269. 1934.
 ≡ *Cordyceps paludosa* (Mains) Mains, Pap. Michigan Acad. Sci. 25: 83. 1940.
 Anamorph: *Polycephalomyces paludosus* Mains
- ²*Ophiocordyceps pentatomae* (Koval) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504321.

- ≡ *Cordyceps pentatomae* Koval, Nov. Sist. Niz. Rast. 1: 166. 1964. (as *C. 'pentatomi'*)
Anamorph: *Hirsutella*
- ²***Ophiocordyceps petchii*** (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504322.
≡ *Cordyceps petchii* Mains, Bull. Torrey Bot. Club 86: 47. 1959.
≡ *Cordyceps ramosa* Petch, Trans. Brit. Mycol. Soc 21: 42. 1937 [non Teng 1936].
- ²***Ophiocordyceps proliferans*** (Henn.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504323.
≡ *Cordyceps proliferans* Henn., Hedwigia 43: 248. 1904.
- ²***Ophiocordyceps pseudolloydii*** (H.C. Evans & Samson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504324.
≡ *Cordyceps pseudolloydii* H.C. Evans & Samson, Trans. Brit. Mycol. Soc. 82: 133. 1984.
- ²***Ophiocordyceps pseudolongissima*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504325.
≡ *Cordyceps pseudolongissima* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 119. 1982.
- ²***Ophiocordyceps purpureostromata*** (Kobayasi) ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504326.
≡ *Cordyceps purpureostromata* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 136. 1980. Type Shimizu No. 128, preserved in TNS; therefore the basionym was valid from the beginning.
- ²***Ophiocordyceps purpureostromata* f. *recurvata*** (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504327.
≡ *Cordyceps purpureostromata* f. *recurvata* Kobayasi, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 138. 1980.
- ¹***Ophiocordyceps ravenelii*** (Berk. & M.A. Curtis) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504328.
≡ *Cordyceps ravenelii* Berk. & M.A. Curtis, J. Linn. Soc. 1: 159. 1857.
- ¹***Ophiocordyceps rhizoidea*** (Höhn.) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.
≡ *Cordyceps rhizoidea* Höhn., Sitzungsber. Kaiserl. Akad. Wiss. Wien 118: 307. 1909.
Anamorph: *Hirsutella*
- ²***Ophiocordyceps ridleyi*** (Masse) Kobayasi, Bull. Biogeogr. Soc. Japan 9: 271. 1939.
≡ *Cordyceps ridleyi* Masse, Bull. Misc. Inform. Roy. Bot. Gard. Kew, p. 173. 1899.
- ¹***Ophiocordyceps robertsii*** (Hook.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504329.
≡ *Sphaeria robertsii* Hook. Icon. Plant. 1 pl. 6. 1837.
≡ *Cordyceps robertsii* (Hook.) Berk., Fl. New Zealand 2: 202. 1855.
- ²***Ophiocordyceps rubripunctata*** (Moureau) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504331.
≡ *Cordyceps rubripunctata* Moureau, Mém. Inst. Roy. Colon. Belge 7: 26. 1949.
Anamorph: *Hirsutella rubripunctata* Samson, H.C. Evans & Hoekstra
- ²***Ophiocordyceps rubiginosiperitheciata*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504332.
≡ *Cordyceps rubiginosiperitheciata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 14. 1983 (as *C. 'rubiginosiperitheciata'*).
- ²***Ophiocordyceps ryogamiensis*** (Kobayasi & Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504333.
≡ *Cordyceps ryogamiensis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 9: 4. 1983.
- ²***Ophiocordyceps salebrosa*** (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504334.
≡ *Cordyceps salebrosa* Mains, Mycologia 39: 541. 1947.
- ²***Ophiocordyceps scottiana*** (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504335.
≡ *Cordyceps scottiana* Olliff, Agric. Gaz. New South Wales 6: 407. 1895.
- ²***Ophiocordyceps selkirkii*** (Olliff) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504338.
≡ *Cordyceps selkirkii* Olliff, Agric. Gaz. New South Wales 6: 411. 1895.
- ²***Ophiocordyceps sichuanensis*** (Z.Q. Liang & B. Wang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504339.
≡ *Cordyceps sichuanensis* Z.Q. Liang & B. Wang, Fungal Diversity 12: 129. 2003.
- ¹***Ophiocordyceps sinensis*** (Berk.) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504340.
≡ *Sphaeria sinensis* Berk., J. Bot. (Hooker) 2: 207. 1843.
≡ *Cordyceps sinensis* (Berk.) Sacc., Michelia 1: 320. 1879.
Anamorph: *Hirsutella sinensis* X.J. Liu, Y.L. Guo, Y.X. Yu & W. Zeng
- ²***Ophiocordyceps smithii*** (Mains) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504341.
≡ *Cordyceps smithii* Mains, J. Elisha Mitchell Sci. Soc. 55: 127. 1939.
- ¹***Ophiocordyceps sobolifera*** (Hill ex Watson) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504342.
≡ *Clavaria sobolifera* Hill ex Watson, Philos. Trans. Roy. Soc. Lond. 53: 271. 1763.
≡ *Sphaeria sobolifera* (Hill ex Watson) Berk., J. Bot. (Hooker) 2: 207. 1843.
≡ *Torrubia sobolifera* (Hill ex Watson) Tul. & C. Tul., Sel. Fung. Carpol. 3: 10. 1865.
≡ *Cordyceps sobolifera* (Hill ex Watson) Berk. & Broome, J. Linn. Soc. 14: 110. 1875.
Anamorph: *Beauveria sobolifera* Z.Y. Liu, Z.Q. Liang, Whalley, A.Y. Liu & Y.J. Yao

¹*Ophiocordyceps sphecocephala* (Klotzsch ex Berk.)G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504343.≡ *Sphaeria sphecocephala* Klotzsch ex Berk., J. Bot. (Hooker) 2: 206. 1843.≡ *Torrubia sphecocephala* (Klotzsch ex Berk.) Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.≡ *Cordyceps sphecocephala* (Klotzsch ex Berk.) Berk. & M.A. Curtis, in Berkeley, J. Linn. Soc., Bot. 10: 376. 1868.Anamorph: *Hymenostilbe*²*Ophiocordyceps stipillata* (Z.Q. Liang & A.Y. Liu)G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504344.≡ *Cordyceps stipillata* Z.Q. Liang & A.Y. Liu, Mycosystema 21: 11. 2002.¹*Ophiocordyceps stylophora* (Berk. & Broome) G.H.Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504345.≡ *Cordyceps stylophora* Berk. & Broome, J. Linn. Soc. 1: 158. 1857.Anamorph: *Hirsutella stylophora* Mains²*Ophiocordyceps subflavida* (Mains) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504346.≡ *Cordyceps subflavida* Mains, Bull. Torrey Bot. Club 86: 47. 1959.≡ *Cordyceps albida* Pat. & Gaillard, Bull. Soc. Mycol. France 7: 116. 1888 [non Berk. & M.A. Curtis ex Cooke 1884].²*Ophiocordyceps subunilateralis* (Henn.) Kobayasi, Bull. Biogeogr. Soc. Japan 9: 271. 1939.≡ *Cordyceps subunilateralis* Henn., Hedwigia 41: 168. 1902.¹*Ophiocordyceps superficialis* (Peck) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504347.≡ *Torrubia superficialis* Peck, Rep. N. Y. State Botanist 28: 70. 1876.≡ *Cordyceps superficialis* (Peck) Sacc., Syll. Fung. 2: 574. 1883.²*Ophiocordyceps superficialis* f. *crustacea* (Kobayasi& Shimizu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504348.≡ *Cordyceps superficialis* f. *crustacea* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 82. 1980.²*Ophiocordyceps takaoënsis* (Kobayasi) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504349.≡ *Cordyceps sobolifera* var. *takaoënsis* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 165. 1939.≡ *Cordyceps takaoënsis* (Kobayasi) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 130. 1941.²*Ophiocordyceps taylorii* (Berk.) G.H. Sung, J.M.Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504350.≡ *Sphaeria taylorii* Berk., J. Bot. (Hooker) 2: 209. 1843 (as *S. 'taylori'*).≡ *Cordyceps taylorii* (Berk.) Sacc., Michelia 1: 320. 1879.²*Ophiocordyceps thyrsoides* (A. Möller) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.**

MycoBank MB504351.

≡ *Cordyceps thyrsoides* A. Möller, Phycomycceten u. Ascomycceten, p. 221. 1901.¹*Ophiocordyceps tricentri* (Yasuda) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504352.≡ *Cordyceps tricentri* Yasuda, in Lloyd, Mycol. Writ. 4: 568. 1915 (as *C. 'tricentrus'*).= *Cordyceps aphrophorae* Yasuda, Bot. Mag. Tokyo 36: 51. 1922.²*Ophiocordyceps uchiyamae* (Kobayasi & Shimizu)G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504353.≡ *Cordyceps uchiyamae* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 125. 1980.¹*Ophiocordyceps unilateralis* (Tul. & C. Tul.) Petch, Trans. Brit. Mycol. Soc. 16: 74. 1931.≡ *Torrubia unilateralis* Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.≡ *Cordyceps unilateralis* (Tul. & C. Tul.) Sacc., Syll. Fung. 2: 570. 1883.= *Torrubia formicivora* Tul. & C. Tul., Sel. Fung. Carpol. 3: 18. 1865.≡ *Cordyceps formicivora* (Tul. & C. Tul.) J. Schröt., Krypt.-Fl. Schlesien 3(2) 276. 1894.Anamorph: *Hirsutella formicarum* Petch²*Ophiocordyceps unilateralis* var. *clavata* Kobayasi, Bull. Biogeogr. Soc. Japan 9: 272. 1939.≡ *Cordyceps unilateralis* var. *clavata* (Kobayasi) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 78. 1941.¹*Ophiocordyceps variabilis* (Petch) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504354.≡ *Cordyceps variabilis* Petch, Trans. Brit. Mycol. Soc. 21: 42. 1937.= *Cordyceps viperina* Mains, Mycologia 29: 674. 1937.Anamorph: *Syngliocladium*²*Ophiocordyceps voeltzkowii* (Henn.) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504355.≡ *Cordyceps voeltzkowii* Henn., in Voeltzkow, Reise Ostafrika 3: 29. 1908.²*Ophiocordyceps volkiana* (A. Möller) G.H. Sung,J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504356.≡ *Cordyceps volkiana* A. Möller, Phycomycceten u. Ascomycceten, p. 233. 1901.Anamorph: *Hirsutella*²*Ophiocordyceps wuyishanensis* (Z.Q. Liang, A.Y. Liu & J.Z. Huang) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504357.≡ *Cordyceps wuyishanensis* Z.Q. Liang, A.Y. Liu & J.Z. Huang, Mycosystema 21: 162. 2002.

Anamorph: paecilomyces-like

¹*Ophiocordyceps yakusimensis* (Kobayasi) G.H.Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504358.≡ *Cordyceps yakusimensis* Kobayasi, Bull. Natn. Sci. Mus. Tokyo 6: 302. 1963.

²***Ophiocordyceps zhangjiajiensis*** (Z.Q. Liang & A.Y. Liu) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **comb. nov.** MycoBank MB504359.

= *Cordyceps zhangjiajiensis* Z.Q. Liang & A.Y. Liu, *Mycosystema* 21: 163. 2002.

Anamorph: *Hirsutella zhangjiajiensis* Z.Q. Liang & A.Y. Liu

CLAVICIPITACEAE Clade C

Clavicipitaceae clade C is a strongly supported group that includes the type species, *C. militaris*, of *Cordyceps* (MP-BP = 100 %, ML-BP = 100 %, PP = 1.00 in Figs 1–2). Because of the non-monophyly of *Cordyceps*, we reintroduce the preexisting family name *Cordycipitaceae* for *Clavicipitaceae* clade C. This family name was not validly published and it is validated herein based on the type genus *Cordyceps*. Most of the species in the family parasitize hosts in leaf litter, moss, or upper soil layers and produce superficial to partially immersed to completely immersed perithecia on a fleshy stroma or subiculum that is pallid or brightly coloured. The family contains species of *Cordyceps* and *Torrubiella* (Figs 5, 7). The unispecific genus *Phytocordyceps* is also recognized as a member of this family and transferred to *Cordyceps* (Fig. 6). In addition, the recent molecular study shows that species of the genera *Ascopolyporus* A. Möller and *Hyperdermium* J. White, R. Sullivan, G. Bills & N. Hywel-Jones 2000 [non Link], both pathogens of scale insects, are also inferred to be members of the family (Sullivan *et al.* 2000, Bischoff *et al.* 2005).

CORDYCIPITACEAE Kreisel 1969 ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, **fam. nov.** MycoBank MB504360.

Cordycipitaceae Kreisel, *Grundz. Natürl. Syst. Pilze*: 112. 1969 [*nom. inval.*, Art. 36].

Stromata vel subiculum pallida vel laete colorata, carnosae. Perithecia superficialia vel omnino immersa, perpendicularia ad superficiem. Asci cylindrici, apice inspissato. Ascospores cylindricae, multiseptatae, maturae diffrangentes vel integrae remanentes.

Stromata or subiculum pallid or brightly pigmented, fleshy. Perithecia superficial to completely immersed, oriented at right angles to the surface of the stroma. Asci cylindrical with thickened ascus apex. Ascospores usually cylindrical, multiseptate, disarticulating into part-spores or remaining intact at maturity.

Type: *Cordyceps* Fr.

Teleomorphic genera: *Ascopolyporus*, *Cordyceps*, *Hyperdermium*, *Torrubiella*.

Anamorphic genera: *Beauveria*, *Engyodontium*, *Isaria*, *Lecanicillium*, mariannaea-like, *Microhilum*, *Simplicillium*.

CORDYCEPS Fr., *Observ. Mycol.* 2 (revis.): 316. 1818 **emend.** G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

= *Phytocordyceps* C.H. Su & H.-H. Wang, *Mycotaxon* 26: 338. 1986.

Stromata or subiculum pallid or brightly pigmented, fleshy. Perithecia superficial to completely immersed, ordinal in arrangement. Asci hyaline, cylindrical with thickened ascus apex. Ascospores hyaline, cylindrical, multiseptate, disarticulating into part-spores or non-disarticulating, rarely possessing a thread-like structure connecting the fusiform ends.

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

Anamorphic genera: *Beauveria*, *Isaria*, *Lecanicillium*, mariannaea-like, *Microhilum*, *Simplicillium*.

Commentary: Species of *Cordyceps* s. s. are characterized by possessing fleshy stromata that are pallid or brightly coloured. Because species of *Torrubiella* are interspersed among *Cordyceps* species in the basal part of the *Cordycipitaceae*, its ultimate application to a monophyletic taxon within the *Cordycipitaceae* is not clear, however (Fig. 10). The genus *Torrubiella* was erected in 1885 by Boudier with the type species *T. aranicida* Boud. (Kobayasi & Shimizu 1982). Our sampling included several species of *Torrubiella* that were interspersed amongst species of *Cordycipitaceae*, but we could not get hold of *T. aranicida*. Thus, *Cordyceps* s. s. is narrowly applied to the strongly supported clade (MP-BP = 98 %, ML-BP = 98 %, PP = 1.00 in Figs 1–2, 10) that includes *Cordyceps* species closely related to *C. militaris*. *Cordyceps* species that are placed outside of the *Cordyceps* s. s. node, but within the *Cordycipitaceae*, are provisionally retained within *Cordyceps* s. l. *Torrubiella* species that are part of the *Cordyceps* s. s. are transferred accordingly. The full extent to which the names *Cordyceps* and *Torrubiella* will ultimately be applied awaits additional sampling of *Torrubiella*, especially that of *T. aranicida* with the possibility that *Torrubiella* will need to be synonymized with *Cordyceps*. Although *Phytocordyceps* is characterized by its possession of bola-ascospores, it is also synonymized with *Cordyceps* because of its phylogenetic placement (Figs 8, 10).

Accepted names and new combinations for *Cordyceps* s. s.

The following taxa are accepted species of *Cordyceps* s. s. based on their inclusion in molecular phylogenies presented herein¹ (see Table 1) or morphological descriptions matching the characters described above². Where known we provide the anamorph connection for the species of *Cordyceps* s. s.

²***Cordyceps ampullacea*** Kobayasi & Shimizu, *Bull. Natn. Sci. Mus. Tokyo, Ser. B*, 8: 112. 1982.

²***Cordyceps bassiana*** Z.Z. Li, C.R. Li, B. Huang & M.Z. Fan, *Chinese Science Bulletin* 46: 751. 2001.

Anamorph: *Beauveria bassiana* (Bals.) Vuill.

²***Cordyceps belizensis*** Mains, *Mycologia* 32: 21. 1940.

¹***Cordyceps bifusispora*** O.E. Erikss., *Mycotaxon* 15: 185. 1982.

- Anamorph: *Septofusidium bifusisporum* Z.Y. Liu, Z.Q. Liang & A.Y. Liu
- ²*Cordyceps brongniartii* Shimazu, Trans. Mycol. Soc. Japan 29: 328. 1988.
Anamorph: *Beauveria brongniartii* (Sacc.) Petch
- ²*Cordyceps chichibuënsis* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 87. 1980.
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Anamorph: *Lecanicillium lecanii* (Zimm.) Zare & W. Gams
- ²*Cordyceps erotyli* Petch, Trans. Brit. Mycol. Soc. 21: 40. 1937.
- ²*Cordyceps exasperata* A.F. Vital, Anais Soc. Biol. Pernambuco 14: 65. 1956.
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≡ *Xylaria militaris* (L.) Gray, Nat. Arr. Brit. Pl. (London), p. 510. 1821.
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Anamorph: *Lecanicillium*
- ²*Cordyceps miryensis* Henn., Hedwigia 43: 247. 1904.
- ²*Cordyceps mitrata* Pat., Bull. Soc. Mycol. France 14: 196. 1898.
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Anamorph: acremonium-like
- ¹*Cordyceps ochraceostromata* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 6: 132. 1980.
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Anamorph: *Mariannaea pruinosa* Z.Q. Liang
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Anamorph: *Beauveria*
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≡ *Acrophyton tuberculatum* Lebert, in Sieb & Köll., Z. Wiss. Zool. 9: 448. 1858.

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Anamorph: *Akanthomyces pistillariiformis* (Pat.) Samson & H.C. Evans

²*Cordyceps tuberculata* var. *tuberculata* [var. *typica* Kobayasi] f. *moelleri* (Henn.) Kobayasi, Sci. Rep. Tokyo Bunrika Daigaku, Sect. B, 5: 88. 1941.

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≡ *Cordyceps crista* A. Möller, Phycomycceten u. Ascomyceten, p. 212. 1901.

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≡ *Cordyceps cockerellii* (Ellis & Everh.) Ellis, in Seaver, North Am. Flora 3: 52. 1910.

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Clavicipitaceae incertae sedis

The following teleomorph genera could not be confidently assigned in the new classification because they were either not sampled as part of this study, were not sampled as part of other molecular phylogenetic studies, or the assessment of their morphology and ecology was inconclusive: *Berkelella* (Sacc.) Sacc., *Cavimalum* Yoshim. Doi, Dargan & K.S. Thind, *Dussiella* Pat., *Epicrea* Petr., *Helminthascus* Tranzschel, *Konradia* Racib., *Moelleriella* Bres., *Mycomalus* A. Möller, *Neobarya* Lowen, *Neocordyceps* Kobayasi, *Podocrella* Seaver, *Romanoa* Thirum., *Sphaerocordyceps* Kobayasi, and *Stereocrea* Syd. & P. Syd.

Residual species of *Cordyceps*

The following species of *Cordyceps s. l.* could not be confidently assigned in the new classification because they were either not assigned in any of the proposed genera in this study, were not sampled as part of this or

other molecular phylogenetic studies, or the assessment of their morphology and ecology was inconclusive. These species are provisionally retained within *Cordyceps s. l.* until further phylogenetic analyses are conducted to classify them in a phylogenetic system. Where known we provide the anamorph connection for the species of *Cordyceps s. l.*

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Cordyceps albocitrina Koval, Nov. Sist. Niz. Rast. 11: 209. 1974.

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Cordyceps atewensis Samson, H.C. Evans & E.S. Hoekstra, Proc. K. Ned. Akad. Wet., Ser. C, Biol. Med. Sci. 85: 590. 1982.

Cordyceps atrobrunnea Penz. & Sacc., Malpighia 11: 522. 1897.

Cordyceps atropuncta Koval, Bot. Mater. Otd. Sporov. Rast. 14: 158. 1961.

Cordyceps atrovirens Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 4: 52. 1978.

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Cordyceps aurea Moureau, Mém. Inst. Roy. Colon. Belge 7: 21. 1949.

Cordyceps barberi Giard ex Masee, Ann. Bot. 9: 18. 1895.

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- Cordyceps baumanniana* Henn., Bot. Jahrb. Syst. 23: 539. 1897.
- Cordyceps bicolor* Pat., Mém. Acad. Malgache 6: 40. 1928.
- Cordyceps bokyoënsis* Kobayasi, J. Jap. Bot. 58: 221. 1983.
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Anamorph: *Nomuraea atypicola* (Yasuda) Samson
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- Cordyceps dimeropoda* Syd., Bot. Jahrb. Syst. 57: 324. 1922.
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- Cordyceps gemella* Moureau, Lejeunia, Mém. 15: 6. 1961.
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Anamorph: *Akanthomyces*
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Anamorph: *Isaria nipponica* Kobayasi
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Anamorph: *Iecanicillium*/*simplicillium*-like
- Cordyceps pseudonelumboides* Kobayasi & Shimizu, Bull. Natn. Sci. Mus. Tokyo, Ser. B, 8: 80. 1982.
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KEY TO THE GENERA OF FUNGI FORMERLY CLASSIFIED IN *CORDYCEPS*

This key is designed to emphasize the most conspicuous field-, host-, and macroscopic characters available to the user for *Cordyceps sensu* Kobayasi and Mains. It is a key to the monophyletic genera described herein and is not a key to the species. As relatively few species occur on *Elaphomyces* and adult stages of Arthropoda, the key begins with these characters so as to expeditiously highlight or remove these taxa from consideration. Host is an exceedingly important character in most species descriptions of arthropod-pathogenic fungi. The host should be collected with the fungal specimen whenever possible, but this often proves problematic. The vast majority of arthropod-pathogenic fungi occur

on immature stages (e.g., larvae, pupae) of arthropods. Therefore, if the host is lacking from a particular specimen or collection, we suggest the user to begin with couplet (6). The multigene phylogeny reveals that colour, texture, and shape of stromata are particularly phylogenetically informative, thus we place special emphasis on these characters where possible but emphasize that, as with most fungal taxa, exceptions are to be expected.

To assist the user we briefly define some characters of stromatal texture and morphology that may not be intuitive:

Fleshy	– stromata that are composed of relatively loosely woven hyphae and are soft in texture (e.g., <i>C. militaris</i>).
Wiry	– filiform stromata that are somewhat brittle and stiff (e.g., <i>O. unilateralis</i>).
Pliant	– filiform stromata that are more pliable and rubbery to the touch; when fresh, they bend easily without breaking; typically slightly more robust than wiry (e.g., <i>O. nutans</i>).
Fibrous	– stromata that are composed of relatively tightly woven hyphae and are firm in texture, similar to the stipe of a mushroom (e.g., <i>E. ophioglossoides</i> , <i>O. heteropoda</i>).
Subicular	– production of perithecia on a net-like structure of mycelium, not on the developed stroma (e.g., <i>C. tuberculata</i>).
Lateral pads	– production of perithecia on a disc-like or cushion-like structure on a subterminal region of the stroma (e.g., <i>O. variabilis</i> , <i>O. unilateralis</i>).
Aperithecial apices	– production of perithecia in subterminal regions of the stroma, resulting in an apical region of the stroma lacking perithecia. (Note: The term sterile apices has also been used to describe this condition, but the apical regions of many stromata produce an anamorph and thus are not technically sterile.)

***Cordyceps* s. s.** consists almost entirely of pallid to brightly coloured species that produce soft fleshy stromata (e.g., *C. militaris*). The majority of species attack larvae and pupae of Lepidoptera and Coleoptera in leaf litter, moss or upper soil layers. Numerous species that produce highly reduced stromata, loosely organized hyphae, or a subiculum on the host also occur in this genus (e.g. *C. tuberculata*), some of which were previously classified in *Torrubiella* (e.g., *T. confragosa*).

Elaphocordyceps includes all species that parasitize *Elaphomyces* and closely related species that attack nymphs of cicadas. The morphology of the *Elaphomyces* parasites and the cicada pathogens are remarkably similar and attest to the recent history of inter-kingdom host-jumps in a common subterranean environment (Nikoh & Fukatsu 2000). The exception to this genus is *E. subsessilis*, which macroscopically and ecologically is distinct from the rest of the species, but is well supported as being a member of the genus based on molecular data and micromorphology.

Metacordyceps includes only a limited number of described species, of which all but one are only known from East Asia. The stromatal colour of fresh specimens ranges from white to lilac, purple or green, and the darker pigments are almost black in dried specimens. The texture of the stromata is fibrous and not fleshy like *Cordyceps* s. s., and the hosts are almost always buried in soil.

Ophiocordyceps is the largest genus of arthropod-pathogenic fungi. Many species are darkly pigmented and occur on immature stages of hosts buried in soil or in decaying wood. Notable exceptions exist for both of these traits among species that attack adult stages of hosts, however. For example, *O. unilateralis* is common on adult ants and occurs on the under sides of leaves, and *O. sphecocephala* is common on adult wasps and is found in leaf litter. Stromatal morphology is diverse, ranging from filiform and wiry to clavate and fibrous, according to species, and many species produce their perithecia in nonterminal regions of the stroma, either distinctly superficial, or in broad irregular patches, or in lateral pads.

1. Host – <i>Elaphomyces</i>	<i>Elaphocordyceps</i> (e.g., <i>E. ophioglossoides</i>)
1. Host – Arthropods.....	2
2. Host – adult Arthropods.....	3
2. Host – immature stage of Arthropods.....	6
3. Perithecia – <i>colour</i> : pallid, cream to white; <i>arrangement</i> : superficial on a subiculum or highly reduced pallid stroma. Host – adult Lepidoptera.....	<i>Cordyceps</i> (e.g., <i>C. tuberculata</i>)
3. On adult Arthropods other than Lepidoptera (e.g., ant, wasp, weevil, dragonfly, etc.) and stroma typically well-developed.....	4

4. **Stroma** – colour: yellow; texture: fleshy; shape: stipitate, clavate. **Perithecia** – colour: like stroma; arrangement: partially immersed to pseudoimmersed at right angles to surface of stroma (ordinal).
Host – typically on adult scarab beetles *Cordyceps* (e.g., *C. scarabaeicola*)
4. **Stroma** – colour: brightly or darkly pigmented; texture: wiry or pliant, not fleshy; shape: stipitate with or without pronounced fertile head region. **Perithecia** – arrangement: immersed at an oblique angle in fertile head region or more or less ordinal in subterminal lateral pads 5
5. **Stroma** – colour: at least partly brightly coloured; texture: pliant; shape: stipitate with globose to elongated fertile head region. **Perithecia** – arrangement: usually completely immersed at oblique angles, often giving the surface of the fertile head region a slightly uneven appearance when mature. **Host** – typically on adult insects (ants, wasps, weevils, dragonflies, etc.)..... *Ophiocordyceps* (e.g., *O. nutans*, *O. sphecocephala*)
5. **Stroma** – colour: darkly pigmented; texture: wiry; shape: filiform. **Perithecia** – colour: darkly pigmented like stroma or darker; arrangement: produced in subterminal region of stroma in lateral pad(s).
Host – adult ants..... *Ophiocordyceps* (e.g., *O. unilateralis*)
6. **Stroma** – colour: pallid to brightly coloured; texture: fleshy to fibrous; shape: usually stipitate, clavate but stroma highly reduced or subicular in some species. **Perithecia** – colour: pallid to brightly coloured like stroma; arrangement: typically partially immersed to pseudoimmersed to superficial on clava or subiculum in some species..... 7
6. **Stroma** – colour: usually darkly pigmented tan to brown to olive or black, rarely white to lilac to purple; texture: wiry, pliant or fibrous; shape: stipitate, club-shaped, or filiform, rarely subicular.
Perithecia – colour: typically pigmented like stroma or darker; arrangement: immersed to partially immersed to pseudoimmersed to superficial 8
7. **Stroma** – colour: pallid, cream to white; texture: fibrous; shape: reduced to pad-like or cushion-like structure on surface of wood, connected to host buried in wood via rhizomorph-like structures.
Perithecia – colour: like stroma; arrangement: immersed to partially immersed on pad-like stroma.
Host – Scarabid beetle larvae buried in decaying wood..... *Elaphocordyceps* (e.g., *E. subsessilis*)
7. **Stroma** – colour: yellow to red to orange; texture: fleshy; shape: usually stipitate clavate but subicular in some species. **Perithecia** – colour: like stroma; arrangement: ordinal, typically partially immersed to pseudoimmersed to superficial on clava or subiculum in some species.
Host – typically on larvae or pupae of arthropods in relatively exposed environments, such as leaf litter, moss, or the uppermost soil layer *Cordyceps* (e.g., *C. militaris*, *C. staphylinidicola*)
8. **Stroma** – colour: olive to brown; texture: fibrous; shape: stipitate, fertile region terminal, distinctly capitate to clavate. **Perithecia** – colour: like that of stroma; arrangement: immersed.
Host – cicada nymphs *Elaphocordyceps* (e.g., *E. paradoxa*)
8. **Stroma** – colour: tan to brown to black or lightly pigmented, white to lilac to purple, rarely brightly pigmented; texture: wiry, pliant, fibrous; shape: stipitate, capitate to clavate to filiform, rarely subicular.
Perithecia – colour: similar to stroma when immersed, often darker when superficial; arrangement: immersed, pseudoimmersed or superficial 9
9. **Stroma** – colour: white to lilac to purple to green, then appearing almost black when dry; texture: fibrous; shape: stipitate, typically with elongated clava. **Perithecia** – colour: like stroma; arrangement: immersed, ordinal or oblique. **Host** – typically buried in soil..... *Metacordyceps* (e.g., *M. taii*)
9. **Stroma** – colour: olive to brown to black rarely brightly coloured; texture: wiry, pliant, or fibrous; shape: stipitate, club-shaped to clavate or filiform, rarely subiculate. **Perithecia** – colour: darkly pigmented like stroma or darker; arrangement: immersed, pseudoimmersed but tightly spaced, or superficial and widely spaced, produced in terminal clava or subterminal patches or lateral pads.
Host – typically embedded in rotten wood or buried in soil
..... *Ophiocordyceps* (e.g., *O. sinensis*, *O. acicularis*, *O. variabilis*)

ACKNOWLEDGEMENTS

The authors wish to thank Dr Walter Gams for assistance with Latin diagnoses for new taxa and for providing editorial comments to early drafts of this manuscript. This research was supported by grants from the National Science Foundation (DEB-0129212 and DEB-0529752 to J.W.S.), the Korea Science and Engineering Foundation (to J-M Sung), and continuing support from Morakot Tanticharoen and BIOTEC (to N.H.J. and J.J.L.).

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