Revisiting *Metarhizium* and the description of new species from Thailand

S. Mongkolsamrit, A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, W. Noisripoom, S. Lamlertthon, W. Himaman, J. Houbraken, R.A. Samson, and J. Luangsa-ard

1National Center for Genetic Engineering and Biotechnology (BIOTEC), 113 Thailand Science Park, Phahonyothin Road, Klong Nueng, Klong Luang, Pathum Thani, 12120, Thailand; 2Center of Excellence in Fungal Research, Faculty of Medical Science, Naresuan University, Phitsanulok, 65000, Thailand; 3Forest Entomology and Microbiology Research Group, Forest and Plant Conservation Research Office, Department of National Parks, Wildlife and Plant Conservation, 61 Phahonyothin Road, Chatuchak, Bangkok, 10900, Thailand; 4Westerdijk Fungal Biodiversity Institute, Uppsalaalan 8, Utrecht, NL-3584 CT, The Netherlands

*Correspondence: J. Luangsa-ard, jajen@biotec.or.th*

**Abstract:**
Over the last two decades the molecular phylogeny and classification of *Metarhizium* has been widely studied. Despite these efforts to understand this enigmatic genus, the basal lineages in *Metarhizium* are still poorly resolved. In this study, a phylogenetic framework is reconstructed for the *Clavicipitaceae* focusing on *Metarhizium* through increased taxon-sampling using five genomic loci (SSU, LSU, tef, rpb1, rpb2) and the barcode marker ITS DNA. Multi-gene phylogenetic analyses and morphological characterisation of green-spored entomopathogenic *Metarhizium* isolates from Thailand and soil isolates of *M. carneum* and *M. marquandii* reveal their ecological, genetic and species diversity. Nineteen new species are recognised in the *Metarhizium* clade with narrow host ranges: two new species are found in the *M. anisopliae* complex – *M. clavatum* on Coleoptera and *M. sulphureum* on Lepidoptera larvae; four new species are found in the *M. flavoviride* complex – *M. biotecense* and *M. fusoidium* on brown plant hoppers (Hemiptera), *M. culicidarum* on mosquitoes, *M. nornnoi* on Lepidoptera larvae; three new species; *M. megaloponomea*; *M. cicaeida*; *M. megaloponomea*; five new species; *M. candelabrum*; *M. cercopidum*; *M. ellipsodeum*; *M. huanamangdense*; *M. oviodosporum* occur on planthoppers, leafhoppers and froghoppers (Hemiptera); one new species; *M. eburneum* on Lepidoptera pupae; and four new species; *M. phueiwiangense*; *M. purpureum*; *M. purpureonigrum*; *M. flavum* on Coleoptera. Of these 19 new species, seven produce a sexual morph (*M. clavatum*; *M. eburneum*; *M. flavum*; *M. phueiwiangense*; *M. purpureum*; *M. purpureonigrum*; *M. sulphureum*); and asexual morphs are found in the remaining new species and also in *M. sulphureum*; *M. purpureonigrum* and *M. purpureum*. *Metarhizium* blattodeae, *M. koreanum* and *M. viridulum* are new records for Thailand. An alternative neotype for *Metarhizium anisopliae* is proposed based on multi-gene and 5*′*ef*′* analyses showing that CBS 130.71 from Ukraine is more suitable, being from a much closer geographical location to Metchnikoff's *Metarhizium anisopliae*. This isolate is distinct from the neotype of *Metarhizium anisopliae* var. anisopliae proposed by M. Tulloch from Ethiopia (ARSEF 7487). Six new genera are established for monophyletic clades subtending the core *Metarhizium* clade, including Keithomyces, Marquandomyces, Papiliomyces, Purpureomyces, Sungia, and Yosiokobayasia. *Metarhizium carneum*, *M. aciculare*, and *M. neogunnii* are combined in *Keithomyces* and one new combination for *M. marquandii* in *Marquandomyces* is proposed. *Purpureomyces* is introduced for species producing purple stromata including a new combination for *M. phueiwiangense* and two new species *P. maesotensis* and *P. pyriformis*. *Papiliomyces* contains two new combinations for *M. liangshanense* and *Metacytocybe* *sphinitensis*. The genus *Sungia* is proposed for the Korean species *M. yongmunense* on Lepidoptera pupa and Yosiokobayasia for the Japanese species *M. kusangiense* also on Lepidoptera pupa. A synoptic and dichotomous key to the accepted taxa is provided together with tables listing distinguishing morphological characters between species, host preferences, and geography.

**Key words:** Biological control, *Clavicipitaceae*, Entomopathogenic fungi.

**Taxonomic novelties:**
*New genera:* Keithomyces samson, Luangsa-ard & Houbraken, Marquandomyces samson, Houbraken & Luangsa-ard, Papiliomyces luangsa-ard, Samson & Thanakitpipattana, Purpureomyces luangsa-ard, Samson & Thanakitpipattana, Sungia luangsa-ard, Samson & Thanakitpipattana, Yosiokobayasia samson, Luangsa-ard & Houbraken, *New species:* Metarhizium biotecense luangsa-ard, Khonsanit, Thanakitpipattana & Samson, M. candelabrum luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. cercopidum luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. cicaeida luangsa-ard, Tasanathai, Thanakitpipattana & Samson, M. clavatum luangsa-ard, Mongkolsamrit, Lamlertthon, Thanakitpipattana & Samson, M. culicidarum luangsa-ard, Khonsanit, Thanakitpipattana & Samson, M. eburneum luangsa-ard, Noisripoom, Thanakitpipattana & Samson, M. ellipsodeum luangsa-ard, Khonsanit, Thanakitpipattana & Samson, M. flavum luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. fusoidum luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. huanamangdense luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. megapomonniae luangsa-ard, Tasanathai, Thanakitpipattana & Samson, M. megalopomoniae luangsa-ard, Noisripoom, Thanakitpipattana & Samson, M. nornnoi luangsa-ard, Khonsanit, Thanakitpipattana & Samson, M. oviodosporum luangsa-ard, Khonsanit, Thanakitpipattana & Samson, M. phueiwiangense luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, M. purpureonigrum luangsa-ard, Tasanathai, Thanakitpipattana & Samson, M. purpureum luangsa-ard, Mongkolsamrit, Lamlertthon, Thanakitpipattana & Samson, M. sulphureum luangsa-ard, Khonsanit, Thanakitpipattana & Samson, Purpureomyces maesotensis luangsa-ard, Noisripoom, Thanakitpipattana & Samson, P. pyriformis luangsa-ard, Noisripoom, Himaman, Mongkolsamrit, Thanakitpipattana & Samson, *New combinations:* Keithomyces aciculatis (H. Iwasaki et al.) Samson, Luangsa-ard & Houbraken, Keithomyces carneus (Duché & R. Heim) Samson, Luangsa-ard & Houbraken, Keithomyces neogunnii (T.C. Wen & K.D. Hyde) Luangsa-ard, Thanakitpipattana & Samson, Marquandomyces marquandii (Massée) Samson, Houbraken & Luangsa-ard, Papiliomyces liangshanense (M. Zang et al) Luangsa-ard, Samson & Thanakitpipattana, Papiliomyces sphinitensis (T.C. Wen et al.) Luangsa-ard & Samson, Thanakitpipattana, Papiliomyces khaoyiensis (Hywel-Jones) Luangsa-ard, Samson & Thanakitpipattana, Sungia yongmunensis (G.H. Sung et al.) Luangsa-ard, Thanakitpipattana & Samson, Yosiokobayasia kusangiensis (Kobayasi & Shimizu) Samson, Luangsa-ard & Thanakitpipattana.

**Neotype:** Metarhizium anisopliae (Metch.) Sorokin.

Available online 5 May 2020; https://doi.org/10.1016/j.stmymco.2020.04.001.
INTRODUCTION

The genus *Metarhizium* is one of the ubiquitous genera of entomopathogenic fungi with diverse asexual reproductive morphologies and life cycle stages (Bischoff et al. 2009, Kepler et al. 2012a, Luangsa-ard et al. 2017). Known to cause the “green muscardine disease”, it was first described by Methchnikoff (1879) occurring in its asexual morph on a wheat cockchafer *Anisoplia austriaca* (scarab beetle, Coleoptera) in Russia (Zimmermann et al. 1995). Tulloch (1976) reviewed the genus and she reduced the genus only to two species — *M. anisopliae* and *M. flavoviride*, but recognising two varieties, *M. anisopliae* var. *anisopliae* with small conidia and *M. anisopliae* var. *majus* with large conidia. Two species published by Petch, *M. album* (Petch 1931) and *M. brunneum* (Petch 1934) were considered synonyms of *M. anisopliae* and with *M. album* considered as an immature specimen of *M. anisopliae*. Rombach et al. (1986, 1987) took into account the shapes of the conidia and phialides, as well as the conidial formation to form prismatic columns of immature specimen of *M. anisopliae*. Before 2000, the classification of *Metarhizium* was mainly based on morphological characters and Driver et al. (2000) increased our understanding of the genetic diversity in *Metarhizium* by studying the ITS regions and RAPD patterns of isolates identified as *M. anisopliae*, *M. flavoviride* and *M. album*. They recognised four varieties within the *M. anisopliae* group, five varieties in *M. flavoviride* group and *M. album*. Sung et al. (2007) erected *Metacordyceps* to accommodate *Cordyceps* spp. within *Clavicipitaceae* s.l. that are associated with *Metarhizium* and *Pochonia*. In a multi-gene phylogenetic study of *M. anisopliae* and *M. flavoviride* lineages, Bischoff et al. (2006, 2009) elevated and accepted *Metarhizium* varieties to species rank by using additional protein-coding genes (tuf, rpb1, rpb2 and *tub*). The authors recognised the synonyms of *M. taii* (Liang et al. 1991) and *M. guizhouense* (Guo et al. 1986, Shimazu 1989) and *M. taiti* with its sexual morph Cordyceps taii (Liang et al. 1991).

Before 2000, the classification of *Metarhizium* was mainly based on morphological characters and Driver et al. (2000) increased our understanding of the genetic diversity in *Metarhizium* by studying the ITS regions and RAPD patterns of isolates identified as *M. anisopliae*, *M. flavoviride* and *M. album*. They recognised four varieties within the *M. anisopliae* group, five varieties in *M. flavoviride* group and *M. album*. Sung et al. (2007) erected *Metacordyceps* to accommodate *Cordyceps* spp. within *Clavicipitaceae* s.l. that are associated with *Metarhizium* and *Pochonia*. In a multi-gene phylogenetic study of *M. anisopliae* and *M. flavoviride* lineages, Bischoff et al. (2006, 2009) elevated and accepted *Metarhizium* varieties to species rank by using additional protein-coding genes (tuf, rpb1, rpb2 and *tub*). The authors recognised the synonyms of *M. taii* (Liang et al. 1991) and *M. guizhouense* (Guo et al. 1986), thus proposing nine species as members of the *M. anisopliae* complex. *Metarhizium brunneum* was resurrected as a species and two new species in the *M. anisopliae* complex, *M. globosum* and *M. robertsi*, as well as one species in the *M. flavoviride* complex, *M. frigidum*, were recognised as valid species. In an effort to follow the concept of single nomenclature, Kepler et al. (2014) proposed the suppression of *Metacordyceps* in favour of a broad concept of *Metarhizium* and subsequently recognising that there are taxa with uncertain placement in their analyses, but favouring taxonomic stability and minimising disruption. *Pochonia* was retained and a new genus, *Metapochonia* was erected to accommodate members of *Pochonia* that did not group with the type species, *Chamaeleomyces*, *Nomuraea* spp. excluding *N. atypica*, and *Paecilomyces viridis* were transferred to *Metarhizium*, recognising a total of 34 species. Over the last decade, with increased availability of sequence data, recognition of new species in *Metarhizium* increased our understanding of its diversity, host affiliation, ecology and distribution with new species described from Argentina (Gutierrez et al. 2019), Brazil (Montalva et al. 2016, Lopes et al. 2018, Luz et al. 2019), China (Li et al. 2010, Chen et al. 2017, Wen et al. 2017, Chen et al. 2018a, c), Japan (Nishi et al. 2017, Iwasaki et al. 2019, Yamamoto et al. 2020), and Thailand (Luangsa-ard et al. 2017, Thanakitpipattana et al. 2020).

Originally known as generalists with a global distribution, many *Metarhizium* species are now described as members of *M. anisopliae* or *M. flavoviride* species complexes with certain species adapted to specific hosts (*M. acridum, M. grillicidicola, M. phasmatodeae*) or ecologies. Over 50 years ago, *Metarhizium anisopliae* was recorded to infect 200 insect species (Zimmermann 2007) and this ability to infect different host species in the field has been exploited in biological control strategies. *Metarhizium anisopliae* is used for control of insect pests in many countries around the world including Brazil, Iran, Japan, Thailand, and the USA (Jackson & Jaronski 2008, Ghayedi & Abdollahi 2013, Thongkaewyuan & Chairin 2018, Beys-da-Silva et al. 2020, Kim et al. 2020a, b) as an environmentally safe alternative to the use of chemical pesticides. Most of the initially identified *M. anisopliae* isolates may belong to any of the species in the *M. anisopliae* complex (Bischoff et al. 2009, Luangsa-ard et al. 2017, Chen et al. 2018a, c, Luz et al. 2019, Yamamoto et al. 2020) and the host range reported for *M. anisopliae* in the past may belong to one of the newly erected species. In this complex, only *M. acridum* was regarded as specific to locusts and grasshoppers (Vega et al. 2012). Later studies in Thailand have also showed *M. grillicidicola*, a species in the *M. anisopliae* complex, occurring on *Orthoptera* (Thanakitpipattana et al. 2020). Recent genome sequencing projects on *Metarhizium* tried to focus on host associations (Hu et al. 2014, Zhang et al. 2019) claiming some species are more host-specific than others. Correct identification of the species and its host-range, thus using the right species for biological control of agricultural pests is paramount to a successful biocontrol strategy.

The aims of this study were (1) to re-evaluate the concept of *Metarhizium*, its phylogenetic relationships and taxonomic stability among closely related clavicipitoid fungi, and (2) to evaluate what morphological and ecological characters could be used in the circumscription of the genus and (3) to identify and describe *Metarhizium* species from insects and soil, collected primarily in Thailand.

MATERIALS AND METHODS

Fungal materials and isolation

The entomogenous specimens in this study were collected from various national parks and community forests in Thailand. Forest floors, leaf litter, twigs, upper and underside of leaves were carefully inspected for the emergence from any attached or buried insects of brown, yellow or green coloured stromata. The specimens were picked up carefully in order not to damage the host, were stored in small plastic boxes before returning to the laboratory for isolation. The material was examined under a dissecting microscope (Olympus SZ61). The isolation from the sexual morph follows Luangsa-ard et al. (2018) with modifications: the fertile head of the stromata containing mature perithecia were placed on the potato dextrose agar plates (PDA; fresh diced potato 200 g/L, dextrose 20 g/L, agar 15 g/L). These were placed in a plastic box with moist tissue paper overnight to
create a humid chamber. The following morning, plates were examined with a dissecting microscope to examine the discharged ascospores. Discharged ascospores were transferred to fresh PDA plates.

Isolation from the asexual morph was done as described in Mongkolsamrit et al. (2018) with modifications: the conidia from sporulating structures were touched by using a flame-sterilized inoculation needle and streaked on PDA plates, then incubated in a plastic box at room temperature (RT) and examined regularly for germinated conidia. The germinated conidia were also transferred to fresh PDA plates. Pure cultures derived from sexual and asexual morphs were incubated at 25 °C under light/dark condition (L:D=14:10) and examined daily for fungal contaminants. Isolations with contaminants were sub-cultured to dark condition (L:D=14:10) and examined daily for fungal conidia. The geminated conidia were bated in a plastic box at room temperature (RT) and examined in a humid chamber. The following morning, plates were incubated, chloroform:isoamyl alcohol (24:1) was added and mixed by inverting the tube. Genomic DNA was precipitated by the addition of ice-cold isopropanol. The pellet was washed with 70 % ethanol and resuspended in 1× TE buffer.

The extracted DNA was preserved at ~20 °C and used as template for PCR amplifications. PCR amplifications for six loci of all strains including nuclear rDNA region encompassing the internal transcribed spacers 1 and 2 along with the 5.8S rDNA (ITS), nuclear ribosomal small and large subunits (SSU and LSU), the largest and second largest subunits of DNA-directed RNA polymerase II (rpb1 and rpb2), translation elongation factor 1-a (tef) and 5′-intron-rich region of elongation factor 1-α (5′tef) were performed in 25 mL reaction volumes consisting of 1× PCR buffer, 200 μM of each of the four dNTPs, 2.5 mM MgCl2, 1 U Taq DNA Polymerase, recombinant (Thermo Scientific, US), 0.5 μM of each primer and 50–100 ng DNA template. PCR primers used to amplify the gene regions for this study were: ITS5, ITS4 for ITS (White et al., 1990), LROR and LR5 for LSU (Vilgalys & Hester 1990, Rehner & Samuels 1994), EF1-983F and EF1-2218R for tef (Rehner & Buckley 2005), CRPB1 and RPB1Cr for rpb1 (Hall 2003, Castlebury et al., 2004), RPB2-5F2 and RPB2-7Cr for rpb2 (Liu et al. 1999, O’Donnell et al. 2007) and EF1T and EF2T for 5′tef (Bischoff et al. 2009). Thermocycler conditions for amplification of the DNA regions used in this study followed previously published protocols (Sung et al. 2007, Mongkolsamrit et al. 2019).

Morphological observations

The macro-morphological characters and relevant data of the fungus, such as the host, host location, colour and shape of the stromata, perithecial orientation (superficial, immersed, semi-immersed; ordinal or oblique) were examined under a dissecting microscope (Olympus SZ61). For micro-morphological characterization, perithecia, asci, ascospores, phialides and conidia were photographed with an Olympus DP70 Digital Camera mounted on an Olympus BX51 compound microscope. The reaction of the stroma obtained in this study with 3 % potassium hydroxide (KOH) was observed as a colour reaction.

Cultures were grown on oatmeal agar (OA, Difco), PDA and one quarter strength SDAY (SDAY/4, Difco) (Bischoff et al. 2009), incubated at 25 °C under light/dark conditions (L:D=14:10). Cultures were studied for comparison of important morphological characters such as shapes and sizes of conidia, phialides, colony growth and colouration. The colour of fresh specimens and cultures incubated on OA, PDA, and SDAY/4 was described and codified following the Online Auction Colour Chart and (abbreviated “oc” herein), Methuen handbook of colour (Kornerup & Wanscher 1963) and Naturalist’s Colour Guide (Smith 1975). The sporulation on three media were daily observed. Images of 2-wk-old cultures on three media were taken. Slow-growing species were allowed to grow longer until sporulation is observed for 20–30 d. Details of phialides and conidia were also described by illustrating structures with a Hitachi scanning electron microscope (Model SU8020).

DNA isolation, amplification and sequencing

Genomic DNA of Metarhizium was extracted using a modified CTAB protocol (Doyle 1987). Samples were prepared by grinding fresh mycelium with a pestle in CTAB buffer including polyvinyl pyrrolidone (PVP) to remove polyphenols (Maliyakal 1992). Ground mycelium was incubated at 65 °C for 30 min. After incubation, chloroform:isoamyl alcohol (24:1) was added and mixed by inverting the tube. Genomic DNA was precipitated by the addition of ice-cold isopropanol. The pellet was washed with 70 % ethanol and resuspended in 1× TE buffer.

The DNA sequences generated in this study were examined for ambiguous bases using BioEdit v. 7.2.3 (Hall 2004) and then submitted to GenBank. The ITS, SSU, LSU, tef, rpb1, rpb2 and 5′tef sequences obtained in this study and their accession numbers are shown in Table 1. Sequences of ITS, SSU, LSU, tef, rpb1, rpb2 and 5′tef from related species in previous studies were downloaded from GenBank to elucidate relationships in Clavicipitaceae (Table 1). ITS sequences were generated only for barcoding purposes and not included in the multi-gene analyses. The phylogenetic relationships among congeneric Metarhizium species and related genera within Clavicipitaceae were further studied using ITS, and a combined rpb1 and rpb2 dataset (Supplementary Figs 1 and 2). Each combined dataset was generated to discriminate closely related species and species-level identification in certain lineages for placement of the clavicipitaceous fungi. All datasets were aligned using MUSCLE v. 3.6 (Edgar 2004). Maximum parsimony analysis was conducted on the combined dataset using PAUP v. 4.0a166 (http://paup.phylosoftolutions.com, Swoford 2019), adopting random addition sequences (10 replications) with gaps treated as missing data. A bootstrap (MPBS) analysis was performed using the maximum parsimony criterion in 1 000 replications. Bayesian phylogenetic inference was performed using MrBayes v. 3.2.7a (Ronquist et al. 2012) with a general time reversible plus proportion invariant plus gamma (GTR+I+G) model of DNA substitution as the best fit model. This model was chosen as the result from a pre-test using MrModeltest v. 2.2 (Nylander 2004) which selected GTR+I+G as the best nucleotide substitution model. Four Markov chains were run from random starting trees for 3 M generations using sampled frequency of 1 000 generations and a burn-in of 10 % of the total run. Bayesian posterior probabilities (BPP) were calculated on the
| Species                  | Strains   | Locality   | Host                          | SSU          | LSU          | tef          | rpb1         | rpb2         | ITS          | 5'tef        | References                  |
|-------------------------|-----------|------------|-------------------------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|-----------------------------|
| Aschersonia badia       | BCC 8105  | Thailand   | Hemiptera: Scale insect       | DQ522537     | DQ518752     | DQ522317     | DQ522363     | DQ522411     | –            | –            | Spatafora et al. (2007)     |
| A. placenta             | BCC 7869  | Thailand   | Hemiptera: Scale insect       | EF469121     | EF469074     | EF469056     | EF469085     | EF469104     | –            | –            | Sung et al. (2007)          |
| Balsansa epichloe       | A.E.G. 96-15a | –          | Poaceae                       | –            | –            | –            | –            | –            | JN049848     | –            | Kepler et al. (2012a)       |
| B. henningsiana         | A.E.G.96-27a | –          | Poaceae: Panicum sp.         | AY545723     | AY545727     | AY489610     | AY489643     | DQ522413     | JN049815     | –            | Sung et al. (2007)          |
| GAM 16112               | –          | Poaceae: Panicum sp.         | –            | –            | –            | –            | –            | JN049815     | –            | Sung et al. (2007)          |
| B. pilutaeformis        | A.E.G. 94-2 | –          | Poaceae                       | AF543764     | AF543788     | DQ522319     | DQ522365     | DQ522414     | JN049816     | –            | Sung et al. (2007)          |
| Chamaeleomyces viridis  | CBS 348.65 | Madagascar | Chameleo lateralis            | –            | –            | –            | –            | –            | AY624197     | –            | Luangsara-ard et al. (2005) |
| CBS 659.71              | –          | Chameleo lateralis            | HO165673     | HO165735     | HO165692     | –            | HO165652     | HO165714     | –            | Luangsara-ard et al. (2017) |
| Claviceps fusiformis     | ATCC 26019 | –          | Poaceae                       | DQ522539     | U17402       | DQ522320     | DQ522366     | –            | –            | Sung et al. (2007)          |
| C. paspali              | ATCC 13892 | –          | Poaceae                       | U32401       | U47826       | DQ522321     | DQ522367     | DQ522416     | –            | Sung et al. (2007)          |
| C. purpurea             | SA sp11    | –          | Poaceae                       | EF469122     | EF469075     | EF469058     | EF469087     | EF469105     | –            | –            | Sung et al. (2007)          |
| Coniocladinea tenuis    | NHJ 6791   | Thailand   | Hemiptera: Scale insect       | –            | –            | –            | –            | –            | JN049863     | –            | Johnson et al. (2009)       |
| Cordyceps brittlebankoiides | G97025   | –          | –                             | –            | –            | –            | –            | –            | A309332      | –            | Liu et al. (2001)           |
| C. chlamydospora        | CBS 101244 | –          | Diplopora: Egg of slug        | DQ522544     | DQ518758     | DQ522327     | DQ522372     | DQ522424     | JN049821     | –            | Sung et al. (2007)          |
| C. cylindrica           | CBS 744.73 | Japan      | Acranthida: Spider            | EF468987     | EF468841     | EF468786     | EF468892     | –            | GU980041     | –            | Sung et al. (2007)          |
| C. fraticida            | TNS 19011  | –          | Fungi                         | JQ257022     | JQ257023     | JQ257028     | JQ257016     | JQ257021     | –            | Kepler et al. (2012b)       |
| C. gunnii               | G97011     | China      | –                             | –            | –            | –            | –            | –            | A243773      | –            | Chan et al. (2011)          |
| G97022                  | China      | –          | –                             | –            | –            | –            | –            | –            | A243773      | –            | Chan et al. (2011)          |
| Cordyceps sp.           | EFCC 2131  | Korea      | Lepidoptera                   | EF468977     | EF468833     | EF468770     | EF468876     | –            | JN049856     | –            | Sung et al. (2007)          |
| EFCC 2135               | Korea      | Lepidoptera                   | EF468979     | EF468834     | EF468769     | EF468877     | –            | –            | –            | Sung et al. (2007)          |
| GNJ020527-04            | China      | –          | –                             | –            | –            | –            | –            | –            | AY913757     | –            | Li et al. (2010)            |
| HMIGD0885               | –          | –          | –                             | –            | –            | –            | –            | –            | DQ150247     | –            | Zhang et al. (2004)         |
| BCC19475                | Thailand   | Lepidoptera                   | –            | –            | –            | –            | –            | –            | KY348781     | –            | Luangsara-ard et al. (2017) |
| BCC19950                | –          | Lepidoptera                   | GU979934     | GU979943     | GU979952     | GU979961     | GU979967     | –            | KY348780     | –            | Luangsara-ard et al. (2017) |
| BCC37521                | –          | Lepidoptera                   | GU979937     | GU979946     | GU979955     | GU979964     | GU979970     | –            | –            | Luangsara-ard et al. (2017) |
| Hypocrella schizostachyi| BCC 14123  | Thailand | Lepidoptera                   | DQ522557     | DQ518771     | DQ522346     | DQ522392     | DQ522447     | –            | –            | Sung et al. (2007)          |
| Hypocrella sp.          | GJS 89–104 | –          | Lepidoptera                   | –            | DQ518772     | DQ522347     | DQ522393     | DQ522448     | –            | –            | Spatafora et al. (2007)     |
| Isaria takamizusanensis | NBRC 110230 | Japan   | Hemiptera                     | –            | –            | –            | –            | –            | –            | –            | Ban et al. (2015)           |
| Keithomyces carneus     | CBS 158.69 | USA        | Soil                          | –            | –            | –            | –            | –            | MT078886     | This study                  |
| Keithomyces sp.         | CBS 126563 | Tanzania | Soil                          | MT078871     | MT078856     | MT078848     | MT078864     | MT078921     | MT078883     | This study                  |
| CBS 127407              | USA        | Soil                   | MT078873     | MT078858     | MT078850     | MT078866     | MT078923     | –            | –            | This study                  |
| Marquandomyces sp.      | CBS 127132 | USA        | Soil                          | MT078872     | MT078857     | MT078849     | MT078865     | MT078922     | MT078882     | This study                  |
### Table 1. (Continued).

| Species                      | Strains       | Locality     | Host                  | SSU       | LSU         | tef         | rpb1         | rpb2         | ITS          | 5’tef       | References                      |
|------------------------------|---------------|--------------|-----------------------|-----------|-------------|-------------|--------------|--------------|--------------|-------------|---------------------------------|
| Marquandomyces sp.           | CBS 129413    | USA          | Soil                  | MT078874  | MT078859    | MT078851    | MT078867     | –            | MT561567     | –           | This study                      |
| Metacordyceps atrovirens    | TNM-F10184    | Japan        | Coleoptera            | JF415950  | JF415966    | –           | JN049884     | JN049882     | –            | –           | Kepler et al. (2012a)           |
| Mc. brittlebankioides        | Hn1           | China        | Coleoptera            | –         | –           | AB778555    | AB778555     | –            | –            | –           | Nishi et al. (2015)             |
| Mc. indigotica              | TNS-F18553    | Japan        | Lepidoptera           | JF415953  | JF415968    | JF416010    | JN049868     | JN049876     | –            | –           | Kepler et al. (2012a)           |
| Mc. indigotica              | TNS-F18554    | Japan        | Lepidoptera           | JF415962  | JF415969    | JF416011    | JN049867     | JN049875     | –            | –           | Kepler et al. (2012a)           |
| Mc. khaoyaiensis            | BCC12687      | Thailand     | Lepidoptera larva     | –         | –           | –           | –            | JN049868     | –            | –           | Kepler et al. (2012a)           |
| Mc. kusanoensis             | BCC14290      | Thailand     | Lepidoptera larva     | JF415970  | –           | KJ398797    | JN049888     | JN049869     | –            | –           | Kepler et al. (2012a)           |
| Mc. liangshanensis          | EFCC 1452     | Korea        | Lepidoptera           | EF468962  | EF468815    | EF468756    | –            | –            | –            | –           | Sung et al. (2007)              |
| Mc. liangshanensis          | EFCC 1523     | Korea        | Lepidoptera           | EF468961  | EF468814    | EF468755    | –            | EF468918     | –            | –           | Sung et al. (2007)              |
| Mc. martialis               | EFCC 6863     | Korea        | Lepidoptera           | –         | JF415975    | JF416016    | JF415995     | –            | –            | –           | Luangsa-ard et al. (2017)       |
| Mc. martialis               | TM561567      | –            | –                     | –         | –           | JN049886    | –            | –            | –            | –           | Luangsa-ard et al. (2017)       |
| Mc. neogunnii               | BUM 415       | China        | Lepidoptera larva     | MH143845  | MH143828    | MH143861    | MH143876     | MH143891     | –            | –           | Chen et al. (2018b)             |
| Mc. owarianensis            | NRBC33258     | Japan        | Hemiptera             | HQ165669  | HQ165730    | HQ165689    | HQ165747     | –            | –            | –           | Luangsa-ard et al. (2017)       |
| Mc. pseudobreviformis       | TNSF-16380    | Japan        | Coleoptera            | –         | JF415977    | –           | JN049893     | JF415997     | JN049870     | –           | Kepler et al. (2012a)           |
| Mc. shibinensis             | GZUH SB13050311 | China    | Lepidoptera           | KR153588  | –           | KR153589    | KR153590     | –            | –            | –           | Wen et al. (2015)               |
| Metacordyceps sp.           | ARSEF 2038    | Korea        | Hemiptera: Delphacidae| –         | –           | –           | –            | –            | –            | –           | Kepler et al. (2014)            |
| Mc. shibinensis             | GZUH SB13050305 | China    | Lepidoptera larva     | KU729724  | KU729729    | KU729734    | –            | KU729735     | KU729736     | –           | Wen et al. (2017)               |
| SK 2014                     | India         | Hymenoptera  | –                     | –         | –           | –           | –            | –            | –            | –           | Sharma & Gautam (2015)          |
| Mc. taii                     | ARSEF 5714    | China        | Lepidoptera           | –         | –           | –           | –            | JN049829     | EU248856     | –           | Bischoff et al. (2009)          |
| Metapochonia bulbillosa     | CBS 145.70    | Denmark      | Picea abies           | AF339591  | AF339542    | AF68796     | AF687902     | AF686943     | AJ292410     | –           | Sung et al. (2007)              |
| Mp. bulbillosa              | CBS 464.88    | Scotland     | Nematode eggs         | AF339615  | AF339566    | AF68797     | AF68803      | AF686944     | AJ292400     | –           | Sung et al. (2007)              |
| CBS 891.72                  | Germany       | Fungi        | –                     | AF339599  | AF339550    | DO522354     | DO522401     | DO522458     | AJ292409     | –           | Sung et al. (2007)              |
| Metarhizium aciculare       | JCM 33284     | Japan        | Soil                  | LC435738  | LC435741    | LC462188    | –            | –            | –            | Iwasaki et al. (2019)          |
| JCM 33285                   | Japan         | Soil         | Orthoptera            | LC435739  | LC435742    | LC462189    | –            | –            | –            | Iwasaki et al. (2019)          |
| M. acidum                   | ARSEF 324     | Australia    | Orthoptera            | –         | –           | –           | –            | –            | –            | EU248844     | Bischoff et al. (2009)          |
| ARSEF 5748                  | Mexico        | Orthoptera   | –                     | –         | –           | –           | –            | –            | –            | EU248879     | Bischoff et al. (2009)          |
| ARSEF 7486                  | Niger         | Orthoptera   | –                     | –         | –           | EU248845    | EU248897     | EU248925     | HO231458     | EU248845     | Bischoff et al. (2009)          |
| M. album                    | ARSEF 1941    | Philippines  | Nephotettix virescens | –         | –           | –           | –            | –            | –            | AF137067     | Driver et al. (2000)            |
| ARSEF 1942                  | Philippines   | Nephotettix virescens | –         | –           | –           | –            | –            | –            | –            | HM05452      | –                         |
| ARSEF 2082                  | Indonesia     | Hymenoptera  | –                     | DO522560  | DO518775    | DO522352    | DO522398     | DO522452     | AY375446     | –           | Sung et al. (2007)              |
| Species          | Strains          | Locality       | Host          | SSU       | LSU       | tef         | rpb1       | rpb2       | ITS        | 5'tef    | References                  |
|------------------|------------------|----------------|---------------|-----------|-----------|-------------|------------|------------|------------|----------|----------------------------|
| M. anisopliae    | ARSEF 6347       | Colombia       | Homoptera     | –         | –         | –           | –          | –          | –          | –        | Mayerhofer et al. (2019)    |
|                  | ARSEF 7450       | Australia      | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | EU248852 Bischoff et al. (2009) |
|                  | ARSEF 7487       | Ethiopia       | Orthoptera    | –         | –         | –           | DQ469365   | DQ468370   | MH604974   | DQ463966 | Bischoff et al. (2009)       |
|                  | CG1233           | Brazil         | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | Lopes et al. (2013)          |
|                  | CG814            | Brazil         | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | Lopes et al. (2014)          |
|                  | IP86             | Brazil         | Soil          | –         | –         | –           | –          | –          | –          | –        | Rocha et al. (2013)          |
|                  | CBS 130.71       | Ukraine        | Avena sativa  | MT078868  | MT078853  | MT078845    | MT078861   | MT078918   | MT078844   | MT078928 | This study                   |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. argentinense  | CEP424           | Argentina      | Blaberidae: Epilamprinae | – | – | – | – | – | – | – | – | Gutierrez et al. (2019) |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. biotecense    | BCC31812T        | Thailand       | Hemiptera: Delphacidae | – | – | – | – | – | – | – | – | This study |
|                  | BCC31813         | Thailand       | Hemiptera: Delphacidae | MN781938 | MN781839 | MN781694 | MN781746  | MN781793  | MN781879  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. blattodeae    | MY08096          | Thailand       | Blattodea     | HQ165657  | HQ165719  | HQ165678   | HQ165638   | HQ165697   | –          | –        | Luangsas-ard et al. (2017)  |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
|                  | NHJ11597         | Thailand       | Blattodea     | –         | –         | –           | –          | –          | –          | –        | Luangsas-ard et al. (2017)  |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. brachyspermum | CM1              | Japan          | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | Yamamoto et al. (2020)       |
|                  | CM2              | Japan          | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | Yamamoto et al. (2020)       |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. brasiliense   | ARSEF 2948       | Brazil         | Hemiptera     | –         | –         | –           | KJ398809   | KJ398620   | –          | –        | Kepler et al. (2014)         |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. brunneum      | ARSEF 2107       | USA            | Coleoptera    | –         | –         | –           | –          | –          | –          | –        | Bischoff et al. (2009)       |
|                  | ARSEF 4152       | Australia      | Soil          | –         | –         | –           | –          | –          | –          | –        | Bischoff et al. (2009)       |
|                  | ARSEF 4179       | Australia      | Soil          | –         | –         | –           | –          | –          | –          | –        | Bischoff et al. (2009)       |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
|                  | CBS 316.51       | USA            | Coleoptera: Elateridae | MT078875 | MT078860  | MT078852   | –          | –          | –          | –        | MT078888 MT078927 This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. candelabrum   | BCC29224         | Thailand       | Hemiptera: leafhopper | MN781952 | MN781853  | MN781708   | MN781755   | MN781804  | MN781881  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. ceropidaruin  | BCC31660T        | Thailand       | Hemiptera: leafhopper | MN781953 | BCC31660  | MN781709   | MN781756   | MN781805  | MN781880  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. chayaphumense | BCC28241         | Thailand       | Hemiptera: Cicadidae | MN781932 | MN781832 | MN781684   | MN781740   | MN781784  | MN781884  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
|                  | BCC78198         | Thailand       | Hemiptera: Cicadidae | KX365996 | KX365953 | KX365989   | KX365993   | KX365994  | KX365995  | MT078881 | –  | Luangsas-ard et al. (2017)  |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. cicadas       | BCC48696         | Thailand       | Hemiptera: Cicadidae | MN781948 | MN781848 | MN781703   | –          | MN781800  | MN781885  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
|                  | BCC48881T        | Thailand       | Hemiptera: Cicadidae | MN781949 | MN781849 | MN781704   | MN781752   | MN781752  | –          | –        | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. clavatum      | BCC84543T        | Thailand       | Coleoptera larva | –         | –         | –           | MN781834   | MN781689   | MN781741  | MN781789  | MN781886 MT078929 This study |
|                  | BCC84558         | Thailand       | Coleoptera larva | –         | –         | –           | MN781835   | MN781690   | MN781742   | –        | –        | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. culicidarum   | BCC2673          | Thailand       | Diptera: Culicidae | MN781950 | MN781851 | MN781706   | MN781753   | MN781802  | MN781867  | –  | This study |
|                  | BCC7600T         | Thailand       | Diptera: Culicidae | MN781951 | MN781852 | MN781707   | MN781754   | MN781803  | MN781889  | –  | This study |
|                  | BCC7625          | Thailand       | Diptera: Culicidae | –         | –         | –           | MN781850   | MN781705   | MN781801  | MN781888  | –  | This study |
|                  |                  |                |               |           |           |             |            |            |            |          |                            |
| M. cylindrosporae| ARSEF 6926       | China          | Hemiptera: Cicadidae | –         | –         | –           | –          | –          | –          | –        | AF368270 – – | Kepler et al. (2012a) |
|                  | RCEF 3632        | China          | Hemiptera: Cicadidae | JF415964 | JF415987  | JF416022   | –          | –          | –          | JN049872 | –        | Kepler et al. (2012a)       |

**Table 1. (Continued).**
| Species               | Strains | Locality          | Host               | SSU       | LSU       | rpb1    | rpb2    | ITS        | 5'tef   | References                      |
|----------------------|---------|-------------------|--------------------|-----------|-----------|---------|---------|------------|---------|---------------------------------|
| *M. cylindrosporae*  | TNS-16371 | Japan             | Hemiptera: Cicadidae | JF415963  | JF415966 | JF416027 | JN049902 | –          | –       | –                               |
| *M. eburneum*        | BCC79252T | Thailand          | Lepidoptera pupa    | –         | MN781829  | MN781682 | MN781736 | MN781914   | –       | –                               |
|                      | BCC79267 | Thailand          | Lepidoptera pupa    | –         | MN781826  | MN781735 | MN781915 | –          | –       | This study                      |
| *M. ellipsoideum*    | BCC12847 | Thailand          | Hemiptera adult     | MN781859  | MN781860  | MN781715 | MN781761 | MN781810   | MN781925 | This study                      |
|                      | BCC49285T | Thailand         | Hemiptera adult     | MN781857  | MN781858  | MN781713 | MN781759 | MN781808   | MT078876 | This study                      |
|                      | BCC53509  | Thailand          | Hemiptera adult     | MN781858  | MN781859  | MN781714 | MN781760 | MN781809   | MT078877 | This study                      |
| *M. flavoviride*     | CBS 700.74 | USA               | –                  | –         | MT078870  | MT078855 | MT078847 | MT078863   | MT078920 | MT078925 |
|                      | ARSEF 2133 | Czech Republic   | Coleoptera         | –         | –         | –       | –       | –          | –       | Bischoff et al. (2006)         |
|                      | CBS 125.65 | USA               | –                  | –         | MT078869  | MT078854 | MT078846 | MT078862   | MT078919 | MT078885 |
|                      | CBS 218.56 | Czech Republic   | Coleoptera         | –         | –         | KJ398787 | KJ398598 | –          | –       | Kepler et al. (2014)           |
| *M. flavum*          | BCC90870T | Thailand          | Coleoptera larva   | MN781965  | MN781874  | MN781731 | MN781776 | MN781822   | –       | This study                      |
|                      | BCC90874  | Thailand          | Coleoptera larva   | MN781966  | MN781875  | MN781732 | MN781777 | MN781823   | –       | This study                      |
| *M. frigidum*        | ARSEF 4124 | Australia        | Coleoptera         | –         | –         | DQ464002 | DQ468361 | DQ468376   | NR132012 | Bischoff et al. (2006)         |
| *M. fusoides*        | BCC28246T | Thailand          | Lepidoptera        | MN781944  | MN781844  | MN781699 | MN781749 | MN781796   | MN781893 | This study                      |
|                      | BCC41242  | Thailand          | Psocoptera         | MN781942  | MN781825  | MN781679 | MN781780 | –          | –       | This study                      |
|                      | BCC53130  | Thailand          | Psocoptera         | MN781943  | MN781843  | MN781698 | –       | MN781795   | MN781894 | This study                      |
| *M. globosum*        | ARSEF 2596 | India             | Lepidoptera        | –         | –         | –       | –       | –          | –       | Bischoff et al. (2009)         |
| *M. granulomatis*    | UAMH 11028 | Denmark           | Chamaeleo calyptrus | HM635076  | HM195304  | KJ398781 | –       | –          | –       | Sigler et al. (2010)           |
|                      | UAMH 11176 | Denmark           | Chamaeleo calyptrus | HM635076  | HM195304  | KJ398781 | KJ398593 | –          | –       | Sigler et al. (2010)           |
| *M. gryllidicola*    | BCC22353  | Thailand          | Orthoptera: Gryllidae: adult cricket | – | – | – | – | – | MT078890 |
|                      | BCC37915  | Thailand          | Orthoptera: Gryllidae: adult cricket | – | – | – | – | – | MN781896 |
|                      | BCC37918  | Thailand          | Orthoptera: Gryllidae | MN781935  | MN781836  | MN781691 | MN781743 | MN781790   | MN781897 | Thanakhipatpattana et al. (2020) |
|                      | BCC53857  | Thailand          | Orthoptera: Gryllidae | – | – | – | – | – | MT078899 |
|                      | BCC82988  | Thailand          | Orthoptera: Gryllidae | MK632117  | MK632091  | MK632062 | MK632166 | MK632143   | –       | Thanakhipatpattana et al. (2020) |
| *M. guizhouense*     | ARSEF 4303 | Australia        | Soil               | –         | –         | –       | –       | –          | –       | Bischoff et al. (2009)         |
|                      | ARSEF 4321 | Australia        | Soil               | –         | –         | –       | –       | –          | –       | Bischoff et al. (2009)         |
|                      | ARSEF 6238 | China             | Lepidoptera        | –         | –         | EU248857 | EU248890 | EU248937   | –       | Bischoff et al. (2009)         |
|                      | CBS 258.90 | China             | Lepidoptera        | –         | –         | EU248862 | EU248914 | EU248942   | HQ314448 | EU248862 |
| *M. huainamdangense* | BCC23190 | Thailand          | Hemiptera: leafhopper | MN781954  | MN781855  | MN781710 | MN781757 | –          | MN781899 | This study                      |
|                      | BCC44270T | Thailand          | Hemiptera: leafhopper | MN781956  | MN781857  | MN781712 | MN781807 | MN781898   | –       | This study                      |
|                      | BCC77672  | Thailand          | Hemiptera: leafhopper | MN781955  | MN781856  | MN781711 | MN781758 | MN781806   | MN781901 | This study                      |
| *M. huflavi*         | IP46     | Brazil            | Soil               | –         | –         | MH837574 | MH837566 | MH837565   | –       | Luz et al. (2019)              |

(continued on next page)
| Species         | Strains     | Locality | Host          | SSU       | LSU       | tef     | rpb1    | rpb2    | ITS       | 5'tef    | References                  |
|-----------------|-------------|----------|---------------|-----------|-----------|---------|---------|---------|-----------|---------|-----------------------------|
| M. indicoticum  | NBRC 100684 | Japan    | Lepidoptera   | –         | –         | –       | –       | –       | –         | KJ398784 | Kepler et al. (2014)         |
| M. kalasinense  | BCC53581    | Thailand | Coleoptera    | –         | –         | –       | –       | –       | –         | KX823944 | Luangsara-ard et al. (2017) |
| M. khaoyaiense  | BCC3176     | Thailand | Coleoptera larva | KC011175  | KC011183 | KC011189 | –       | –       | –         | KX823945 | Luangsara-ard et al. (2017) |
| M. koreanum     | BCC27998    | Thailand | Hemiptera: Fulgoromorpha | MN781945  | MN781845 | MN781700 | –       | MN781797 | MN781903 | –         | This study                  |
| M. lepidiotae   | ARSEF 7412  | Australia | Coleoptera   | –         | –         | –       | –       | –       | –         | EU248864 | Bischoff et al. (2009)      |
| M. megapomponiae| ARSEF 2037  | Philippines | Hemiptera | AF339580  | AF339531 | DQ522353 | DQ522400 | DQ522454 | AF138271 | –         | Sung et al. (2007)          |
| M. minus        | ARSEF 1099  | Philippines | Hemiptera | –         | –         | –       | –       | –       | –         | KJ398979 | Kepler et al. (2014)        |
| M. niveum       | BCC524007   | Thailand | Hemiptera: Cicadidae | MN781933  | MN781832 | MN781685 | –       | MN781785 | MN781907 | –         | This study                  |
| M. normoi       | BCC19364    | Thailand | Lepidoptera larva | MN781940  | MN781841 | MN781696 | MN781747 | –       | MN781891 | –         | This study                  |
| M. novozealandicum| ARSEF 4661 | Australia | Soil         | –         | –         | –       | –       | –       | –         | KJ398811 | Kepler et al. (2014)        |
| M. ovoidosporum | BCC29223    | Thailand | Hemiptera: Cercopidae | MN781960  | MN781861 | MN781716 | MN781762 | –       | MN781909 | –         | This study                  |
| M. pemphigi     | ARSEF 6569  | United Kingdom | Hemiptera | –         | –         | KJ398813 | KJ398624 | DQ68378 | –         | –         | Kepler et al. (2014)        |
| M. phasmatodeae | BCC2841     | Thailand | Orthoptera: Phasmatodea | MN781931  | MN781828 | MN781681 | MN781738 | MN781782 | MN781911 | –         | Thanakitpipattana et al. 2020 |
| M. phuwiangense | BCC78206    | Thailand | Coleoptera adult | –         | –         | MN781719 | MN781765 | MN781812 | MN787887 | –         | This study                  |
| M. phuwiangense | BCC65068    | Thailand | Coleoptera adult | –         | –         | MN781864 | MN781720 | MN781766 | MN781813 | MN781912 | This study                  |
| Species            | Strains         | Locality       | Host               | SSU     | LSU      | tef     | rpb1    | rpb2    | ITS     | 5'tef | References                  |
|--------------------|-----------------|----------------|--------------------|---------|---------|---------|---------|---------|---------|------|-----------------------------|
| M. phuwiangense    | BCC85069T       | Thailand       | Coleoptera adult   | –       | MN781865| MN781721| MN781767| MN781814| MN781913| –     | This study                  |
| M. pingshaense     | ARSEF 3210      | India          | Coleoptera         | –       | –       | –       | –       | –       | –       | –    | DQ463995 Bischoff et al. (2006) |
| ARSEF 4342         | Solomon Islands | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | EU248851 Bischoff et al. (2009) |
| ARSEF 7929         | Australia       | Isoptera       | –                  | –       | –       | –       | –       | –       | –       | –    | EU248847 Bischoff et al. (2009) |
| CBS 257.90         | China           | Coleoptera     | –                  | –       | EU248850| EU248902| EU248930| HQ331450| EU248850| –    | Bischoff et al. (2009)       |
| M. prachinense     | BCC47950        | Thailand       | Lepidoptera        | KCO11172| KCO11180| KCO11186| KCO11184| KCO11185| KCO11177| –    | Luangsa-ard et al. (2017)    |
|                    |                 |                |                    |         |         |         |         |         |         |       |                              |
| M. purpureonigrum  | BCC89247T       | Thailand       | Coleoptera larva   | –       | MN781725| MN781771| MN781817| –       | –       | –    | Bischoff et al. (2009)       |
|                    | ARSEF 3210       | India          | Coleoptera         | –       | –       | –       | –       | –       | –       | –    | Bischoff et al. (2009)       |
| ARSEF 4342         | Solomon Islands | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | Bischoff et al. (2009)       |
| ARSEF 7929         | Australia       | Isoptera       | –                  | –       | –       | –       | –       | –       | –       | –    | Bischoff et al. (2009)       |
| CBS 257.90         | China           | Coleoptera     | –                  | EU248850| EU248902| EU248930| HQ331450| EU248850| –       | Bischoff et al. (2009)       |
| M. purpureum       | BCC89248        | Thailand       | Coleoptera larva   | MN781964| MN781870| MN781728| MN781816| MN781919| –       | –    | This study                  |
|                    | BCC89249        | Thailand       | Coleoptera larva   | MN781963| MN781869| MN781726| MN781772| MN781818| –       | –    | This study                  |
| M. robertsii       | ARSEF 6472      | USA            | Coleoptera         | –       | –       | –       | –       | –       | –       | –    | EU248884 Bischoff et al. (2009) |
|                    | ARSEF 727       | Brazil         | Orthoptera         | –       | –       | –       | –       | –       | –       | –    | DQ463994 Bischoff et al. (2009) |
| ARSEF 7501         | Australia       | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | Bischoff et al. (2009)       |
| ARSEF 2575         | USA             | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | EU248849 Bischoff et al. (2009) |
| ARSEF 4739         | Australia       | Coleoptera     | –                  | –       | –       | –       | –       | EU248848| EU248928| EU248848 Bischoff et al. (2009) |
| M. samlanense      | BCC17091        | Thailand       | Hemiptera adult    | HQ165665| HQ165727| HQ165686| HQ165727| HQ165846| HQ165707| –    | Luangsa-ard et al. (2017)    |
|                    | BCC39752        | Thailand       | Hemiptera adult    | MN781939| MN781840| MN781695| MN781794| MN781794| MN781918| –    | Luangsa-ard et al. (2017)    |
| Metapochonia sp.   | BUM3.5          | China          | Coleoptera         | –       | –       | –       | –       | –       | –       | –    | Chen et al. (2016c)          |
|                    | BUM263.4        | China          | Coleoptera         | –       | –       | –       | –       | –       | –       | –    | Chen et al. (2018a)          |
| CBS 64867          | France          | Coleoptera     | –                  | LC126075| LC125907| LC125923| –        | –       | –       | –    | Nishi et al. (2017)          |
| CTTCC M 2016588    | China           | Coleoptera     | –                  | LC126075| LC125907| LC125923| –        | –       | –       | –    | Nishi et al. (2017)          |
| CTTCC M 2016589    | China           | Coleoptera     | –                  | LC126075| LC125907| LC125923| –        | –       | –       | –    | Nishi et al. (2017)          |
| CEP414             | Argentina       | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | Chen et al. (2018a)          |
| CG1123             | Brazil          | Coleoptera     | –                  | –       | KY007614| KY007612| KY007613| –       | –       | –    | Lopes et al. (2018)          |
| GZAC-IFR1006       | China           | Coleoptera     | –                  | KT166031| KT961694| KT166032| –        | –       | –       | –    | Chen et al. (2017)          |
| MAFF 243305        | Japan           | Coleoptera     | –                  | AB700552| LC126078| LC125913| LC125920| –        | –       | –    | Nishi et al. (2017)          |
| MAFF 244762        | Japan           | Coleoptera     | –                  | LC126078| LC125911| LC125922| –        | –       | –       | –    | Nishi et al. (2017)          |
| NBRC 112661        | Japan           | Coleoptera     | –                  | LC126078| LC125908| LC125924| –        | –       | –       | –    | Nishi et al. (2017)          |
| RCEF 2001          | China           | Coleoptera     | –                  | –       | –       | –       | –       | –       | –       | –    | Li et al. (2010)             |

(continued on next page)
| Species                      | Strains          | Locality       | Host                      | SSU              | LSU              | tef         | rpb1        | rpb2        | ITS          | 5'tef       | References                  |
|------------------------------|------------------|----------------|---------------------------|------------------|------------------|-------------|-------------|-------------|--------------|-------------|----------------------------|
| *M. sulphureum*              | BCC36585         | Thailand       | Lepidoptera larva         | –                | –                | MN781686    | MN781766    | MN781786    | –            | MT078931    | This study                  |
| *M. takense*                 | BCC36599<sup>2</sup> | Thailand       | Lepidoptera larva         | –                | –                | MN781687    | MN781787    | –            | –            | –           | This study                  |
| *M. vinidulum*               | BCC39045         | Thailand       | Lepidoptera larva         | MK632120         | MK632095         | MK632066    | MK632147    | MK632037    | MT078930    | –           | This study                  |
| *M. takense*                 | BCC30934         | Thailand       | Hemiptera                | HQ165658         | HQ165720         | HQ165679    | HQ165740    | HQ165639    | HQ165698    | –           | Luangsaa-ard et al. (2017) |
| *M. takense*                 | BCC30939         | Thailand       | Hemiptera                | HQ165659         | HQ165721         | HQ165741    | HQ165640    | HQ165669    | –            | Luangsaa-ard et al. (2017) |
| *M. vinidulum*               | ARSEF 6927       | Taiwan         | Hemiptera                | –                | –                | KJ398815    | KJ398681    | –            | –            | –           | Kepler et al. (2014)        |
| *M. vinidulum*               | BCC36261         | Thailand       | Hemiptera: Cicadidae     | MN781930         | MN781827         | MN781680    | MN781737    | MN781781    | MT078878    | –           | This study                  |
| *Myriogenospora atramentosa* | A.E.G 96–32      | –              | Plant                     | AY489701         | AY489733         | AY489628    | AY489665    | DQ522455    | –            | –           | Sung et al. (2007)          |
| *Nomuraea rileyi*            | AF368501         | –              | –                         | –                | –                | –           | –           | –           | –            | –           | Driver et al. (2000)        |
| *CBS 806.71*                 | USA              | Trichoplusia ni | Tissue                    | AY526491         | –                | EF468787    | EF468893    | EF468937    | AY624205    | –           | Sung et al. (2007)          |
| *NRBC 8560*                  | Japan            | Lepidoptera     | Tissue                    | HQ165667         | HQ165729         | HQ165688    | –            | –           | AY647742    | –           | Luangsaa-ard et al. (2017) |
| *Paecilomyces carneus*       | CBS 239.32       | France         | Sand dune                 | EF468988         | EF468843         | EF468789    | EF468894    | EF468938    | AY624171    | –           | Spatafora et al. (2007)     |
| *CBS 399.59*                 | USA              | Soil           | Tissue                    | EF468989         | EF468842         | EF468788    | EF468895    | EF468939    | MT078887    | –           | Spatafora et al. (2007)     |
| *Pa. gunnii*                 | G845-19          | China          | Tissue                    | –                | –                | –           | –           | –           | –            | AY643943    | Chu et al. (2011)           |
| *Pa. ilicinus*               | CBS 284.36       | USA            | Soil                      | AY662475         | AY662427         | EF468792    | EF468898    | EF468941    | –            | –           | Sung et al. (2007)          |
| *Pa. marquandi*              | CBS 182.27       | USA            | Soil                      | EF468990         | EF468845         | EF468793    | EF468999    | EF468942    | AY624193    | –           | Sung et al. (2007)          |
| *Pa. reniformis*             | ARSEF 429        | Philippines    | Orthoptera: Tettigoniidae | HQ165671         | HQ165733         | HQ165690    | –            | HQ165650    | –            | Luangsaa-ard et al. (2017) |
| *IndGH96*                    | Philippines      | –              | Tissue                    | HQ165670         | HQ165732         | –            | –           | HQ165649    | –            | Luangsaa-ard et al. (2017) |
| *Petchia siamensis*          | BCC66420         | Thailand       | Ootheca of Mantidae       | MK632113         | MK632087         | MK632163    | MK632140    | –            | –           | Thanakitpipattana et al. (2020) |
| *BCC73637*                   | Thailand         | Ootheca of Mantidae | Tissue                  | MK632115         | MK632089         | MK632060    | MK632138    | –            | –           | Thanakitpipattana et al. (2020) |
| *Pochonia chloridaspore*     | CBS 504.66       | Canada         | Soil                      | AF339593         | AF339544         | AF469097    | AF469098    | AF469120    | AJ292398    | –           | Sung et al. (2007)          |
| *Purpureocillium lavendulum* | FMR 10376        | Venezuela      | Soil                      | –                | FR775489         | FR775516    | FR775512    | –            | –           | Perdomo et al. (2017)       |
| *Pur. ilicinus*              | CBS 431.87       | Philippines    | Meloidogyne sp.           | –                | –                | –           | –           | –           | HQ842812    | –           | Luangsaa-ard et al (2011)   |
| *Pur. takamiaconense*        | NHJ 3582         | Thailand       | Hemiptera: Cicadidae      | EU369097         | EU369034         | EU369015    | –            | –           | –           | Johnson et al. (2009)       |
| *Purpureomyces maesotensis*  | BCC88441         | Thailand       | Lepidoptera larva         | –                | –                | MN781877    | MN781734    | MN781779    | MN781824    | MN781916    | This study                  |
| *P. pyriformis*              | BCC89300<sup>2</sup> | Thailand       | Lepidoptera larva         | –                | –                | MN781876    | MN781733    | MN781776    | –            | MN781917    | This study                  |
| *P. pyriformis*              | BCC85047<sup>3</sup> | Thailand       | Lepidoptera larva         | –                | –                | MN781873    | MN781730    | MN781775    | MN781821    | MN781929    | This study                  |
| *P. pyriformis*              | BCC85348         | Thailand       | Lepidoptera larva         | –                | –                | MN781781    | MN781728    | MN781773    | MN781820    | MN781927    | This study                  |
| *P. pyriformis*              | BCC85349         | Thailand       | Lepidoptera larva         | –                | –                | MN781872    | MN781729    | MN781774    | –            | MN781928    | This study                  |
| *Regiocrella camerunensis*   | ARSEF 7682       | –              | Hemiptera                 | –                | –                | DQ118735    | DQ118743    | DQ127234    | –            | –           | Chavert et al. (2005)       |
| *Rotiferophthora angustispora* | CBS 101437     | –              | Bdelloid rotifers         | AF339584         | AF339535         | AF543776    | DQ522402    | DQ522460    | AJ292412    | –           | Sung et al. (2007)          |
| *Shimizuiomyces paradoxus*   | EFC 6279         | Korea          | Smilax sieboldii         | EF469131         | EF469084         | EF469071    | EF469100    | EF469117    | JN049647    | –           | Sung et al. (2007)          |

<sup>1</sup> This study
<sup>2</sup> Luangsaa-ard et al. (2017)
<sup>3</sup> Sung et al. (2007)
RESULTS

Molecular phylogeny

We generated 135 ITS, 43 SSU, 61 tef, 49 rpb1, 49 rpb2 and 12 5’tef sequences in this study from 62 living cultures (Table 1). The combined dataset of 173 taxa with concatenated multilocus sequences totalling 4,226 bp (SSU 1,014 bp, LSU 856 bp, tef 895 bp, rpb1 667 bp and rpb2 794 bp) provided 4,302 characters in the combined alignment where 2,729 were constant and 1,280 were parsimony-informative. Sequences of the genus Purpureocillium in the Ophiocordycipitaceae were used as outgroup. The maximum parsimony analyses resulted in a single most parsimonious tree which is shown in Fig. 1 (tree length, 9,736 steps; CI, 0.258; RI, 0.684; RC, 0.177; HI, 0.742). The result of MrModeltest selected the General Time Reversible (GTR) model with proportion in invariable sites (I) and gamma distribution (G) (GTR+I+G; Lanave et al. 1984) as the best-fit model by AIC in MrModeltest v. 2.2. A = 0.2216, C = 0.2876, G = 0.2744, T = 0.2164 and the rate matrix for the substitution model: [A-C] = 1.0968, [A-G] = 4.4130, [A-T] = 1.1698, [C-G] = 0.8387, [C-T] = 7.3758, [G-T] = 1.0000. For the among-site variation the proportion of invariable sites (I) was 0.5552, and the gamma distribution shape parameter was 0.6802. This model was used in MrBayes on XSEDE v. 3.2.7a and RAxML v. 8.2.12. Bayesian analyses resulted in 2,000 “burn-in” trees; the consensus of the remaining 10,000 trees resulted in identical topology (−lnL 52275.3594) as the Maximum Parsimony tree. For the ML analysis in RAxML (Stamatakis 2014), the GTRCAT model was used for the nucleotide partitions and the default setting for binary (indel) data was chosen. Phylogenetic analyses based on a combined dataset comprising SSU, LSU, tef, rpb1 and rpb2 strongly support 19 new Metarhizium species in the core Metarhizium clade (sensu Kepler et al. 2014) as a monophyletic clade with moderate support (MPBS 77 %, BPP 60 %, MLBS < 70 %). Two new species clustered with M. khaoyaiense outside the core Metarhizium clade and these species are accommodated in the new genus Purpureomyces. New combinations are proposed for Metarhizium aciculare, M. carneum and Metacordyceps neogunnii in Keithomyces, M. kusangajense in Yosiokobayasia, Metacordyceps liangshanensis and Metacordyceps shibinensis in Papiliomyces, M. marquandii in Marquandomyces and M. yongmunense in Sungia; including some genera which formed independent groups and are designated as new genera.

Phylogeny of species in Metarhizium anisopliae complex

The concatenated alignment of 5’tef included 50 taxa, with 716 bp providing 740 characters in the alignment where 554 were constant and 27 were parsimony-uninformative. For the Bayesian inference, the HKY+I model was selected as the best-
Fig. 1. Phylogenetic reconstruction of Metarhizium and related genera in the Clavicipitaceae obtained from the combined SSU, LSU, tef, rpb1 and rpb2 sequences based on Maximum Parsimony, Bayesian analysis and RAxML. Numbers on the nodes are MP bootstrap / Bayesian posterior probability / ML bootstrap values above 70% (MPBS-MLBS) or 0.7 (BPP). Thickened lines mean support for the three analyses was 100% (MPBS-MLBS) or 1.0 (BPP).
fit model by AIC in MrModeltest v. 2.2. A = 0.2234, C = 0.2612, G = 0.2384, T = 0.2770 and the rate matrix for the substitution model: Ti/tv ratio = 2.1669. For the ML analysis in RAxML v. 8.2.12, the GTRCAT model was used for the nucleotide partitions and the default setting was chosen.

Seventeen species had available 5′tef sequences and were included in analyses of the *M. anisopliae* species complex. *Metarhizium flavoviride* is used as the outgroup taxon. Based on our analyses, it is apparent that morphological characters are not reliable to delineate species in this group. The type of *M. lepidiotae* (ARSEF 7488) did not group with other ARSEF strains identified as such, but grouped with CBS 130.71, a *M. anisopliae* strain from Ukraine. *Metarhizium sulphureum* nested with strains of *M. guizhouenze*.

**TAXONOMIC REVISION**

The present analyses using MP, Bayesian and RAxML analyses gave similar topologies and agreed with one another, except for some of the branches where there is no support from either MP or RAxML. The multi-gene analyses identified a *Metarhizium* clade (77% support on the branch) that is partly similar to previous studies (Fig. 1). Several clades comprising the *Metarhizium anisopliae* species complex, members of the *Metarhizium flavoviride* species complex, on cicada, nomuraea-like clade and a clade occurring on small plant hoppers are all well-supported. The *M. anisopliae* and *M. flavoviride* species complexes both produce a candelabrum-like arrangement of the phialides from compact conidiophores that form a hymenial layer and occasionally having conidia adhering laterally to form prismatic columns, as in some species of *Aspergillus*. Species in these clades belong to *Metarhizium* s. str. The remaining basal clades constitute other well-supported clades but only in their terminal branches. What we identify as the *Metarhizium* clade includes green-spored species that correspond with Kepler et al.'s core *Metarhizium D Clade* (2014). These clades include species that produce nomuraea-like and paecilomyces-like asexual morphs. The taxonomic relationships at the base of the tree comprising *Metarhizium sensu* Kepler et al. (2014), despite the extensive taxon sampling is still poorly resolved. While the current classification of *Metarhizium* is based on multi-gene phylogenetic analyses and should only reflect relationships based on monophyletic clades, the inclusion of species outside the *Metarhizium* branch remains doubtful as the morphological characters of the species subtending this group do not reflect in any way our present understanding of *Metarhizium*. *Pochonia* and *Rotiferophthora* belong to a clade subtending *Metarhizium* while species previously belonging to the basal clades in *Metarhizium sensu* Kepler et al. (2014) are now in a clade which is also subtended by *Metapochonia* and is basal to the *Pochonia-Rotiferophthora* and *Metarhizium* clades. This clade comprises the six new genera proposed in this study (Fig. 1).
Fig. 2. Phylogenetic reconstruction of *Metarhizium* anisopliae species complex 5′ef sequences based on Maximum Parsimony, Bayesian analysis and RAxML. Number on the nodes are MP bootstrap / Bayesian posterior probability / ML bootstrap values above 70% (MPBS-MLBS) or 0.7 (BPP). Thickened lines mean support for the three analyses was 100% (MPBS-MLBS) or 1.0 (BPP).
Six new genera (Keithomyces, Marquandomyces, Papiliomyces, Purpureomyces, Sungia, Yosiokobayasia) and twenty-one new species are described in this study, nineteen in *Metarhizium* and two in *Purpureomyces*. Three species are combined in *Keithomyces*, two in *Papiliomyces*, and one each in *Marquandomyces*, *Purpureomyces*, *Sungia* and *Yosiokobayasia*.

**TAXONOMY**

Fig. 3. Keithomyces carneus. Colonies after 14 d. A–B. CBS 239.32. A. On MEA. B. On OA. C–D. CBS 339.59. C. On MEA. D. On OA. E–G. Conidiophores and conidia on MEA. H–J. Conidiophores and conidia on OA. Scale bars = 10 μm.
Keithomyces Samson, Luangsa-ard & Houbraken, gen. nov. MycoBank MB834876.

Etymology: Named after Dr Keith A. Seifert, in recognition for his contributions to our knowledge of asexually reproducing fungi.

Description: Asexual morph paecilomyces-like, producing conidiophores with divergent whorls of 2–4 phialides; conidia echinulate to aciculate, in chains.

Type species: Keithomyces carneus (Duché & R. Heim) Samson, Luangsa-ard & Houbraken

Fig. 4. Marquandomyces marquandii. Colonies after 14 d A–B, CBS 182.27. A. On MEA. B. On OA. C–D. CBS 282.53. C. On MEA. D. On OA. E–G. Conidiophores and conidia on MEA. H–J. Conidiophores and conidia on OA. Scale bars = 10 μm.
| Species               | Substrate                        | Countries found                                                                 | References                                      |
|----------------------|----------------------------------|----------------------------------------------------------------------------------|------------------------------------------------|
| **Metarhizium acridum** | Orthoptera: Acrididae, Pygromorphidae | Australia, Benin, Chad, Guinea-Bissau, Madagascar, Mali, Mexico, Niger, Senegal, Tanzania, Thailand, USA | Driver et al. (2000), Bischoff et al. (2009), Database of ARSEF |
| M. album              | Hemiptera: Cicadellidae          | Indonesia, Philippines                                                            | Petch (1931), Database of ARSEF                |
| M. alvesii            | Soil                             | Brazil                                                                           | Lopes et al. (2018)                             |
| M. anisopliae         | Coleoptera: Chrysomelidae, Curculionidae, Elateridae, Scarabaeidae, Diptera: Stratiomyidae, Hemiptera: Pentatomidae, Cercopidae, Cicadellidae, Delphacidae, Lepidoptera: Noctuidae, Pyralidae, Orthoptera: Acrididae, Grylloidae, Isoptera: Mastotermitidae, Rhinotermitidae, Termitidae, Soil | Brazil, Colombia, Ethiopia, France, India, Indonesia, Japan, Moldova, Myanmar, New Zealand, Papua, New Guinea, Philippines, USA, Western Samoa | Bischoff et al. (2009), Database of ARSEF |
| M. argentinense       | Blattodea: Blaberidae (Epilampra sp.) | Argentina                                                                        | Gutierrez et al. (2019)                         |
| M. atrovirens         | Coleoptera larva                 | Japan                                                                            | Koyabasi & Shimizu (1978), Kepler et al. (2014) |
| M. baoshanense        | Soil                             | China                                                                            | Chen et al. (2018a)                             |
| M. bibionidarum       | Diptera: Bibionidae, Coleoptera: Scarabaeidae, Soil | Japan, France                                                                    | Nishi et al. (2017)                             |
| M. biotecense         | Hemiptera: Delphacidae           | Thailand                                                                         | This study                                      |
| M. blattodeae         | Blattodea (Cockroach)            | Brazil, Thailand                                                                 | Montalva et al. (2016), This study              |
| M. brachyspermum      | Coleoptera (Elaterid larva)      | Japan                                                                            | Yamamoto et al. (2020)                          |
| M. brasiliense        | Hemiptera: Cicadellidae          | Brazil                                                                           | Kepler et al. (2014)                            |
| M. brittlebankiosoides| Coleoptera: Scarabaeida          | China, Japan                                                                     | Liu et al. (2001), Kepler et al. (2014), Gutierrez et al. (2019) |
| M. brunneum           | Acari: Ixodidae, Araneida, Coleoptera: Cerambycidae, Curculionidae, Elateridae, Scarabaeidae, Tenebrionidae, Diptera: Culicidae, Hemiptera: Delphacidae, Hymenoptera: Formicidae, Isoptera: Rhinotermitidae, Termitidae, Lepidoptera: Bombycidae, Hepialidae, Lyonellidae, Noctuidae, Pyralidae, Tortricidae, Orthoptera: Acrididae, Soil | Argentina, Australia, Austria, Canada, Denmark, Finland, France, Germany, Indonesia, Italy, Japan, Mexico, Myanmar, New Zealand, Norway, Philippines, Portugal, Republic of Georgia, Switzerland, Turkey, UK, USA | Bischoff et al. (2009), Database of ARSEF |
| M. candelabrum         | Hemiptera (Leafhopper)           | Thailand                                                                         | This study                                      |
| M. campospermi        | Coleoptera: Scarabaeida          | China                                                                            | Zhang et al. (2004), Kepler et al. (2014)       |
| M. cercopidaran       | Hemiptera: Cercopidae            | Thailand                                                                         | This study                                      |
| M. chaigaphumense     | Hemiptera: Cicadidae (Cicada nymph) | Thailand                                                                        | Luangsa-ard et al. (2017)                       |
| M. ciliacea           | Hemiptera: Cicadidae             | Thailand                                                                         | This study                                      |
| M. clavatum           | Coleoptera (Larva of Oxynopterus sp.) | Thailand                                                                        | This study                                      |
| M. culicidaran        | Diptera: Culicidae               | Thailand                                                                         | This study                                      |
| M. cylindrosorum      | Hemiptera: Cicadidae (Adult cicada) | China, Japan, Taiwan                                                             | Guo et al. (1986), Tzean et al. (1993), Kepler et al. (2014), Database of ARSEF |
| M. dendrolimatis      | Lepidoptera (Dendrolimus sp.)    | China                                                                            | Chen et al. (2017)                              |
| M. eburneum           | Lepidoptera pupa                 | Thailand                                                                         | This study                                      |
| M. ellipsoideum       | Hemiptera (Leafhopper)           | Thailand                                                                         | This study                                      |

(continued on next page)
| Species          | Substrate | Countries found                                      | References                                      |
|------------------|-----------|-----------------------------------------------------|------------------------------------------------|
| *M. flavoviride* | Coleoptera: Curculionidae,Scarabaeidae, Orthoptera: Acrididae, Soil | Australia, Czech Republic, France, Germany, Malaysia, Netherlands | Gams & Rozsypal (1973), Database of ARSEF |
| *M. flavum*      | Coleoptera larva | Thailand | This study |
| *M. frigidum*    | Coleoptera: Scarabaeidae, Isoptera: Rhinotermitidae, Soil | Australia | Bischoff et al. (2009), Database of ARSEF |
| *M. fusoidum*    | Lepidoptera, Psocoptera | Thailand | This study |
| *M. gaoligongense* | Soil | China | Chen et al. (2018b) |
| *M. globosum*    | Lepidoptera: Pyralidae | India | Bischoff et al. (2009), Database of ARSEF |
| *M. granulomatis* | Chameleo calyptratus | Denmark | Sigler et al. (2010), Kepler et al. (2014) |
| *M. gryllidicola* | Orthoptera: Gryllidae (Cricket adult) | Thailand | Thanakitpipattana et al. (2020) |
| *M. guizhouense* | Lepidoptera | Thailand | Li et al. (2010) |
| *M. humberi*     | Coleoptera, Lepidoptera, Hemiptera, Soil | Brazil, Mexico | Luz et al. (2019) |
| *M. indigolicum* | Lepidoptera larva (Cossidae) | Japan | Kobayasi & Shimizu (1978), Kepler et al. (2012a, 2014) |
| *M. kalasinense* | Coleoptera larva | Thailand | Luangsra-ard et al. (2017) |
| *M. koreanum*    | Hemiptera: Delphacidae, Fulgoromorpha, Tropiduchidae | Japan, South Korea, Thailand | Kepler et al. (2014), Nishi & Sato (2017), This study |
| *M. lepidiotae*  | Coleoptera: Scarabaeidae, Isoptera: Rhinotermitidae, Soil | Australia, Japan, Papua New Guinea | Driver et al. (2000), Bischoff et al. (2009), Database of ARSEF |
| *M. majus*       | Coleoptera: Scarabaeidae, Lepidoptera: Bombycidae, Noctuidae, Soil | Australia, France, Indonesia, Japan, Malaysia, Philippines, Poland, Western Samoa | Bischoff et al. (2009), Database of ARSEF |
| *M. megapomponiae* | Hemiptera: Megapomponia | Thailand | This study |
| *M. minus*       | Hemiptera: Cicadellidae, Delphacidae, Pentatomidae, Orthoptera: Acrididae | Benin, Ecuador, Philippines, Solomon Islands, Thailand | Driver et al. (2000), Kepler et al. (2014), Database of ARSEF, This study |
| *M. niveum*      | Hemiptera: Cicadidae (Cicada adult) | Thailand | This study |
| *M. normosoi*    | Lepidoptera larva, Coleoptera adult | Thailand | This study |
| *M. novozealandicum* | Coleoptera, Lepidoptera, Soil | Australia, New Zealand | Driver et al. (2000), Kepler et al. (2014), Database of ARSEF |
| *M. ovoidosporum* | Hemiptera: Cercopidae, Eurybrachidae | Thailand | This study |
| *M. owariense*   | Hemiptera: Cicadidae | Japan | Kobayasi (1939), Kepler et al. (2014) |
| *M. pemphigii*   | Hemiptera: Aphididae, Isoptera: Rhinotermitidae, Soil | Canada, China, Georgia, Japan, UK | Guo et al. (1986), Kepler et al. (2014), Database of ARSEF |
| *M. phasmatoidea* | Orthoptera: Phasmatoidea | Thailand | Thanakitpipattana et al. (2020) |
| *M. phuwiangense* | Coleoptera adult | Thailand | This study |
| *M. pingshaense* | Coleoptera: Cerambycidae, Chrysomelidae, Curculionidae, Scarabaeidae, Diptera: Stratiomyidae, Hemiptera: Coccidae, Cydnidae, Delphacidae, Pentatomidae, Pseudococcidae, Isoptera: Kalotermitidae, Rhinotermitidae, Termesidae, Lepidoptera: Noctuidae, Orthoptera: Gryllidae, Soil | Australia, Brazil, China, Colombia, India, Indonesia, Japan, Myanmar, New Zealand, Oman, Pakistan, Papua New Guinea, Philippines, Solomon Islands, Thailand | Guo et al. (1986), Bischoff et al. (2009), Database of ARSEF |
| *M. prachinense* | Lepidoptera larva | Thailand | Luangsra-ard et al. (2017) |
| *M. pseudocatrinires* | Coleoptera larva | Japan | Kobayasi & Shimizu (1982), Kepler et al. (2012a, 2014) |
in contrast to the pink-shaded conidia of

2 = The phialides are globose with a long cylindrical neck but is not tapering.

1 = Sexual morph found in nature.

or borne directly on stalk. Phialides consisting of a globose basal portion and a distinct thin neck, conidia in chains.

indiscernible neck; conidia in dry basipetal chains. Paecilomyces-like: Conidiophores mononematous, verticillate, bearing short branches with whorls of two to four phialides

aciculate conidia.

Notes

De Eurotiales

Entomopathogenic Fungal Cultures (ARSEF). U.S. Department of Agriculture, Agricultural Research Service. https://doi.org/10.15482/USDA.ADC/1326695. Accessed

Database of ARSEF: U.S. Department of Agriculture, Agricultural Research Service, Biological Integrated Pest Management Research Unit. (2016). ARS Collection of

Entomopathogenic Fungal Cultures (ARSEF). U.S. Department of Agriculture, Agricultural Research Service. https://doi.org/10.15482/USDA.ADC/1326695. Accessed

2019-12-12.

Table 2. (Continued).

| Species                      | Substrate          | Countries found    | References             |
|------------------------------|--------------------|--------------------|------------------------|
| M. purpureogenum            | Soil               | Japan              | Nishi et al. (2017)    |
| M. purpureonigrum           | Coleoptera larva   | Thailand           | This study             |
| M. purpureum                | Coleoptera (Oxyopterus sp.) | Thailand           | This study             |
| M. reniforme                | Orthoptera: Tettigoniidae | Ghana, Indonesia, Philippines, USA | Kalkar et al. (2006) |
| M. rileyi                   | Hemiptera: Cercopidae, Delphacidae, Lepidoptera: Bombycidae, Lymantriidae, Noctuidae, Pyralidae | Argentina, Australia, Brazil, China, France, India, Indonesia, Japan, Mexico, Palestine, Philippines, Russian Federation, Solomon Islands, Thailand, USA | Samson (1974), Database of ARSEF |
| M. robertii                 | Coleoptera: Carabidae, Cerambycidae, Chrysomelidae, Curculionidae, Elateridae, Scarabaeidae, Tenebrionidae, Hemiptera: Cicadidae, Cydnidae, Hymenoptera: Formicidae, Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae, Lepidoptera: Nymphalidae, Plutellidae, Pyralidae, Orthoptera: Tettigoniidae, Sol | Argentina, Australia, Brazil, Canada, Colombia, Germany, Italy, Japan, Mexico, Myanmar, Norway, Portugal, Republic of Georgia, Romania, USA | Bischoff et al. (2009), Kepler et al. (2014), Database of ARSEF |
| M. samlanense               | Hemiptera: Cicadellidae | Thailand           | Luangs-a-ard et al. (2017) |
| M. sulphureum               | Lepidoptera larva   | Thailand           | This study             |
| M. takense                  | Hemiptera: Cicadidae (Cicada nymph) | Thailand           | Luangs-a-ard et al. (2017) |
| M. viride                   | Chameleoidea lateralis | Madagascar        | Samson (1974), Kepler et al. (2014) |
| M. viridulum                | Hemiptera: Cicadidae (Cryptotympana facialis adult) | Taiwan, Thailand | Tzean et al. (1992), Kepler et al. (2014) |

Table 3. Phialide characteristics of asexual morphs in Metarhizium.

| Phialide morphology | Species |
|---------------------|---------|
| Metarhizium-like    | M. acridum, M. album, M. alvesii, M. anisopliae, M. argentinense, M. baoshanense, M. bivionidurum, M. biotecense, M. blattodeae, M. brachyspermum1, M. brasilisense, M. brittlebanksisoides1, M. bruneum, M. candelabrum, M. campsoidei1, M. cercopidae, M. clavatum1, M. cilicidianum1, M. ellipsoidum, M. flavoviridi1, M. flavum, M. frigidum, M. fuscidium, M. gaojiangense, M. globosum, M. gryllicola, M. guizhouense1, M. gunjinjapense1, M. huanamdangense, M. humberi, M. indigocitum1, M. kalasinense1, M. koreanum, M. lepidiaceae, M. majus, M. minus, M. nomoi, M. novozealandicum, M. pemphi, M. phasmatodeae, M. pingshaense, M. purpureogenum, M. purpureonigrum1, M. purpureum1, M. robertii, M. sulphureum1 |
| Nomuraea-like        | M. chayaphumense1, M. cicadae, M. cylindrosporum, M. dendrolmatilis, M. megapomponiae, M. niveum, M. ovoidosporum, M. owaniense1, M. prachinensi1, M. rileyi, M. samalense, M. takense1, M. viridulum |
| Paecilomyces-like    | M. granulomatis, M. phuwiangense1,2, M. reniforme, M. viride |
| Unknown              | M. atrovirens2, M. eburneum1, M. pseudoatrovirens1 |

Definitions: Metarhizium-like: Candelabrum-like arrangement of phialides from compact conidiophores that form a hymenial layer; conidia ovoid, cylindrical, or globose, which often aggregate into prismatic columns. Nomuraea-like: Conidiophores mono- or symnematous, phialides in whorls, oval-cylindrical with very short or almost indiscernible neck; conidia in dry basipetal chains. Paecilomyces-like: Conidiophores mononematous, verticillate, bearing short branches with whorls of two to four phialides or borne directly on stalk. Phialides consisting of a globose basal portion and a distinct thin neck, conidia in chains.

1 = Sexual morph found in nature.  
2 = The phialides are globose with a long cylindrical neck but is not tapering.

Notes: This genus comprises species isolated mainly from soil and produce paecilomyces-like asexual morphs and echinulate or aciculate conidia. Paecilomyces sensu stricto is classified in the Eurotiales. Metarhizium produces green or brown coloured conidia in contrast to the pink-shaded conidia of Keithomyces.

Keithomyces carneus (Duché & R. Heim) Samson, Luangsa-ard & Houbraken, comb. nov. MycoBank MB834877. Fig. 3. Basisynym: Spicaria carneus Duché & R. Heim, Recl. Trav. Cryptogam. Dédies à Louis Mangin: 454. 1931. Synonyms: Paecilomyces carneus (Duché & R. Heim) A.H.S. Br. & G. Sm., Trans. Br. Mycol. Soc. 40: 70.1957.
| Species             | Stromata                                                                 | Perithecia (μm)                                                                 | Asci (μm)                  | Ascospores (μm)                                      | Asexual morph                           |
|---------------------|----------------------------------------------------------------------------|--------------------------------------------------------------------------------|----------------------------|-----------------------------------------------------|------------------------------------------|
| *Metarhizium atrovirens* | Multiple, cylindrical to clavate, 20–50 mm long                          | Obliquely immersed, ovoid, 475–550 × 240–250                                    | 210–250 × 3.5             | Lanceolate with tapering ends, 50–52 × 2.5–3         | Unknown                                  |
| M. brachyspermum     | Single or multiple, clavate, pale green to olive green, up to 30 mm long | Obliquely immersed, flask-shaped, 500–795 × 190–300                             | Cylindrical, 230–400 × 2.5–4.5 | Filiform, 190–270 × 1                               | Metarhizium-like                         |
| M. brittlebankiosoides | Multiple, cylindrical, pale green, 100 mm long                          | Ordinarily immersed, flask-shaped, 406–531 × 170–200                            | Cylindrical, 188–313 × 3–3.2 | Part-spores, 5.7–8.1 × 0.94                         | Metarhizium-like                         |
| M. campossterni      | Simple, cylindrical, greenish yellow, 160 mm long                        | Ordinarily immersed, pyriform, obovoid, 275–433 × 165–276                      | Lanceolate with tapering | Metarhizium-like                                     | Metarhizium-like                         |
| M. chalayphumense    | Solitary, cylindrical, simple, or 2–3 branched, greyish yellow, 30–35 mm long | Obliquely immersed, ovoid to obpyriform, 550–870 × 320–380                      | Cylindrical, 520–650 × 3–4 | Filiform, 225–375 × 1                               | Metarhizium-like                         |
| M. clavatum          | Single or multiple, cylindrical to clavate, yellow to greyish green, 35 mm long | Obliquely immersed, flask-shaped, 600–700 × 210–290                             | Cylindrical, up to 420 × 5–6 | Filiform, 224–420 × 1–1.5                           | Metarhizium-like                         |
| M. eburneum          | Solitary, cylindrical, white to creamy, 10 mm long                      | Ordinarily semi-immersed, ovoid to obclavate, 603–640 × 275–300                 | Cylindrical, 235–462.5 × 2–3 | Filiform, 222.5–360 × 1                             | Unknown                                  |
| M. flavum            | Simple, multiple, clavate, pale yellow to olive yellow, up to 45 mm long | Ordinarily semi-immersed, ovoid, 500–650 × 270–330                              | Cylindrical, 280–320 × 5–6 | Filiform, 200–315 × 1–1.5                           | Metarhizium-like                         |
| M. guizhouense (M. tai) | Cylindrical, tapering, yellowish, 20–35 mm long, 2–5 mm wide            | Obliquely immersed, 267–794(–1061) × 247–354                                    | –                          | Part-spores, 17–34 × 1–1.4                          | Metarhizium-like                         |
| M. guniijiangense    | Multiple, dark green, 40.3–42.5 mm long, confluent at base, apically subulate with acute, yellow and glabrous tip | Obliquely immersed, amoupleaceous, 640–770 × 240–320                            | Cylindrical, 310–380 × 4–4.8 | Filiform, 240–330 × 0.8–1                           | Metarhizium-like                         |
| M. indigoticum       | Multiple, dark green elastic, irregularly, curved stroma, 40–50 mm, 3–5 mm wide | Obliquely immersed, 700–750 × 275–325                                           | –                          | Part-spores, 4.5–5 × 1                              | Metarhizium-like                         |
| M. kalasinense       | Simple or sparingly branched, olive green to greenish brown, 150 mm long | Obliquely immersed, 700–800 × 250–350                                           | Cylindrical, 500–650 × 4–5 | Filiform, 400–500 × 1–1.5                          | Metarhizium-like                         |
| M. owariense         | Solitary, dark brown, straight, cylindrical, 57 mm long                  | Obliquely immersed, amoupleaceous, 460–530 × 200–270                            | –                          | Part-spores, 4.2–5.6 × 1                             | Nomuraea-like                           |
| M. phuwiangense      | Multiple, clavate, orange brown, up to 15 mm long, 1.5–2 mm wide        | Obliquely semi-immersed, ovoid, 540–700 × 290–400                                | Cylindrical, 225–320 × 3–4 | Part-spores, 8–12 × 1–1.5                           | Paecilomyces-like                        |
| M. prachinense       | Multiple, cylindrical to clavate, white cream to pale brown, 50–86 mm long, 1–2 mm wide | Obliquely immersed, clavate to ovoid, 320–470 × 180–300                          | Cylindrical, 100–271 × 3–5 | Filiform, 94–107 × 1                                 | Nomuraea-like                           |
| M. pseudoatrovirens  | Multiple, cylindrical, fertile part fusoid to ovoid, olive green, 14 mm long | Ordinarily immersed, ovoid, 520–550 × 250–320                                    | –                          | LANCEOLATE WITH TAPERING ENDS, 50 × 2.5              | Unknown                                  |
| M. purpureonigrum    | Multiple, purple to dark, 100–150 mm long, up to 10 mm wide             | Ordinarily immersed, elongate ovoid, 600–870 × 250–500                           | Cylindrical, 245–280 × 6–8 | Filiform, 200–275 × 1–1.5                           | Metarhizium-like                         |
| M. purpureum         | Multiple, clavate, branched, dark purple, up to 40 mm long, 2.5–3 mm wide | Ordinarily immersed, ovoid, 370–520 × 210–300                                    | Cylindrical, 150–250 × 5–8 | Filiform, 160–240 × 1–1.5                           | Metarhizium-like                         |
| M. sulphureum        | Solitary, multiple, sulphur-yellow, greenish-olive, 25–45 mm long, 2–3 mm wide | Obliquely semi-immersed, ovoid, 600–700 × 420–450                                | Cylindrical, 300–420 × 3–6 | Filiform, 200–300 × 2–3                              | Metarhizium-like                         |
**Metarhizium carneum** (Duché & R. Heim) Kepler et al., Mycologia 106: 821. 2014.

**Penicillium nophoroense** [as ‘nophoroensum’] Y. Sasaki & Nakane, J. Agric. Chem. Soc. Japan: 775. 1943.

**Spicaria carnosa** J.H. Mill. et al., Mycologia 49: 800. 1957.

?? **Spicaria decumbens** Oudem., Archives Néerlandaises 7: 290. 1902.

**Description and illustration:** See Samson (1974).

**Typus:** France, Hills of Vauville, sandy soil, collection date unknown, J. Duche (holotype CBS H-7449, culture ex-type CBS 239.32, type culture of **Spicaria carnea**).

**Habitat:** Dune sand, Thysanoptera (Thripidae), Coleoptera (Staphylinidae), soil.

**Known distribution:** China, France, Japan, Netherlands, USA.

**Notes:** *Keithomyces carneus* is a common soil fungus in temperate regions and could be easily recognized by its echinulate conidia and green reverse.

**Keithomyces acicularis** (H. Iwasaki et al.) Samson, Luangsa-ard & Houbraken, *comb. nov*. MycoBank MB834945.

**Basionym:** *Metarhizium aciculare* H. Iwasaki et al., Mycoscience 60: 315. 2019.

**Description and illustration:** See Iwasaki et al. (2019).

**Typus:** Japan, Tokyo, Izu Islands, Nii-jima, from soil under *Angelica keiskei*, 13 Mar. 2013, Nonaka (holotype JCM 33284, culture ex-type FKI-7236).

**Habitat:** Soil.

**Known distribution:** Japan.

**Notes:** *Keithomyces acicularis* is closely related to *K. carneus* and can be distinguished from it by the size and presence of aciculate conidia.

**Keithomyces neogunnii** (T.C. Wen & K.D. Hyde) Luangsa-ard, Thanakitpipattana & Samson, *comb. nov*. MycoBank MB834878.

**Basionym:** *Metarhizium aciculare* H. Iwasaki et al., Mycoscience 60: 315. 2019.

**Synonyms:** ‘*Paecilomyces gunnii*’ sensu Z.Q. Liang, Acta Mycol. Sin. 4: 163. 1985.

*Cordyceps gunnii* var. minor Z.Z. Li et al., Korean J. Mycol. 27: 232. 1999.

*Paecilomyces gunnii* var. minor, Z.Z. Li et al., Korean J. Mycol. 27: 233. 1999.

**Description and illustration:** See Wen et al. (2017).

**Typus:** China, Guizhou Province, Shibin County, Yuntai Mountain, on larva of Lepidoptera in soil, 23 Apr. 2013, L.P. Chen (holotype GZUH SB1 3050302, culture ex-type GZUCC SB1 30503021).

**Habitat:** Lepidoptera larvae living in soil.

**Known distribution:** China.

**Notes:** *Cordyceps gunnii* (Berk.) Berk. is known from Australia and resembles *C. hawkesii* Gray, which has also been reported from Australia and Japan. Molecular studies by Wen et al. (2017) has shown that what had been identified as *C. gunnii* in China is phylogenetically different from the Australian isolate. *Cordyceps gunnii* from Australia has been transferred by Spatafora et al.
| Species                  | Countries found                                      | Phialides (μm)           | Conidia (μm)                  | Colony description                |
|--------------------------|------------------------------------------------------|---------------------------|-------------------------------|-----------------------------------|
| *Metarhizium acridum*    | Australia, Benin, Guinea-Bissau, Madagascar, Mali, Mexico, Niger, Senegal, Tanzania, Thailand, Tschad, USA | Cylindrical or ellipsoid, 4.5–12.5 × 2.5–4.5 | Ellipsoid, globose, 4.5–5.5 × 3–4 | Greyish yellow                    |
| *M. album*               | Indonesia, Philippines                               | Cylindrical, 5–14 × 1.5–2  | Ellipsoid, cylindrical, 5–6 × 1.5–2 | Pale brown                       |
| *M. alvesii*             | Brazil                                               | Ovoid to broadly ellipsoid, 7.55–14.46 × 1.6–2.8 | Cylindrical, 3.86–6.55 × 2.16–3.25 | Yellow to greenish               |
| *M. anisopliae*          | Brazil, Colombia, Ethiopia, France, India, Indonesia, Japan, Moldova, Myanmar, New Zealand, Papua New Guinea, Philippines, USA, Western Samoa | Cylindrical, 8–11.5 × 2–3 | Cylindrical to ellipsoid, 5–7 × 2–3.5 | Greyish green                    |
| *M. bibionidarum*        | Japan, France                                        | Cylindrical, 9.5–24.5 × 1.5–2 | Cylindrical to ellipsoid, 4.5–6 × 2–3 | Brownish yellow                  |
| *M. biotecense*          | Thailand                                             | Cylindrical, 6–16 × 2–3    | Cylindrical, ellipsoid, 5–7 × 2–3 | White                            |
| *M. blattodeae*          | Brazil, Thailand                                     | Ellipsoid, cylindrical, 5–15 × 2–2.5 | Ellipsoid to cylindrical, 6–8 × 2–3 | Pale yellow                      |
| *M. brachyspernum*       | Japan                                                 | Cylindrical, 7.5–10.5 × 1.5–2.5 | Cylindrical, 6–8 × 2.5–3 | Olive green                      |
| *M. brasiliense*         | Brazil                                                | Cylindrical, 7–10 × 1.5–2  | Ovoid to cylindrical, 3–10 × 2–3 | Cream to pale yellow             |
| *M. bruneum*             | Argentina, Australia, Austria, Canada, Denmark, Finland, France, Germany, Indonesia, Italy, Japan, Mexico, Myanmar, New Zealand, Norway, Philippines, Portugal, Republic of Georgia, Switzerland, Turkey, UK, USA | Cylindrical, 7–22 × 1.5–2 | Cylindrical, ellipsoid, 4.5–9 × 2–3 | White cream                      |
| *M. candelabrum*         | Thailand                                              | Cylindrical, 5–10 × 1.5–2  | Cylindrical, 7–9 × 1.5–2 | White to pale green              |
| *M. cercopidum*          | Thailand                                              | Cylindrical to ellipsoid, 5–8 × 2–3 | Cylindrical, 6–10 × 1.5–3 | Pale yellow to pale green        |
| *M. chaiyaphumense*      | Thailand                                              | Clavate, 10–12 × 2–3      | Two types of conidia; ovoid, ellipsoid or subglobose, 3–6 × 2–3; cylindrical, ellipsoid, 12–15 × 3–5 | Leaf green                       |
| *M. cicadae*             | Thailand                                              | Cylindrical, 4–7 × 2–3.5   | Two types of conidia; ovoid, ellipsoid, 2–6 × 2.5–4; cylindrical, 10–17 × 3–4 | Dark green                       |
| *M. clavatum*            | Thailand                                              | Cylindrical, 6–10 × 1.5–3  | Cylindrical, 5–6 × 2–3 | Pale green                       |
| *M. culicidarum*         | Thailand                                              | Cylindrical, 4–12 × 1.5–2.5 | Fusiform-elliptical, ellipsoid, 4–7 × 1–1.5 | White                            |
| *M. cylindrosporum*      | China, Japan, Taiwan                                  | Ovoid, 4–7 × 2–3           | Two types of conidia; ovoid, subglobose, 3–8 × 2–3; cylindrical, 14–22 × 3–4 | Pale yellow                      |
| *M. eburneum*            | Thailand                                              | NA                        | NA                            | White to creamy                  |
| *M. ellipsiodeum*        | Thailand                                              | Cylindrical, 4–7 × 1.5–3   | Cylindrical, ellipsoid, 4–7 × 1.5–2 | Olive yellow, sulphur yellow      |
| *M. flavoviride*         | Australia, Czech Republic, France, Germany, Malaysia, Netherlands | Cylindrical, 9–26 × 1.5–2 | Pyriform, reniform, ovoid 4–10 × 1.5–3 | Yellowish white                  |
| *M. flavum*              | Thailand                                              | Cylindrical, 7–12 × 2–3    | Cylindrical, 7–10 × 2–3 | Pale yellow                      |
| *M. frigidum*            | Australia                                             | Cylindrical to ellipsoid, 6–12 × 2–3 | Cylindrical, 4–8 × 2–4 | Dark green                       |
| *M. fusioideum*          | Thailand                                              | Cylindrical, 6–10 × 2–3    | Ellipsoid to cylindrical, 6–10 × 2–3 | White to pale cream              |
| *M. globosum*            | India                                                 | Clavate, ovoid 5–12 × 3–4 | Globose, 4–5 × 4–5 | Greyish green                    |
| *M. gryllidicola*        | Thailand                                              | Cylindrical, utriform, 6–11 × 2–3 | Cylindrical to ovoid, obclavate, 4–7 × 2–3 | Sulphur yellow                   |
| *M. guiuzhouense*        | China                                                 | 7–12 × 2–3                | 7–10 × 2–3 | Olive                            |
| Species               | Countries found                                      | Phialides (μm)                        | Conidia (μm)                               | Colony description                      |
|----------------------|------------------------------------------------------|---------------------------------------|--------------------------------------------|-----------------------------------------|
| **M. huainamdangense** | Thailand                                             | NA                                    | NA                                         | Grey pink                               |
| **M. humberi**        | Brazil, Mexico                                        | Ovoid to broadly ellipsoid, 6.6–12.85 × 1.77–2.45 | Cylindrical, 4.14–6.05 × 1.69–2.59         | Grey green                              |
| **M. kalasinense**    | Thailand                                             | Clavate, 8–12 × 2–3                   | Cylindrical, 6–8 × 2–3                      | Greenish olive with spectrum yellow     |
| **M. koreanum**       | Japan, South Korea, Thailand                         | Cylindrical, 5–13 × 2–2.5             | Cylindrical, ellipsoid, 4–7.5 × 1.5–2.5     | White to yellow                         |
| **M. lepidiotae**     | Australia, Japan, Papua New Guinea                   | Cylindrical, 8–15 × 2–3               | Ovoid to ellipsoid, cylindrical, 5–7.5 × 3–4 | White                                   |
| **M. majus**          | Australia, France, Indonesia, Japan, Malaysia, Philippines, Poland, Western Samoa | Cylindrical to ellipsoid, 11–22 × 2–3 | Oblong-elliptical, 10–14 × 2–4              | Yellowish orange to green               |
| **M. megapomponiae**  | Thailand                                             | Cylindrical, 5–11 × 2–4               | Cylindrical, ellipsoid, 7–11 × 3–4          | Cream to yellow brown                   |
| **M. minus**          | Benin, Ecuador, Philippines, Solomon Islands, Thailand | Cylindrical, 6–14 × 2.5–4             | Cylindrical, ellipsoid, 4–6 × 2.5–3         | White                                   |
| **M. niveum**         | Thailand                                             | Cylindrical, 4 × 2                    | Ovoid, ellipsoid, 2–5 × 2–3                 | White to cream                          |
| **M. nornnoi**        | Thailand                                             | Cylindrical, 4–9 × 2–3                | Cylindrical, 4–7 × 1.5–2                    | Sulphur yellow                          |
| **M. novozealandicum**| Australia, New Zealand                               | Cylindrical, 6–19 × 2–3               | Cylindrical, ellipsoid, 5–7.5 × 2–3         | White to pale yellow                    |
| **M. ovoidosporum**   | Thailand                                             | Oblpyriform, ovoid, 3–7 × 2–4         | Ovoid, ellipsoid, subglobose, 3–5 × 2–4     | Olive yellow                            |
| **M. owariense**      | Japan                                                | Ovoid, 5–8 × 3–4                      | Ovoid, ellipsoid, 7–10 × 4–5                | Greenish yellow                         |
| **M. pemphigi**       | Canada, China, Japan, Republic of Georgia, UK        | Cylindrical, ellipsoid, 6–12 × 2–3    | Cylindrical, 3–8 × 1.5–2                    | Pale yellow                             |
| **M. phasmatodeae**   | Thailand                                             | Cylindrical, utriform, 5–11 × 2–3     | Cylindrical, ovoid, obclavate, 5.5–8 × 2–3  | Sulphur yellow                          |
| **M. phuwiangense**   | Thailand                                             | Paecilomyces-like, swollen globose, 5–12 × 2–3, with distinct necks, 2–5 × 1 | Ellipsoid to cylindrical, 7–8 × 2.5–4 | Brown orange                            |
| **M. pinghaense**     | Australia, Brazil, China, Colombia, India, Indonesia, Japan, Myanmar, New Zealand, Oman, Pakistan, Papua New Guinea, Philippines, Solomon Islands, Thailand | Cylindrical, 7–17 × 2.5–3.5            | Ellipsoid, 6–8 × 2.5–3.5                  | Olive                                   |
| **M. prachinense**    | Thailand                                             | Ovoid to obpyriform, 2–5 × 2–2.5      | Subglobose, 3–5 × 2–3                       | Sulphur yellow                          |
| **M. purpureogenum**  | Japan                                                | Cylindrical, flask-shaped, 7–19 × 2–2.5 | Ovoid to ellipsoid, 4.5–5.5 × 3.5–4         | Pale ochre or tan                       |
| **M. purpureonigrum** | Thailand                                             | NA                                    | NA                                         | NA                                      |
| **M. purpureum**      | Thailand                                             | NA                                    | NA                                         | Pale cream                              |
| **M. reniforme**      | Indonesia, Ghana, Philippines, USA                   | Spherical to broadly ellipsoid, 2.5 ± 0.4 × 2.3 ± 0.2 | Reniform, 4.5 ± 0.7 ± 2.2 ± 0.4 | Greyish green, olive, dull green        |
| **M. robertsi**       | Argentina, Australia, Brazil, Canada, Colombia, Germany, Italy, Japan, Mexico, Myanmar, Norway, Portugal, Republic of Georgia, Romania, USA | Cylindrical, 7–13 × 2–2.5              | Cylindrical, ellipsoid, 5–9 × 2–3         | White to pale yellow                    |
| **M. samlanense**     | Thailand                                             | Ovoid, subglobose, cylindrical, 5–7 × 2–3 | Globose, 3–5                              | Sulphur yellow to straw yellow          |
| **M. sulphureum**     | Thailand                                             | Cylindrical, 5–11 × 1.5–2             | Cylindrical, 6–9 × 2–3                      | Olive yellow and greenish olive         |
Table 5. (Continued).

| Species | Countries found | Phialides (μm) | Conidia (μm) | Colony description |
|---------|-----------------|----------------|--------------|--------------------|
| *M. takense* | Thailand | Fusiform to narrowly ovoid, 5–8 × 2–3 | Ovoid, ellipsoid, subglobose, 3–5 × 2–3 | Greenish olive |
| *M. viridulum* | Taiwan, Thailand | Oval-cylindrical to ellipsoid, 5–9 × 3–5 | Ellipsoid, cylindrical, 7–13 × 3–4 | Pale yellow |
| *Purpureomyces khaoyaensis* | Thailand | Lecaniciellum-like, tapering gradually towards the apex, 7–18 × 1–3 | Ovoid, 2–3 × 1–5–3 | White to cream |
| *Pu. maesotensis* | Thailand | Lecaniciellum-like, tapering gradually towards the apex, 4–21 × 1.5–2 | Ovoid, 3 × 1–2.5 | White to lilac |
| *Pu. pyriformis* | Thailand | Lecaniciellum-like, tapering gradually towards the apex, 8–22 × 1–2 | Ovoid, 2–4 × 1.5–2 | White to cream |

NA: Sporulation not observed.

(2015) to Drechmeria in Ophiocordycipitaceae, while *C. gunnii* from China was transferred to Metarhizium by Wen et al. (2017) in Clavicipitaceae and renamed the species as *M. neogunnii*. This sexually reproductive species is nested with asexually reproductive isolates of what was previously identified as *Paecilomyces carneus* (= *Metarthizium carneum*).

**Marquandomyces** Samson, Houbraken & Luangsa-ard, *gen. nov*. MycoBank MB834879.

**Etymology**: Named after an estate in Guernsey (UK).

**Type species**: *Verticillium marquandii* Samse, Trans. Br. Mycol. Soc. 1: 24. 1898.

**Description and illustration**: See Samson (1974).

**Habitat**: On mushrooms, soil.

**Known distribution**: Brazil, Netherlands, Russia, UK, USA.

**Notes**: Samson (1898) found the species parasitic on the gills of *Hygrocybe virginus*. To date, strains of *M. marquandii* are often found in soil.

**Metarhizium** Sorokin, Veg. Parasitenk. Mensch Tieren: 268. 1879.

**Synonyms**: Chamaeleomyces Sigler, J. Clin. Microbiol. 48: 3186. 2010.

**Metarhizycpes** G.H. Sung et al., Stud. Mycol. 57: 27. 2007.

**Nomuraea** Maubl., Bull. Soc. Mycol. France 19: 296. 1903.

**Type species**: *Metarhizium anisopliae* (Metschn.) Sorokin, Plant Paras. Man Anim.: 268. 1883.

**Notes**: The concept of the genus *Metarhizium* is revised to exclude species not belonging in the *Metarhizium* clade in Fig. 1. Relationships between species in the *Metarhizium anisopliae* complex were elucidated using 5′*tef* sequences in Fig. 2. A list of strains used in this study and their GenBank accession numbers is found in Table 1. Table 2 lists the hosts, substrates and geographical locations of all *Metarhizium* species. Table 3 shows the types of conidiation and Table 4 shows the differences between the sexual morphs of *Metarhizium* and closely related taxa. The micromorphologies and colour of most species on SDAY/4 are shown in Table 5. Conidigenous structures and conidial shapes of known species from ARSEF (type strains) on SDAY/4 after 7 d are shown in Figs 5–8. The morphological differences of most species on OA and PDA are shown in Supplementary Table S1. The phylogenetic relationships of *Metarhizium* and related taxa were analysed using the ITS barcode in Supplementary Fig. S1 and using combined *rpb1* and *rpb2* sequences in Supplementary Fig. S2.

We recommend the use of SDAY/4 for studying the micromorphologies and colony colour in *Metarhizium*. Growth on
both PDA and SDAY/4 are fast as well as the sporulation, but in SDAY/4 sporulation is less compared to PDA making it easier to observe the shapes of the phialides for a better diagnosis. The use of PDA and OA is suitable only in two species in *Metarhizium*, *M. purpureonigrum* and *M. purpureum*, where using SDAY/4 does not result in sporulation. OA is suitable for slow-growing species in *Metarhizium*.

**Fig. 5.** Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A**–**D.** *M. acridum* ARSEF 7486. **E**–**H.** *M. album* ARSEF 1942. **I**–**K.** *M. anisopliae* ARSEF 7487. **L**–**O.** *M. blattodeae* BCC 20250. **P**–**R.** *M. brasiliense* ARSEF 2948. **S**–**V.** *M. brunneum* ARSEF 2107. Scale bars = 10 μm.
**Metarhizium anisopliae** (Metsch.) Sorokin, Plant Paras. Man Anim. 2: 268. 1883.

*Basionym*: *Entomophthora anisopliae* Metsch. Zap. Imp. Obshch. Khoz. Ross.: 45. 1879.

*Synonyms*: *Isaria anisopliae* (Metsch.) Pettit, Cornell Univ. Agric. Exp. St. Bull. 97: 356. 1895.  
*Penicillium anisopliae* (Metsch.) Vuill., Bull. Trimest. Soc. Mycol. Fr. 20: 221. 1904.

Fig. 6. Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–D.** *M. cylindrosporum* ARSEF 6926. **E–G.** *M. trigidum* ARSEF 4124. **H–J.** *M. globosum* ARSEF 2596. **K–M.** *M. gryllidicola* BCC 82988. **N–P.** *M. kalasinense* BCC 53582. **Q–S.** *M. koreanum* AFSEF 2038. Scale bars = 10 μm.
**Isaria destructor** Metsch., Zool. Anz. 3: 45. 1880.

**Oospora destructor** (Metsch.) Delacroix, Bull. Trimest. Soc. Mycol. Fr. 9: 260. 1893.

**Isaria anisopliae** var. **americana** Pettit, Cornell Univ. Agric. Exp. St. Bull. 97: 354. 1895.

**Penicillium cicadinum** Höhn., Sber. Akad. Wiss. Wien 118: 405. 1909.

---

*Fig. 7.* Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–D.** *M. lepidiotae* ARSEF 7488. **E–G.** *M. majus* ARSEF 1914. **H–J.** *M. minus* ARSEF 2037. **K–M.** *M. novozelandicum* ARSEF 8214. **N–P.** *M. owariense* NBRC 33258. **Q–T.** *M. pemphigi* ARSEF 7491. Scale bars = 10 μm.
Metarhizium cicadinum (Höhn.) Petch, Trans. Br. Mycol. Soc. 16: 68. 1931.

Sporotrichum paranense Marchionatto, Bol. Mens. Min. Agric. Noac. Buenos Aires 34: 241. 1933.

Neotype: Ukraine, isolated from Avena sativa root, collection date unknown, collector unknown (Neotype CBS H-14432 preserved in a metabolically inactive state, culture ex-neotype CBS

Fig. 8. Colonies on SDAY/4 after 7 d, phialides and conidia of known Metarhizium species: A–C. M. phasmatodeae BCC 47272. D–F. M. prachinense BCC 47979. G–J. M. robertsii ARSEF 8820. K–M. M. samlanense BCC 17091. N–P. M. takense BCC 30939. Q–T. M. viridulum ARSEF 6927. Scale bars = 10 μm.
130.71 = ATCC 22269 = VKM F-1490 Metarhizium anisopliae var. anisopliae, type of Myrothecium commune Pidopl.)

Habitat: Various insect hosts, soil.

Known distribution: Worldwide.

Notes: The Metarhizium anisopliae species complex comprises 21 species. Metarhizium anisopliae was first reported by Metchnikoff from Anisoplia austriaca, a cockchafer found on wheat in Russia. Four varieties were recognised by Driver et al. (2000), M. anisopliae var. acridum, M. anisopliae var. anisopliae, M. anisopliae var. lepidiotae and M. anisopliae var. majus in an ITS molecular phylogeny. Bischoff et al. (2009) elevated the varieties to species rank based on a multi-gene phylogenetic analyses that included M. guizhouense, M. pingshaense and M. tali. In the past decade, additional species were recognised using multi-gene analyses (Bischoff et al. 2009, Luangsa-ard et al. 2017, Chen et al. 2018a, c, Lopes et al. 2018, Luz et al. 2019, Yamamoto et al. 2020, Thanakitpipattana et al. 2020) and members of the complex now include M. acridum, M. alvesii, M. anisopliae, M. baoshanense, M. brachyspermum, M. brittlebankisoides, M. brunneum, M. campsosterni, M. clavatum, M. globosum, M. guizhouense, M. humberi, M. indigoticum, M. majus, M. lepidiotae, M. kalasinense, M. pingshaense, M. robertsi, M. phasmatodeae, M. Gryllidicola and M. sulphureum.

Tulloch (1976) designated an isolate from a desert locust (Orthoptera, Acrididae) in Ethiopia that threatens agricultural crops as the neotype of M. anisopliae var. anisopliae while Metchnikoff (1879) described M. anisopliae from a scarab beetle from Russia, a harmful pest of cereal crops. It was during Metchnikoff’s research time at the Univ. of Odessa, which is now in present day Ukraine, when an outbreak of the pest Anisoplia austriaca and related species was reported from southern parts of Russia. He then aimed to find a method to control these scarab (Zimmermann et al. 1995). A strain from Ukraine, CBS 130.71, isolated from Avena sativa root, a cereal crop, is considered the closest strain to Metchnikoff’s Metarhizium anisopliae in terms of geography which is nested with M. lepidiotae, and not with the Ethiopian neotype strain (Figs 1 and 2). We therefore reject the neotype (ARSEF 7487 = CSIRO Fl-
1029 = IMI (168777ii) proposed by Tulloch (1976) and followed by Driver et al. (2000), Bischoff et al. (2009), Kepler et al. (2014) and papers resulting thereafter, because it is isolated from a different locality and substrate. Our phylogenetic analyses clearly demonstrated it is different from the isolate originating from Ukraine and therefore we propose CBS 130.71 as the neotype.

Fig. 10. *Metarhizium candelabrum* (BBH 22654, culture ex-type BCC 29224). A. Fungus on adult leafhopper (Hemiptera). B. Conidia on insect host. C. Colonies on OA. D–F. Phialides and conidia on OA. G. Colonies on PDA. H–I. Phialides and conidia on PDA. J. Colonies on SDAY/4. K–M. Phialides and conidia on SDAY/4. Scale bars: A = 1 mm; B = 8 μm; D–F, H, I, K, L, M = 10 μm.
Metarhizium acridum (Driver & Milner) J.F. Bisch. et al., Mycologia 101: 519. 2009.
Basionym: Metarhizium anisopliae var. acridum Driver & Milner, Mycol. Res. 104: 144. 2000.

Description and illustration: See Driver et al. (2000).

Typus: Niger, West Africa, isolated from Ornithacris cavroisi (Orthoptera: Acrididae), 29 Aug. 1992, collector unknown, (holotype Locusta migratoria laboratory infected with FI-987 dried over silica gel, DAR 74297; paratype DAR 74298-74301, culture ex-type ARSEF 7486 = FI-0987 = IMI 330189 used by Driver et al. (2000) to describe M. anisopliae var. acridum, culture ex-paratype ARSEF 324, ARSEF 3391).

Habitat: Orthoptera: Acrididae, soil.
Known distribution: Australia, Benin, Chad, Madagascar, Mali, Mexico, Niger, Senegal, Tanzania, Thailand (Orthoptera: Acrididae: Patanga succincta).

Notes: Strains forming *M. anisopliae* var. *acidum* were originally identified as *M. anisopliae* var. *minus* and *M. anisopliae* var. *anisopliae* (Driver et al. 2000) and were also known from grasshoppers and locusts in Africa, Asia, South America and Australia. Unlike most species in the *M. anisopliae* complex having cylindrical conidia, *M. acidum* produces ovoid conidia.

**Metarhizium album** Petch, Trans. Br. Mycol. Soc. 16: 71. 1931.

Description and illustration: See Petch (1931), Rombach et al. (1987).

Typus: Sri Lanka, southern province, on leafhopper (*Tettigoniella spectra*) on rice, Jan. 1928, J.C. Hutson.

Habitat: Hemiptera: Cicadellidae: *Tettigoniella spectra* (Cofana spectra).

Known distribution: Indonesia, Philippines, Sri Lanka, Thailand.

Notes: Petch (1931) noted that this species on planthoppers produces conidiophores from a basal stroma that forms a continuous palisade layer and that conidia in chains form prismatic columns. Tulloch (1976) considered this species only an immature specimen of *M. anisopliae*. Rombach et al. (1986) restored *M. album* for a pathogen of homopterans from Asia that form clavate phialides with conidia that do not form prismatic columns. The conidia of the Sri Lankan specimen on OA are ovoid to oblong oval (3–4 × 1.8 μm), shorter that those found in Thailand, which are cylindrical to ellipsoidal. Within the *M. anisopliae* group, the conidia in *M. album* are not as long as in *M. majus*.

**Metarhizium alvesii** R.B. Lopes et al., J. Invert. Path. 151: 166. 2018.

Description and illustration: See Lopes et al. (2018).

Typus: Brazil, isolated from soil in banana plantation, 2 Feb. 2009, R.B. Lopes (holotype UFG 50750, culture ex-type CG1123 = ARSEF 13308).

Habitat: Soil.

Known distribution: Brazil.

Notes: *Metarhizium alvesii* is difficult to be distinguished from other species in the *M. anisopliae* complex based on the shape of conidia (cylindrical) and phialides. It is closely related to other species also found in soil, such as *M. acidum* and is closest to *M. lepidioides*. Both *M. acidum* and *M. lepidioides* have ellipsoidal conidia while *M. alvesii* produces cylindrical conidia.

**Metarhizium argentinense** A.C. Gutierrez et al., Fungal Biol. 123: 368. 2019.

Description and illustration: See Gutierrez et al. (2019).

Typus: Argentina, on Epilampra sp. (Blaberidae: Epilamprinae), 14 Aug. 2013, A.G. Gutierrez (holotype LPS 49098, culture ex-type CEP424 = ARSEF 13510).

Habitat: Cockroaches in the genus Epilampra (*Blaberidae, Epilamprinae*).

Known distribution: Argentina.

Notes: Our multi-gene phylogeny shows *M. argentinense* is closely related to another cockroach pathogen, *M. blattodeae*. It is a member of the *M. flavoviride* complex of 13 species comprising *M. argentinense*, *M. binonidurum*, *M. biotecense*, *M. blattodeae*, *M. culicidarum*, *M. flavoviride*, *M. frigidum*, *M. gaoligongense*, *M. koreanum*, *M. fusoidum*, *M. minus*, *M. normai*, and *M. pemptgii*. Contrary to the notion that members of the *M. flavoviride* complex produces ovoid to ellipsoidal conidia as opposed to the cylindrical conidia of species in the *M. anisopliae* complex, *M. argentinense* produces cylindrical, olive to dull green conidia in parallel chains forming columns or plate-like masses. Its conidial sizes are similar to *M. blattodeae* and *M. frigidum* but can be distinguished by its cylindrical phialides and conidia.

**Metarhizium atrovirens** (Kobayasi & Shimizu) Kepler et al., Mycologia 106: 821. 2014.

Basionym: *Cordyceps atrovirens* Kobayasi & Shimizu, Bull. Nat. Sci. Mus. Tokyo 4: 52. 1978.

Synonym: *Metacordyceps atrovirens* (Kobayasi & Shimizu) Kepler et al., Mycologia 104: 185. 2012.

Description and illustration: See Kobayasi & Shimizu (1978).

Typus: Japan, Tsugawa, Yamagata Prefecture, on Coleoptera larva, 21 Aug. 1960, Y. Kobayasi & D. Shimizu (holotype in TNS).

Habitat: Coleoptera larva.

Known distribution: Japan.

Notes: Kobayasi & Shimizu (1978) noted the production of ellipsoidal conidia (microcyclic sporulation) on the germinating ascospores. This is a phenomenon often seen in discharged ascospores in *Cordyceps nelumboides*, *Purpureomycetes khaoyaiensis*, *Metarhizium phiwiangense*, and some species of *Ophiocordyceps* (*Ophiocordyceps unilateralis sensu stricto, Ophiocordyceps pseudocommunis*). *Metarhizium atrovirens* differs from *M. pseudoatrovirens* in the oblique arrangement of the perithelia and protruding ostioles. *Metarhizium pseudoatrovirens* has ordinarily arranged, completely immersed perithecia.

**Metarhizium baoshanense** Z.H. Chen et al., Pakist. J. Zool. 50: 1745. 2018.

Description and illustration: See Chen et al. (2018a).

Typus: China, Yunnan Province, Taibao mountain, isolated from soil of mid-montane of humid evergreen broad-leaved forest, 3 May 2015, Z.H. Chen (holotype CCTCC M2016589, culture ex-type BUM 63.4).

Habitat: Soil.

Known distribution: China.

Notes: *Metarhizium baoshanense* is a member of the *M. anisopliae* complex and is close to *M. brittlebankisoides*, *M. clavatum* and *M. gryllidicola*. However, the conidia of *M. baoshanense* are shorter than those reported for *M. clavatum* and *M. gryllidicola* although the shapes and sizes of the conidia do not differ significantly and seem to be all a part of a continuum in this complex.

**Metarhizium bibionidarum** O. Nishi & H. Sato, Mycol. Prog. 16: 993. 2017.
**Description and illustration:** See Nishi et al. (2017).

**Typus:** Japan, woods on Hongo campus of Univ. of Tokyo, on cadaver of March fly larva (Bibionidae), 1993, K. Nijima (holotype TNS-F-53529, culture ex-type NBRC 112661).

**Habitat:** Diptera: Bibionidae, Coleoptera: Scarabaeidae, soil.

**Known distribution:** France, Japan.

**Notes:** *Metarhizium bionidarum* is a member of the *M. flavoviride* complex and is closely related to *M. pemphigi, M. gaoligongense* and *M. normoi*. *Metarhizium gaoligongense* was isolated from soil, *M. pemphigi* was found predominantly on Hemiptera while *M. normoi* was found on larva of Lepidoptera. It
can be distinguished from *M. pemphigi* by its larger conidia (Nishi et al. 2017).

**Metarhizium biotecense** Luangsa-ard, Khonsanit, Thanakitpattana & Samson, sp. nov. MycoBank MB834881. Fig. 9.

**Etymology:** In reference to the BIOTEC Greenhouse, National Science and Technology Development Agency (NSTDA), Pathum Thani Province, where the type specimen was collected.

Specimens were found on brown planthoppers (*Nilaparvata lugens*, Delphacidae, Hemiptera) on the underside of rice leaves. The host's body was covered with white to smoke grey (No.44–45) mycelium and powdery cream to smoke grey conidia. *Phialides* smooth-walled, cylindrical with semi-papillate apices, (5.5–7)–10.5(–12) × 2–3 μm. *Conidia* smooth-walled, cylindrical with rounded apices or ellipsoidal, (4–) 5–6.5(–9) × 2–3 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 21 mm in 14 d, mycelium densely appressed, flat, white at the margins turning to peacock-green (No.162C), powdery while sporulating. Sporulation starts 5 d after inoculation, reverse olivaceous (No.52). *Conidiophores* arising from aerial mycelium, erect, smooth-walled. *Phialides* smooth-walled, cylindrical with semi-papillate apices, (6.5–7)–10(–12) × 2–3 μm. *Conidia* smooth-walled, peacock-green (No.162C), cylindrical with rounded apices or ellipsoidal, (5–)5.5–7.5(–9) × 2–3 μm.

Colonies on SDAY attaining a diam of 21–22 mm in 20 d, mycelium dense, floccose, cottony, slightly convex to the agar surface, white turning to peacock-green (No.162C), powdery while sporulating. Sporulation starts at 12 d after inoculation, reverse verona brown (No.223B) in the middle of colony and straw yellow (No.56) with white cream at the margin. *Conidiophores* arising from aerial mycelia, erect, smooth-walled. *Phialides* smooth-walled, cylindrical with semi-papillate apices, (6–)6.5–9.5(–14) × 2–3 μm. *Conidia* smooth-walled, peacock-green (No.162C), ellipsoidal, 5–6(–7) × 2–3 μm.

Colonies on SDAY/4 attaining a diam of 25–28 mm in 20 d, mycelium dense, floccose, cottony, slightly convex to the agar surface, white. Sporulation starts 14 d after inoculation, reverse citrino (No.51) in the middle of colony and olive yellow (No.52) with white cream at the margin. *Conidiophores* arising from aerial mycelia, erect, smooth-walled. *Phialides* smooth-walled, cylindrical with semi-papillate apices, (6–)8–12(–16) × 2–3 μm. *Conidia* smooth-walled, white, cylindrical with rounded apices and ellipsoidal, 5–6(–7) × 2–3 μm.

**Typus:** Thailand, Pathum Thani Province, Klong Luang, National Science and Technology Development Agency, BIOTEC Greenhouse, on *Nilaparvata lugens* on the underside of rice leaves, 2 Mar. 2012, C. Sunyachadkun (holotype BBH 32704 preserved in a metabolically inactive state, culture ex-type BCC 51812).

**Habitat:** On adult brown planthopper, *Nilaparvata lugens* (Hemiptera: Delphaciidae) on the underside of rice leaves.

**Known distribution:** Thailand, found in BIOTEC Greenhouse, National Science and Technology Development Agency, Klong Luang, Pathum Thani Province.

Additional materials examined: Thailand, Pathum Thani Province, Klong Luang, National Science and Technology Development Agency, BIOTEC Greenhouse, 14.076383 N, 100.61442 E, on adult of *Nilaparvata lugens*, 2 Mar. 2012, C. Sunyachadkun (BBH 32705, BCC 51813).

**Notes:** *Metarhizium biotecense* is a member of the *M. anisopliae* species complex and is closely related to *M. minus* and *M. culicidarum*. The micro-morphologies of the conidiophores, phialides and conidia of *M. biotecense* are indistinguishable from *M. minus* (Supplementary Table S1) but could be differentiated by its growth on PDA. The colony colour of *M. biotecense* on PDA is pale yellow, and white in *M. minus*.

**Metarhizium blattodeae** Montalva et al., Fungal Biol. 120: 660. 2016.

**Description and illustration:** See Montalva et al. (2016). The description below is based on specimens collected in Thailand.

**Description from the asexual morph.** Host's head and thorax are covered with pale green mycelium and by sporulating conidiophores. *Phialides* ellipsoidal to cylindrical with semi-papillate apices, (5–)7–10 × (2)–2.5–3 μm. *Conidia* smooth-walled, Paris green (No.63), ellipsoidal to cylindrical, (5–)7–10 × (2–) 2.5–3(–4) μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 15–18 mm in 14 d, white, flat, floccose, entire edge, reverse uncoloured. *Conidia* and reproductive structures not observed.

Colonies on PDA attaining a diam of 20–22 mm in 14 d, white to pale yellow, abundant aerial mycelium, fluffy, entire edge, poor sporulation with dark green conidia produced on aerial mycelium. Sporulation starts at 12 d after inoculation, reverse uncoloured. *Conidiophores* terminating in branches, with 1–4 phialides per branch. *Phialides* ellipsoidal to cylindrical with semi-papillate apices, (5–)6.5–9.5(–10) × 2–3 μm. *Conidia* smooth-walled, dark green (No.262), ellipsoidal to cylindrical with rounded apices, (6–)6.5–7.5(–8) × 2–2.5(–3) μm.

Colonies on SDAY/4 attaining a diam of 15 mm in 14 d, pale yellow, flat, floccose, undulate edge, white margin. Sporulation starts at 12 d after inoculation, reverse uncoloured. *Conidiophores* unbranched. *Phialides* solitary along the hyphae, ellipsoidal to cylindrical with semi-papillate apices, (5–) 6.5–12(–15) × 2–2.5 μm. *Conidia* smooth-walled, hyaline, ellipsoidal to cylindrical with rounded apices, (6–)7–8 × 2–3 μm.

**Typus:** Brazil, Bacupari Reserve, Calvante, Goias, on undetermined species of Dictyoptera: Blattodea: Ectobiidae, 4 Feb. 2015, C. Montalva (holotype UFG 49886, culture ex-type ARSEF 12850 = IP 414).

**Habitat:** On Dictyoptera: Blattodea: Ectobiidae in South America and on Blattaria, Blattidae in Thailand; all forest cockroaches.

**Known distribution:** Brazil; Thailand; known from Khlong Nakha Wildlife Sanctuary and Kaeng Krachan National Park.

**Additional materials examined:** Thailand, Ranong Province, Khlong Nakha Wildlife Sanctuary, 9.459589 N, 98.504486 E, on adult cockroach (*Blattodea: Blattellidae*), 11 Jan. 2006, K. Tasanathai, W. Chaygate, S. Mongkolsamrit, P. Srikitikulchai, B. Thongnuch, Le Tan Hung & Lam Ngu Yen (BBH 16548, BCC 20255); Phetchaburi Province, Kaeng Krachan National Park, 12.866783 N 99.400444 E, on adult cockroach (*Blattodea: Blattellidae*), 24 Aug. 2001, R. Nasit, G. Samuels & R. Reblova (NHU 11597).

**Notes:** *Metarhizium blattodeae* (Montalva et al. 2016) is a member of the *M. flavoviride* species complex and was isolated from an infected forest cockroach from Brazil as well as in Thailand. *Metarhizium blattodeae* is closely related to *M. argentinense* (Gutierrez et al. 2019) occurring on forest cockroaches.
Fig. 13. *Metarhizium clavatum* (BBH 43330, culture ex-type BCC 84543). A–B. Stromata arising from host. C–D. Oblique perithecial orientation. E. Asci. F. Ascus tip. G. Ascospore. H. Whole ascospore showing septa (arrows). I. Colonies on OA. J–L. Phialides and conidia on OA. M. Colonies on PDA. N–P. Phialides and conidia on PDA. Q. Colonies on SDAY/4. R–T. Phialides and conidia on SDAY/4. Scale bars: A, B = 10 mm; C = 350 μm; D, E = 150 μm; F–H, J–L, N, O, R, S = 10 μm; P, T = 5 μm.
Metarhizium blattodeae is rarely reported in Thailand. The colony colour on PDA and SDAY/4 of M. blattodeae from the Thai strain is white to pale yellow with poor sporulation while no sporulation can be observed on OA. The micro-morphology of M. blattodeae from Thailand on SDAY/4 differs from the Brazilian strain by producing solitary phialides along the hyphae and not in branches, while phialides of the Brazilian type species are produced in branches (1–5 branches). Conidial form from both countries are cylindrical and are in the same size range.

Metarhizium brachyspermum Koh. Yamam. et al., Mycoscience 61: 38. 2019.

Description and illustration: See Yamamoto et al. (2020).

Typus: Japan, Togichi Prefecture, Utsunomiya-shi, Nagaokacho, on elaterid pupa in underground pupal chamber, 2 Jul. 2017, K. Yamamoto (holotype KY170702-1, culture ex-type CM1 = IFM 65744 = TNS-F-70755).

Habitat: Coleoptera: Elaterid larva.

Known distribution: Japan.

Notes: Metarhizium brachyspermum shows similarity to M. kalasinense but produces shorter ascospores compared to the latter. The sexual morph of both species is found occurring on Coleoptera larva in nature and are members of the M. anisopliae complex. Metarhizium campsomertii also shows similarity to M. brachyspermum and M. kalasinense in infecting larva of Elateridae (Coleoptera) but differs in the colour of the stromata, which are greenish yellow, as well as in the size of the perithecia. Metarhizium kalasinense has bigger perithecia than M. brachyspermum. The perithecia in M. campsomertii are smaller than the two aforementioned species.
Metarhizium brittlebankisoides (Zuo Y. Liu et al.) Kepler et al., Mycologia 106: 821. 2014.
Basionym: Cordyceps brittlebankisoides Zuo Y. Liu et al., J. Invert. Pathol. 78: 179. 2001.
Synonym: Metacordyceps brittlebankisoides (Zuo Y. Liu et al.) G.H. Sung et al., Stud. Mycol. 57: 35. 2007.

Description and illustration: See Liu et al. (2001).

Typus: China, Wawu Mountains, Sichuan, on Coleoptera larva, Scarabaeidae, Jul. 1997, collector unknown (holotype CGAC 9728 in Guizhou University, Guiyang, Guizhou, culture ex-type CGAC 9728-C = IMI 385941 in CABI Bioscience Collection, Surrey, UK).

Habitat: Coleoptera: Scarabaeidae.

Known distribution: China.

Notes: Based on the data presented by Liu et al. (2001), the asexual morph M. brittlebankisoides shares similar morphological characters such as shape of phialides and conidia as M. majus, only the conidia are shorter in M. brittlebankisoides (9–10 μm) than in M. majus (10–14 μm). Many species in this species complex have similar conidial sizes that seem to be in the same range or are in a continuum and is therefore difficult to use for identification. We believe more loci have to be sequenced for the type of M. brittlebankisoides to clarify its position in Metarhizium. Multi-gene sequence data is available for a M. brittlebankisoides strain from Japan (MAFF243306), which places this strain in the M. anisopliae complex (Gutierrez et al. 2019). Our ITS phylogeny using the sequence from the type material (Liu et al. 2001) shows M. brittlebankisoides nested with M. candelabrum and M. huainamdangense and not in the M. anisopliae complex (Supplementary Fig. S1). Unfortunately, no ITS sequence for the Japanese strain is provided to compare with the Chinese type material, which did not group with other members of the M. anisopliae complex in the ITS phylogeny by Gutierrez et al. (2019). Strains of M. majus were not only reported from Scarabaeidae, Coleoptera but also from other hosts/substrate such as Lepidoptera, Orthoptera (Gryllidae), Phasmatodea, and soil.

Metarhizium brasiliense Kepler et al., Mycologia 106: 821. 2014.

Description and illustration: See Kepler et al. (2014).

Typus: Brazil, Campinas, Sao Paulo, on Hemiptera: Cicadellidae, 30 Apr. 1989, L.G. Leite (holotype BPI 892884, culture ex-type ARSEF 2948).

Habitat: Hemiptera.

Known distribution: Brazil.

Notes: This species was originally considered by Driver et al. (2000) to be the M. flavoviride “Type E” clade. However, this species shows a sister relationship to M. album and M. ellipsoideum. The latter two new species produce only one size class of conidia while M. brasiliense was reported to be producing two differing size classes, a habit observed in some species of the clade occurring on cicada adults comprising M. chaiyaphumense, M. cicadae, M. cylindrosporum, M. niveum and M. takense.

Metarhizium brunneum Petch, Trans. Br. Mycol. Soc. 19: 189. 1935 [1934].

Description and illustration: See Petch (1934), Bischoff et al. (2009).

Typus: USA, Forest Grove, Oregon, on larva of Agriotes sp. (Coleoptera: Elateridae), 29 Jun. 1933, K.B. Raper & L.P. Rockwood (culture ex-type CBS 316.51 = IMI 014746 = NRRL 1944 = QM 191, culture ex-epitype ARSEF 2107, identified by Petch (1934), was designated when no viable ex-type culture available).

Habitat: Coleoptera: Acari (Ixodidae), Diptera, Lepidoptera, Hymenoptera, soil.

Known distribution: Argentina, Australia, Canada, Denmark, Finland, France, Indonesia, Italy, Japan, Mexico, New Zealand, Philippines, Switzerland, USA.

Notes: A member of the M. anisopliae complex, M. brunneum produces chains of brown (olivaceous) conidia that adhere to each other and form columns (Petch 1934). Petch’s description was based on a Cicadellidae (Hemiptera) from Laguna, the Philippines. As the type was not readily accessible, Bischoff et al. (2009) designated a dried culture (BPI 878293) as an epitype occurring on Elateridae larva from the USA.

Metarhizium candelabrum Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, sp. nov. MycoBank MB834882. Fig. 10.

Etymology: Named after the arrangement of phialides looking like a candelabra.

Specimen found on leafhopper (Hemiptera), Host’s head and thorax were covered with pale green mycelium and sporulating conidiophores. Conidia smooth-walled, pale green (oac875-876), cylindrical with rounded apices, (6–)6.5–8 × 2–3 μm.

Cultural characteristics: Colonies on OA attaining a diam of 15 mm in 14 d, white mycelium, fluffy, abundant aerial hyphae, entire edge, dark green in the centre of colonies due to production of conidia. Sporulation starts at 10 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2–3 phialides per branch. Phialides cylindrical with semi-papillate apices, (5–)6–7.5–8.5 × 2–2.5–3 μm. Conidia smooth-walled, pale green (oac103-104), cylindrical with rounded apices, (6–)7–8(–8.5) × 1.5–2.5 μm.

Colonies on PDA attaining a diam of 15 mm in 30 d, white mycelium, fluffy, abundant aerial hyphae, entire edge, dark green in the centre of colonies due to production of conidia. Sporulation starts at 30 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2–3 phialides per branch. Phialides cylindrical with semi-papillate apices, (5–)6–7–8(–9) × 1.5–2 μm.

Colonies on SDA/Y attaining a diam of 15 mm in 30 d, pale green, floccose, abundant aerial hyphae, white border, pale yellow in the centre of colonies. Sporulation starts at 30 d, reverse uncoloured. Conidiophores terminating in branches, with 2–3 phialides per branch. Phialides cylindrical with semi-papillate apices, (5–)6–8(–10) × 1.5–2 μm. Conidia pale green (oac36) and pale yellow (oac4-5), cylindrical with rounded apices, 7–8(–9) × 1.5–2 μm.
**Typus:** Thailand, Kamphaeng Phet Province, Khlong Lan National Park, on adult leafhopper (Hemiptera), 2 Oct. 2007, B. Thongnuch, K. Tasanathai, S. Mongkolsamrit, P. Srikitikulchai, R. Ridkaew & A. Khonsanit (holotype BBH 22654 preserved in a metabolically inactive state, culture ex-type BCC 29224).

**Habitat:** Adult leafhopper (Hemiptera), on the underside of dicotyledonous plants.

**Known distribution:** Thailand; known from Khlong Lan National Park.

**Notes:** Metarhizium candelabrum is closely related to *M. cercopidarum* and *M. huainamdangense*. It sporulates profusely on three kinds of media followed by *M. cercopidarum* and then *M. huainamdangense*. The micro-morphologies, especially in the size and shapes of the conidia and phialides, of these three species are almost in a continuum but their growth on three kinds of media vary from each other. No sporulation could be observed after 30 d in *M. huainamdangense* while in *M. candelabrum* a floccose overgrowth of mycelium could be found on three media with heavy sporulation in the middle of the colonies.
Metarhizium camposterni (W.M. Zhang & T.H. Li) Kepler et al., Mycologia 106: 821. 2014.
Basionym: Cordyceps camposterni [as ‘campsosterna’] W.M. Zhang & T.H. Li, Fungal Diversity 17: 240. 2004.
Synonym: Metacordyceps camposterni (W.M. Zhang & T.H. Li) G.H. Sung et al., Stud. Mycol. 57: 35. 2007.

Description and illustration: See Zhang et al. (2004).

Typus: China, Huidong County, Gutian Nature Reserve, Guangdong Province, on nymph and adult of Campsosternus auratus buried in soil, 25 Jun. 2002, W.M. Zhang (holotype HMIGD 20885, deposited in Herbarium of Microbiology of Guangdong).

Habitat: Coleoptera: Scarabaeidae.

Known distribution: China.

Notes: Phylogenetic analyses of Yamamoto et al. (2020) have shown M. camposterni as a member of the M. anisopliae species complex together with M. baoshanense, M. brachyspermum, M. guizhouense, M. indigoticum, M. kalasinense, and M. majus. It is one of the sexual morphs reported in the M. anisopliae complex together with M. taii (= M. guizhouense), M. brachyspermum, M. brittlebankisoides, M. clavatum, M. kalasinense, and M. sulphureum.

Metarhizium cercopidarum Luangsara, Mongkolsamrit, Thanakitpipattana & Samson, sp. nov. MycoBank MB834883. Fig. 11.
**Etyymology:** Named after the family of insect host, *Cercopidae*.

Specimen found on leafhopper (*Hemiptera*). Host’s head and thorax were covered with pale green mycelium and sporulating conidiophores. Conidia smooth-walled, pale green (oac875-876), cylindrical with rounded apices, (7–)8.5–10 × 2 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 18 mm in 14 d, white mycelium, floccose, abundant aerial hyphae, dark green in the centre of colonies due to production of conidia. Sporulation starts at 7 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2–3 phialides per branch. Phialides cylindrical to ellipsoidal with semi-papillate apices, (5–)6–9(–10) × 2–2.5 μm. Conidia smooth-walled, dark green (oac125-127), cylindrical with rounded apices, 6–8 × 1.5–2 μm. Colonies on PDA attaining a diam of 15 mm in 14 d, white mycelium, floccose, abundant aerial hyphae, dark green in the centre of colonies due to production of conidia. Sporulation starts at 10 d after inoculation, reverse uncoloured. Conidiophores dense, terminating in branches, with 2–3 phialides per branch. Phialides cylindrical to ellipsoidal with semi-papillate apices, 5–8(–10) × 2–2.5(–3) μm. Conidia cylindrical with rounded apices, (6–)6.5–8 × 2 μm.

Colonies on SDAY/4 attaining a diam of 15 mm in 21 d, pale yellow mycelium, floccose, abundant aerial hyphae, with pale green border of colonies due to production of conidia. Sporulation starts at 21 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2–3 phialides per branch. Phialides cylindrical to ellipsoidal with semi-papillate apices, 5–6.5(–8) × 2–2.5(–3) μm. Conidia smooth-walled, pale green (oac48), cylindrical with rounded apices, (6–) 7–10 × 1.5–2(–3) μm.

**Typos:** Thailand, Loei Province, Phu Suan Sai National Park, on adult leafhopper (*Hemiptera*), 15 Jul. 2008, K. Tasanathai, B. Thongnuch, S. Mongkolsamrit, P. Sritikitkulchai & A. Khonsanit (holotype BBH 24005 preserved in a metabolically inactive state, culture ex-type BCC 31660).

**Habitat:** Adult leafhopper in the order Hemiptera: Cercopidae, on the underside of a dicotyledonous plant.

**Known distribution:** Thailand, known from Phu Suan Sai National Park.

**Notes:** Ecologically, *M. cercopidarum* is most similar to *M. candelabrum*, *M. huainamdangense*, *M. ellipsoideum*, *M. brasiliense* and *M. album* by infecting leafhoppers (*Hemiptera*). The conidia of *M. cercopidarum* on specimens and on media are of only one kind, cylindrical with rounded apices, similar to those reported in *M. candelabrum* and *M. huainamdangense*, and their conidial sizes are in the same range. The conidial shape of *M. cercopidarum* from the specimens differs from *M. ellipsoideum*, *M. brasiliense* and *M. album*. Conidia in *M. ellipsoideum* are ellipsoidal, occasionally ovoid, while conidia in *M. cercopidarum* are cylindrical with rounded apices. Additionally, *M. brasiliense* produces two differing size classes of conidia (short and long form) on PDA (Kepler et al. 2014) and *M. album* produces oval to oblong-ovoid conidia on OA (Petch 1931).

**Metarthizium chaiyaphumense** Tasanathai et al., Mycol. Prog. 16: 380. 2017.

**Description and illustration:** See Luangsra-ard et al. (2017) and this study. Description on OA is based on this study. Description on stroma, PDA and SDAY/4 were taken from Luangsra-ard et al. (2017).

Stroma arising from the head of the cicada nymphs, solitary or multiple, simple or 2–3 branched, greyish yellow (1C6) to yellowish olive green (1F7), straight, cylindrical, 30–35 mm long. Fertile area on the upper part of the stroma tapering or rounded, 10–15 mm long, 1–1.2 mm thick; terminal part mostly sterile, white to cream. Perithecia ovoid to obpyriform, immersed, 550–670 × 320–380 μm, oblique in arrangement. Asci cylindrical, 520–650 × 3–4 μm. Ascospores hyaline, filliform, 225–375 × 1 μm, smooth-walled, multi-septate with cells 9–21.5 μm long, remaining whole after discharge (non-fragmenting). Asexual morph found only on adult cicada of the genus Platyleura (*Hemiptera, Cicadidae*). Conidiophores arising all over the adult cicada, at first white turning green due to the production of conidia.

**Cultural characteristics:** Colonies on OA attaining a diam of 15–17 mm in 14 d, white to cream, floccose, entire margin, poor sporulation with green conidia produced on aerial mycelium. Sporulation starts at 14 d after inoculation, reverse uncoloured. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, ovoid, occasionally subglobose and cylindrical, (3–)4.5–6.5(–8) × 1.5–2 μm. Conidia smooth-walled, dimorphic; microconidia formed first, ovoid, ellipsoidal, 3–5 × 2–3 μm; macroconidia formed later, cylindrical, 8–10 × 2 μm.

Colonies on PDA attaining a diam of 18 mm in 7 d, at first white turning to parrot green (No.60) due to heavy sporulation, velvety to floccose. Colony reverse cream to pale green. Mycelium hyaline, branched, septate, smooth-walled. Conidiophores consisting of divergent, terminal, often verticillate metulae, broadly clavate, or cylindrical, 5–9 × 2–3 μm, smooth-walled. Phialides hyaline, ovoid or ellipsoidal, appressed, 5–8 × 2–3 μm. Conidia catenulate, dimorphic; microconidia formed first, ovoid, ellipsoidal or subglobose, 2–4 × 2–3 μm, macroconidia formed later, cylindrical, clavate, 4–9 × 2–3 μm.

Colonies on SDAY/4 attaining a diam of 17 mm in 14 d, at first white becoming leaf green (No.146) at 7 d in colony centre due to the production of conidia. Vegetative hyphae smooth-walled. Conidiophores densely packed, terminating in branches with 2–5 phialides per branch. Phialides clavate, 10–12 × 2–3 μm. The colony isolated from sexual morph grown on the SDAY/4 produced catenulate, dimorphic conidia; microconidia formed first, ovoid, ellipsoidal or subglobose, 3–6 × 2–3 μm; macroconidia formed later, mostly cylindrical, ellipsoidal, 12–15 × 3–5 μm.

**Typos:** Thailand, Chaiyaphum Province, Phukhiao Wildlife Sanctuary, on cicada nymph (*Hemiptera*) underground, 13 Aug. 2015, S. Mongkolsamrit, A. Khonsanit, N. Kobmoo, D. Thana-kittipattana, W. Noisripoom, P. Sritikitkulchai, S. Wongkanoun & R. Promhan (holotype BBH 41326 preserved in a metabolically inactive state, culture ex-type BCC 78198).

**Habitat:** Hemiptera: Cicadidae.

**Known distribution:** Thailand.

**Notes:** Metarthizium chaiyaphumense is closely related to *M. takense*, as well as *M. cicadae*, *M. cylindrosporum*, *M. megapomponia*, *M. niveum*, and *M. viridulum*. All species
Fig. 17. *Metarhizium flavum* (BBH 47499, culture ex-type BCC 90870). A–B. Stromata arising from host. C–E. Ordinal perithecial orientation. F. Asci. G. Ascus tip. H. Ascospores. I. Whole ascospore showing septa (arrows). J. Conidia on insect host. K. Colonies on OA. L–M. Phialides and conidia on OA. O. Colonies on PDA. P–R. Phialides and conidia on PDA. S. Colonies on SDAY/4. T–U. Phialides and conidia on SDAY/4. V. Chlamydospores. W. Conidia. Scale bars: A = 10 mm; B = 20 mm; C = 4 mm; D, F = 100 μm; E = 350 μm; G, L = 5 μm; H = 20 μm; I, M, N, P, Q, R, T–W = 10 μm.
in this subclade produce nomuraea-like asexual morphs and conidia that adhere laterally to produce columns. Two differing size classes of conidia (dimorphic) are produced by _M. chayaphumense_, a characteristic also seen in _M. takense_, _M. cicadae_ and _M. cylindrosporum_.

**Metarhizium cicadae** Luangsa-ard, Tanasanathi, Thanakitipattana, & Samson, *sp. nov*. MycoBank MB834887. Fig. 12.

**Etymology**: Name refers to cicada host.

Specimens found on adult cicadas. Hosts covered by mycelium, pale green to greyish green, with heavy sporulation. _Synnemata_ absent, mononematous. _Conidium_ smooth-walled, dimorphic; microconidia ovoid, ellipsoidal, (3–)4–5.5(–6) × (2–)2.5–3(–4) μm; macroconidia cylindrical, (12–)16.5–20(–22) × 3–4 μm.

**Cultural characteristics**: Colonies on OA attaining a diam of 20 mm in 14 d, mycelium floccose, cottony, cream (oac900) to olive green (oac82), powdery while sporulating. Sporulation starts at 7 d after inoculation. _Conidiophores_ arising from hyphae, smooth-walled. _Phialides_ solitary or in a group of three to ten borne directly on metulae, nomuraea-like, smooth-walled, cylindrical, 4–6(–9) × 3 μm. _Conidia_ smooth-walled, dimorphic; microconidia formed first, ovoid, ellipsoidal, (2–)3.5–5.5(–6) × (2–)2.5–4(–5) μm; macroconidia formed later, cylindrical, (10–)13.5–18.5(–22) × (2–)2.5–4 μm.

Colonies on PDA attaining a diam of 15 mm in 14 d, floccose, cream to green with age (oac892–oac39). Sporulation starts at 7 d after inoculation, reverse uncoloured. _Conidiophores_ arising from hyphae, smooth-walled. _Phialides_ solitary or in a group of three to ten borne directly on metulae, nomuraea-like, smooth-walled, cylindrical, (4.5–)5(–7)–(10) × 2–3 μm. _Conidia_ smooth-walled, dimorphic; microconidia formed first, ovoid, ellipsoidal, 4–5.5(–7) × 2–3.5 μm; macroconidia formed later, cylindrical, (10–)15.5–22(–24) × 3–3.5(–4) μm.

Colonies on SDAY/4 attaining a diam of 12 mm in 14 d, powdery, dark green (oac38). Sporulation starts at 7 d after inoculation, reverse uncoloured. _Conidiophores_ arising from hyphae, smooth-walled. _Phialides_ solitary or in a group of three to ten borne directly on metulae, nomuraea-like, smooth-walled, cylindrical, 4–6(–7) × 2–3.5 μm. _Conidia_ smooth-walled, dimorphic; microconidia formed first, ovoid, ellipsoidal, (2–)3.5–5(–6) × 2.5–4 μm; macroconidia formed later, cylindrical, (10–)11.5–17 × 3–4 μm.

**Typus**: Thailand, Nakhon Phanom Province, Ban Don Sala, on adult cicada (_Hemiptera_), 15 Jun. 2011, K. Tasanathi, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon & W. Noisripoom (holotype BBH 30616 preserved in a metabolically inactive state, culture ex-type BCC 48881).

**Habitat**: Adult cicada (_Hemiptera_).

**Known distribution**: Thailand, found at Ban Don Sala, Nakhon Phanom Province.

Additional material examined: _Thailand_, Nakhon Phanom Province, Ban Don Sala, 17.581925 N, 104.1285 E, on adult cicada (_Hemiptera_), 15 Jun. 2011, K. Tasanathi, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon & W. Noisripoom (BCC 48696).

**Notes**: This species is morphologically similar to _M. chayaphumense_ and _M. takense_ but differs in the life stage of the infected host. _Metarhizium cicadae_ occurs on adult cicadas while _M. chayaphumense_ and _M. takense_ parasitize cicada nymphs. In _M. cicadae_ the sizes of phialides and conidia on OA and PDA are bigger than in _M. chayaphumense_ and _M. takense_ (Supplementary Table S1).

**Metarhizium clavatum** Luangsa-ard, Mongkolsamrit, Lamlertthon, Thanakitipattana & Samson, *sp. nov*. MycoBank MB834888. Fig. 13.

**Etymology**: Named after the clavate shape of the stromata.

**Stromata** two to several, simple, cylindrical to clavate, branched, up to 3.5 cm long, 3–5 mm wide. _Rhizoids_ flexuous, arising from the region between head and thorax of _Coleoptera_ larva buried ca. 6–7 cm deep under the ground. Upper part of the stromata fertile, yellow to greyish green (oac106–107), 2.5 cm long, 3–5 mm wide. _Perithecia_ immersed, oblique in arrangement with slightly protuberant ostioles, flask-shaped, (600–)625–685(–700) × (210–)240–280(–290) μm. _Asci_ cylindrical, 8-spored, up to 420 μm long, 5–6 μm wide, apical cap prominent, 3–4 × 4 μm. _Ascospores_ filiform, with septa but do not dissociate into part-spores, (224–)280–405(–420) × 1.5–1.5 μm. _Asexual morph_ not seen in nature.

**Cultural characteristics**: Colonies on OA attaining a diam of 15 mm in 14 d, leaf green mycelium with white border, floccose, entire edge, velvety to woolly. Sporulation starts at 14 d after inoculation, reverse uncoloured. _Conidiophores_ dense, terminating in branches, with 2–3 phialides per branch, forming a palisade-like layer. _Phialides_ cylindrical with semi-papillate apices, (5–)6–9.5(–10) × 2–3 μm. _Conidia_ smooth-walled, leaf green (No.146), cylindrical with rounded apices, 5–8(–10) × 2.5–(3) μm.

Colonies on PDA attaining a diam of 15 mm in 21 d, dense white mycelium, fluffy, entire edge, white turning to leaf green (No.146) in the centre of colonies due to production of conidia. Sporulation starts at 21 d after inoculation, reverse uncoloured. _Conidiophores_ terminating in branches, with 2–3 phialides per branch, forming a palisade-like layer. _Phialides_ cylindrical with semi-papillate apices, (5–)6–8(–9) × (1.5–)2–3 μm. _Conidia_ smooth-walled, leaf green (No.146), cylindrical with rounded apices, (4–)5–6.5(–7) × 2–3 μm.

Colonies on SDAY/4 attaining a diam of 15 mm in 21 d, pale green mycelium dense, fluffy with abundant aerial hyphae, circular, pulvinate, entire edge, grey border. Sporulation starts at 21 d after inoculation, reverse uncoloured. _Conidiophores_ dense, terminating in branches, with 2–3 phialides per branch. _Phialides_ cylindrical with semi-papillate apices, (6–)7–9(–10) × 1.5–2.5(–3) μm. _Conidia_ smooth-walled, pale green (No.150), cylindrical with rounded apices, 5–6 × 2–3 μm.

**Typus**: Thailand, Phitsanulok Province, Ban Phathai Community Forest, on larva of _Oxynopterus_ sp. (_Coleoptera_), 30 May 2017, S. Mongkolsamrit, W. Noisripoom & S. Lamlertthon (holotype BBH 43330 preserved in a metabolically inactive state, culture ex-type BCC 84543).

**Habitat**: Larva of _Oxynopterus_ sp. (_Coleoptera_), buried in the ground.

**Known distribution**: Thailand, known from Ban Phathai Community Forest, Phitsanulok Province.

Additional materials examined: _Thailand_, Phitsanulok Province, Ban Phathai Community Forest, 16.735031 N, 100.659608 E, on larva of _Oxynopterus_ sp.
Notes: The macromorphologies of the natural samples of *M. clavatum* are most similar to *M. kalasinense* (Luangsaa-ard et al. 2017) by having yellow to greyish green stromata and oblique perithecial arrangement. It differs significantly from *M. kalasinense* in the size of the perithecia and asci. In *M. clavatum*, perithecia and asci are smaller and shorter than those reported for *M. kalasinense* (700–800 × 250–350 μm; 500–650 × 4–5 μm). In addition, based on the multi-gene phylogeny (Fig. 1) *M. clavatum* is closest to *M. gryllidicola* on Orthoptera producing an asexual morph and to the Japanese *M. brittlebankisoides* strain Hn1. On SDAY/4, the conidia of *M. clavatum* are cylindrical while in *M. gryllidicola* they could be cylindrical, ovoid to obclavate. *Metarhizium clavatum* produces pale green colonies in contrast to the spectrum yellow to sulphur yellow colonies in *M. gryllidicola*. Members of the *M. anisopliae* species complex occurs on various insect hosts and can be isolated from the soil.
**Metarhizium culicidarum** Luangsa-ard, Khonsanit, Thanakitpattana & Samson, *sp. nov*. MycoBank MB8334889. Fig. 14.

**Etymology:** In reference to the family of the host, *Culicidae (Diptera).*

Specimens found only on adult mosquitoes (*Diptera, Culicidae*) on the underside of leaves. The thorax and wings of the hosts were covered with lime-green (No.59) powdery conidia. Phialides smooth-walled, ovoid with semi-papillate apices, 6–11 × 2–3 μm. *Conidia* smooth-walled, lime-green (No.59), fusiform-elliptical, (5–)6–7.5(–8) × 1.5–2 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 26 mm in 20 d, flat, closely appressed and slightly convex in the middle of agar surface, while to olive green (No.46), powdery while sporulating. Sporulation starts at 14 d after inoculation, reverse tawny olive (No.223D). *Conidiophores* arising from aerial mycelium, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical with semi-papillate apices, (5–)6–7.5(–9) × 2–3 μm. *Conidia* smooth-walled, olive green (No.46), fusiform-elliptical, ellipsoidal, (4–)6–7.5(–8) × 1.5–2 μm.

Colonies on PDA attaining a diam of 22–24 mm in 20 d, dense mycelium, floccose, slightly convex to the agar surface, white while turning to parrot-green (No.60), powdery while sporulating. Sporulation starts at 7 d after inoculation, reverse tawny olive (No.223D) in the middle of colony and white cream at the margin. *Conidiophores* arising from aerial mycelium, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical with semi-papillate apices, 6–8(–10) × 2–3 μm. *Conidia* smooth-walled, parrot-green (No.60), fusiform-elliptical, (5–)6.5–8 × 1.5–2 μm.

Colonies on SDAY/4 attaining a diam of 18–19 mm in 20 d, mycelium floccose, cottony, closely appressed to the agar surface, while. Sporulation starts at 5 d after inoculation, reverse smoke grey (No.45) in the middle of colony and white cream at the margin. *Conidiophores* arising from aerial mycelium, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical with semi-papillate apices, (4–)7–10(–12) × 1.5–2(–2.5) μm. *Conidia* smooth-walled, white, fusiform-elliptical, ellipsoidal, (4–)5–6.5(–7) × 1–1.5 μm.

**Typos:** Thailand, Phetchaburi Province, Kaeng Krachan National Park, on adult mosquitoes (*Diptera, Culicidae*), 28 Sep. 2000, A. Lathisungnoen, R. Nasit & W. Chaygate (*holotype* BBH 8129 preserved in a metabolically inactive state, culture ex-type BCC 7600).

**Habitat:** Adult mosquitoes (*Diptera, Culicidae*).

**Known distribution:** Thailand, found at Kaeng Krachan National Park.

**Additional materials examined:** Thailand, Phetchaburi Province, Kaeng Krachan National Park, 12.866756 N, 99.400444 E, on adult mosquitoes (*Diptera, Culicidae*), 28 Sep. 2000, A. Lathisungnoen, R. Nasit & W. Chaygate (BBH 8121, BCC 7625), (BBH 8142, BCC 12764), (BBH 8140, BCC 7601), (BBH 8742, BCC 12749).

**Notes:** *Metarhizium culicidarum* occurs on mosquitoes (*Diptera*), while *M. minus* and *M. biotecense* are found on brown planthoppers (*Hemiptera*). *Metarhizium culicidarum* shares similarities with *M. biotecense* in the cylindrical shape and size of the phialides with semi-papillate apices, which are 4–12 × 1.5–2.5 μm in *M. culicidarum* and 6–16 × 2–3 μm in *M. biotecense*. Both species differ from *M. minus* in the shape of the phialides, which is clavate in *M. minus*, 8.4 ± 1.2 × 2.8 ± 0.3 μm on Sabouraud dextrose agar+1 % yeast extract (Rombach et al. 1986). The conidia of *M. culicidarum* are fusiform-elliptical (4–7 × 1–1.5 μm), while in *M. minus* it is ellipsoidal, 4.5–7 × 2–3 μm, and in *M. biotecense* cylindrical with rounded apices or ellipsoidal, 4–7 × 2–3 μm. The colonies on SDAY/4 of *M. culicidarum* and *M. biotecense* are white, while in *M. minus* they are grey-green.

**Metarhizium cylindrosporum** [as ‘cylindrosporum’] Q.T. Chen & H.L. Guo, Acta Mycol. Sin. 5: 180. 1986.

**Synonym:** Nomuraea cylindrospora (Q.T. Chen & H.L. Guo) Tzean et al., Mycologia 85: 514. 1993.

**Description and illustration:** See Guo et al. (1986), Tzean et al. (1993).

**Typos:** China, Guizhou, unknown tea tree insect pest, collection date and collector unknown (*holotype* ACCC 30114).

**Habitat:** Adult cicada (*Hemiptera*).

**Known distribution:** China, Japan, Taiwan.

**Notes:** *Metarhizium cylindrosporum* is one of the cicada pathogens that produces dimorphic conidia (two different size classes). Other dimorphic species in this subclade include *M. cicadae, M. chaiyaphumense, M. cylindrosporum, M. niveum* and *M. takense*. Three species in this subclade occurring on cicadas, *M. owariense, M. viridulum* and *M. megapompaniae*, produce only one size class of conidia (monomorphic). Tzean et al. (1993) transferred *M. cylindrosporum* (Guo et al. 1986) based on the nature of the metulae and phialides growing along the length of the conidiophores to Nomuraea. Molecular phylogenetic studies done by Kepler et al. (2014), however, did not result in a well-supported clade for Nomuraea and green-spored Nomuraea were subsequently transferred to *Metarhizium* and henceforth synonymized Nomuraea with *Metarhizium*.

**Metarhizium dendrolimatis** Z.Q. Liang et al., Mycosphere 8: 33. 2017.

**Description and illustration:** See Chen et al. (2017).

**Typos:** China, Guizhou Province, Guiyang, Tongmuling, on *Dendrolimus* sp. in pine wood, 6 Oct. 2013, W.H. Chen (*holotype* HXDX.1006, culture ex-type GZAC IFR1006).

**Habitat:** Lepidoptera larva.

**Known distribution:** China.

**Notes:** On the natural substrate, the fungus produces nomuraea-like conidiophores consisting of whorls of flask-shaped phialides. It is closely related to *M. eburneum* occurring on *Lepidoptera* pupae and to *M. rileyi* predominantly found on *Lepidoptera* larvae. These three species produce nomuraea-like conidiophores in culture.

**Metarhizium eburneum** Luangsa-ard, Noisripoom, Thanakitpattana & Samson, *sp. nov*. MycoBank MB8334890. Fig. 15.

**Etymology:** Named after the Latin “eburneus”, meaning white as ivory. Refers to the colour of the stroma and the colonies in culture.
Stroma on Lepidoptera pupa cylindrical, solitary, simple, 10 mm long, 1–2 mm wide, white to cream. Rhizoids flexuous, arising from the pupa of Lepidoptera, ca. 8 mm long under the ground. Fertile part terminal, discoid, ovoid, 2 mm long, 2 mm wide, white to creamy. Perithecia semi-immersed, ordinal in arrangement, ovoid to obclavate with protruding apices, (603–)610–637(640) × (275–)280–298(300) μm. Asci cylindrical, (235–)270–344(462.5) × (2–)2.5–3 μm, apical cap prominent, 2–2.5 μm wide. Ascospores hyaline, filiform, whole, multi-septate, (225–)251–298.5(–360) × 1 μm. Conidia cylindrical, 2.5–3(–4) × 1 μm, seen as microcyclic sporulation of the ascospores on glass slide. Asexual morph not seen in nature.

Cultural characteristics: Colonies on OA attaining a diam of 30 mm in 14 d, white, floccose, dense mycelium, reverse cream. Hyphae smooth-walled, hyaline, 1–1.5 μm diam in diam, conidia and reproductive structure not observed.

Colonies on PDA attaining a diam of 25 mm in 14 d, white, cottony, high mycelial density, reverse cream. Hyphae smooth-walled, hyaline, 1–1.5 μm diam, conidia and reproductive structure not observed.

Colonies on SDA/Y4 attaining a diam of 25 mm in 14 d, white to creamy, cottony, high mycelial density, reverse pale yellow to cream. Hyphae smooth-walled, hyaline, 1–1.5 μm diam, conidia and reproductive structure not observed.

Typus: Thailand, Phitsanulok Province, Ban Phaothai Community Forest, on Lepidoptera pupa buried in the ground, 5 Nov. 2015, K. Tasanathai, S. Mongkolsamrit, A. Khonsanit, W. Noisripoom & D. Thanakitpipattana (holotype BBH 42744 preserved in a metabolically inactive state, culture ex-type BCC 79252).

Habitat: Lepidoptera pupa underground.

Fig. 19. Metarhizium huainamdangense (BBH 29715, culture ex-type BCC 44270). A. Fungus on adult leafhopper (Hemiptera). B. Conidia on insect host. C. Colonies on OA. D–F. Phialides and conidia on OA. G. Colonies on PDA. H–J. Phialides and conidia on PDA. Scale bars: A = 1 mm; B = 8 μm; D, E, I = 5 μm; F, H, J = 10 μm.
Known distribution: Thailand, known from Ban Phaithai Community Forest.

Additional materials examined: Thailand, Phitsanulok Province, Ban Phaithai Community Forest, on Lepidoptera pupa, buried in the ground, 5 Nov. 2015, K. Tasanathai, S. Mongkolsamrit, A. Khonsanit, W. Nairopoom & D. Thanakitpattana (BBH 42748, BCC 79266), (BBH 42749, BCC 79267).

Notes: In our phylogenetic reconstruction Metarhizium eburneum is closely related to M. viride and M. granulomatis (Sigler et al. 2010), basal to M. rileyi and M. dendromatolitis (Chen et al. 2017). Metarhizium eburneum produces the sexual morph only on Lepidoptera pupa, with cylindrical stipe, solitary, simple, white to creamy, no conidiogenous structures on cultures after 14 d. The next clade above it comprises species on Coleoptera. Metarhizium ellipsoideum differs from species on Coleoptera such as M. atrovirens, M. flavum, M. phuwiangense, M. pseudatoxirovirens, M. purpureonigrum, and M. purpureum in the host, size and shape of the stroma, and perithecia. Most of these species that parasitize Coleoptera produce immersed perithecia and only M. flavum, like M. eburneum, produces semi-immersed perithecia.

Metarhizium ellipsoideum Luangsara, Khonsanit, Thanaikitpattana & Samson, sp. nov. MycoBank MB834891. Fig. 16.

Etymology: In reference to the conidial shape on the host and on OA, PDA and SDAY/4 media.

Specimens found only on leafhoppers (Hemiptera) on the underside of leaves. Host's body was covered with parrot-green (No.60) powdery conidia. Conidia smooth-walled, parrot-green (No.60), ellipsoidal, occasionally ovoid, (3–) 4–5(–5.5) × 2.2–5 μm.

Cultural characteristics: Colonies on OA attaining a diam of 19–21 mm in 14 d, flat, closely appressed to the agar surface, white, with parrot-green (No.60), powdery conidia while sporulating. Sporulation starts at 3 d after inoculation, reverse pale horn colour (No.92). Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, 4–5.5(–6) × 1.5–3 μm. Conidia smooth-walled, parrot-green (No.60), cylindrical with rounded apices or ellipsoidal, 5–6.5(–7) × 1.5–2 μm.

Colonies on OA attaining a diam of 14–15 mm in 14 d, mycelium closely appressed to the agar surface, flat, white at the margins, white turning to parrot-green (No.60) powdery conidia while sporulating. Sporulation starts at 3 d after inoculation, reverse white cream. Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, 4–5.5(–6) × 2–3 μm. Conidia smooth-walled, parrot-green (No.60), cylindrical with rounded apices or ellipsoidal, 5–6.5(–7) × 1.5–2 μm.

Colonies on PDA attaining a diam of 14–15 mm in 14 d, mycelium closely appressed to the agar surface, white turning to olive-yellow (No.52) to sulphur yellow (No.57). Sporulation starts 3 d after inoculation, reverse tawny olive (No.223D). Conidiophores arising from aerial mycelium, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, 4–5.5(–7) × 1.5–3 μm. Conidia smooth-walled, sulphur yellow (No.57), cylindrical with rounded apices or ellipsoidal, (4–) 4.5(–6)(–7) × 1.5–2 μm.

Typus: Thailand, Chiang Mai Province, Chiang Dao Wildlife Sanctuary, on adult leafhopper (Hemiptera), 17 Aug. 2011, A. Khonsanit, K. Sansatchanon, K. Tasanathai, P. Srikulchulchai & S. Mongkolsamrit (holotype BBH 30724 preserved in a metabolically inactive state, culture ex-type BCC 49285).

Habitat: Adult leafhoppers (Hemiptera) on the underside of monocotyledonous and dicotyledonous leaves.

Known distribution: Thailand, found from Chiang Dao Wildlife Sanctuary, Khaosoi Dao Wildlife Sanctuary, Khaoyai National Park and Phu Kaeng Waterfall.

Additional materials examined: Thailand, Chanthaburi Province, Khaoyai Wildlife Sanctuary, 13.103906 N, 102.194322 E, on adult leafhopper (Hemiptera), 26 Mar. 2000, R. Nasit (BBH 2566, BCC 7550); Nakhon Ratchasima Province, Khaoyai National Park, 14.439089 N, 101.372228 E, on adult leafhopper (Hemiptera), 5 Sep. 2001, R. Nasit (BBH 9730, BCC 8516); on adult leafhopper (Hemiptera), 1 Oct. 2002, R. Nasit & W. Chegade (BBH 12847, BCC 8687); on adult leafhopper (Hemiptera), 10 Dec. 2009, A. Khonsanit, K. Tasanathai, M. Sudhadham, P. Srikulchulchai, R. Rirdkaew, S. Mongkolsamrit & T. Chohmee (BBH 27327, BCC 40161); on adult leafhopper (Hemiptera), 16 May 2012, A. Khonsanit, K. Tasanathai, M. Sudhadham, P. Srikulchulchai, R. Rirdkaew, S. Mongkolsamrit & T. Chohmee (BBH 32448, BCC 53509); Chiang Rai Province, Phu Kaeng Waterfall nature trail, on adult leafhopper (Hemiptera), 17 Jan. 2009, A. Khonsanit, K. Tasanathai, P. Srikulchulchai, R. Promharn, S. Mongkolsamrit & T. Chohmee (BBH 26421, BCC 34770).

Notes: Metarhizium ellipsoideum shares similarity with M. album, M. brasiliense, M. candelabrum, M. ceropidium, and M. huainamdangense in the production of cylindrical phialides with rounded ends. It differs in the size, which is shorter than those from the above-mentioned species (Table 5 and Supplementary Table S1). Metarhizium ellipsoideum also produces cylindrical conidia with rounded apices but the conidia are shorter than in M. candelabrum, M. ceropidium and M. huainamdangense. Metarhizium brasiliense produces two differing size classes of conidia, ellipsoidal and cylindrical, and M. album produces oval to oblong-ovoid conidia (Petch 1931, Kepler et al. 2014). The colony colour of these species also vary. In M. ellipsoideum it is white to parrot green while in M. ceropidium and M. candelabrum they are pale green to pale yellow. Metarhizium huainamdangense produces grey pink colonies while M. brasiliense produces white to cream, dark green, bluish green colonies (Kepler et al. 2014).

Metarhizium flavoviride as Metarhizium flavoviride’ W. Gams & Rozsypal, Acta Bot. Neerl. 22: 519. 1973.

Description and illustration: See Gams & Rozsypal (1973).

Typus: Czech Republic, on larvae & pupae of Ceutorhynchus maculata-alba (Coleoptera, Curculionidae), 1956, J. Rozsypal (culture ex-type ARSEF 2133 = CBS 218.56 = IMI 170146 = ATCC 32969).

Habitat: Coleoptera, soil.

Known distribution: Australia, Czech Republic, Germany.

Notes: Metarhizium flavoviride was separated from M. anisopliae by Gams & Rozsypal (1973) based on the yellow-green colonies on larvae and pupae of curculionids and broadly ellipsoidal conidia with faintly differentiated basal end in fresh strains and cylindrical with a rounded upper and a tapering truncate basal end in older strains. Molecular phylogenetic studies by Driver et al. (2000) and Bischoff et al. (2009) have shown it as a species complex distinct from M. anisopliae. Strains of M. flavoviride seem to be cold-active, germinating and sporulating at low temperatures (Driver et al. 2000).
Metarhizium flavum Luangsara, Mongkolsamrit, Thanakitipattana & Samson, *sp. nov.* MycoBank MB834892. Fig. 17.

**Etymology:** Name refers to the yellow colour of stromata.

**Stromata** are buried in the ground, dark green (oac104). Conidiophores are arising from region between head, thorax, and abdomen of Coleoptera larvae, ca. 2 – 3 cm buried in the ground. Upper part of the stromata fertile, pale yellow to olive yellow (No. 52), 0.5 – 3 cm long, 2 – 4 mm wide. *Perithecium* semi-immersed, ordinal in arrangement with slightly protuberant ostioles, ovoid, (500 –) 545 – 640 – 650) × (270 –) 280 – 320 – 330) μm. Ascii cylindrical, 8-spored, 280 – 320 × 5 – 6 μm, apical cap prominent, 5 – 6 × 5 – 6 μm. Ascospores filiform, with septa but do not dissociate into part-spores, hyaline, (200 –) 225 – 295 – 315) × 1.5 – 2 μm. The asexual morph was seen only on one sample in nature. The sporulating conidiophores are produced on the body and on rhizoids from the insect host which are buried in the ground, dark green (oac104-105). Conidia smooth-walled, cylindrical with rounded apices, (8 – 8) 5 – 11( – 12) × 3 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 10 mm in 14 d, white mycelium with low density, flat, entire edge, turning to pale green (oac104-105) in the centre of colonies due to production of conidia. Sporulation starts at 7 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2 – 3 phialides per branch, single phialides produced along the hyphae. *Phialides* cylindrical with semi-papillate apices, (5 –) 6.5 – 9( – 10) × 2 – 3 μm. *Conidia* smooth-walled, pale green (oac104–105), cylindrical with rounded apices, (6 – 6) 5 – 9( – 10) × 2 – 3 μm.

Colonies on PDA attaining a diam of 8 mm in 14 d, white mycelium, low density, fluffy, irregular edge, turning to dark green in the centre of colonies due to production of conidia. Sporulation starts at 14 d after inoculation, reverse brown. Conidiophores terminating in branches, with 2 – 3 phialides per branch, single phialides produced along the hyphae. *Phialides* cylindrical with semi-papillate apices, (7 – 8) 10 × (2 –) 2) 5 – 3 μm. *Conidia* smooth-walled, dark green (oac104-105), cylindrical with rounded apices, (7 –) 7.5 – 9.5( – 10) × 2 – 3 μm.

Colonies on SDA4/4 attaining a diam of 3 mm in 14 d, pale yellow mycelium, less dense, fluffy, irregular edge. Sporulation starts at 14 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2 – 3 phialides per branch, single phialides produced along the hyphae. *Phialides* cylindrical with semi-papillate apices, (7 –) 8.5 – 10.5( – 12) × 2 – 2.5( – 3) μm. *Chlamydospores* present, singly or in short chains, subglobose, up to 10 μm in diameter. *Conidia* smooth-walled, hyaline, cylindrical with rounded apices, 7 – 9( – 10) × 2 – 2.5( – 3) μm.

**Typus:** Thailand, Chiang Mai Province, San Buak Wai Community Forest, on Coleoptera larva, 20 Aug. 2019, S. Mongkolsamrit, N. Kobmoo, P. Sritikitkulchai, U. Pinruan, P. Khamsumton & S. Sommai (holotype BBH 47499 preserved in a metabolically inactive state, culture ex-type BCC 90870).

**Habitat:** Coleoptera larva, buried in the ground.

**Known distribution:** Thailand.

**Additional materials examined:** Thailand, Chiang Mai Province, San Pa Pao Community Forest and San Buak Wai Community Forest, Chiang Mai Province.

Notes: Phylogenetically, *M. flavum* is closely related to *M. purpureum* and *M. purpureonigrum* but differs in the colour of its stromata. *Metarhizium flavum* has pale yellow to olive yellow stromata while *M. purpureum* and *M. purpureonigrum* have purple stromata. The perithecia of *M. flavum* are semi-immersed but in *M. purpureum* and *M. purpureonigrum* the perithecia are immersed. However, *M. flavum* shares similarity to *M. purpureum* and *M. purpureonigrum* by having perithecia in ordinal arrangement. The sporulation of *M. flavum* can be observed on three media while in *M. purpureum* and *M. purpureonigrum* the sporulation can be observed only on OA. On OA these three species produce cylindrical conidia that are all in the same size range.

**Metarhizium frigidum** J. Bisch. & S.A. Rehner, Mycologia 98: 741. 2006.

**Description and illustration:** See Bischoff et al. (2006).

**Typus:** Australia, Victoria, Ballarat, on larva of *Adyorphus* sp. (Coleoptera, Scarabaeidae), 10 Jun. 1994, Reinganum (holotype BPI 872114, culture ex-type ARSEF 4124).

**Habitat:** Coleoptera, Isoptera, soil.

**Known distribution:** Australia.

Notes: *Metarhizium frigidum* and *M. flavoviride* are closely related in the *M. flavoviride* clade. The colour of the conidia of *M. frigidum* is reminiscent of those of *M. anisopliae*, while the conidia of *M. flavoviride* are bright yellow green on SDA4/4.

**Metarhizium fusoidema** Luangsara, Mongkolsamrit, Thanakitipattana & Samson, *sp. nov.* MycoBank MB834893. Fig. 18.

**Etymology:** In reference to the fusoid shape of conidia in natural specimens.

Specimen found on adult moth (*Lepidoptera*). Hosts’ head and thorax were covered with pale green mycelium and sporulating conidiophores. *Conidia* smooth-walled, parrot green (No.260), broadly fusoid, 5 – 6 × 2 – 3 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 22 mm in 14 d, dark green, flat, entire edge, white border, dark green of colonies due to production of conidia. Sporulation starts at 5 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2 – 3 phialides per branch. *Phialides* cylindrical with semi-papillate apices, (7 –) 7.5 – 10 × 2 μm. *Conidia* smooth-walled, parrot green (No.260), ellipsoidal to cylindrical with rounded apices, (5 –) 7 – 10 × 2 – 3 μm.

Colonies on PDA attaining a diam of 22 mm in 14 d, dark green, flat, entire edge, white border, dark green of colonies due to production of conidia. Sporulation starts at 5 d after inoculation, reverse uncoloured. Conidiophores terminating in branches, with 2 – 3 phialides per branch. *Phialides* cylindrical with semi-papillate apices, (5 –) 7 – 10 × 2 – 3 μm. *Conidia* smooth-walled, parrot green (No.260), ellipsoidal to cylindrical with rounded apices, (5 –) 6.5 – 9.5( – 10) × 2 – 2.5( – 3) μm.

Colonies on SDA4/4 attaining a diam of 15 mm in 14 d, white to pale cream, abundant aerial mycelium, fluffy, undulate edge, pale brown margin (oac776), brown due to production of conidia. Sporulation starts at 10 d after inoculation, reverse uncoloured.
**Conidiophores** terminating in branches, with 2–3 phialides per branch. **Phialides** cylindrical with semi-papillate apices, (6–) 7.5–9.5(–10) × 2–2.5(–3) μm. **Conidia** smooth-walled, hyaline, ellipsoidal to cylindrical with rounded apices, (6–) 7–9.5(–10) × 2–2.5(–3) μm.

**Typus:** Thailand, Chaiyaphum Province, Phu Khiao Wildlife Sanctuary, on moth (*Lepidoptera*) on underside of a dicot leaf, 24 Oct. 2007, K. Tasanathai, S. Mongkolsamrit, P. Srikitikulchai, B. Thongnuch, R. Ridkaew & A. Khonsanit (holotype BBH 22698)

**Fig. 20.** *Metarhizium megapomponiae* (BBH 19660, culture ex-type BCC 25100). **A–B.** Fungus on adult cicada. **C.** Phialides and conidia on host. **D–E.** Conidium on insect host. **F.** Colonies on OA. **G–H.** Phialides and conidia on OA. **I.** Conidia on OA. **J.** Colonies on PDA. **K–L.** Phialides and conidia on PDA. **M.** Conidia on PDA. **N.** Colonies on SDAY/4. **O–P.** Phialides and conidia on SDAY/4. **Q.** Conidia on SDAY/4. Scale bars: A, B = 10 mm; C = 8 μm; D–Q = 5 μm.
preserved in a metabolically inactive state, culture ex-type BCC 28246).

**Habitat:** On moth (Lepidoptera) and on barklice (Psocoptera), on the underside of dicotyledonous plants.

**Known distribution:** Thailand, known from Phu Khiao Wildlife Sanctuary and Khao Yai National Park.

**Additional materials examined:** Thailand, Nakhon Ratchasima Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on Psocoptera, 22 Sep. 2012, K. Tasanathai, S. Mongkolsamrit, A. Khonsanit & W. Noisripoom (BBH 32443, BCC 53130); idem., on Psocoptera, 7 Apr. 2010, K. Tasanathai, S. Mongkolsamrit, T. Chohme, A. Khonsanit & R. Ridkaew (BBH 28541, BCC 41242).

*Notes:* *Metarhizium fusoideum* is a member of the *M. flavoviride* species complex and is closely related to *M. koreanum* (Kepler et al. 2014). Based on natural specimens from Thailand, the conidia of *M. fusoideum* are distinguishable from *M. koreanum*. Conidia in *M. fusoideum* are broadly fusoid while conidia in *M. koreanum* are cylindrical, ellipsoidal, or ovoid. The colony colour of *M. fusoideum* and *M. koreanum* on OA and PDA are green with conidial mass. The phialides are cylindrical and conidia are ellipsoidal to cylindrical with rounded apices. However, on SDAY/4 *M. fusoideum* produces white to cream colonies with brown border while the colony of *M. koreanum* is brownish yellow. Both species have similar micro-morphologies – the
Metarhizium gaoligongense Z.H. Chen & L. Xu, Int. J. Agric. Biol. 20: 2272. 2018.

Description and illustration: See Chen et al. (2018c).

Typus: China, Yunnan Province: Gaoligong Mountains, soil of a coffee farmland, 12 May 2015, Z.H. Chen (culture ex-type CCTCC M 2016588).

Habitat: Soil.

Known distribution: China.

Notes: Metarhizium gaoligongense, found in soil, is closely related to M. nomnoi, M. pempigii and M. bibiniodarum occurring on insects.

Metarhizium globosum J.F. Bisch et al., Mycologia 101: 520. 2009.

Description and illustration: See Bischoff et al. (2009).

Typus: India, on Pyrausta machaeraulis (Lepidoptera. Pyralidae) on teak, Tectona grandis, 12 Sep. 1988, R.C. Rajak (holotype BPI 878294, culture ex-type ARSEF 2596).

Habitat: Lepidoptera.

Known distribution: India.

Notes: The globose conidia of M. globosum is a distinguishing character that is not found in any other species in the M. anisopliae complex. It forms a close relationship with M. acridum and can both be distinguished by conidial shape. Metarhizium acridum produces ovoid conidia.

Metarhizium granulomatis (Sigler) Kepler et al., Mycologia 106: 822. 2014.

Basionym: Chamaeleomycetes granulomatis Sigler, J. Clin. Microbiol. 48: 3188. 2010.

Description and illustration: See Sigler et al. (2010).

Typus: Denmark, Copenhagen, from liver of a chameleon, collection date and collector unknown (culture ex-type UAMH 11028).

Habitat: Chamaeleo calyptratus.

Known distribution: Denmark.

Notes: Metarhizium granulomatis and M. viride belong to the basal-most subclade in Metarhizium. Both species were isolated from diseased Chamaeleo species. It shares similarity with M. viride in producing yeast-like cells as well as the curved phialide necks. These two species produce paecilomyces-like phialides.

Metarhizium gryllidicola Khons. et al., Persoonia 44: 150. 2020.

Description and illustration: See Thanakitpipattana et al. (2020). The following descriptions are based on other specimens examined from Thailand.

Specimens found only on adult of crickets (Gryllidae) on the leaf litter on the forest floor. The host body was covered with leaf green (No.146), bunting green (No.150) and dark green (28F8) powdery conidia. Phialides smooth-walled, ovoid with semi-papillate apices, occasionally cylindrical, 5–10 × 2–3 μm. Conidia smooth-walled, ellipsoidal, cylindrical, 5–6.5(–7) × 2–3 μm.

Cultural characteristics: Colonies on OA attaining a diam of 26–27 mm in 14 d, flat, closely appressed to the agar surface, at first white turning bunting green (No.150) and leaf green (No.146), powdery while sporulating, white at the margins. Sporulation starts at 3 d after inoculation, reverse pale horn (No.92). Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical, (5–)6.5–9(–11) × 2–3 μm. Conidia smooth-walled, bunting green (No.150), leaf green (No.146), ovoid to ellipsoidal, occasionally cylindrical, (4.5–)5–6.5(–7) × 2–3 μm.

Colonies on PDA attaining a diam of 25–27 mm in 14 d, flat, closely appressed to the agar surface, at first white turning leaf green (No.146), white at the margins, powdery while sporulating. Sporulation starts at 5 d after inoculation, reverse white. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical, utriform, without a distinct neck, (5–)6–9(–12) × 2–3 μm. Conidia smooth-walled, leaf green (No.146), cylindrical, ovoid, (5–)5.5–7 × 2–3 μm.

Colonies on SDAY/4 attaining a diam of 25–26 mm in 20 d, mycelium dense, floccose, cottony, white turning to sulphur yellow (No.57) and chamois (No.123D), powdery while sporulating. Sporulation starts at 15 d after inoculation, reverse white. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical, utriform, without a distinct neck, (6–)7–9.5(–11) × 2–3 μm. Conidia smooth-walled, sulphur yellow (No.57) and chamois (No.123D), cylindrical to ovoid to obclavate, (4–)5–6(–7) × 2–3 μm.

Typus: Thailand, Nakhon Ratchasima Province, Khao Yai National Park, on adult crickets, 1 Nov. 2016, D. Thanakitpipattana, N. Kobmoo & R. Somnuk (holotype BBH 44436 preserved in a metabolically inactive state, culture ex-type BCC 82988).

Habitat: On adult crickets (Gryllidae) on the leaf litter in the forest.

Known distribution: Thailand, Khao Yai National Park.

Additional materials examined: Thailand, Nakhon Ratchasima Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on adult of crickets, 18 Jun. 2008, B. Thongnuch, J. Luangsa-ard, K. Tasanathai, P. Srikitikulchai, R. Prinnum, R. Ridkaew, S. Mongkolsumrat & W. Chaygaye (BBH 23876, BCC 30917); idem., 14 Aug. 2009, K. Tasanathai, P. Sritikutichai, R. Ridkaew, S. Mongkolsumrat & T. Chohmee (BBH 26529, BCC 37915), (BBH 26533, BCC 37918); idem., 11 Jul. 2012, A. Khonsanit, K. Sansatchanon, K. Tasanathai, P. Sritikutichai, R. Somnuk, S. Mongkolsumrat & W. Noisriroom (BBH 32733, BCC 53857); Nakhon Nayok Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on adult of cricket, 5 Jul. 2006, B. Thongnuch, J. Luangsa-ard, K. Tasanathai, P. Sritikutichai, S. Mongkolsumrat & W. Chaygaye (BBH 18647, BCC 22353).

Notes: Metarhizium gryllidicola is a member of the M. anisopliae complex and is close to M. brittlebankisioides and M. clavatum. It is only found occurring on adult crickets (Gryllidae), while M. brittlebankisioides and M. clavatum are from Coleoptera. Both M. clavatum and M. gryllidicola produce cylindrical conidia that are of the same size range and shape on SDAY/4 and PDA. However, on OA M. gryllidicola produces ovoid to ellipsoidal, occasionally cylindrical conidia while M. clavatum produces only cylindrical conidia.
Metarhizium guizhouense Q.T. Chen & H.L. Guo, Acta Mycol. Sin. 5: 181. 1986.

Synonyms: Metarhizium taii Z.Q. Liang & A. Y. Liu, Acta Mycol. Sin. 10: 260. 1991.
Metacordyceps taii (Z.Q. Liang & A.Y. Liu) G.H. Sung et al., Acta Mycol. Sin. 10: 257. 1991.

Description and illustration: See Guo et al. (1986) and Liang et al. (1991).

Typus: China, Guizhou Province, on Hepialis, Lepidoptera, 30 Oct.1980, Z.Q. Liang (holotype ACCC 30115 (asexual morph), SGA-C88-601 (M. taii, sexual morph), culture ex-type CBS 258.90).

Habitat: Lepidoptera.

Known distribution: China.

Notes: Metacordyceps taii was recognised by Bischoff et al. (2009) to be the sexual morph of Metarhizium guizhouense and therefore Mc. taii is considered a synonym of M. guizhouense. It is closely related to M. sulphureum which also occurs on Lepidoptera larva. Both M. sulphureum and the sexual state of M. guizhouense have obliquely arranged perithecia. However, M. guizhouense (= Mc. taii) has distinctly bigger perithecia, 267–794(–1061) × 247–354 μm, which are curved, ampullaceous and completely immersed in the stroma than M. sulphureum, which has semi-immersed, ovoid perithecia, 600–700 × 420–450 μm. Metarhizium guizhouense produces ascospores that break into part-spores while M. sulphureum produces whole, filiform ascospores.
Metarhizium gunjiangiense  (C.R. Li et al.) Kepler et al., Mycologia 106: 822. 2014.

Conidia pale green mycelium and sporulating conidiophores.

Location of the specimen.

Etymology

Smooth-walled, pale green (oac875-876), cylindrical with rounded apices, 5–9.5(–10) × 2.5(–3) μm.

Conidia 8–10(–12) μm, are longer than those of M. owariense (640–800 × 4–6 μm), M. viridiscens (440–640 × 180–320 μm and 180–300 × 5–6.5 μm, respectively).

Notes: This species is placed in Metarhizium based on morphological and molecular data presented in Li et al. (2010). The ITS phylogeny (Supplementary Fig. S1) shows it closely related to M. cylindrosporum, M. niveum and M. viridulum. Metarhizium gunjiangiense produces the largest conidia followed by M. cylindrosporum and M. viridulum (Li et al. 2010). Morphologically, it is similar to M. owariense f. viridescens in occurring on cicada nymphs but differs in the colour of the stomata. Furthermore, the sizes of phialidia and asci of M. gunjiangiense (640–770 × 240–320 μm and 310–380 × 4–4.8 μm) are longer than those of M. owariense f. viridescens (440–640 × 180–320 μm and 180–300 × 5–6.5 μm, respectively).

Metarhizium huainamdangense Luangs-a-ard, Mongkolsrir, Thanakitpipattana & Samson, sp. nov. MycoBank MB838498. Fig. 19.

Etymology: Named after Huai Nam Dang National Park, the type location of the specimen.

Specimens found on the adult leafhoppers (Hemiptera) attached to the underside of dicotyledonous and monocotyledonous leaves in the forest. Hosts’ head and thorax were covered with pale green mycelium and sporulating conidiophores. Conidia smooth-walled, pale green (oac875-876), cylindrical and rounded at the apices, 5–7(–8) × 2–5.5(–3) μm. Conidiophores terminating in branches, with 2–3 phialides per branch, 3–5(–6) × 1.5–2.5 μm.

Cultural characteristics: Broths on OA attaining a diam of 15 mm in 14 d, pale cream, floccose, irregular edge, velvety to woolly, pale yellow to dark green in the centre of cultures due to production of conidia. Conidiophores terminating in branches, with 2–3 phialides per branch, 3–5(–6) × 1.5–2.5 μm.

Notes: Multi-gene phylogenetic analyses supported the recognition of this species in the M. anisopliae complex, close to M. anisopliae, M. pingshaense and M. robertsi. First reported from soil, M. humeri was also found occurring on various insect orders and have proven to be a favorable candidate to be used in biological control of insect pests.

Metarhizium indigoticum (Kobayasi & Shimizu) Kepler et al., Mycologia 108: 823. 2014.

Conidia 6.5–8.5(–10) × 2–3 μm.

Notes: Metarhizium indigoticum is one of the sexually reproductive species in the Metarhizium anisopliae complex and is closely related to M. majus and M. phasmatodeae.
**Description and illustration:** See Luangsa-ard et al. (2017) and this study. Description on OA is based on this study. Description on stroma, PDA and SDAY/4 were taken from Luangsa-ard et al. (2017).

**Stromata** simple to sparingly branched, yellow brown (5D8) when young turning olive green (1F7) to greenish brown (8F3) with age, dark green (30F3) ostioles. **Rhizoids** flexuous, up to 30 cm buried deep in the ground. Stipe of the stroma brownish yellow (5C8) to olive green (1F7), up to 0.5 cm broad. Sterile stipe emerging from the ground, cylindrical, mustard yellow (4B7) to olive green (1F7), 3–5 cm long, 0.5 cm wide. Fertile part clavate, 25–30 × 3–5 mm. **Perithecia** flask-shaped, immersed, oblique in arrangement, 700–800 × 250–350 μm, each wall with a layer of closely arranged parallel hyphae, 20–30 μm thick. **Asci** hyaline, cylindrical, 500–650 × 4–5 μm, with a prominent apical cap, 5–8 × 3–5 μm. **Ascospores** filiform, hyaline, without septations and not fragmenting into part-spores, 400–500 × 1–1.5 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 15 mm in 14 d, green black to black. Sporulation starts at 7 d after inoculation, reverse uncoloured. **Conidiophores** arising from aerial mycelia, erect, smooth-walled, cylindrical. **Phialides** smooth-walled, ovoid, occasionally cylindrical, (6–) 7–9(–10) × 2 μm. **Conidia** smooth-walled, globose, (4–) 5–6(–7) × 2.5–3(–4) μm.

Colonies on PDA attaining a diam of 10 mm in 14 d, at first white turning pale yellow green (No.58) with the production of conidia, velvety to fumicolose, reverse cream to yellow. **Phialides** cylindrical, narrowing at the tip, to lanceolate. **Conidia** cylindrical with rounded ends, forming long chains, 6–7 × 2–3 μm.

---

**Fig. 23.** *Metarhizium ovoidosporum* (BBH 25358, culture ex-type BCC 32600). A. Fungus on adult Lophopid planthopper. B. Phialides and conidia on insect host. C. Conidia on insect host. D. Colonies on OA in 14 d. E. Conidiophores bearing phialides and conidia on OA. F. Conidia on OA. G. Colonies on PDA in 20 d. H. Conidiophores bearing phialides and conidia on PDA. I. Conidia on PDA. J. Colonies on SDAY/4 in 20 d. K. Conidiophores bearing phialides and conidia on SDAY/4. L. Conidia on SDAY/4. Scale bars: A = 5 mm; B, C, E, F, H, I, K, L = 5 μm.
Colonies on SDAY/4, attaining a diam of 10 mm in 14 d, at first white becoming greenly pigmented after 5 d (Greenish Olive, No.49) turning yellow (No.55) in the middle and surrounding the colonies. Colonies floccose, with areas appearing powdery due to production of conidia. Conidiophores dense, terminating in branches, with 2–3 phialides per branch. Phialides clavate, 8–12 × 2–3 μm. Conidia cylindrical with rounded ends, 6–8 × 2–3 μm.

**Typus: Thailand,** Kalasin Province, Khok Pa Si Community forest, on Coleoptera larva, 15 Jun. 2012, K. Tasanathai, S. Mongkolsamrit, P. Srikittikulchai, A. Khonsanit & W. Noisriprom (holotype BBH 34585 preserved in a metabolically inactive state, culture ex-type BCC 53582).

**Habitat:** Coleoptera larva.

**Known distribution:** Thailand, known from Kalasin Province.

**Additional materials examined:** Thailand, Kalasin Province, Khok Pa Si Community forest, 16.562794 N, 104.103092 E, on Coleoptera larva, 15 Jun. 2012, K. Tasanathai, S. Mongkolsamrit, P. Srikittikulchai, A. Khonsanit & W. Noisriprom (BBH 34584, BCC 53581); idem., 26 Jun. 2012, A. Khonsanit & W. Noisriprom (BBH 32209, BCC 53629); idem., 19 Jul. 2012, K. Tasanathai, A. Khonsanit & W. Noisriprom (BBH 34586, BCC 53874), (BBH 34590, BCC 53876), (BBH 34592, BCC 53877).

**Notes:** This species is morphologically very similar to *M. camposterni* but differs not only in having 8-spored ascii but also in the size of the perithecia, ascii and ascospores.

**Metarhizium koreanum** Kepler et al., Mycologia 106: 823. 2014.

**Description and illustration:** See Kepler et al. (2014). The description below is based on specimens collected in Thailand.

Specimens found on plant hopper (Fulgoromorpha, Hemiptera) on the underside of leaves. Hosi’s head and thorax were covered with Paris green (No.63) powdery conidia. *Conidia* smooth-walled, cylindrical, ellipsoidal, ovoid, (4–)4.5–5.5(–6) × 2.2–5 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 24 mm in 14 d, flat, closely appressed to the agar surface, at first white turning olive-green (No.47) and powdery while sporulating, white at the margins, producing bunting green (No.150) pigmentation in agar culture. Sporulation starts 4 d after inoculation, reverse citrine (No.51), olive yellow (No.52) in the middle of colony and white cream at the margin. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. **Phialides** smooth-walled, cylindrical, (5–)8–11.5(–13) × 2–2.5 μm. *Conidia* smooth-walled, buff (No.24), cylindrical with rounded apices, ellipsoidal, (4–)5.5–7(–7.5) × 1.5–2.5(–3) μm.

Colonies on SDAY/4 attaining a diam of 19–20 mm in 14 d, flat, closely appressed to the agar surface, at first white turning to buff (No.24) and spectrum yellow (No.55), powdery while sporulating, white at the margin. Sporulation starts at 5 d after inoculation, reverse citrine (No.51), olive yellow (No.52) in the middle of colony and white cream at the margin. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. **Phialides** smooth-walled, cylindrical, (5–)8–11.5(–13) × 2–2.5 μm. *Conidia* smooth-walled, buff (No.24), cylindrical with rounded apices, ellipsoidal, (4–)5.5–7(–7.5) × 1.5–2(–2.5) μm.

**Typus: Republic of Korea,** on Nilaparvata lugens (Hemiptera: Delphacidae) on rice, 16 Oct. 1985, S.B. Ahn (culture ex-type ARSEF 2038).

**Habitat:** On adult plant hoppers (Hemiptera: Fulgoromorpha and Delphacidae) on the underside of leaves.

**Known distribution:** Japan, South Korea, Thailand - found from Khlong Lan National Park, Thung Yai Naresuan Wildlife Sanctuary and Namtok Samlan National Park.

**Additional materials examined:** Thailand, Kamphaeng Phet Province, Khlong Lan National Park, 16.129661 N, 99.278694 E, on adult planthopper, 2 Oct. 2007, A. Khonsanit, B. Thongnuch, K. Tasanathai, P. Srikittikulchai, R. Ridkaew & S. Mongkolsamrit (BBH 22655, BCC 27998); Saraburi Province, Namtok Samlan National Park, 14.440100 N, 100.963038 E, on adult planthopper, 15 Jul. 2004, K. Tasanathai, N. Boonyuen, P. Puynang, S. Sivichai & V. D. Khanh (BBH 10087, BCC 16762); Kanchanaburi Province, Thung Yai Naresuan Wildlife Sanctuary, 15.333364 N, 98.916483 E, on adult planthopper, 11 Dec. 2007, B. Thongnuch, K. Tasanathai, R. Ridkaew & S. Mongkolsamrit (BBH 23160, BCC 30455).

**Notes:** This species is a member of the *M. flavoviride* species complex, however the green pigmentation of conidia en masse is considerably darker than in other species of this complex. Conidial and phialidic morphology is apparently variable between isolates.

**Metarhizium lepidiotae** (Driver & Milner) J.F. Bisch. et al., Mycologia 101: 520. 2009.

**Basionym:** Metarhizium anisopliae var. lepidiotae Driver & Milner [as Metarhizium anisopliae var. lepidiotum], Mycol. Res. 104: 145. 2000.

**Description and illustration:** See Driver et al. (2000), Bischoff et al. (2009).

**Typus:** Australia, Queensland, near Cairns, on Lepidoptera conobrina (Coleoptera, Scarabaeidae), 5 Mar. 1994, collector unknown (holotype DAR 74302, culture ex-type ARSEF 7488 = ARSEF 7453 = CSIRO FI-1042 used by Driver et al. (2000) to describe Metarhizium anisopliae var. lepidiotum, paratypes DAR 74303–74306).

**Habitat:** Coleoptera, Isoptera, soil.

**Known distribution:** Australia, Japan, Papua New Guinea.

**Notes:** Metarhizium lepidotae is morphologically indistinguishable from *M. anisopliae* except in molecular data (Bischoff et al. 2009). Our multi-gene analyses show *M. lepidotae* nested together with *M. anisopliae* CBS 130.71 from Ukraine but not with *M. anisopliae* ARSEF 7487, which was Tulloch’s neotype (1979). Our S7/tef analysis (Fig. 2) supports this result but also shows other species identified as *M. lepidotae* (ARSEF 7412, ARSEF 4628) distinct from the type strain and forming the second basal-most clade in the complex, suggesting that we could be dealing with a different species.
Fig. 24. *Metarhizium phuwiangense* (BBH 47443, culture ex-type BCC 85069). A. Stromata arising from host. B–D. Oblique perithecial orientation. E. Asci. F. Ascus. G. Ascospores. H–J. Ascospores showing part ascospores. K. Microcyclic sporulation of ascospores. L. Colonies on OA. M–P. Phialides and conidia on OA. Q. Colonies on PDA. R–U. Phialides and conidia on PDA. V. Colonies on SDAY/4. W–Z. Phialides and conidia on SDAY/4. Scale bars: A = 10 mm; B = 5 mm; C = 120 μm; D = 300 μm; E = 60 μm; F, G, I–K = 8 μm; H = 50 μm; M, O, R = 5 μm; N, P, S–U, W, X = 10 μm; Y, Z = 7 μm.
Metarhizium majus (J.R. Johnst.) J.F. Bisch. et al., Mycologia 101: 520. 2009.  
Basionym: Metarhizium anisoplae f. major J.R. Johnst., Entomogenous Fungi of Porto Rico: 27. 1915.  
Synonyms: Metarhizium anisoplae f. oryctophagum Friederichs, Die Grundfragen und Gesetzmassigkeiten der Land-und Forstwirtschaftlichen Zoologie: 199. 1930.  
Metarhizium anisoplae var. major (J.R. Johnst.) M.C. Tulloch, Trans. Br. Mycol. Soc. 66: 409. 1976.  

**Description and illustration:** See Tulloch (1976), Bischoff et al. (2009).

**Habitat:** Coleoptera: Scarabaeidae, Isoptera, Lepidoptera, Orthoptera, Gryllidae, Phasmatodea, soil.

**Known distribution:** Australia, France, Japan, Malaysia, Philippines, Poland, Puerto Rico, USA.

**Typus:** In the absence of a useful type for Metarhizium majus, Bischoff et al. (2009) designated a dried culture stored at the US National Fungus Collection (epitype BPI 878297). This epitype was prepared from a plate of the isolate ARSEF 1914.

**Note:** Metarhizium majus is a member of the *M. anisoplae* complex that is closely related to *M. phasmatodeae* and *M. indigoticum*.

**Metarhizium megapomponiae** Luangsa-ard, Tasanathai, Thanakitpipattana & Samson, sp. nov. MycoBank MB834895. Fig. 20.

**Etymology:** Named after cicada host in the genus *Megapomponia*.

Specimens found on adult cicada (*Hemiptera*). Host was covered by mycelium, initially white, then turning pale green to greyish green, with heavy sporulation. Synnemata absent. *Conidiophores* borne on hyphae, erect, septeate, smooth-walled, hyaline, bearing divergent, terminal, verticillate metulae or phialides. Metulae broadly clavate or cylindrical. *Phialides* oval-cylindrical, ellipsoidal, (4–)5–7–(8) × 3–4 μm. *Conidia* aseptate, smooth-walled, cylindrical, ellipsoidal, usually slightly curved or allantoid, (6–)7–10–(11) × 3–4(–5) μm.

**Cultural characteristics:** Colonies on OA attaining a diameter of 15 mm in 14 d, mycelium floccose, cottony, cream (oac900) in the middle of agar surface, margin floccose, olive green (oac38), powdery while sporulating, reverse uncoloured. Sporulation starts at 7 d after inoculation. *Conidiophores* arising from hyphae, erect, smooth-walled, metulae broadly clavate. *Phialides* solitary or in groups of three to eight per metula, borne directly on the conidiophores, smooth-walled, oval-cylindrical, 5–7.5(–10) × 3–4 μm. *Conidia* smooth-walled, hyaline, cylindrical to ellipsoidal, (7–)9–11(–13) × 3–4 μm.

Colonies on SDAY/4 attaining a diam of 15 mm in 14 d, cream to yellow brown, margin floccose, white, reverse uncoloured. Sporulation starts at 7 d after inoculation. *Conidiophores* arising from hyphae, erect, smooth-walled, cylindrical. *Phialides* solitary or in groups of three to eight per metula, borne directly on the conidiophores, smooth-walled, cylindrical, (5–)5.5–8.5(–11) × (2–)2.5–4 μm. *Conidia* smooth-walled, cylindrical, ellipsoidal, usually slightly curved or allantoid, (7–)7.5–9.5(–11) × 3–4 μm.

**Typs:** Thailand. Trang Province, Khao Ban That Wildlife Sanctuary, on adult cicada, *Megapomponia* sp., 19 Mar. 2007, K. Tasanathai, S. Mongkolsumrit, P. Srikitikulchai, R. Promham & T. Chohmee (holotype BBH 19860 preserved in a metabolically inactive state, culture ex-type BCC 25100).

**Habitat:** On adult cicada (*Hemiptera, Megapomponia*).

**Known distribution:** Thailand, found at Khao Ban That Wildlife Sanctuary.

**Notes:** Phylogenetically *M. megapomponiae* is closely related to *M. viridulum* and *M. owariense*, producing monomorphic conidia. Like *M. viridulum* it produces curved or allantoid conidia. Tzean et al. (1992) reported monomorphic conidia for *M. viridulum* on MEA but it produced larger conidia (14.4–19.4 × 3.6–4.4 μm) than *M. megapomponiae*.

**Metarhizium minus** (Rombach et al.) Kepler et al., Mycologia 106: 823. 2014.  
Basionym: Metarhizium flavoviride var. minus Rombach et al., Mycotaxon 27: 89. 1986.

**Description and illustration:** See Rombach et al. (1986).

**Typs:** Philippines, IRRI, Los Banos, Manila, on *Nilaparvata lugens*, *Hemiptera: Delphacidae*, 5 Nov. 1985, MC Rombach (culture ex-type ARSEF 2037).

**Habitat:** Hemiptera.

**Known distribution:** Benin, Ecuador, Philippines, Solomon Islands, Thailand.

**Notes:** This species seems to have a narrow host range, only found occurring on leafhoppers. It is closely related to *M. biotencene*, also found on leafhoppers, but they differ in the colony growth and colour on PDA.

**Metarhizium niveum** Luangsa-ard, Tasanathai, Thanakitpipattana & Samson, sp. nov. MycoBank MB834896. Fig. 21.

**Etymology:** In reference to the colour of colony on OA, PDA and SDAY/4.

Specimens found on adult cicadas (*Hemiptera*). Hosts covered by mycelium, pale green to greyish green, with heavy sporulation. Synnemata absent. *Conidia* smooth-walled, dimorphic; microconidia ovaloid, ellipsoidal, (3–)3.5–5(–6) × 2–3 μm; macroconidia cylindrical, (16–)17.5–20 × 3.5–4 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 20 mm in 14 d, mycelium floccose, cottony, white to cream, green edge due to production of conidia. Sporulation starts at 20 d after inoculation, reverse uncoloured. *Phialides* solitary or in
a group of three borne directly on the metulae, smooth-walled, cylindrical, 6–7 × 2 μm. Conidiophores nomurae-like, hyaline, smooth-walled. Conidia smooth-walled, dimorphic: microconidia ovoid, ellipsoidal, (3–)3.5–5(–6) × 2–3 μm; macroconidia cylin-
drical, (10–)12.5–18.5(–25) × 3–4 μm.

Colonies on OA containing a diam of 24–27 mm in 14 d, mycelium closely appressed to the agar surface, flat, white in the margin with parrot-green (No.60), powdery while sporulating. Sporulation starts at 3 d after inoculation, reverse pale horn (No.92). Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, (5–)5.5–8(–10) × 1.5–2 μm. Conidia smooth-walled, cylindrical with rounded apices, (4–)4.5–6(–8) × 1.5–2 μm.

Colonies on PDA containing a diam of 21–24 mm in 14 d, mycelium closely appressed to the agar surface, flat, white at the margins turning to parrot-green (No.60), powdery while sporulating. Sporulation starts at 3 d after inoculation, reverse white cream. Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, (5–)6.5–9(–10) × 2–3 μm. Conidia smooth-walled, parrot-green (No.60), cylindrical with rounded apices, (4–)4.5–6(–8) × 1.5–2 μm.

Colonies on SDA/Y4 attaining a diam of 20–21 mm in 14 d, mycelium closely appressed and slightly convex to the agar surface, white at the margins turning to sulphur-yellow (No.57), powdery while sporulating in the middle of colony. Sporulation starts at 5 d after inoculation, reverse sulphur yellow (No.57) in the middle of colony and white cream at the margin. Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical with semi-papillate apices, (4–)4.5–6(–7) × 2–3 μm. Conidia smooth-walled, sulphur-yellow (No.57), cylindrical with rounded apices, (4–)4.5–6(–7) × 1.5–2 μm.

**Typus:** Thailand, Chaiyaphum Province, Phu Khiao Wildlife Sanctuary, on Lepidoptera larva, 13 Oct. 2005, B. Thongmunk, K. Tasanathai, P. Sritikitkulchai, R. Cheoeyklin, R. Ridkaew, S. Mongkolsamrit & W. Chaygate (holotype BBH 14938 preserved in a metabolically inactive state, culture ex-type BCC 19364).

**Habitat:** Lepidoptera larva and Coleoptera adult on the leaf litter.

**Known distribution:** Thailand, found in Phu Khiao Wildlife Sanctuary and Khao Yai National Park.

Additional material examined. Thailand: Nakhon Ratchasima Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on adult of beetle (Coleoptera), 12 Jun. 2007, C. Chuaseeharonnachai, J. Luangsa-ard, J. Sakayaroj & S. Mongkolsamrit (BBH 24540, BCC 25948).

**Notes:** Three species in the *M. flavoviride* complex are closely related to each other – *M. gaoligongense*, *M. novozealandicum*, and *M. pemphigi*. This clade is subtended by *M. bibionidarum*. On PDA *M. gaoligongense*, *M. novozealandicum* and *M. pemphigi* produce cylindrical conidia (5.4–7.7 × 1.9–2.8 μm, 4–6 × 1.5–2 μm and 5–8 × 1.5–2 μm, respectively). There is no clear distinction on the morphological characters on other media. The only difference between each of the species is their host. *Metarhizium novozealandicum* occurs on Lepidoptera and Coleoptera while *M. pemphigi* is found on Hemiptera, *M. bibionidarum* on Diptera. *Metarhizium gaoligongense* was isolated from soil.

**Metarhizium novozealandicum** Kepler et al., Mycologia 106: 823. 2014.

**Basionym:** Metarhizium flavoviride var. novozealandicum Driver & R.J. Milner, Mycol. Res. 104: 143. 2000.

**Description:** See Driver et al. (2000).

**Typus:** New Zealand, on Lepidoptera larva, Hepialidae, (holotype DAR 74293: FI-698, paratype DAR 74294).

**Habitat:** Coleoptera: Platypus sp., soil.

**Known distribution:** Australia, New Zealand.

**Notes:** All isolates studied by Driver et al. (2000) are cold-active and grow well at low temperatures (<10 °C). It is closely related to *M. purpureogenum* isolated from soil in Japan. It differs from *M. purpureogenum* in the shape of the conidia, which is ovoid to ellipsoidal in *M. purpureogenum* and cylindrical to ellipsoidal, often twisted conidia in *M. novozealandicum*.

**Metarhizium ovoidosporum** Luangsa-ard, Khonsanit, Thanakitipattana & Samson, sp. nov. MycoBank MB834898. Fig. 23.

**Etymology:** In reference to the predominantly ovoid shape of conidia.
Specimens found on Lophopid planthopper and froghopper (*Hemiptera*) on the underside of leaves. Host's body was covered with olive-grey (No.42) powdery conidia. Phialides smooth-walled, globose to subglobose 2.5–3 × 3–5 μm. Conidia smooth-walled, olive-grey (No.42), subglobose, occasionally ovoid, 3–3.5(–4) × 2–3 μm.

Cultural characteristics: Colonies on OA attaining a diam of 22–23 mm in 14 d, mycelium dense, floccose, at first white turning to olive-grey (No.42) or olive green (No.46), powdery texture while sporulating, white and cottony at the margins, slightly convex to the agar surface, producing olive-yellow (No.52) pigmentation around the margin of colony. Sporulation starts at 7 d after inoculation, reverse olive yellow (No. 52). Conidiophores arising from aerial mycelium, erect, smooth-walled, cylindrical. Phialides smooth-walled, obpyriform, ovoid, 4–5.5(–6) × 2–3 μm. Conidia smooth-walled, olive green (No.46), ovoid, occasionally ellipsoidal, (3.5–) 4–5(–5.5) × 2–2.5(–3) μm.

Colonies on PDA attaining a diam of 20 mm in 20 d, mycelium dense, floccose, cottony, slightly convex to the agar surface,
white turning to olive-grey (No.42). Sporulation starts at 6 d after inoculation, reverse citrine (No.52) with olive yellow (No. 52) in the middle of colony and white cream at the margin. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, obpyriform, ovoid, 3–5 × 1.5–2 μm. Conidia smooth-walled, olive-grey (No.42), ovoid, occasionally ellipsoidal, 3–4.5(–5) × 2–3 μm.

Colonies on SDAY/4 attaining a diam of 21–23 mm in 20 d, mycelium dense, floccose, cottony, slightly convex to the agar surface, white. Sporulation starts at 3 d after inoculation, reverse citrine (No.52) with yellowish olive-green (No.50) and olive yellow (No.52) in the middle of colony and white cream at the margin. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides obpyriform, ovoid, (3–) 3.5–5.5(–7) × 2–2.5(–4) μm. Conidia smooth-walled, white, ovoid, occasionally ellipsoidal, subglobose, 3–4(–5) × (2–) 2.5–4 μm.

**Typus**: Thailand, Kamphaeng Phet Province, Khlong Lan National Park, 16.129661 N, 99.278694 E, on adult of Lophopid planthopper (*Eurybrachidae*), 26 Sep. 2008, A. Khonsanit, K. Tasanathai, P. Srikitikulchai, R. Ridkaew & W. Chaygate (*holotype* BBH 25358 preserved in a metabolically inactive state, culture ex-type BCC 32600).

**Habitat**: On adult of lophopid planthopper and froghopper (*Hemiptera: Lophopidae, Cercopidae*) on the underside of leaves.

**Known distribution**: Thailand, found in Khlong Lan National Park.

Additional materials examined: Thailand. Phetchaburi Province, Kaeng Krachan National Park, 12.866756 N, 99.400444 E, on adult of leafhopper, 29 Sep. 2000, P. Lutthisungneon, R. Nast & W. Chaygate (BBR8126, BCC7634); Kamphaeng Phet Province, Khlong Lan National Park, 16.129661 N, 99.278694 E, on adult of froghoppers (*Cercopidae*), 2 Oct. 2007, B. Thongnuch, A. Khonsanit, K. Tasanathai, P. Srikitikulchai, R. Ridkaew & S. Mongkolmsrit (BBB 22653, BCC 29223).
Notes: *Metarhizium ovoidosporum* shares similarity with *M. prachinense* and *M. samlanense* in producing nomuraea-like phialides in culture. These three species are found in different localities in Thailand, *M. ovoidosporum* is found in Khong Lan National Park, *M. prachinense* is from Khao Yai National Park while *M. samlanense* was found in Namtok Samlan National Park. *Metarhizium ovoidosporum* occurs on lophopid planthoppers (Eurybrachidae) and froggoppers (Cercopidae) while *M. prachinense* is found on Lepidoptera larva and *M. samlanense* is found on planthoppers. Both *M. ovoidosporum* and *M. samlanense* were found with their asexual morphic states while *M. prachinense* was found in its sexual morph state. *Metarhizium ovoidosporum* produces ovoid, occasionally subglobe conidia, 3–5 × 2–4 μm, while *M. prachinense* produces subglobose conidia, 3–5 × 2–3 μm. The conidia of *M. samlanense* are globose, 3–5 μm in diam.

*Metarhizium owariense* (Kobayasi) Kepler et al., Mycologia 106: 823. 2014.

*Basionym*: Cordycipes owariensis Kobayasi, Bull. Biogeogr. Soc. Jpn. 9: 166. 1939.

*Synonyms*: Ophiocordycepsoviariensis (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, Stud. Mycol. 57: 45. 2007. *Cordycipes owariensis* f. viridescens Uchiy. & Udagawa, Mycologia 43: 136. 2002.

*Ophiocordycpes owariensis* f. viridescens (Uchiy. & Udagawa) G.H. Sung et al., Stud. Mycol. 57: 45. 2007.

*Metacordycpes owariensis* f. viridescens (Uchiy. & Udagawa) Kepler et al., Mycologia, 104: 185. 2012.

Nomuraea owariensis Uchiy. & U dagawa, Mycoscience 43: 136. 2002.

*Metarhizium owariense* f. viridescens (Uchiy. & Udagawa) Kepler et al., Mycologia 106: 823. 2014.

**Description and illustration**: See Kobayasi (1939), Uchiyama & Udagawa (2002).

**Typus**: Japan, Owari Prov. On *Platylepura kaempferi* (Hemiptera, Cicadidae), Aug 1938, Y. Kobayasi, (holotype in Kato’s Cicadidae Museum).

**Habitat**: Hemiptera: Cicadidae.

**Known distribution**: Japan.

**Notes**: *Metarhizium owariense* is in the same clade as *M. viridulum* and *M. megapomponiae*. All three species produce only one kind of conidial size and shape (monomorphic) and nomuraea-like phialides. *Metarhizium owariense* is pathogenic to cicada nymphs while *M. viridulum* and *M. megapomponiae* occur on adult cicadas. Other species occurring on cicada are usually dimorphic. *Metarhizium owariense* f. viridescens on cicada nymph (*Platylepura kuroiwa*) differs from *Metarhizium owariense* in the coloration of its stroma, which is green, as opposed to the pale yellow stroma of the latter. It is similar to *M. owariense* in the size and morphology of stromata, asci and ascospores. However, the ascospores of *M. owariense* dissociate into parts while those reported for *Metarhizium owariense* f. viridescens are whole. More collections and sequenced loci for *M. owariense* f. viridescens are necessary to transfer it to species rank.

**Metarhizium pemphigi** (Driver & R.J. Milner) Kepler et al., Mycologia 106: 824. 2014.

*Basionym*: Metarhizium flavoviride var. pemphigi Driver & R.J. Milner, Mycol. Res. 104: 144. 2000.

**Typus**: UK, Norfolk, 1975, Foster (holotype laboratory infected *Pep rhigus bursarius* DAR 74295, culture ex-type Fl-72, paratype DAR 74296).

**Habitat**: Hemiptera, Homoptera: Melanotus cribicollis.

**Known distribution**: China, UK.

**Notes**: Initially known only from the UK where it occurs on root aphids (*Pep rhigus treherenii*), the conidia of *M. pemphigi* resemble *M. anisopliae* but it is a member of the *M. flavoviride* complex and is closely related to *M. bibionidarum*, *M. gaoligongense* and *M. normai*.

**Metarhizium phasmatodeae** Khons. et al., Persoonia 44: 151. 2020.

**Description**: See Thanakitpipattana et al. (2020). The following descriptions and illustrations are from other specimens examined from Thailand.

Specimens found on stick insects (*Phasmatodea*) on the leaf litter of the forest floor. Hosts’ bodies were covered with opaline green (No.162D) and peacock green (No. 162C) powdery conidium. *Phialides* smooth-walled, ovoid with semi-papililate apices, cylindrical, (6–)8.3–10.2(–12) × (2.5–)3–4(–5) μm. *Conidia* smooth-walled, ovoid, occasionally cylindrical, (6–)6.6–8.6(–9.5) × (2–)2.6–3(–3.5) μm.

**Cultural characteristics**: Colonies on OA attaining a diam 20–21 mm in 8 d, flat, closely appressed to the agar surface, at first white turning to bunting green (No.150), leaf green (No.146), white at the margins, powdery while sporulating. Sporulation starts at 5 d after inoculation, reverse sulphur yellow (No.57). *Conidiophores* arising from aerial mycelia, erect, smooth-walled. *Phialides* smooth-walled, cylindrical, utriform, without a distinct neck, (5–)7.8–11.2(–15) × 3 μm. *Conidium* smooth-walled, bunting green (No.150), leaf green (No.146), cylindrical, oblong-elliptical, obovoid, (7–)7.6–9.2(–10) × 2–3 μm.

Colonies on PDA attaining a diam 26–27 mm in 14 d, flat, closely appressed to the agar surface, floccose, at first white turning to dark green (No.162A), white cream at the margins, powdery while sporulating. Sporulation starts at 5 d after inoculation, reverse raw umber (No.123), sulphur yellow (No.57) in the middle of colony and pearl gray (No.81) at the margin. *Conidiophores* arising from aerial mycelia, erect, smooth-walled. *Phialides* smooth-walled, cylindrical, utriform, without a distinct neck, (6–)7.7–10.6(–12) × 2–2.5(–3) μm. *Conidium* smooth-walled, dark green (No. 162A), cylindrical, ovoid, obclavate, (7–)7.6–9.2(–10) × 2–2.7(–3) μm.

Colonies on SDAY/4 attaining a diam of 24–25 mm in 14 d, flat, closely appressed to the agar surface, at first white turning to greenish olive (No.49) in the middle of colony, straw yellow (No.56), olive yellow (No.52) and pearl gray (No.81) in the margin, powdery while sporulating, white mycelium at the margin, producing olive-yellow (No.52) pigmentation in the agar medium. Sporulation starts at 5 d after inoculation, reverse
greenish olive (No.49) and yellowish olive-green (No.50). Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical, utriform, without a distinct neck, (5–)6.8–9.8(–11) × (2–)2.6–3(–3.2) μm. Conidia smooth-walled, straw yellow (No.56), olive yellow (No.52) cylindrical, ovoid, obclavate (5.5–)6.6–7.7(–8) × 2–2.5(–3) μm.

Typus: Thailand, Chiang Mai Province, Ban Hua Thung Community Forest, on stick insects (Phasmatodea) on the leaf litter, 16 Aug. 2011, A. Khonsanit, J. Kumsao, K. Tasanathai, P. Sritikitkulchai & S. Mongkolsamrit (holotype BBH 32532 preserved in a metabolically inactive state, culture ex-type BCC 49272).

Habitat: On stick insects (Phasmatodea) on the leaf litter on the forest floor.

Known distribution: Thailand, known from Ban Hua Thung Community Forest, Wat Hin Mak Peng, Chet Kot Waterfall National Park.

Fig. 27. Metarhizium sulphureum (BBH 29463, culture ex-type BCC 36592). A. Immature stroma (arrow) with developing and mature stromata on Lepidoptera larvae. B. Fertile head. C. Perithecia. D. Ascus and ascus cap showing ascospores inside. E. Ascospores. F. Colonies on OA in 20 d. G. Conidiophores bearing phialides and conidia on OA. H. Conidia on OA. I. Colonies on PDA. J. Conidiophores bearing phialides and conidia on PDA. K. Conidia on PDA. L. Colonies on SDAY/4. M. Conidiophores bearing phialides and conidia on SDAY/4. N. Conidia on SDAY/4. Scale bars: A = 10 mm; B = 1 mm; C = 200 μm; D, G, J, M = 10 μm; E = 50 μm; H, K, N = 5 μm.
Additional materials examined. **Thailand**, Chiang Mai Province, Ban Hua Thung Community Forest, 19.367814 N, 98.964903 E, on stick insects, on the leaf litter, 25 Oct. 2013, A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Sritikulchai, S. Watcharapayungkit & W. Noisripong (BBH 37785, BCC 68409); Nong Khai Province, Wat Hin Mak Peng, 17.963328 N, 102.628481 E, on stick insects, on the leaf litter, 30 Aug. 2009, K. Tasanathai, N.T. Thanh, N.T. Toan, P. Sritikulchai & T. Chomme (BBH 27078); Saraburi Province, Khao Yai National Park, 14.439069 N, 101.372228 E, on stick insects, on the leaf litter, 27 Aug. 2012, A. Khonsanit, D. Thanakitpipattana, J. Luangsa-ard, S. Mongkolsamrit & W. Noisripong (BBH 32525, BCC 55003).

**Notes:** **Metarhizium phasmatoideae** is in a clade with *M. brachyspernum*, *M. indigotica* and *M. majus*. **Metarhizium phasmatoideae** has cylindrical, obclavate, ovoid conidia, 5.5–8 × 2–3 μm, which are shorter than those reported for *M. majus* (10.5–13 × 2.5–4 μm). Both species were found in their asexual states.

**Metarhizium phuwiangense** Luangsa-ard, Mongkolsamrit, Himaman, Thanakitpipattana & Samson, sp. nov. MycoBank MB834899. Fig. 24.

**Etyymology:** Named after Phu Wiang National Park, where the type specimen was found.

**Stromata** two to three, clavate, branched. 1–1.5 cm long, 1.5–2 mm wide, becoming purple in 3 % potassium hydroxide (KOH). *Rhizoida* flexuosus, arising from region between head and thorax of Coleoptera adults, ca. 3.5 cm buried deep under the ground in the leaf litter. Upper part of the stromata fertile, orange brown (oac868-867), 0.5–1 cm long, 1.5–2.5 mm wide. *Perithecia* semi-immersed, oblique in arrangement with slightly protuberant ostiole, ovoid, (540–)575–695–(700) × (200–)295–375–(400) μm. Asci cylindrical, 8-spored, 225–320 × 3–4 μm, apical cap prominent, 3 μm wide with thin ascus tip, 1–2 μm. Ascospores filiform with septa that dissociate into 16 cylindrical part-spores, hyaline, 8–12 × 1.5–1.5 μm. Secondary conidia produced within 24 h directly on ascospores, cylindrical with rounded apices, 3–5 × 1.5–3 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 20 mm in 14 d, pale green (oac874-875) with slightly white mycelium, floccose, pale red pigmented (oac868-669) in media. Sporulation starts at 14 d after inoculation. *Phialides* produced singly along the hyphae, not in whors, with swollen globose basal portion, paecilomyces-like, 5–7.5(–10) × 2–3 μm, and distinct necks, (1–)1.5–3(–4) μm. *Conidia* smooth-walled, hyaline, ellipsoidal to cylindrical with rounded apices, in imbricate chains, 7–8 × (2.5–)3–3.5(–4) μm.

**Typus:** **Thailand**, Khon Kaen Province, Phu Wiang National Park, on Coleoptera adult, 19 Jul. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripong, W. Himaman, P. Jangsannteer & B. Sakolkrak (holotype BBH 47443 preserved in a metabolically inactive state, culture ex-type BBC 85069).

**Habitat:** Coleoptera adult, buried in the ground.

**Known distribution:** Thailand, known from Phu Wiang National Park, Phu Khiao Wildlife Sanctuary.

**Metarhizium pingshaense Q.T. Chen & H.L. Guo, Acta Mycol. Sin. 5: 181. 1986.**

**Description and illustration:** see Guo et al. (1986).

**Typus:** **China**, on pupa of Allissonotum, (Coleoptera, Scarabaeidae), collection date and collector unknown (culture ex-type CBS 257.90).

**Habitat:** Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Isopota, Orthoptera, soil.

**Known distribution:** Australia, Brazil, China, India, Indonesia, Japan, Papua New Guinea, Philippines, Solomon Islands, Thailand.

**Notes:** Based on the multi-gene phylogenetic analyses, *Metarhizium phuwiangense* is closely related to *M. reniforme*. It shares similarity with *M. reniforme* in the production of spherical to broadly ellipsoidal phialides with distinct necks. It differs distinctly from *M. reniforme* in the arrangement of conidia as well as its shape. In *M. phuwiangense* the conidia are cylindrical to ellipsoidal with rounded apices while in *M. reniforme* the conidia are kidney-shaped. *Metarhizium reniforme* is only known to occur on tettigonid grasshoppers while *M. phuwiangense* occurs on Coleoptera adults. We never found the asexual morph in nature so comparisons with the morphology on the host with *M. reniforme* could not be made. In culture, the phialides of *M. reniforme* are in whors of 2–3 but in *M. phuwiangense* they occur singly along the mycelium. It produces a unique form of conidio genesis and resembles that of *Chloridium virescens* (Cole & Samson, 1979) in being phialidic with a sympodial sequence of conidial succession.

**Metarhizium pingshaense Q.T. Chen & H.L. Guo, Acta Mycol. Sin. 5: 181. 1986.**

**Description and illustration:** see Guo et al. (1986).

**Typus:** **China**, on pupa of Allissonotum, (Coleoptera, Scarabaeidae), collection date and collector unknown (culture ex-type CBS 257.90).

**Habitat:** Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Isopota, Orthoptera, soil.

**Known distribution:** Australia, Brazil, China, India, Indonesia, Japan, Papua New Guinea, Philippines, Solomon Islands, Thailand.

**Notes:** *Metarhizium pingshaense* is a member of the ping- shaense, anisopliae, robertsi, brunneum – PARB clade – of the *M. anisopliae* complex that now includes *M. humberi* to the original four species (Fig. 2). However, members of *M. anisopliae* in this PARB clade are considered different species to the *M. anisopliae* neotype from Ukraine.

**Metarhizium prachinense** Tasanathai et al., Mycol. Prog. 16: 382. 2017.
Description and illustration: See Luangsra-ard et al. (2017) and this study. Description on OA is based on this study. Description of stroma, on PDA and SDAY/4, were taken from Luangsra-ard et al. (2017).

Stromata usually branched, on Lepidoptera larva, 50–86 × 1–2 mm, broad; stipe cylindrical, somewhat flat, pale yellow (1A3) to greyish yellow (4C6); fertile area cylindrical with pointed ends, white, pale yellow to greyish yellow, 0.8–1.7 × 1 mm. Rhizoids flexuous, up to 7 cm underground. Perithecia scattered or crowded, greyish yellow (4C6) to brown (6E5), oblique in arrangement, clavate to ovoid with slightly protruding, bent ostioles, 320–470 × 180–300 μm. Ascii hyaline, cylindrical, 100–271 × 3–5 μm, apical cap prominent, 1 × 2 μm. Ascospores filliform, hyaline, whole, 94–107 × 1 μm.

Cultural characteristics: Colonies on OA attaining a diam of 15 mm in 14 d, white to cream, floccose, entire margin, poor sporulation with green conidia produce on aerial mycelium. Sporulation starts at 14 d after inoculation, reverse uncoloured. Conidiophores arising from aerial mycelia, erect, smooth-walled, cylindrical. Phialides smooth-walled, cylindrical, (5–) 6–10 × 2–3 μm. Conidia smooth-walled, globose, (2–) 2.6–3.7(–4) × 2–3 μm. Conidia on PDA initially colourless, turning green due to the production of green conidia after 7 d. Vegetative hyphae smooth-walled. Conidiophores erect, resembling Isaria but not having tapering long necks, bearing dense whorls of branches, each bearing 3–5 conidiogenous cells. Phialides ovoid to obpyriform with short distinct neck, 3–5 × 2 μm. Conidia subglobose, green, 3–5 × 1.5–2.5 μm. Colonies on PDA initially colourless, turning green due to the production of green conidia after 7 d. Vegetative hyphae smooth-walled. Conidiophores erect, resembling Isaria but not having tapering long necks, bearing dense whorls of branches, each bearing 2–5 conidiogenous cells. Phialides ovoid to obpyriform with short distinct neck, 2–5 × 2–2.5 μm. Conidia hyaline, subglobose, 3–5 × 2–3 μm.

Typus: Thailand, Prachin Buri Province, Khao Yai National Park, on Lepidoptera larva, 2 Jun. 2011, K. Tasanathai, S. Mongkolsamrit, P. Sritikulchaisri, A. Khonsanit & W. Noisipoom (holotype BBH 30607 preserved in a metabolically inactive state, culture ex-type BCC 47979).

Habitat: Lepidoptera larva.

Known distribution: Thailand.

Additional material examined: Thailand, Prachin Buri Province, Khao Yai National Park, 14 439 069, N 101 372 228 E, on Lepidoptera larva, 12 May 2011, J. Luangsra-ard, K. Tasanathai, S. Mongkolsamrit & A. Khonsanit (BBH 30600, BCC 47950).

Notes: Metarhizium prachinense shares similarity with M. ovoidosporum and M. samlanense in producing nomuraea-like phialides in culture. Metarhizium prachinense was found in sexual morph state while M. ovoidosporum and M. samlanense were found with their asexual morph states. Metarhizium prachinense and M. samlanense produce subglobose conidia (3–5 × 2–3 μm and 3–5 μm, respectively) but M. ovoidosporum produces ovoid, occasionally subglobose conidia, 3–5 × 2–4 μm.

Metarhizium pseudoatrovirens (Kobayasi & Shimizu) Kepler et al., Mycologia 106: 824. 2014.

Basionym: Cordyceps pseudoatrovirens Kobayasi & Shimizu, Bull. Nat. Sc. Mus. Tokyo 8: 111. 1982.

Synonym: Metacordyceps pseudoatrovirens (Kobayasi & Shimizu) Kepler et al., Mycologia 104: 190. 2012.

Typus: Japan, Aomori Prefecture, Towada, Oirase, on larva of Coleoptera, 13 Sep. 1979, D. Shimizu (holotype TA 225, deposited in TNS).

Habitat: Coleoptera larva.

Known distribution: Japan.

Notes: This species differs from M. atrovirens in the ordinal arrangement of the perithecia that are completely immersed, including the ostioles.

Metarhizium purpureogenum O. Nishi et al., Mycol. Prog. 16: 994. 2017.

Description and illustration: See Nishi et al. (2017).

Typus: Japan, Nagasaki, isolated from soil in grass lawn, 2008, collector unknown (holotype NIAES 20610, culture ex-type MAFF 243305 = ARSEF 12571).

Habitat: Soil.

Known distribution: Japan.

Notes: Metarhizium purpureogenum, found in soil samples, is closely related to M. novozealandicum which was isolated from Lepidoptera, Coleoptera larva and from soil. Metarhizium purpureogenum excretes a red-purple pigment into the agar which is characteristic of this species.

Metarhizium purpureonigrum Luangsra-ard, Tasanathai, Tha- naktipattana & Samson, sp. nov. MycoBank MB834913. Fig. 25.

Etymology: Named after colour of the fresh stromata, from the Latin ‘purpura’ meaning purple and ‘nigrum’ meaning black.

Stromata protruding from the ground with several loosely connected stromata emerging from the host, 10–15 cm long, up to 10 mm wide. Fertile part on the terminal end ca. one-third of the stroma, purple to black. Perithecia crowded, ordinal in arrangement, completely immersed, elongate ovoid, (600–) 685–846(–870) × (250–)275–420(–500) μm. Ascii cylindrical, 8-spored, (245–)250–275(–280) × 6–8 μm. Ascospores hyaline, filiform, multi-septate (200–)228–270(–275) × 1.5–2 μm. From the asexual morph, conidiophores consisting of verticillate branches with whorls of phialides. Phialides cylindrical, 5–7.2(–8) × 2–3 μm. Conidia smooth-walled, hyaline, fusiform, (4–)5.4–7.7(–10) × 2–3 μm.

Cultural characteristics: Colonies on OA attaining a diam of 20 mm in 20 d, mycelium floccose, cottony, closely appressed and slightly convex in the middle of agar surface, cream (oac486) to olive green (oac873), powdery while sporulating. Sporulation starts at 14 d after inoculation. Conidiophores arising from aerial mycelia, erect, smooth-walled. Phialides smooth-walled, cylindrical, 10–12 × 3–4 μm. Conidia smooth-walled, hyaline, cylindrical, (6–)7–9.2(–10) × 2–3 μm.
Colonies on PDA extremely slow growing. Conidia and reproductive structures not observed.

Colonies on SDAY/4 extremely slow growing. Conidia and reproductive structures not observed.

**Typus:** Thailand, Nakhon Ratchasima Province, Khao Yai National Park, on Coleoptera larva, 19 Sep. 2018, J. Luangsa-ard, K. Tasanathai, D. Thanakitipipattana, B. Sakolrak, R. Somnuk, S. Mongkolsamrit, W. Noisripoom & W. Himaman (holotype BBH 47504 preserved in a metabolically inactive state, culture ex-type BCC 89247).

**Habitat:** Coleoptera larva.

**Known distribution:** Thailand, from at Khao Yai National Park.

**Additional materials examined:** Thailand, Nakhon Ratchasima Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on Coleoptera larva, 19 Sep. 2018, J. Luangsa-ard, K. Tasanathai, D. Thanakitipipattana, B. Sakolrak, R. Somnuk, S. Mongkolsamrit, W. Noisripoom & W. Himaman (BBH 44518, BCC 89248), (BBH 47505, BCC 89244), (BBH 43816, BCC 89249), (BBH 43814, BCC 89250).

**Notes:** Phylogenetically *M. purpureonigrum* is closely related to *M. purpureum"* and *M. flavum"*. Differs in the colour of its stromata in specimens producing the sexual morph. *Metarhizium purpureonigrum* and *M. purpureum* have purplish to dark stromata while *M. flavum* has pale yellow to olive yellow stromata. The perithecia of *M. purpureonigrum* and *M. purpureum* are immersed but in *M. flavum* they are semi-immersed. These three species share similarity in having perithecia in ordinal arrangement.

**Metarhizium purpureum** Luangs-ard, Mongkolsamrit, Lam- lethorn, Thanakitipipattana & Samson, sp. nov. MycoBank MB834900. Fig. 26.

**Etymology:** Refers to the purple colour of stroma on the host.

Stromata two to eight, clavate, branched, up to 4 cm long, 2.5–3 mm wide. Rhizoids flexuous, arising from region between head and thorax of Coleoptera larva, up to 3 cm buried deep underground. Upper part of the stromata fertile, dark purple (oac524–525), 1–2.5 cm long, 2.5–5 mm wide. Peri-thecia immersed, ordinal in arrangement with slightly protuberant ostiole, ovoid, (370–412–495–520) × (210–230–285–300) μm. Asci cylindrical, 8-spored, 150–250 × 5–8 μm, prominent apical cap, 5 × 5 μm. Asco-spores flliform, with septa but do not dissociate into part-spores, hyaline, (160–)200–240 × 1.5–2 μm. Asexual morph seen in nature. Stipe erect, clavate, unbranched, flattened, covered with pale blue greenish (oac175–176) to dark green (oac159–160) mycelium covered by sporulating conidio- spores. Terminal part of stroma purple. Conidiophores dense, consisting of 1–3 phialides in whorls, nomuraea-like. Phialides cylindrical or subglobose and blunt at the ends, 5–10 × 3–3.5 μm. Conidia cylindrical with rounded apices, (5–)5.5–8 × (2–)2.5–3 μm.

**Cultural characteristics:** Colonies on OA attaining a diameter of 10 mm in 21 d, pale green with slightly, flat, floccose, velvety to woolly, reverse uncoloured. Sporulation starts at 21 d after inoculation. Conidiophores terminating in single phialides or branches with 2–3 phialides. Phialides cylindrical, 5–8–10 × 2–2.5–3 μm. Conidia smooth-walled, pale green (oac101), cylindrical with rounded apices, (7–)7.5–10 × 2 μm.

Colonies on PDA attaining a diam of 5 mm in 14 d, pale cream mycelium, fluffy, reverse colorless. Conidia and reproductive structures not observed.

Colonies on SDAY/4 attaining a diam of 5 mm in 14 d, pale cream mycelium, fluffy, reverse colorless. Conidia and reproductive structures not observed.

**Typus:** Thailand, Phitsanulok Province, Ban Phaothai Community Forest, on Coleoptera larva, 4 Sep. 2016, K. Tasanathai, S. Mongkolsamrit, D. Thanakitipipattana, W. Noisripoom, R. Somnuk, P. Srikitkulchait, S. Wongkanon & S. Lamlethorn (holotype BBH 42769 preserved in a metabolically inactive state, culture ex-type BCC 82642).

**Habitat:** On larva of Oxynopterus sp. (Coleoptera), underground.

**Known distribution:** Thailand, known from Ban Phaothai Community Forest.

**Additional materials examined:** Thailand, Phitsanulok Province, Ban Phaothai Community Forest, 16.735031 N, 100.659606 E, on Coleoptera larva, 2 Aug. 2016, K. Tasanathai, S. Mongkolsamrit, D. Thanakitipipattana, W. Noisripoom, R. Somnuk, P. Srikitkulchait, S. Wongkanon & S. Lamlethorn (BBH 42769, BCC 82642), (BBH 41293, BCC 82173); idem., 27 Sep. 2016, J. Luangsa-ard, S. Mongkolsamrit, D. Thanakitipipattana, R. Somnuk, W. Noisripoom & S. Lamlethorn (BBH 41815, BCC 83564).

**Notes:** In sexual morph specimens found in nature, *M. purpureum* is mostly similar to *M. purpureonigrum* by producing multiple purplish stromata and perithecia that are ordinal in arrangement. The perithecia and ascii in *M. purpureum* are smaller and shorter than those reported in *M. purpureonigrum* (600–870 × 250–500 μm; 245–280 × 6–8 μm). The asexual morph of these two species in nature differ significantly, in *M. purpureum* only a single flattened stroma is produced and the apex of the stroma is purple while *M. purpureonigrum* has branched, multiple stromata with attenuated tips. These two species sporulate only on OA. Additionally, *M. purpureum* and *M. purpureonigrum* are sibling species to *M. flavum*. The sexual morphs of these three species differ in the colour of their stromata. *Metarhizium purpureum* and *M. purpureonigrum* have purple stromata while *M. flavum* has pale yellow to olive yellow stromata.

**Metarhizium reniforme** (Samson & Evans) Luangs-ard et al., Mycol. Prog. 16: 386. 2017.

**Basionym:** Paecilomyces reniformis Samson & Evans, Stud. Mycol. 6: 43. 1974.

**Typus:** No type has been designated for this species. An Indonesian strain was sequenced but was not deposited in a culture collection.

**Habitat:** Seems specific only to Orthoptera: Tettigoniidae.

**Known distribution:** Ghana, Indonesia, Philippines, USA.

**Notes:** The conidigenous structures of *Metarhizium reniforme* are reminiscent of *M. rileyi* consisting of a globose basal portion with a short neck and less compact conidiophores. It produces pale green conidia that are kidney-shaped, reminiscent of those of *Isaria tenuipes* (*Paecilomyces tenuipes*), hence the previous placement in *Paecilomyces* section *Isarioidea* by Samson (1974). *Metarhizium reniforme* appears to have a specificity for *Tettigoniidae* grasshoppers and the conidial shape of *M. reniforme* remains reniform (kidney-shaped) after culture.
Fig. 28. Purpureomyces khaoyaiensis (NHU00855.01, BCC1376). A. Stroma arising from Lepidoptera larva. B. Oblique perithecial. C. Section through the stroma showing perithecia. D. Whole ascospore. E. Germination and microcyclic sporulation of the ascospores on slide. F. Colonies on OA. G–I. Phialides and conidia on OA. J. Colonies on PDA. K–M. Phialides and conidia on PDA. N. Colonies on SDAY/4. O–Q. Phialides and conidia on SDAY/4. Scale bars: A = 5 mm; B = 4 mm; C = 200 μm; D, E = 20 μm; G–I, K–M, O–Q = 10 μm.
Metarhizium rileyi (Farl.) Kepler et al., Mycologia 106: 824. 2014.

Basionym: Botrytis rileyi Farl., Riley, Rep. U.S. Dep. Agric.: 121. 1883.

Synonyms: Spicaria rileyi (Farl.) Charles, Mycologia 28: 398.1936.
Beauveria rileyi (Farl.) Gösswald, Arb. biol. BundAnst. Land- u. Forstw.: 434. 1939
Nomuraea rileyi (Farl.) Samson, Stud. Mycol. 6: 81. 1974

Fig. 29. Purpureomyces maesotensis (BBH 44500, culture ex-type BCC 89300). A–B. Stroma arising from Lepidoptera larva. C. Perithecia. D. Asci. E. Whole ascospores. F. Colonies on OA. G–I. Phialides and conidia on OA. J. Colonies on PDA. K–M. Phialides and conidia on PDA. N. Colonies on SDAY/4. O–Q. Phialides and conidia on SDAY/4. Scale bars: A = 5 mm; B = 1 mm; C = 200 μm; D, E = 20 μm; G–I, K, L, O, P = 10 μm; M, Q = 5 μm.
**Nomuraea prasina** Maubl., Bull. Soc. Mycol. France 19: 296. 1903.

*Description and illustration:* See Samson (1974).

**Typus:** USA, Washington D.C., on *Plusia brassicae*, collection date unknown, R. Thaxter.

**Habitat:** Lepidoptera, Hemiptera.

**Known distribution:** Argentina, Brazil, China, France, Indonesia, Japan, Philippines, Solomon Islands, Thailand, USA.

**Notes:** *Metarhizium rileyi* is more common in agricultural ecosystems than in the forest and is used in biological control of certain *Lepidoptera* species especially the larva in cabbage farms.

**Metarhizium robertsii** J.F. Bisch. et al., Mycologia 101: 520. 2009.

*Description and illustration:* See Bischoff et al. (2009).

**Typus:** USA, South Carolina, on *Curculio caryae* (Coleoptera, *Curculionidae*), 21 Jul. 1988, R.J. St. Leger, (*holotype* BPI 878819, culture ex-type ARSEF 2575 = ATCC MYA-3093 = IMI 191-613).

**Habitat:** Coleoptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, soil.

**Known distribution:** Argentina, Australia, Brazil, Canada, Italy, Japan, Portugal, USA.

**Notes:** *Metarhizium robertsii* is morphologically indistinguishable from *M. anisopliae*, and is also a member of the PARB clade together with *M. alvesii*, *M. humberi* and *M. lepidiotae*. It was diagnosed from other members of the *M. anisopliae* complex by unique fixed nucleotide characters in the *tef* alignment which can be evaluated by downloading the alignment S2169 from www.TreeBase.org (Bischoff et al. 2009). Like most species in this species complex, the best method to use to identify the species is to sequence multiple loci and run a phylogenetic analysis to have a better idea of its placement and relationships with other species.

**Metarhizium samlanense** Luangsa-ard et al., Mycol. Prog. 16: 387. 2017.

*Description and illustration:* See Luangsa-ard et al. (2017). The description below is based on specimens collected in Thailand.

Specimens found only on leafhoppers (*Hemiptera, Cicadellidae*) on the underside of leaves. The host body was covered with bunting-green (No.150) powdery globose conidia, 3–4 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 20–22 mm in 14 d, flat, closely appressed to the agar surface, at first white turning peacock-green (No.162C) and powdery while sporulating, white at the margins, produced olive-yellow (No.52) pigmentation in agar culture. Sporulation starts at 3 d after inoculation, reverse olive-yellow (No.52) to straw yellow (No.56), powdery while sporulating, white mycelium at the margin. Sporulation starts at 3 d after inoculation, reverse olive-brown (No.28), olive yellow (No.52) in the middle of colony and white cream at the margin. *Conidiophores* arising from aerial mycelia, erect, smooth-walled, cylindrical, nomuraea-like in forming of branches. *Phialides* smooth-walled, ovoid, occasionally subglobose and cylindrical, 5–7 × 2–3 μm. *Conidia* smooth-walled, straw yellow (No.56), globose, 3–5 μm.

**Typus:** Thailand, Saraburi Province, Namtok Samlan National Park, 14.440100 N, 100.960308 E, on adult leafhopper, 2 Feb. 2005, J. Luangsa-ard & S. Mongkolsamit (*holotype* BBH 14640 preserved in a metabolically inactive state, culture ex-type BCC 17091).

**Habitat:** Adult leafhopper (*Hemiptera: Cicadellidae*), on the underside of monocotyledonous leaves.

**Known distribution:** Thailand, only from Namtok Samlan National Park.

**Additional materials examined:** Thailand, Saraburi Province, Namtok Samlan National Park, 14.440100 N, 100.960308 E, on adult leafhopper, 25 Oct. 2006, K. Tasanathai (MY01747, BCC 23818), 8 Sep. 2009, D. Thanakitpipattana, J. Luangsa-ard & R. Rikitak (BBH 27086, BCC 39752), (BBH 27087, BCC 39753), (BBH 27088, BCC 39755).

**Notes:** *Metarhizium samlanense*, *M. ovoidosporum* and *M. prachinense* share similarity in producing nomuraea-like conidiophores in culture. All three species were found in different localities in Thailand. *Metarhizium samlanense* was found only in Namtok Samlan National Park, *M. prachinense* in Khao Yai National Park and *M. ovoidosporum* in Khlong Lan National Park. *Metarhizium samlanense* and *M. ovoidosporum* were both found in their asexual states while *M. prachinense* was found in its sexual state. Both *M. ovoidosporum* and *M. samlanense* were found occurring on *Hemiptera* on the underside of leaves while *M. prachinense* was found occurring on *Lepidoptera* larva buried in the ground. On SDAY/4, the conidial shape of *M. samlanense* is globose while it is ovoid, occasionally ellipsoidal or subglobose in *M. ovoidosporum* and only subglobose in *M. prachinense*.

**Metarhizium sulphureum** Luangsa-ard, Khonsanit, Thanaktipattana & Samson, sp. nov. MycoBank MB834901. Fig. 27.

**Etymology:** In reference to the colour of stromata on the host. Specimens were found on *Lepidoptera* larva, mostly buried in the soil, seldom in the leaf litter. *Stromata* solitary to several,
Fig. 30. Purpureomyces pyriformis (BBH 43364, culture ex-type BCC 85074). A–B. Stroma arising from Lepidoptera pupa. C. Perithecia. D. Asci. E. Whole ascospore. F. Colonies on OA. G–I. Phialides and conidia on OA. J. Colonies on PDA. K–M. Phialides and conidia on PDA. N. Colonies on SDAY/4. O–Q. Phialides and conidia on SDAY/4. Scale bars: A = 5 mm; B = 2 mm; C = 150 μm; D, E, H, L = 20 μm; G, I, K, M, O–Q = 10 μm.
25–45 × 2–3 mm, arising from head of infected Lepidoptera larva, sulphur-yellow (No.57) to greenish-olive (No.49), the host’s bodies were covered with apple-green (No.61), Paris-green (No.63) mycelium. Perithecia semi-immersed, oblique in arrangement, ovoid, dark ostiolates, 600–700 × 420–450 μm. Asci cylindrical, 300–420 × 3–6 μm. Asci caps rounded, 5 × 5 μm. Ascospores hyaline, filiform, 300–300 × 2–3 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 20–21 mm in 14 d, mycelium closely appressed and white, slightly convex in the middle of agar surface, olive-yellow (No.52) at the margins, powdery while sporulating. Sporulation starts at 3 d after inoculation, reverse olive-yellow (No.52). Conidiophores arising from aerial mycelium, erect, smooth-walled, cylindrical. *Phialides* smooth-walled, cylindrical with semi-papillate apices, 7–10(–12) × 1.5–2 μm. *Conidia* smooth-walled, greenish-olive (No.49), cylindrical with rounded apices or ellipsoidal, (5–)6–7.5(–8) × 2–2.5 μm.

Colonies on PDA attaining a diam of 18–21 mm in 14 d, mycelium closely appressed and slightly convex in the middle of agar surface, flat, white at the margins turning greenish-olive (No.49) and powdery while sporulating. Sporulation starts at 3 d after inoculation, reverse olive-yellow (No.52) in the middle of colony and white cream at the margin. *Conidiophores* arising from aerial mycelium, erect, smooth-walled, cylindrical. *Phialides* smooth-walled, cylindrical with semi-papillate apices, 7–8.5(–10) × 1.5–2 μm. *Conidia* smooth-walled, greenish-olive (No.49), cylindrical with rounded apices or ellipsoidal, (5–)6–7(–9) × 2–2.5 μm.

Colonies on SDAY/4 attaining a diam of 14–17 mm in 14 d, mycelium closely appressed and slightly convex to the agar surface, white at the margins turning olive-yellow (No.52) and greenish-olive (No.49), powdery while sporulating around the middle of colony. Sporulation starts at 3 d after inoculation, reverse buff in the middle of colony and white cream at the margin. *Conidiophores* arising from aerial mycelium, erect, smooth-walled, cylindrical. *Phialides* smooth-walled, cylindrical with semi-papillate apices, (5–)6.5–9.5(–11) × 1.5–2 μm. *Conidia* smooth-walled, greenish-olive (No.49), cylindrical with rounded apices, 6–7.5(–9) × 2–3 μm.

**Typus:** Thailand, Nakhon Ratchasima Province, Khaoyai National Park, on Lepidoptera larva, 21 May 2009, K. Tasanathai, P. Puyngain, P. Srikitikulchai, R. Ridkaew, S. Mongkolamsamrit & T. Chohmee (**holotype** BBH 29463 preserved in a metabolically inactive state, culture ex-type BCC 36992).

**Habitat:** Lepidoptera larva buried in the soil or lying in the leaf litter.

**Known distribution:** Thailand, found only in Khaoyai National Park.

**Additional materials examined:** Thailand, Nakhon Ratchasima Province, Khaoyai National Park, Mo Sing To Nature Trail, 14.439089 N, 101.372228 E, on Lepidoptera larva, 19 May 2009, K. Tasanathai, P. Puyngain, P. Srikitikulchai, R. Ridkaew, S. Mongkolamsamrit & T. Chohmee (BBH 26200, BCC 36568); **idem.,** 20 May 2009, K. Tasanathai, P. Puyngain, P. Srikitikulchai, R. Ridkaew, S. Mongkolamsamrit & T. Chohmee (BBH 26213, BCC 36585); **idem.,** 13 Sep. 2009, K. Tasanathai, P. Srikitikulchai, R. Ridkaew, S. Mongkolamsamrit & T. Chohmee (BBH 27261, BCC 39045).

**Notes:** Metarhizium sulphureum was found occurring on Lepidoptera larva and both sexual and asexual states were collected.

Only eight species with sexual morphic states are known in the *Metarhizium* anisopliae complex including *M. brachyspermum*, *M. brittlebankisoides*, *M. campossterni*, *M. clavatum*, *M. guizhouense* (*M. tail*), *M. indigoticum*, *M. kalasinense,* and *M. sulphureum*. All eight species differ in the size and shape of the perithecia, asci, and ascospores (Table 4). *Metarhizium indigoticum* and *M. sulphureum* were found occurring on Lepidoptera larva, while *M. brachyspermum*, *M. brittlebankisoides*, *M. campossterni*, *M. clavatum* and *M. kalasinense* were found on Coleoptera larva. *Metarhizium guizhouense* was found occurring on various insect orders including Coleoptera, Diptera, Lepidoptera, and is also found in the soil.

**Metarhizium takense** Tasanathai et al., Mycol. Prog. 16: 388. 2017.

**Description and illustration:** See Luangs-ard et al. (2017) and this study. Description on OA is based on this study. Description on stroma, PDA and SDAY/4 were taken from Luangs-ard et al. (2017).

**Stromata** simple, cylindrical, greyish-green (27D5) to almost dark green (29F5) arising from the head of the cicada nymphs, 70–130 × 0.6–1.8 mm. Terminal part of the stroma fertile, cylindrical. *Perithecia* flask-shaped, oblique in arrangement, 510–550 × 250–350 μm. Asci hyaline, cylindrical, 275–400 × 5 μm. Ascospores filiform, hyaline, not fragmenting into part-spores, 155–230 × 1.25 μm.

**Cultural characteristics:** Colonies on OA attaining a diam of 15 mm in 14 d, floccose, cream to green with age (oac892-oac39). Sporulation starts at 7 d after inoculation, reverse uncoloured. *Conidiophores* arising from hyphae, smooth-walled, cylindrical. *Phialides* smooth-walled, cylindrical, (3–)4–5(–6) × 2–3 μm. *Conidia* smooth-walled, ovoid, ellipsoidal, (2–3)–5 × 2–3 μm.

Colonies on PDA attaining a diam of 10 mm in 10 d, at first white turning greenish olive (No.49) due to the production of conidia in the middle of colony. *Phialides* fusiform to narrowly ovoid, 3–5 × 2 μm. *Conidia* catenulate, dimorphic; microconidia formed first, ovoid, ellipsoidal or subglobose, 3–5 × 2–3 μm, macroconidia formed later, cylindrical, clavate, 8–16 × 3–4 μm.

Colonies on SDAY/4 attaining a diam of 10 mm in 14 d, at first white becoming greenish olive (No.49) at 7 d due to the production of conidia. Vegetative hyphae smooth walled. *Conidiophores* dense, terminating in branches with 2–3 phialides per branch. *Phialides* fusiform to narrowly ovoid, 5–8 × 2–3 μm. *Conidia* catenulate, ovoid, ellipsoidal or subglobose, 3–5 × 2–3 μm.

**Typus:** Thailand, Tak Province, Umphang Wildlife Sanctuary, on cicada nymph (*Hemiptera*), 24 Jun. 2008, J. Luangsa-ard, K. Tasanathai, S. Mongkolamsamrit, P. Srikitikulchai, A. Khonsanit & B. Thongnuch (**holotype** BBH 25192 preserved in a metabolically inactive state, culture ex-type BCC 30939).

**Habitat:** Cicada nymph (*Hemiptera*).

**Known distribution:** Thailand.

**Additional materials examined:** Thailand, Tak Province, Umphang Wildlife Sanctuary, on cicada nymph (*Hemiptera*), 24 Jun. 2008, J. Luangsa-ard, K. Tasanathai, S. Mongkolamsamrit, P. Srikitikulchai, A. Khonsanit & B. Thongnuch (BBH 23893, BCC 30934), (BBH 23898, BCC 30940).
Notes: Metarhizium takense closely related to M. chaiyaphumense but they differ in the shape of the perithecia as well as in the length of their asci and ascospores. Metarhizium chaiyaphumense has longer asci than in M. takense. The colour of the stroma in M. takense is greenish brown to dark green while in M. chaiyaphumense the stroma is greyish yellow to yellowish olive green. The stroma in M. takense is significantly bigger (70–130 mm) than in M. chaiyaphumense, measuring only 30–35 mm (Luangsarut et al. 2017).

Metarhizium viride (Segretain et al. ex Samson) Kepler et al., Mycologia 106: 824. 2014.
Basionym: Paecilomyces viridis Segretain et al. ex Samson, Stud. Mycol. 6: 64. 1974.
Synonym: Chamaeleomyces viridis (Segretain et al. ex Samson) Sigler, J. Clin. Microbiol. 48: 3188. 2010.

**Description and illustration:** See Samson (1974).

**Typus:** Madagascar, from Chamaeleo lateralis (holotype IP 850), culture ex-type CBS 348.65 = ATCC 28695 = IHEM 3281, isotype IP 850.64.

**Habitat:** Chamaeleo lateralis (Reptilia: Chamaeleonidae).

**Known distribution:** Expected in countries with Chamaeleo spp.

Notes: As pathogens of reptiles, M. viride and M. granulomatis occupy the basal most position of the *Metarhizium* clade producing pale green to greenish-grey colonies. Both species produce paecilomyces-like phialides consisting of a globose or flask-shaped basal portion and a distinct thin, sometimes long neck, globose to subglobose conidia, and a yeast-like fragmentation in culture. Both species are rare but seem to be aggressive pathogens of chameleons (Sigler et al. 2010).

Metarhizium viridulum (Tzean et al.) B. Huang & Z.Z. Li, Mycosystems 23: 36. 2004.
Basionym: Nomuraea viridula Tzean et al., Mycologia 84: 781. 1992.

**Description and illustration:** See Tzean et al. (1992). The description below is based on specimens in Thailand.

**Description from the asexual morph:** Specimens found on adult cicadas. Hosts covered with pale green mycelium and sporulating conidiophores. Conidia smooth-walled, ellipsoidal to cylindrical, allantoid, (9–10)(12–14) × 3–4(5) μm.

**Cultural characteristics:** Colonies on OA attaining a diameter of 18 mm in 14 d, white to cream, floccose, entire margin, poor sporulation with green conidia produced on aerial mycelium. Sporulation starts at 14 d after inoculation, reverse uncoloured, *Conidia* smooth-walled, ellipsoidal to cylindrical, allantoid, (6–)8–10(–12) × 3–4 μm.

Colonies on PDA attaining a diameter of 15 mm in 14 d, white to pale yellow, green in the middle, margin floccose, white. Sporulation starts at 12 d after inoculation, reverse uncoloured. *Conidia* smooth-walled, ellipsoidal to cylindrical, (7–)8–10(–11) × 3–4 μm.

Colonies on SDA/Y4 attaining a diameter of 15 mm in 14 d, pale yellow, flat, floccose, undulate edge. Sporulation starts at 12 d after inoculation, reverse uncoloured. *Phialides* one to three borne directly on metulae, oval-cylindrical to ellipsoidal, 5–7.5(–9) × 3–4(–5) μm. *Conidia* smooth-walled, hyaline, ellipsoidal to cylindrical, (7–)8.5–11(–13) × 3–4 μm.

**Typus:** Taiwan, Hsientien, Taipei, on Cryptotympana facialis (Homoptera), 22 Jun. 1989, collector unknown (holotype PPH14, culture ex-type PPH 14E = CCRC 32589, isotype in IMI).

**Habitat:** Cryptotympana facialis (Hemiptera) in Taiwan and on adult cicada (Hemiptera) in Thailand.

**Known distribution:** Taiwan, Thailand, known from Khaok Luang National Park.

Additional material examined: Thailand, Nakhon Si Thammarat Province, Khaok Luang National Park, 8.376111 N, 99.734842 E, on adult cicada, 18 Feb. 2009, K. Tasanathai, S. Mongkolsarit, P. Srikitikulchai, R. Promharn & T. Choohmee (BBH 26010, BCC 36261).

Notes: Metarhizium viridulum is closely related to *M. megapompomiae* occurring on adult cicada but differs in the size of conidia. Based on specimens from Thailand, the conidia of *M. viridulum* are longer (9–14 × 3–5 μm) than those of *M. megapompomiae* (6–11 × 3–5 μm). This is the first report of *M. viridulum* in Thailand.

Papiliomyces Luangsarut, Samson & Thanakitpipattana, gen. nov. MycoBank MB834902.

**Etymology:** From the Latin “papilio”, meaning butterfly or moth.

**Description:** Lepidoptera larva buried in the ground. Stromata solitary to multiple (branched), robust to wiry. *Perithecia* superficial to completely immersed in the stroma, ampulliform, ellipsoid to ovoid. *Asci* cylindrical, ascospores whole with septation or breaking into cylindrical part-spores. There are no similarities between the two species in this genus except for the lepidopteran host buried in the ground.

**Type species:** Papiliomyces liangshanensis (M. Zang et al.) Luangsarut, Samson & Thanakitpipattana.

Notes: This genus is phylogenetically distinct from *Metarhizium*. It can morphologically be differentiated from *Metarhizium* in the production of superficial perithecia and wiry, branched stromata in *Papiliomyces liangshanensis* and the white to faint yellow robust stroma in *P. shibinensis*. Sexual morphs of *Metarhizium* produce semi-immersed to completely immersed perithecia on robust, almost fleshy dark green or purplish stromata. Phylogenetically, it is closely related to *Purpureomyces*. However, in *Purpureomyces*, the stromata are fleshy, purple and the perithecia are obliquely immersed in the stroma while perithecia in *P. shibinensis* are ordinal in arrangement.

*Papiliomyces liangshanensis* (M. Zang et al.) Luangsarut, Samson & Thanakitpipattana, comb. nov. MycoBank MB834903.

**Description and illustration:** See Zang et al. (1982).

**Typus:** China, Sichuan, Liangshan, on *Lepidoptera* larva in a bamboo forest *Phyllostachys pubescentius* var. *heterocyclae*, 10 Nov. 1980, Liu Dao-qing (holotype KUN 7723).

**Habitat:** Lepidoptera larva.

**Known distribution:** China.
Notes: Papiliomyces liangshanensis is one of the few species of entomopathogenic fungi with superficial perithecia and wiry stromata that have been reported with aboveground branched stromata. Ophiocordyceps petchii (Mains) G.H. Sung et al. (≡ Cordyceps ramosa Petch, non-Teng 1936) on Lepidoptera larva has similar morphological features as P. liangshanensis but differs from O. petchii in the production of cylindrical parts - spores while the latter produces whole ascospores. The gross morphology of P. liangshanensis could easily be assigned to Ophiocordyceps in the production of dark wiry stromata and superficial perithecia like in the O. acicularis group (Luangsa-ard et al. 2018). A recollection of O. petchii in Trinidad would help elucidate if this species belongs to Ophiocordyceps or Papiliomyces. Another species producing branched stromata in the Clavicipitaceae is Sungia yongmunensis (≡ Metacordyceps yongmunensis, fig. 5B in Sung et al. 2007) on Lepidoptera pupa, but differs in the character of the stroma, which is not wiry but robust and the fertile part is not differentiated from the stroma.

Papiliomyces shibinensis (T.C. Wen et al.) Luangsa-ard Samson & Thanakitpipattana, comb. nov. MycoBank MB834904.

Basionym: Metacordyceps shibinensis T.C. Wen et al., Phytotaxa 226: 57. 2015.

Description and illustration: See Wen et al. (2015).

Typus: China, Shibin County, Yuntai mountains, Guizhou province, on Lepidoptera larva, in the soil, 3 May 2013, L.P. Chen (holotype GZUH SB 13050311, culture ex-type SB13050311).

Habitat: Lepidoptera larva.

Known distribution: China.

Notes: This species is closely related to Papiliomyces liangshanensis (Metacordyceps liangshanensis) but differs significantly in their morphologies. Papiliomyces liangshanensis produces branched, wiry stromata with superficial perithecia and ascospores that dissociate into part-spores while P. shibinensis produces robust stroma with completely immersed perithecia and multi-septate, whole ascospores.

Purpureomyces Luangsa-ard, Samson & Thanakitpipattana gen. nov. MycoBank MB834905.

Etymology: Named after the colour of the stromata in nature.

Description: Stroma solitary, white at the tip when young (immature) to purple, especially around the ostioles, cylindrical to clavate with tapering end, flexuous. Hosts are Lepidoptera larva or pupa underground. Perithecia immersed to semi-immersed, ovoid, oblique in arrangement. Asci cylindrical, 8-spored; ascospores hyaline, filiform, whole, septate, not breaking into part - spores. Asexual morph lecanicillium-like.

Type species: Purpureomyces khaoyaiensis (Hywel-Jones) Luangsa-ard, Samson & Thanakitpipattana.

Notes: Three species are recognised in this genus that all produce purple stromata and obliquely immersed perithecia. Phylogenetically, it is closely related to Marquandomyces and Papiliomyces. The asexual morph in Marquandomyces is paecilomyces-like and in Purpureomyces it is lecanicillium-like. There is no record of the asexual morph in Papiliomyces.

Purpureomyces khaoyaiensis (Hywel-Jones) Luangsa-ard, Samson & Thanakitpipattana, comb. nov. MycoBank MB834906. Fig. 28.

Basionym: Cordyceps khaoyaiensis Hywel-Jones, Mycol. Res. 98: 939. 1994.

Synonyms: Metacordyceps khaoyaiensis (Hywel-Jones) Kepler et al., Mycologia 104: 185. 2012.

Metarhizium khaoyaiense (Hywel-Jones) Kepler et al., Mycologia 106: 823. 2014.

Description and illustration: See Hywel-Jones (1994).

Cultural characteristics: Colonies on OA attaining a diam of 25 mm in 7 d, white, cottony, floccose, dense mycelium, reverse verona brown (223B). Hyphae septate, smooth-walled, hyaline, 1–2 μm wide. Phialides lecanicillium-like, arising from aerial hyphae, cylindrical, tapering gradually towards the apex, hyaline, solitary or more often 2 or 4 in whorls on each node, (3–) 5.5–14.(-20) × 1–2 μm. Conidia in long chains, hyaline, ovoid, 2–3 × 1.5–2(–3) μm.

Colonies on PDA attaining a diam of 15–17 mm in 7 d, white to creamy, cottony, dense mycelium, reverse tawny olive (223D). Hyphae septate, smooth-walled, hyaline, 1–2 μm diam. Phialides lecanicillium-like, arising from aerial hyphae, cylindrical, tapering gradually towards the apex, hyaline, solitary or more often 2 or 4 in whorls on each node, (3–) 9.5–14.5(–18) × 1–2 μm. Conidia in long chains, hyaline, ovoid, 2–3(–3.5) × (1–) 1.5–2 μm.

Colonies on SDA/Y attaining a diam of 16–20 mm in 7 d, white to creamy, cottony, dense mycelium. Colonies reverse rufous (340). Hyphae septate, smooth-walled, hyaline, 1–2 μm diam. Phialides lecanicillium-like, arising from aerial hyphae, cylindrical, tapering gradually towards the apex, hyaline, solitary or more often 2 or 4 in whorls on each node, (7–) 9.5–14.5(–18) × (1–)1.5–2(–3) μm. Conidia in long chains, hyaline, ovoid, 2–3 × 1.5–2(–3) μm.

Typus: Thailand, Nakhon Nayok Province, Khoai Yai National Park, on Lepidoptera larva, in leaf litter, 14 Apr. 1997, N.L. Hywel-Jones (holotype NHU 00885 preserved in metabolically inactive state, culture ex-type BCC 1376).

Habitat: Lepidoptera larva.

Known distribution: Thailand.

Additional materials examined: Thailand, Chiang Mai Province, Ban Hua Thung Community forest, 19.367814 N, 98.964903 E, on Lepidoptera larva, in leaf litter, 23 Sep. 2010, K. Tanasathan, P. Siritikulchu & A. Khonsant (BBH 30160, BCC 44287); idem., 5 Oct. 2012, K. Tanasathan, A. Khonsant, W. Noisripoom, P. Siritikulchu & R. Pongham (BBH 32908, BCC 55765), (BBH 32909, BCC 55766); idem., 29 Oct. 2012, K. Tanasathan, A. Khonsant, W. Noisripoom, D. Thanakitpipattana, P. Siritikulchu & S. Wongkanoun (BBH 40315, BCC 75721), (BBH 40208, BCC 75753), (BBH 40319, BCC 76485).

Notes: Purpureomyces khaoyaiensis is similar to P. pyriformis in having the same host and colour of the stroma. Both species occur on Lepidoptera larvae and produce purple stromata. They differ in the size and shape of perithecia, asci and ascospores. In culture, the asexual morph of P. khaoyaiensis and P. pyriformis is lecanicillium-like. Both P. khaoyaiensis and P. pyriformis produce...
white to cream mycelium on OA, PDA and SDAY/4, with similar sizes and shapes of the phialides and conidia.

*Purpureomyces maesotensis* Luangsa-ard, Noisripoom Thanakitpipattana & Samson, sp. nov. MycoBank MB834907. Fig. 29.

**Etymology:** Name after the type locality.

*Stroma* arising from the middle joints of the *Lepidoptera* larvae, solitary, cylindrical, 26 mm long, 1–1.5 mm wide. Stipe cylindrical, club-shaped, purple base (No.1) to whitish-purple, fertile part deep vinaceous (No.4). *Perithecia* semi-immersed, oblique in arrangement, ovoid, hyaline wall, (360–373–445–470) × (260–264–308–320) μm. *Asci* hyaline, cylindrical, (100–110.5–160–192.5) × (3–4–5–6) μm. *Ascospores* smooth, filiform, hyaline, whole, multi-septate, (107–127–160–177.5) × 1 μm. *Asexual morph* not seen in nature.

**Cultural characteristics:** Colonies on OA attaining a diam of 25 mm in 7 d, white, cottony, floccose, high mycelial density, reverse white. Hyphae septate, rough-walled, hyaline, 1–2 μm wide. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or up to 2–3 per branch, narrow, cylindrical, tapering gradually towards the apex, (10–11–19.5–32) × 1.5–2 μm. *Conidia* in long chains, hyaline, ovoid to globose, 2–3 × 1.5–2–(3) μm.

Colonies on PDA attaining a diam of 15 mm in 7 d, white to creamy, cottony, reverse tawny (No.38) to yellow ochre (No.123C). Hyphae septate, rough-walled, hyaline, 1–2 μm wide. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or up to 2 per branch, narrow, cylindrical, tapering gradually towards the apex, (7–9.5–17–(22) × 1–2 μm. *Conidia* in long chains, hyaline, ovoid to globose, 2–3(–4) × 1.5–2 μm.

Colonies on SDAY/4 attaining a diam of 20 mm in 7 d, white to lilac (No.76), high mycelial density, reverse deep vinaceous (No.4) to flesh (No.5). Hyphae septate, rough-walled, hyaline, 1–2 μm wide. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or up to 2–3 per branch, narrow, cylindrical, tapering gradually towards the apex, (4–9–17.5–(21) × 1.5–2 μm. *Conidia* in long chains, hyaline, ovoid, 3 × (1–)1.5–2–(2.5) μm.

**Typus:** Thailand, Tak Province, Mae Sot District, Pha Daeng Waterfall Nature Trail, on *Lepidoptera* larva, on the leaf litter, 6 Sep. 2018, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom & D. Thanakitpipattana (holotype BBH 44500 preserved in metabolically inactive state, culture ex-type BCC 89300).

**Habitat:** *Lepidoptera* larva.

**Known distribution:** Thailand, known from Pha Daeng Waterfall Nature Trail, Mae Sot District, Tak Province.

**Additional material examined:** Thailand, Tak Province, Mae Sot District, Pha Daeng Waterfall Nature Trail, 16.667367 N, 98.657300 E, on *Lepidoptera* larva, on the leaf litter, 6 Sep. 2018, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom & D. Thanakitpipattana (BBH 44501, BCC 88441).

**Notes:** *Purpureomyces maesotensis* is similar to *P. khaoyaiensis* in producing a purple stroma arising from the middle joints of the *Lepidoptera*. It differs from *P. khaoyaiensis* in the size of the stroma, perithecia, asci and ascospores. In *P. khaoyaiensis* these characters are longer than in *P. maesotensis* (stoma 55 mm long, cylindrical asc 200–350 × 5–6 μm, ascospores filiform, whole, 160–250 × 1 μm). Additionally, *P. maesotensis* shares similarity with *P. khaoyaiensis* in producing a lecanicillium-like asexual morph in culture. The colony of both species have white to cream mycelium in obverse on OA and PDA, conidia in long chains, ovoid to globose. It differs from *P. khaoyaiensis* in the colony on SDAY/4, which is cream in *P. khaoyaiensis* and lilac in *P. maesotensis*.

*Purpureomyces pyriformis* Luangsa-ard, Noisripoom, Hima-man, Mongkolsamrit, Thanakitpipattana & Samson, sp. nov. MycoBank MB834908. Fig. 30.

**Etymology:** Named after the pear-shaped perithecia on the stroma.

*Stroma* arising from the head of *Lepidoptera* pupa, cylindrical, solitary, simple, 18 mm long, 3 mm wide, purple (C1). Upper part of the stroma fertile, fleshy, expanded, parted, 11 mm long, 3 mm wide, white to purple (C1). *Perithecia* immersed, oblique in arrangement, ovoid, (304–310–341–(350) × (212.5–220–242.5–250) μm. *Asci* cylindrical, (100–109–159–182) × 4–5 μm, apical cap prominent, 4–5 μm wide. *Ascospores* smooth-walled, hyaline, filiform, (125–)143–178(–190) × 1 μm, whole, multi-septate. *Asexual morph* not seen in nature.

**Cultural characteristics:** Colonies on OA attaining a diam of 25 mm in 7 d, white, cottony, floccose, dense mycelium, reverse cream. Hyphae septate, smooth-walled, hyaline, 1–2.5 μm wide. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or more often 2–4 in whors on each branch, cylindrical, tapering gradually towards the apex, (10–11–20–(32) × 1–2(–3) μm. *Conidia* in long chains, hyaline, ovoid, (2–)2.5–3.5–(4) × 1.5–2–(2.5) μm.

Colonies on PDA attaining a diam of 15–17 mm in 7 d, white to cream, cottony, high mycelial density, reverse cream. Hyphae septate, smooth-walled, hyaline, 1–2 μm diam. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or more often 2–4 in whors on each branch, cylindrical, tapering gradually towards the apex, (5–)8.5–14–(17) × 1–2(–3) μm. *Conidia* in long chains, hyaline, ovoid, (2–)2.5–3.5–(4) × 1.5–2–μm.

Colonies on SDAY/4 attaining a diam of 16–20 mm in 7 d, white to cream, cottony, high mycelial density, reverse pale yellow to cream. Hyphae septate, smooth-walled, hyaline, 1–2 μm diam. *Phialides* arising from aerial hyphae, lecanicillium-like, hyaline, solitary or more often 2–4 in whors on each branch, cylindrical, tapering gradually towards the apex (8–10–16–(22) × 1–2 μm. *Conidia* in long chains, hyaline, ovoid, (2–2.5–4 × 1.5–2 μm.

**Typus:** Thailand, Khon Kaen Province, Phu Wiang National Park, on *Lepidoptera* pupa, underground, 19 Jul. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom & W. Himaman, P. Jangsantear & B. Sakolrak (holotype BBH 43364 preserved in metabolically inactive state, culture ex-type BCC 85074).

**Habitat:** *Lepidoptera* pupa.

**Known distribution:** Thailand, known from Phu Wiang National Park.

**Additional materials examined:** Thailand, Khon Kaen Province, Phu Wiang National Park, 16.661017 N, 102.237069 E, on *Lepidoptera* pupa, buried in the ground, 19 Jul. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom, W. Luangsa-ard, Noisripoom.
Notes: Purpureomyces pyriformis is similar to *P. khaoyaiensis* in parasitizing small *Lepidoptera* larva and producing purple stroma. Both species produce ovoid perithecia and whole ascospores. It differs from *P. khaoyaiensis* in the larger size and shape of its stroma. Purpureomyces pyriformis produces white to cream mycelium in obverse and reverse of PDA plate, while *P. khaoyaiensis* produces a tawny olivine pigment in obverse of the plate. Additionally, *P. pyriformis* shares similarity to *P. khaoyaiensis* and *P. maesotensis* by having a lecanicillium-like asexual morph in culture. It is similar to *P. khaoyaiensis* in producing white to cream mycelium in obverse on OA, PDA and SDAY/4 as well as in size and shape of the phialides and conidia. It differs from *P. khaoyaiensis* in the size and shape of the stroma, peritheca, asc and ascospores. In *P. khaoyaiensis* the perithecia are semi-immersed, oblique in arrangement and have larger perithecia measuring, 300–420 × 200–270 μm compared to the ordinal, immersed perithecia, measuring 304–350 × 212.5–250 μm in *P. pyriformis*. Similarly, the asci in *P. pyriformis* (100–182 × 4–5 μm) and ascospores (125–190 × 1 μm) are shorter than those reported for *P. khaoyaiensis*, 200–350 × 5–6 μm for the asc and 160–250 × 1 μm for the ascospores.

*Sungia* Luangsa-ard, Samson & Thanakitpipattana, *gen. nov.* MycoBank MB834909.

**Etymology:** Named after Prof. Jae-Mo Sung in recognition for his work on entomopathogenic fungi in South Korea.

**Description:** Stromata erect, cylindrical to clavate, robust, multiple, predominantly branched or simple, gregarious, on large *Lepidoptera* pupa. Fertile part white to pale yellow, not differentiated from stipe. Perithecia fusiform to clavate, oblique in arrangement, immersed, loosely scattered or crowded. Asci 8-spored, hyaline, cylindrical with a prominent cap. Ascospores filiform, hyaline, multi-septate, whole. Conidiophores erect with solitary, awl-shaped phialides, pachonia-like. Conidia in slimy heads, elliptical to oblong, hyaline. Chlamydoospores present, cylindrical to subglobose, submerged in agar.

**Type species:** *Sungia yongmunensis* (G.H. Sung et al.) Samson, Luangsa-ard & Thanakitpipattana.

Notes: This species is phylogenetically close to *Yosiokobayasia*. Both genera produce pallid stromata — white to pale yellow in *Sungia* and white in *Yosiokobayasia* which is not observed in any sexual morph of *Metarhizium*.

*Sungia yongmunensis* (G.H. Sung et al.) Luangsa-ard, Thanakitpipattana & Samson, *comb. nov.* MycoBank MB834910.

**Basionym:** Metacordyceps yongmunensis G.H. Sung et al., Stud. Mycol. 57: 27, 2007.

**Synonym:** Metarhizium yongmunense (G.H. Sung et al.) Kepler et al., Mycologia 106: 824. 2014.

**Description and illustration:** See Sung et al. (2007, 2010).

**Habitat:** *Lepidoptera* pupa.

**Known distribution:** South Korea.

Notes: This species was originally erected in Metacordyceps and transferred to *Metarhizium* but our multi-gene phylogenetic analyses have shown that it belonged to one of the least supported clades subtending the *Metarhizium* clade and is therefore transferred to a new genus *Sungia*. Sungia yongmunensis is reminiscent of *Pochonia chlamydospora* in the shape of perithecia and the pachonia-like asexual morph.

**Type:** *South Korea*, Mt. Yongmun, Gyunggi Province, on *Lepidoptera* pupa, 13 Jun. 1998, J.M. Sung (holotype EFCC 2131, culture ex-type EFCC 2131).

*Yosiokobayasia* Samson, Luangsa-ard & Thanakitpipattana, *gen. nov.* MycoBank MB834911.

**Etymology:** Named after Prof. Yosio Kobayasi in recognition for his work on entomopathogenic fungi in Japan.

**Description:** Stromata white, erect with terminal oblong fertile part. Perithecia superficial, ovoid, ordinal in arrangement, on pupa of *Lepidoptera* underground. Ascospores hyaline, filiform, breaking into part-spores.

**Type species:** *Yosiokobayasia kusanagiensis* (Kobayasi & Shimizu) Samson, Luangsa-ard & Thanakitpipattana.

**Habitat:** *Lepidoptera* pupa.

**Known distribution:** Japan.

Notes: *Yosiokobayasia* is an entomopathogenic genus proposed from a single lineage as shown in Fig. 1. This genus belongs to one of the basal lineages in a supported clade that includes *Rotiferophthora*, *Pochonia*, *Metapochonia*, *Papiliomyces*, *Sungia*, *Keithomyces* and *Metarhizium*.

*Yosiokobayasia kusanagiensis* (Kobayasi & Shimizu) Samson, Luangsa-ard & Thanakitpipattana, *comb. nov.* MycoBank MB834912.

**Basionym:** Cordyceps kusanagiensis Kobayasi & Shimizu, Bull. Nat. Sci. Mus. Tokyo, Ser. B, 9: 7. 1983.

**Synonyms:** Metacordyceps kusanagiensis (Kobayasi & Shimizu) Kepler et al., Mycologia 104: 185. 2012.

**Metarhizium kusanagiense** (Kobayasi & Shimizu) Kepler et al., Mycologia 106: 823. 2014.

**Description and illustration:** See Kobayasi & Shimizu (1983).

**Type:** *Japan*, Yamagata Prefecture, Kusanagi Spa, on pupa of *Lepidoptera*, 5 Jul. 1981, Y. Kobayasi & S. Shimizu (holotype TY 93 in TNS).

Note: This monotypic genus is one of the basal lineages in a supported clade that is separated from plant-associated genera as well as scale insect and whitefly pathogens of the Clavicipitaceae.

**DISCUSSION**

Many new species were added to *Metarhizium* in the last five years (Montalva et al. (2016), Chen et al. (2017), Luangsa-ard et al. (2017), Chen et al. (2018a, c), Luz et al. (2019), Yama moto et al. (2020)), including the discovery of 19 new *Metarhizium* species and two new *Purpureomyces* species in this study. Despite all the works on *Metarhizium* and the increase in the number of species studied the support of the clades
separating *Metarhizium*, *Pochonia*, *Metapochonia* and other related genera did not improve. However, this study has shed light on the relationships of basal species previously considered in the *Metarhizium* clade by past authors, such as *M. carneum* which is now in *Keithomyces*, *M. khaoayaiense* in *Purpureomyces*, *M. kusanagiense* in *Yoshiokobayasia*, *M. marquandii* in *Marquandomyces*, *M. liangshanensis* and *M. shibinensis* in *Papiliomyces*, and *M. yongmunense* in *Sungia*.

**How do we recognise *Metarhizium***?

**From natural materials**

It is not so simple to recognise if a specimen belongs to *Metarhizium* or not, but there are characteristics that one could look for to facilitate classification.

The sexual morphs have predominantly cylindrical or clavate stromata, either solitary or multiple and irregularly branched in shades of pale yellow, green to greenish brown or dark purple. Hosts are mostly insect larvae or nymphs buried in the ground ranging from 2–5 cm deep (e.g. *M. chayaphumense*, *M. prachinense*, *M. takense*) to 30 cm (e.g. *M. kalasinense*), rarely on adults buried in the ground (e.g. *M. phuwiangense*). Rhizoids that connect the host to the stromata emerging from the ground are sometimes covered with green conidia. Perithecial orientation varies from oblique to ordinal arrangement. The majority of the ascospores are filiform and whole with septation while in a few species they dissociate into part-spores, such as *M. campososterni* (Zhang et al. 2004) and *M. phuwiangense* (this study).

Species in *Purpureomyces* whose type species *Purpureomyces khaoayaiensis* was previously transferred by Kepler et al. (2014) to *Metarhizium* have purple stroma but are mostly solitary and produce semi-immersed perithecia that are oblique in orientation while species in *Metarhizium* with purple stromata have immersed perithecia in ordinal arrangement.

Other species in *Metarhizium* were transferred to other genera such as *M. liangshanensis* and *M. shibinensis* to *Papiliomyces*; *M. yongmunense* to *Sungia*; *M. kusanagiense* to *Yoshiokobayasia*. The sexual morphs in these genera do not produce green or dark stromata but are rather in shades of white, cream and pallid yellow or orange. Species known mainly from soil such as *M. carneum*, *M. aciculare* were transferred to *Keithomyces* and *M. marquandii* to *Marquandomyces* have only been seen in the asexual states.

In some species the asexual morph develops first on the surface of the stroma while the sexual morph development progresses later. On other species the sexual morph develops on the stroma but the asexual morph develops on the rhizoids in the soil and on the cuticle of the insect (*M. flavum*, *M. kalasinense*).

The asexual morphs are mostly found on the underside of leaves and banks of trees or plants. *Metarhizium* could easily be mistaken for a *Penicillium* in producing abundant green conidia. Normally if an insect dies of other reasons apart from being killed by an entomopathogen, ubiquitous soil and saprobiotic fungi such as *Penicillium* will use the insect as a substrate to grow on. Slide preparations, even just a simple cellophane tape method (Harris 2000), can be made to see important morphological characters such as the phialides and conidia. *Penicillium* produces a penicillate, brush-like appearance of flask-shaped or lanceolate phialides with distinct necks while *Metarhizium* produces a palisade layer of cylindrical or flask-shaped phialides. So far, there have been no reports of *Penicillium* species occurring as pathogens on insects.

**Habits**

*Metarhizium* species are well-known entomopathogens but are also reported as endophytes or soil and rhizosphere inhabitants (Keyser et al. 2014, Vega et al. 2009, Clifton et al. 2018, Luz et al. 2019), resulting in increased plant growth and providing increased tolerance against pests and diseases (Liao et al. 2017, Liu et al. 2017). In Asia (China, Japan and Thailand), reports of *Metarhizium* are mainly from insects and only few studies focus on its presence in soils and roots of plants.

Recently, studies on *Metarhizium* from soils in China were made but only two new species were found, namely *M. baoshanense* and *M. gaoligongense* (Chen et al. 2018a, b). In Japan, two new species, *M. bibionidarum* and *M. purpureogenum*, were isolated from forest soils (Nishi et al. 2017) although *M. bibionidarum* was originally isolated from a March fly larva in Japan as well as from the fruit beetle *Cetonia aurata* (*Coleoptera: Scarabaeidae*) in France (CBS 648.67), formerly assigned to the *M. flavoviride* species complex. Abundance and diversity of *Metarhizium* associated with plant roots were also investigated (Nishi & Sato 2019). In Thailand, despite the enormous diversity of *Metarhizium* species found on insects, common global species such as *M. anisopliae*, *M. flavoviride*, etc. were never encountered. This could be due to the lack of study on the diversity of these fungi in soil, especially in agricultural ecosystems, or rhizosphere and plant endophytic fungi.

**Phylogeny-based re-evaluation of *Metarhizium***

It is a real challenge to distinguish species of *Metarhizium* using only morphological characters, as several species in the genus are morphologically cryptic species (Bischoff et al. 2009, Luangsda-ard et al. 2017). The defining concept of *Metarhizium* in this study lies only in the production of conidia that are predominantly in various shades of green, could also be white or in shades of brown or yellow, and not only in the production of a palisade layer of conidiophores with cylindrical phialides that form a hymenium-like layer on an arthropod host. Presence of normurarea-like, palisclomyces-like phialides in certain species are found dispersed along the tree and do not form monophyletic subclades (Fig.1, Table 3). The systematics of *Metarhizium* which is predominantly asexual, has to rely heavily on multi-gene approaches to study cryptic speciation among closely related species. The genealogical concordance phylogenetic species recognition (GCP SR) which focuses on multi-gene genealogies allows us to recognise and identify phylogenetically distinct lineages suggesting the formation of new species even though morphologically they are still not recognisable. Our phylogenetic analyses using multi-gene sequences identified 19 new species in *Metarhizium* and the segregation of species such as *M. carneum*, *M. khaoayaiense*, *M. kusanagiense*, *M. liangshanense*, *M. marquandii* and *M. yongmunense* to other genera in *Clavicipitaceae*. We have demonstrated that in sequencing more gene regions, even when not using the same molecular markers as used in previous reports (Bischoff et al. 2009, Kepler et al. 2014), identification and inferring boundaries between species could also be achieved. We have also demonstrated that while ITS as a barcode marker will not aid in proper identification
of the species (Supplementary Fig. S1), results of the ITS phylogeny give insights about the presence of species complexes that enables one to make a review of the species by making a thorough morphological examination and additional gene sequencing to achieve an accurate identification.

Diversity of the *Metarhizium anisopliae* species complex

Twenty-one species are accepted in this complex although only 19 species were included in the multi-gene phylogenetic analyses (Fig. 1) due to incomplete sequences of various loci in some reported taxa. Kepler et al. (2014) accepted *M. brittlebankioideae* and *M. campossterni*, as members of the *M. anisopliae* complex on the basis of their asexual morphologies described by Liu et al. (2001) and Sung et al. (2007), respectively. *Metarhizium brachyspermum* was recently published by Yamamoto et al. (2020) as another member of this complex based on morphology and molecular phylogeny but whose molecular data, only ITS and *tef*, are insufficient to be added to our analyses. Members of the *M. anisopliae* complex comprise *M. acidum*, *M. alvesii*, *M. anisopliae*, *M. baoshanense*, *M. brachyspermum*, *M. brittlebankioideae*, *M. brunneum*, *M. campossterni*, *M. clavatum*, *M. globosum*, *M. gryllidicola*, *M. guizhouense*, *M. humberi*, *M. indicoticum*, *M. kalasinense*, *M. lepidiotae*, *M. majus*, *M. phasmatodeae*, *M. pingshaense*, *M. robertsii* and *M. sulphureum*. The sexual morphs of eight species were found in nature – *M. brachyspermum*, *M. brittlebankioideae*, *M. campossterni*, *M. clavatum*, *M. guizhouense*, *M. indicoticum*, *M. kalasinense* and *M. sulphureum* while it is the asexual morphs that are predominantly encountered. Members of this complex have usually dark green colonies and cylindrical phialides packed in a hymenium-like layer or palisade, with cylindrical conidia, except in *M. globosum* with globose conidia that adhere laterally to form prismatic columns. Our understanding of what Metchnikoffs *M. anisopliae* could be was enhanced by the inclusion of an Ukrainian strain of *M. anisopliae* in our analyses. Three ARSEF strains were also included in the S*tef* analyses of the *M. anisopliae* complex including the neotype of *M. anisopliae* var. *anisopliae* from Ethiopia, and which has shown them to be distantly related to *M. anisopliae* from a previous Soviet Republic.

Diversity of the *Metarhizium flavoviride* species complex

All species in this complex are found in their asexual states in nature. No sexual state was observed. There are thirteen species recognised in this complex including *M. argentinense*, *M. bibionidarum*, *M. biocencense*, *M. blattodeae*, *M. culicidarum*, *M. flavoviride*, *M. frigidum*, *M. fusoidenum*, *M. gaolgongense*, *M. koreanum*, *M. minus*, *M. normoi* and *M. pemphigi*. While some species seem to have a global distribution (e.g. *M. bibionidarum*, *M. flavoviride*, *M. pemphigi*), others have been reported only from the tropics (e.g. *M. minus* and new species in this study).

Diversity in the conidiogenesis of the taxa in *Metarhizium*

Different kinds of conidiogenesis were observed in *Metarhizium*. All forms are phialidic and the most predominant phialide morphology is the production of cylindrical phialides with short necks as is understood of *Metarhizium* in the last century. Most importantly, most of the species identified morphologically as *Metarhizium* possess these characters having a candelabrum-like arrangement of cylindrical phialides forming a compact hymenium. These types of conidiogenesis are shown in Table 3 and in Fig. 1 belonging to the *M. anisopliae*, *M. flavoviride* species complexes, pathogens of Coleoptera in the Coleoptera clade, and those occurring on small hoppers comprising *M. album*, *M. brasiliense*, *M. candelabrum*, *C. cercopidae*, *M. ellipsoidae* and *M. huaiamandangense*. Nomuraea-like and paeclomycytes-like phialides are found interspersed in the basal branches of the *Metarhizium* clade. Species on cicada produce nomuraea-like phialides with two differing classes of conidial shapes, while nomuraea-like species belonging to *M. dendromatilis*, *M. ovaspora*, *M. prachinense*, *M. rileyi* and *M. samlanense* form only one kind of conidia. *Metarhizium granulomatis*, *M. phuwiangense*, *M. reniforme*, and *M. viride* produce paeclomycytes-like phialides. All species in *Metarhizium* form mononematous conidiophores except for *M. dendromatilis* that is synnematous.

Generalists and specialists in *Metarhizium*

*Metarhizium* species can have either broad or narrow insect host ranges. Several studies revealed that some species of *Metarhizium*, especially in the *M. anisopliae* and *M. flavoviride* species complexes, have broad insect host ranges, such as *M. brunneum*, *M. flavoviride*, *M. minus*, *M. pingshaense* and *M. robertsii*. However, an increasing number of fungal pathogens initially reported as dispersed generalists are now described as collections of populations or sister species undergoing speciation or have adapted to new habitats or new hosts (Burnett 2003, Giraud et al. 2008, Bischoff et al. 2009, Kobmoo et al. 2019, Thanakitpipattana et al. 2020).

Nishi & Sato (2017) revealed that isolates of *M. pingshaense* in Japan have a broad insect host ranges. They came from six orders (14 families) of insects (Lepidoptera: Noctuidae, Geometridae; Coleoptera: Scarabaeidae, Cerambycidae, Curculionoidea, Lucanidae; Orthoptera: Gryllidae, Diptera: Tabanidae; Hymenoptera: Formicidae, Vespidae; Hemiptera, Cydnidae, Diinoridae, Pentatomidae, Largidae). New records of insect hosts (crickets and stick insects) were seen in *M. majus*, while previously, *M. majus* was reported only from scarabaeid insects (Ferron et al. 1972, Nishi et al. 2015).

In the case of species with narrow insect hosts ranges, *M. koreanum*, which was originally described from Korea (Kepler et al. 2014) and reported from Japan (Nishi & Sato, 2017) and Thailand (this study) were all found occurring on planthoppers belonging to Delphacidae, Tropiduchidae and Fulgoromorpha, respectively. The results from these studies suggests that *M. koreanum* has a narrow insect host range and is only specific to planthoppers. Additionally, *M. acridum* is another species known as a specialist with a narrow insect host range found only on certain locusts and grasshoppers (Driver et al. 2000, Wang et al. 2011) as are *M. blattodeae* and *M. argentinense* that only occur on forest cockroaches (Montalva et al. 2016, Gutierrez et al. 2019).

Several species in *Metarhizium* from Asia are found in their sexual states. These species are members of the *M. anisopliae* species complex as well cicadicolous species. Cordycipitoid
fungi has been known for repeated inter-kingdom host jumps (Nikoh & Fukatsu 2000, Sung et al. 2007). In the Clavicipitaceae the mode of nutrition varies from insects, plants or animals. However, in *Metarhizium* alone, these shifts in nutritional mode are clearly manifested. The highest diversity for *Metarhizium* is now recorded for SE Asia, although no studies of their presence in soil or rhizosphere has been made. In Thailand, for instance, the ubiquitous *M. anisopliae* or *M. flavoviride* were never found, as they were never looked for in the soil. Only few records were made from Africa, South and Central America (Samson 1974, Montalva et al. 2016, Lopes et al. 2018, Gutierrez et al. 2019).

While most of the species discovered in *Metarhizium* are considered entomopathogenic, studies of their plant-growth promoting and endophytic, rhizosphere or soil-dwelling properties have been increasing (Hu & St. Leger. 2002, Chad et al. 2014, Iwanicki et al. 2019). As they continue to promote plant health by increasing nutrient absorption through the roots and killing insect pests (Sasan & Bidochka 2012, Liao et al. 2014, 2017) and being used for biological control, reports have also showed *Metarhizium* implicated in human infections (Neurisson et al. 2017). The first infection caused by *Metarhizium* was reported almost two decades ago (Roberts & St Leger 2004) and since then reports of human infection have been made, especially in immunocompromised patients (Revankar et al. 1999, Osorio et al. 2007, Marsh et al. 2008, Eguchi et al. 2015). These reports have serious consequences for those who use *Metarhizium* in agriculture. More studies on these tripartite interactions between plants, fungus and insects, as well as their interactions with humans, will enable us to have a better understanding of the role of these fungi in the natural habitat.

**KEY TO *METARHIZIUM* SPECIES**

Below are two different keys to help identify species in *Metarhizium*. Most species are members of species complexes and are therefore very difficult to find diagnostic characters to separate the species. It is recommended, however, that after a strain has been narrowed down to a certain species, multi-gene sequencing should also be done.

**Synoptic key for sexually reproductive species in *Metarhizium***

List of sexually reproductive species in *Metarhizium*.

1. *M. atrovirens*
2. *M. brachyspermum*
3. *M. brittlebankisoides*
4. *M. campossterni*
5. *M. chaiyaphumense*
6. *M. clavatum*
7. *M. eburneum*
8. *M. flavum*
9. *M. guizhouense* (*M. taii)*
10. *M. guniujiangense*
11. *M. indigoticum*
12. *M. kaeanse*
13. *M. owariense*
14. *M. phuviangense*
15. *M. prachinense*
16. *M. pseudoatrovirens*
17. *M. purpureonigrum*
18. *M. purpureum*
19. *M. sulphureum*
20. *M. takense*

Description: Stromata single or multiple, solitary, cylindrical, branched. Ascospores lanceolate with tapering ends, filiform, part-spires.

**Insect host**

1. Coleoptera (larva, adult)........1–4, 6, 8, 12, 14, 16–18
2. Lepidoptera (pupa, larva).................7, 9, 11, 15, 19
3. Hemiptera (cicada nymph)...........5, 10, 13, 20

**Stromata (length)**

10–50 mm................................1, 2, 5–11, 14–16, 18, 19
>50–100 mm................................................................3, 13, 15, 20
>100 mm..................................................4, 12, 17, 20

**Perithecial arrangement with position**

1. Obliquely with immersed........1, 2, 5, 6, 9–13, 15, 20
2. Obliquely with semi-immersed..............14, 19
3. Ordinally with immersed......................3, 4, 16–180
4. Ordinally with semi-immersed...............7, 8

**Ascospores**

1. Lanceolate with tapering ends..................1, 16
2. Filiform........................................2, 5–8, 10, 12, 15, 17–20
3. Part-spires........................................3, 4, 9, 11, 13, 14

**Phialide characteristics of asexual morph**

1. Unknown.............................................1, 7, 16
2. *Metarhizium*-like........................2–6, 8–12, 17–19
3. Nomuraea-like.................................13, 15, 20
4. Paecilomyces-like..........................14

**Known geographical distribution**

1. China...............................................3, 4, 9, 10
2. Japan...............................................1–3, 11, 13, 16
3. Thailand.........................................5–8, 12, 14, 15, 17–20
Key to Metarhizium species

Sexual state present: ................................................................. 1
Sexual state not observed: .......................................................... 6

1a. Ascospores not dissociating in part-spores
1b. Ascospores dissociate into part-spores

2a. Ascospores lanceolate with tapering ends
2b. Ascospores filiform

3a. Ascospores 50–52 × 2.5–3 μm, obliquely immersed perithecia, on Coleoptera larva, stromata 20–50 mm long.................................................. M. atrovirens
3b. Ascospores 50 × 2.5 μm, ordinarily immersed perithecia, on Coleoptera larva, stromata 14 mm long.................................................. M. pseudoatrovirens
4a. Ascospores 94–107 × 1 μm, obliquely immersed perithecia, nomuraea-like phialides, on Lepidoptera larva, stromata 50–86 mm long.................................................. M. prachinense
4b. Ascospores 155–230 × 1.25 μm, obliquely immersed perithecia, nomuraea-like phialides, on cicada nymph, stromata 70–130 mm long.................................................. M. takense
4c. Ascospores 200–275 × 1.5–2 μm, ordinarily immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata 100–150 mm long.................................................. M. purpureonigrum
4d. Ascospores 160–240 × 1.5–2 μm, ordinarily immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata 40 mm long.................................................. M. purpureum
4e. Ascospores 190–270 × 1 μm, obliquely immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata up to 30 mm long.................................................. M. brachyspermum
4f. Ascospores 200–300 × 2–3 μm, obliquely semi-immersed perithecia, metarhizium-like phialides, on Lepidoptera larva, stromata 25–45 mm long.................................................. M. sulphureum
4g. Ascospores 200–315 × 1.5–2 μm, ordinarily semi-immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata up to 45 mm long.................................................. M. flavum
4h. Ascospores 222.5–360 × 1 μm, ordinarily semi-immersed perithecia, no sporulation in culture, on Lepidoptera pupa, stromata 10 mm long.................................................. M. eburneum
4i. Ascospores 225–375 × 1 μm, obliquely immersed perithecia, nomuraea-like phialides, on cicada nymph (Hemiptera), stromata 30–35 mm long.................................................. M. chaiyaphumense
4j. Ascospores 240–330 × 0.8–1 μm, obliquely immersed perithecia, metarhizium-like phialides, on cicada nymph (Hemiptera), stromata 40–42.5 mm long.................................................. M. guniujiangense
4k. Ascospores 400–500 × 1–1.5 μm, obliquely immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata 150 mm long.................................................. M. kalasinense
4l. Ascospores 224–420 × 1–1.5, obliquely immersed perithecia, metarhizium-like phialides, on Coleoptera larva, stromata 35 mm long.................................................. M. clavatum

5a. Part-spores cylindrical, 2.9–5.9 × 1 μm, ordinarily immersed perithecia, metarhizium-like phialides, on Coleoptera larva (Scarabaeidae), stromata 160 mm long.................................................. M. campososerni
5b. Part-spores cylindrical, 4.5–5 × 1 μm, ordinarily immersed perithecia, metarhizium-like phialides, on Lepidoptera larva, stromata 40–50 mm long.................................................. M. indigoticum
5c. Part-spores cylindrical, 4.2–5.6 × 1 μm, obliquely immersed perithecia, nomuraea-like phialides on cicada nymph (Hemiptera), stromata 57 mm long.................................................. M. ovaniense
5d. Part-spores cylindrical, 5.7–8.1 × 0.94 μm, ordinarily immersed perithecia, metarhizium-like phialides, on Coleoptera larva (Scarabaeidae), stromata 100 mm long.................................................. M. brittlebankisoides
5e. Part-spores cylindrical, 8–12 × 1–1.5 μm, obliquely semi-immersed perithecia, paecilomyces-like phialides, on adult Coleoptera, stromata up to 15 mm long.................................................. M. phuwiangense
5f. Part-spores cylindrical, 17–34 × 1–1.4 μm, obliquely immersed perithecia, metarhizium-like phialides, on Lepidoptera larva, stromata 20–35 mm long.................................................. M. guizhouense

6a. Metarhizium-like phialides.................................................. M. acridum, M. album, M. alvesii, M. anisopliae, M. argentinense, M. baoshanense, M. bibionidarum, M. biotecense, M. blattoideae, M. brasiensiense, M. bruneum, M. candelabrum, M. cercopidariurn, M. culicidarium, M. ellipsoideum, M. flavoviride, M. frigidum, M. fuscoideum, M. gaoligongense, M. globosum, M. gryllidicola, M. huainamdangense, M. humberi, M. koreanum, M. lepidioti, M. majus, M. minus, M. normoi, M. novozealandicum, M. pemphigi, M. phasmatodeae, M. pingshaense, M. purpureogenum, M. robertssii
6b. Nomuraea-like phialides.................................................. M. cincadae, M. cylindrosorum, M. dendrolimatis, M. megapomponia, M. niveum, M. ovoidosorum, M. rileyi, M. samiennense, M. viridulum

THE GENUS METARHIZIUM AND RELATED GENERA

www.studiesinmycology.org 247
6c. Paecilomyces-like phialides. ................................................................. M. granulomatis, M. reniforme, M. viride

7a. on multiple hosts .......................................................... M. anisopliae, M. bibionidarum, M. brunneum, M. flavoviride, M. frigidum, M. fusoidenum, M. humberi, M. lepidiotae, M. majus, M. minus, M. normoii, M. novozealandicum, M. pemphigi, M. pingshaense, M. robertsii

7b. on cockroaches (Blattodea) .............................................. M. argentinense, M. blattodeae

7c. on Diptera .............................................................. M. globosum

7d. on Hemiptera (small hoppers: Cicadellidae, Cercopidae, Delphacidae) ........................................... M. album, M. biotecense, M. brasiliense, M. candelabrum, M. cercopidum, M. ellipsoideum, M. huainamdongense, M. koreanum

7e. on Lepidoptera larva and pupa ........................................... M. rileyi

9a. Conidia dimorphic, host chameleon ................................................................. M. granulomatis, M. viride

9b. Conidia reniform, 4–5.5 × 1.5–2.5 μm, greyish green, olive, dull green colony ................................................................. M. reniforme

10a. Conidia cylindrical to ellipsoid, 5–7 × 2–3.5 μm, greyish green colony ................................................................. M. anisopliae

10b. Conidia cylindrical to ellipsoid, 4.5–6 × 2–3 μm, brownish yellow colony ................................................................. M. bibionidarum

10c. Conidia cylindrical to ellipsoid, 4.5–9 × 2–3 μm, white cream yellow colony ................................................................. M. brunneum

10d. Conidia pyriform, reniform, ovoid, 4–10 × 1.5–3 μm, yellowish white colony ................................................................. M. flavoviride

10e. Conidia cylindrical, 4–8 × 2–4 μm, dark green colony ................................................................. M. frigidum

10f. Conidia ellipsoid to cylindrical, 6–10 × 2–3 μm, white to pale cream ................................................................. M. fusoidenum

10g. Conidia cylindrical, 4.14–6.05 × 1.69–2.59 μm, grey green colony ................................................................. M. humberi

10h. Conidia ovoid to ellipsoid cylindrical, 5–7.5 × 3–4 μm, white colony ................................................................. M. lepidiotae

10i. Conidia oblong-elliptical, 10–14 × 2–4 μm, yellowish orange to green ................................................................. M. majus

10j. Conidia cylindrical, ellipsoid, 4–6 × 2.5–3 μm, white ................................................................. M. minus

10k. Conidia cylindrical, 4–7 × 1.5–2 μm, sulphur yellow ................................................................. M. normoii

10l. Conidia cylindrical, ellipsoid, 5–7.5 × 2–3, white to pale yellow colony ................................................................. M. novozealandicum

10m. Conidia cylindrical, 3–8 × 1.5–2 μm, pale yellow colony ................................................................. M. pemphigi

10n. Conidia ellipsoid, 6–8 × 2.5–3.5 μm, olive colony ................................................................. M. pingshaense

10o. Conidia cylindrical, ellipsoid, 5–9 × 2–3 μm, white to pale yellow colony ................................................................. M. robertsii

11a. Conidia ellipsoid to cylindrical, 6–8 × 2–3 μm, pale yellow colony (on SDAY/4) ................................................................. M. blattodeae

11b. Conidia cylindrical, 5.1–7.7 × 1.7–2.9 μm, olivaceous green colony (on PDA) ................................................................. M. argentinense

12. Conidia fusiform-elliptical, ellipsoid, 4–7 × 1–1.5 μm, white colony ................................................................. M. culicidum

13a. Conidia ellipsoid, cylindrical, 5–6 × 1.5–2 μm, pale brown colony ................................................................. M. anisopliae

13b. Conidia cylindrical, ellipsoid, 5–6 × 2–3 μm, white colony ................................................................. M. album

13c. Conidia ovoid to cylindrical, 3–10 × 2–3 μm, cream to pale yellow colony ................................................................. M. brasiliense

13d. Conidia cylindrical, 7–9 × 1.5–2 μm, white to pale green colony ................................................................. M. candelabrum

13e. Conidia cylindrical, 6–10 × 1.5–3 μm, pale yellow to pale green colony ................................................................. M. cercopidarum

13f. Conidia cylindrical, ellipsoid, 4–7 × 1.5–2 μm, olive yellow, sulphur yellow colony ................................................................. M. ellipsoideum

13g. Conidia cylindrical, 5–10 × 2–3, pale yellow to dark green colony (on PDA) ................................................................. M. huaianamdongense

13h. Conidia cylindrical, ellipsoid, 4–7.5 × 1.5–2.5 μm, white to yellow colony ................................................................. M. koreanum

14. Conidia globose, 4–5 μm, greyish green colony ................................................................. M. globosum

15a. Conidia ellipsoid, globose, 4–5.5 × 3–4 μm, greyish yellow colony ................................................................. M. acridum

15b. Conidia cylindrical to ovoid, obclavate, 4–7 × 2–3 μm, sulphur yellow colony ................................................................. M. gryllidicola

15c. Conidia cylindrical, ovoid, obclavate, 5.5–8 × 2–3 μm, sulphur yellow colony ................................................................. M. phasmatodeae
Conidia cylindrical, 3.88–6.55 × 2.16–3.25 μm, yellow to greenish colony ................................................. *M. alvesii*

Conidia long oval, cylindrical, 6.7–8.5 × 2.6–3.3 μm, greyish green colony (on PDA) ................................................. *M. baoshanense*

Conidia cylindrical, 5.4–7.7 × 1.9–2.8 μm, green colony (on PDA) ................................................................. *M. gaoligongense*

Conidia ovoid to ellipsoid, 4.5–5.5 × 3.5–4 μm, pale ochre or tan colony .......................................................... *M. purpureogenum*

Conidia ellipsoid, 3.8–10 × 2–2.5 μm, light yellow green colony (on PDA) ......................................................... *M. dendrolimatilis*

Conidia two types of conidia; ovoid, ellipsoid, 2–6 × 2.5–4 μm; cylindrical, 10–17 × 3–4 μm, dark green colony ... *M. cicadas*

Conidia two types of conidia; ovoid, subglobose, 3–8 × 2–3 μm; cylindrical, 14–22 × 3–4 μm, pale yellow colony ... *M. cylindrosporum*

Conidia cylindrical, ellipsoid, 7–11 × 3–4 μm, cream to yellow brown colony .................................................... *M. megapomponia*

Conidia ovoid, ellipsoid, 2–5 × 2–3 μm, white to cream colony ............................................................................ *M. niveum*

Conidia cylindrical, 10–16 × 3–4 μm, pale yellow colony ..................................................................................... *M. viridulum*

Conidia ovoid, ellipsoid, subglobose, 3–5 × 2–4 μm, olive yellow colony ............................................................. *M. ovoidosporum*

Conidia globose, 3–5 μm, sulphur yellow to straw yellow colony ........................................................................... *M. samlanense*

**ACKNOWLEDGEMENTS**

This work is dedicated to Keith A. Seiffert for his invaluable contributions to mycology and the IMA on the occasion of his retirement from Ottawa Research and Development Centre, Agriculture and Agri-Food Canada (Biodiversity; Mycology and Microbiology). Thanks to Bart Kraak and Martin Meijer for their help sequencing of CBS strains. This study was supported by National Science and Technology Development Agency (NSTDA). The authors are grateful to the Platform Technology Management Section, National Center for Genetic Engineering and Technology Development Agency (NSTDA). The authors are grateful to the Community forest, Phitsanulok Province) for their cooperation and support of our biodiversity studies of invertebrate-pathogenic fungi in Thailand. Thanks to the Department of National Parks for their kind support and permission to collect fungi in the national parks. We thank Samet Phussaneri (Head of Phu Wang National Park), Sangsao Veeraping (Village headman of Banphao Thai community forest, Phitsanulok Province) for their cooperation and support of our project research. We thank Thayarat Chaitika, Aundaman Mouchoo for their help in generating molecular data and Kewarin Klamchoo for insect identification. We thank USDA ARS EF (Louela Castrillo) for providing known strains of *Metarhizium* for this study. We thank Konstanze Bensch for her help in species names. We are grateful to the two anonymous reviewers whose comments and suggestions helped improve the manuscript.

**APPENDIX A. SUPPLEMENTARY DATA**

Supplementary data to this article can be found online at https://doi.org/10.1016/j.simyco.2020.04.001.

**REFERENCES**

Ban S, Azuma Y, Sato H, et al. (2015). *Isaria takamizusanensis* is the anamorph of *Cordyceps rygaminomontana*, warranting a new combination, *Purpureoscladium takamizusanensis* comb. nov. International Journal of Systematic and Evolutionary Microbiology 65: 2459–2465.

Beys-da-Silva WO, Rosa RL, Berger M, et al. (2020). Updating the application of *Metarhizium* anisopliae to control cattle tick *Rhipicephalus microplus* (Acari: Ixodidae). Experimental Parasitology 208: 107812.

Bischoff JP, Rehner SA, Humber RA (2006). *Isaria takamizusanensis* nov. sp., a cryptic species of *M. anisopliae* and a member of the *M. flavoviride* complex. Mycologia 98: 737–745.

Bischoff JP, Rehner SA, Humber RA (2009). A multilocus phylogeny of the *Metarhizium* anisopliae lineage. Mycologia 101: 512–530.

Burnett J (2003). Fungal population and species. Oxford University Press, Oxford, UK.

Castlebury LA, Rossman AY, Sung GH, et al. (2004). *Entomophaga* species parasitic on *Metarhizium* from soybean aphid and identification of *Metarhizium* isolates from agricultural fields. Fungal Ecology 7: 174–192.

Chan WH, Ling KH, Chiu SW, et al. (2011). Molecular analyses of *Cordyceps* gunnii in China. Journal of Food and Drug Analysis 19: 18–25.

Chen WH, Ling KH, Chiu SW, et al. (2010).更新 *Cordyceps* species parasitic on *Metarhizium* anisopliae in China. Mycologia 92: 1255–1265.

Chen WH, Han YF, Liang JD, et al. (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1896–1908.

Chen Z, Xu L, Yang X, et al. (2018a). *Metarhizium baoshanense* sp. nov., a new entomopathogenic fungus from southwestern China. Pakistan Journal of Zoology 50: 1739–1746.

Chen Z, Yang X, Sun N, et al. (2018b). Species diversity and vertical distribution characteristics of *Metarhizium* in Gaoligong Mountains, southwestern China. Biodiversity Science 26: 1308–1317.

Chen ZH, Zhang YG, Yang XN, et al. (2018c). A new fungus *Metarhizium gaoligongense* from China. International Journal of Agriculture and Biology 20: 2271–2276.

Cliffon EH, Jaronski ST, Coates BS, et al. (2018). Effects of endophytic entomopathogenic fungi on soybean aphid and identification of *Metarhizium* isolates from agricultural fields. FcOs ONE 13: e0194815.

Cole GT, Samson RA (1979). Patterns of development in conidial fungi. Pitman Publishing Ltd., London, San Francisco, Melbourne: 68–69.

Doyle JJ (1987). A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19: 11–15.

Driver F, Milner RJ, Trueman JH (2000). *Fusarium* sp.: sample preparation and DNA sequence data. Mycological Research 104: 134–150.

Edgar RC (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Edgar RC (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Edgar RC (2004). MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Ferron P, Hurpin B, Robert PH (1972). Sur la spécificité de *Metarhizium anisopliae* (Metschn.) Sorok. Entomophaga 17: 165–178.

Gams W, Rozsypal J (1973). *Metarhizium* flavoviride nov. sp. isolated from insects and the soil. Acta Botanica Neerlandica 2: 518–521.

Ghaderi S, Abdollahi M (2013). Biocontrol potential of *Metarhizium anisopliae* (Hypocreales, Clavicipitaceae) isolated from suppressive soils of the Boyer-Ahman region, Iran, against *J2a* of *Heterodera avenae*. Journal of Plant Protection Research 53: 165–171.

Giraud T, Relfregier G, Le Gac M, et al. (2008). Speciation in Fungi. *Fungal Genetics and Biology* 45: 791–802.

Guo HL, Ye BL, Yue YY, et al. (1996). Three new species of *Metarhizium*. Acta Mycologica Sinica 5: 185–190.

Gutiérrez AC, Lacleque A, Manfrin RG, et al. (2019). Natural occurrence in Argentina of a new fungal pathogen of cockroaches, *Metarhizium argenti- nense* sp. nov. *Fungal Biology* 123: 364–372.

Hall B (2003). Molecular systematics using gene sequences encoding nuclear RNA polymerase subunits. http://faculty.washington.edu/ bhalli/.

Hall T (2004). BioEdit version 6.0.7. Department of Microbiology, North Carolina State University, Harris JL (2000). Safe, low-distortion tape touch method for fungal slide mounts. Journal of Clinical Mycology 38: 4683–4684.
Liu ZY, Liang ZQ, Whalley AJS, Iwasaki H, Tokiwa T, Shiina M, Kornerup A, Wanscher JH (1963).
Lanave C, Preparata G, Saccone C, Li C, Huang B, Fan MZ (2010).
Jackson MA, Jaronski ST (2008). Production of microsclerotia of the fungal
Kalkar et al
Kim JC, Baek S, Park SE, Keyser CA, Thorup-Kristensen K, Meyking NV (2014).
Cordyceps Kobayasi Y (1939). On the genus Metarhizium
9
Metarhizium
842
new pathogen of grubs and its asexual morph,
Metarhizium anisopliae
98
application of
fungal-pathogen speciation and host adaptation.
Neotropical Entomology 42: 436–438.
Lopes RB, Souza DA, Rocha LFN, et al. (2018). Metarhizium alvesii sp. nov.: a new member of the Metarhizium anisopliae species complex. Journal of Invertebrate Pathology 151: 165–168.
Luangsard J, Houbraiken J, van Doorn T, et al. (2011). Purpureocillium, a new genus for the medically important Paecilomyces lilacinus. EMBO Microbiology 321: 141–149.
Luangsard J, Hywel-Jones NL, Manoch L, et al. (2005). On the relationships of Paecilomyces sect. Isaria dubious species. Mycological Research 109: 581–588.
Luangsard J, Mongkolsamrit S, Thanakitpipattana D, et al. (2017). Clavicipitaceae entomopathogenic: new species of Metarhizium and a new species Nigelia. Mycological Progress 16: 389–391.
Luangsard J, Tanatanathi K, Thanakitpipattana D, et al. (2018). Novel and interesting Ophiocordycipstis spp. (Ophiocordycipstids, Hypocreales) with superficial perithecia from Thailand. Studies in Mycology 89: 125–142.
Luz C, Rocha LFN, Montalva C, et al. (2019). Metarhizium humberi sp. nov. (Hypocreales: Cordycipstidaceae), a new member of the PARB clade in the Metarhizium anisopliae complex from Latin America. Journal of Invertebrate Pathology 166: 107216.
Malyskaj EL (1992). An efficient method for isolation of RNA and DNA from plants containing polyphenols. Nucleic Acids Research 20: 2381.
Marsh RA, Lucky AW, Walsh TJ, et al. (2008). Cutaneous infection with Metarhizium anisopliae in a patient with hypohydrotic ectodermal dysplasia and immune deficiency. Pediatric Infectious Disease Journal 27: 283–284.
Mayerhofer J, Lutz A, Dennert F, et al. (2019). A species-specific multiplex PCR amplicon assay for distinguishing between Metarhizium anisopliae, M. brunneum, M. pinghaesaen and M. robertsi. Journal of Invertebrate Pathology 161: 23–28.
Massée G (1898). British Mycology. Transactions of the British Mycological Society 1: 20–24.
Metchnikoff E (1879). Maladies des hannetons duble. Zapiski imperatorskogo obchestev se’iskago Kh Zoozaytstra yuzhnoi rosii, 17–50.
Mongkolsamrit S, Nolipoom W, Amarnatt N, et al. (2019). Resurrection of Parasims in the Ophiocordycipstidaceae with three new species from Thailand. Fungal Diversity 92: 131–1320.
Mongkolsamrit S, Nolipoom W, Thanakitpipattana D, et al. (2018). Disentangling cryptic species with isaria-like morphs in Cordycipstidaceae. Mycologia 110: 230–257.
Montalva C, Collier K, Rocha LFN, et al. (2016). A natural fungal infection of a sylvatic cockroach with Metarhizium blattodaeo sp. nov., a member of the M. flavovirens species complex. Fungal Biology 120: 655–665.
Nikke N, Fukutsu T (2000). Interkingdom host jumping underground: phylogenetic analysis of entomopathogenic fungi of the genus Cordyceps. Molecular Biology and Evolution 17: 629–638.
Nishi O, Iiyama K, Yasunaga-Aoki C, et al. (2015). Phylogenetic status and pathogenicity of Metarhizium majus isolated from a fruit beetle larva in Japan. Mycological Progress 14: 58.
Nishi O, Iiyama K, Yasunaga-Aoki C, et al. (2015). Phylogenetic status and pathogenicity of Metarhizium majus isolated from a fruit beetle larva in Japan. Mycological Progress 14: 58.
Nishi O, Sato H (2017). Species diversity of the entomopathogenic fungi Metarhizium anisopliae and M. flavovirens species complexes isolated from insects in Japan. Mycoscience 58: 472–479.
Nishi O, Sato H (2019). Isolation of Metarhizium spp. from rhizosphere soils of wild plants reflects fungal diversity in soil but not plant specificity. Mycology 10: 22–31.
Nishi O, Shimizu S, Sato H (2017). Metarhizium biondiadura and M. purpureogenum: new species from Japan. Mycological Progress 16: 987–998.
Noussou M, Duport D, Lavernerie RA, et al. (2017). Species of Metarhizium anisopliae complex implicated in human infections: retrospective sequencing study. Clinical Microbiology and Infection 23: 994–995.
Nylander JAA (2004). MrModeltest 2.2: program distributed by the author. Evolutionary Biology Centre, Uppsala University.
