WESTERDIJK FUNGAL BIO DIVERSITY INSTITUTE

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

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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 rDNA. 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* larvae and *M. sulphureum* on *Lepidoptera* larvae; four new species are found in the *M. flavoviride* complex – *M. biotecense* and *M. fusoideum* on brown plant hoppers (*Hemiptera*), *M. culicidarum* on mosquitoes, *M. nornnoi* on *Lepidoptera* larvae; three new species *M. megapomponiae, M. cicadae, M. niveum* occur on cicadas; five new species *M. candelabrum, M. cercopidarum, M. ellipsoideum, M. huainamdangense M. ovoidosporum* occur on planthoppers, leafhoppers and froghoppers (*Hemiptera*); one new species *M. eburneum* on *Lepidoptera* pupae; and four new species *M. phuwiangense, 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. phuwiangense, M. purpureonigrum, M. purpureum,* and *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′*tef* 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. khaoyaiense* and two new species *P. maesotensis* and *P. pyriformis. Papiliomyces* contains two new combinations for *M. liangshanense* and *Metacordyceps shibinensis*. The genus *Sungia* is proposed for the Korean species *M. yongmunense* on *Lepidoptera* pupa and *Yosiokobayasia* for the Japanese species *M. kusanagiense* 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 & Thanakitpipattana. **New species:** *Metarhizium biotecense* Luangsa-ard, Khonsanit, Thanakitpipattana & Samson, *M. candelabrum* Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, *M. cercopidarum* Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, *M. cicadae* 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. ellipsoideum* Luangsa-ard, Khonsanit, Thanakitpipattana & Samson, *M. flavum* Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, *M. fusoideum* Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, *M. huainamdangense* Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, *M. megapomponiae* Luangsa-ard, Tasanathai, Thanakitpipattana & Samson, *M. niveum* Luangsa-ard, Tasanathai, Thanakitpipattana & Samson, *M. nornnoi* Luangsa-ard, Khonsanit, Thanakitpipattana & Samson, *M. ovoidosporum* Luangsa-ard, Khonsanit, Thanakitpipattana & Samson, *M. phuwiangense* Luangsa-ard, Mongkolsamrit, Himaman, 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 acicularis* (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* (Massee) Samson, Houbraken & Luangsa-ard, *Papiliomyces liangshanensis* (M. Zang *et al.*) Luangsa-ard, Samson & Thanakitpipattana, *Papiliomyces shibinensis* (T.C. Wen *et al.*) Luangsa-ard Samson & Thanakitpipattana, *Purpureomyces khaoyaiensis* (Hywel-Jones) Luangsa-ard, Samson & Thanakitpipattana, *Sungia yongmunensis* (G.H. Sung *et al.*) Luangsa-ard, Thanakitpipattana & Samson, *Yosiokobayasia kusanagiensis* (Kobayasi & Shimizu) Samson, Luangsa-ard & Thanakitpipattana.
Neotype: *Metarhizium anisopliae* (Metsch.) Sorokīn.

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

Peer review under responsibility of Westerdijk Fungal Biodiversity Institute.
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Studies in Mycology

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 Metchnikoff (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 and presence or absence of subhymenial zones as the diagnostic criteria for delimiting species. They also added *M. flavoviride* var. *minus* to accommodate Asian isolates with shorter conidia and resurrected *M. album* as a separate species. China and Japan reported *M. pingshaense, M. cylindrosporum, M. guizhouense* (Guo *et al.* 1986, Shimazu 1989) and *M. taii* 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 (*tef, rpb1, rpb2* and *tub*). The authors recognised the synonymy 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. robertsii*, 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. atypicola,* 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. gryllidicola, 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. gryllidicola,* 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 geminated 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 fresh PDA plates. The cultures were then allowed to grow for 2–4 wk, pure cultures were deposited in the BIOTEC culture collection. Specimens were dried in an electric food dryer (50–55 °C) overnight and stored in plastic boxes before storage at the BIOTEC Bangkok Herbarium (BBH).

Seventeen ex-type strains from the USDA, ARSEF were included to study the phenotypical characters (Table 3, Supplementary Table S1).

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 mounted in lactophenol cotton blue solution and measured using a compound microscope (Olympus CX31). Twenty to fifty perithecia, asci, ascospores, phialides and conidia were measured and the range and standard deviations calculated. Specimens were photographed with an Olympus DP70 Digital Camera mounted on an Olympus BX51 compound microscope. The reaction of the stromata 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 "oac" herein), Methuen handbook of colour (Kornerup & Wanscher 1963) and Naturalist's Colour Guide (Smithe 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 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-α (*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 $MgCl_2$, 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 *rpb*1 (Hall 2003, Castlebury *et al.* 2004), RPB2-5F2 and RPB2-7Cr for *rpb*2 (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 previousy published protocols (Sung *et al.* 2007, Mongkolsamrit *et al.* 2019).

Phylogenetic analyses

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.phylosolutions.com, Swofford 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

Table 1. List of specimens and GenBank accession numbers of sequences used in this study. Bold accession numbers were generated from this study.

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)
Balansia 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. pilulaeformis	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	–	Luangsa-ard *et al.* (2005)
	CBS 659.71	–	*Chameleo lateralis*	HQ165673	HQ165735	HQ165692	–	HQ165652	HQ165714	–	Luangsa-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 cp11	–	*Poaceae*	EF469122	EF469075	EF469058	EF469087	EF469105	–	–	Sung *et al.* (2007)
Conoideocrella tenuis	NHJ 6791	Thailand	*Hemiptera*: Scale insect	–	–	–	–	–	JN049863	–	Johnson *et al.* (2009)
Cordyceps brittlebankisoides	G97025	–	–	–	–	–	–	–	AJ309332	–	Liu *et al.* (2001)
C. chlamydosporia	CBS 101244	–	*Diplopoda*: Egg of slug	DQ522544	DQ518758	DQ522327	DQ522372	DQ522424	JN049821	–	Sung *et al.* (2007)
C. cylindrica	CBS 744.73	Japan	*Arachnida*: Spider	EF468987	EF468841	EF468786	EF468892	–	GU980041	–	Sung *et al.* (2007)
C. fratricida	TNS 19011	–	Fungi	JQ257022	JQ257023	JQ257028	JQ257016	JQ257021	–	–	Kepler *et al.* (2012b)
C. gunnii	G97011	China	–	–	–	–	–	–	AJ243773	–	Chan *et al.* (2011)
	G97022	China	–	–	–	–	–	–	AJ309340	–	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)
	HMIGD20885	–	–	–	–	–	–	–	DQ150247	–	Zhang *et al.* (2004)
	BCC19475	Thailand	*Lepidoptera*	–	–	–	–	–	KY348781	–	Luangsa-ard *et al.* (2017)
	BCC19950	Thailand	*Lepidoptera*	GU979934	GU979943	GU979952	GU979961	GU979967	KY348780	–	Luangsa-ard *et al.* (2017)
	BCC37621	Thailand	*Lepidoptera*	GU979937	GU979946	GU979955	GU979964	GU979970	–	–	Luangsa-ard *et al.* (2017)
Hypocrella schizostachyi	BCC 14123	Thailand	*Hemiptera*	DQ522557	DQ518771	DQ522346	DQ522392	DQ522447	–	–	Sung *et al.* (2007)
Hypocrella sp.	GJS 89–104	–	*Hemiptera*: Scale insect	–	DQ518772	DQ522347	DQ522393	DQ522448	–	–	Spatafora *et al.* (2007)
Isaria takamizusanensis	NBRC 110230	Japan	*Hemiptera*	–	–	–	–	–	LC008202	–	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. brittlebankisoides	Hn1	China	*Coleoptera*	–	–	AB778556	AB778555	AB778554	–	–	Nishi *et al.* (2015)
Mc. indigotica	TNS-F18553	Japan	*Lepidoptera*	JF415953	JF415968	JF416010	JN049886	JF415992	JN049874	–	Kepler *et al.* (2012a)
	TNS-F18554	Japan	*Lepidoptera*	JF415952	JF415969	JF416011	JN049887	JF415993	JN049875	–	Kepler *et al.* (2012a)
Mc. khaoyaiensis	BCC12687	Thailand	*Lepidoptera* larva	–	–	–	–	–	JN049868	–	Kepler *et al.* (2012a)
	BCC14290	Thailand	*Lepidoptera* larva	JF415970	–	KJ398797	JN049888	–	JN049869	–	Kepler *et al.* (2012a)
Mc. kusanagiensis	TNS-F18494	Japan	*Coleoptera*	JF415954	JF415972	JF416014	JN049890	–	JN049873	–	Kepler *et al.* (2012a)
Mc. liangshanensis	EFCC 1452	Korea	*Lepidoptera*	EF468962	EF468815	EF468756	–	–	–	–	Sung *et al.* (2007)
	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)
	HMAS 197472	China	*Coleoptera*: *Cerambycidae*	JF415955	JF415973	JF416015	JN049892	JF415994	JN049881	–	Luangsa-ard *et al.* (2017)
	TTZ070716-04	–	–	–	–	–	–	–	JN049871	–	Luangsa-ard *et al.* (2017)
Mc. neogunnii	BUM 415	China	*Lepidoptera* larva	MH143845	MH143828	MH143861	MH143876	MH143891	–	–	Chen *et al.* (2018b)
Mc. owariensis	NBRC33258	Japan	*Hemiptera*	HQ165669	HQ165730	HQ165689	HQ165747	–	–	–	Luangsa-ard *et al.* (2017)
Mc. pseudoatrovirens	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*	–	–	KJ398806	KJ398616	–	–	–	Kepler *et al.* (2014)
	GZUH SB13050305	China	*Lepidoptera* larva	KU729724	–	KU729729	KU729734	–	KY423507	–	Wen *et al.* (2017)
	SK 2014	India	*Hymenoptera*	–	–	–	–	–	KJ179838	–	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	EF468796	EF468902	EF468943	AJ292410	–	Sung *et al.* (2007)
Mp. bulbillosa	CBS 464.88	Scotland	Nematode eggs	AF339615	AF339566	EF468797	EF468903	EF468944	AJ292400	–	Sung *et al.* (2007)
	CBS 891.72	Germany	Fungi	AF339599	AF339550	DQ522354	DQ522401	DQ522458	AJ292409	–	Sung *et al.* (2007)
Metarhizium aciculare	JCM 33284	Japan	Soil	LC435738	LC435741	LC462188	–	–	–	–	Iwasaki *et al.* (2019)
	JCM 33285	Japan	Soil	LC435739	LC435742	LC462189	–	–	–	–	Iwasaki *et al.* (2019)
M. acridum	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	HQ331458	EU248845	Bischoff *et al.* (2009)
M. album	ARSEF 1941	Philippines	*Nephotettix virescens*	–	–	–	–	–	AF137067	–	Driver *et al.* (2000)
	ARSEF 1942	Philippines	*Nephotettix virescens*	–	–	–	–	–	HM055452	–	–
	ARSEF 2082	Indonesia	*Hemiptera*	DQ522560	DQ518775	DQ522352	DQ522398	DQ522452	AY375446	–	Sung *et al.* (2007)

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Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5'*tef*	References
M. anisopliae	ARSEF 6347	Colombia	*Homoptera*	–	–	–	–	–	–	MH604976	Mayerhofer *et al.* (2019)
	ARSEF 7450	Australia	*Coleoptera*	–	–	–	–	–	–	EU248852	Bischoff *et al.* (2009)
	ARSEF 7487	Ethiopia	*Orthoptera*	–	–	DQ463996	DQ468355	DQ468370	MH604974	DQ463996	Bischoff *et al.* (2009)
	CG1233	Brazil	*Coleoptera*	–	–	–	–	–	–	KC832296	Lopes *et al.* (2013)
	CG814	Brazil	*Coleoptera*	–	–	–	–	–	–	KF357928	Lopes *et al.* (2014)
	IP86	Brazil	Soil	–	–	–	–	–	–	JQ061186	Rocha *et al.* (2013)
	CBS 130.71	Ukraine	*Avena sativa*	**MT078868**	**MT078853**	**MT078845**	**MT078861**	**MT078918**	**MT078884**	**MT078928**	This study
M. argentinense	CEP424	Argentina	*Blaberidae*: *Epilamprinae*	–	–	MF966624	MF966625	MF966626	–	–	Gutierrez *et al.* (2019)
M. biotecense	BCC51812^{T}	Thailand	*Hemiptera*: *Delphacidae*	**MN781937**	**MN781838**	**MN781693**	**MN781745**	**MN781792**	**MN781878**	–	This study
	BCC51813	Thailand	*Hemiptera*: *Delphacidae*	**MN781938**	**MN781839**	**MN781694**	**MN781746**	**MN781793**	**MN781879**	–	This study
M. blattodeae	MY00896	Thailand	*Blattodea*	HQ165657	HQ165719	HQ165678	HQ165739	HQ165638	HQ165697	–	Luangsa-ard *et al.* (2017)
	NHJ11597	Thailand	*Blattodea*	–	–	–	–	–	HQ165703	–	Luangsa-ard *et al.* (2017)
M. brachyspermum	CM1	Japan	*Coleoptera*	–	LC469749	LC469751	–	–	LC469747	LC469752	Yamamoto *et al.* (2020)
	CM2	Japan	*Coleoptera*	–	–	–	–	–	LC469748	–	Yamamoto *et al.* (2020)
M. brasiliense	ARSEF 2948	Brazil	*Hemiptera*	–	–	KJ398809	KJ398620	–	–	–	Kepler *et al.* (2014)
M. brunneum	ARSEF 2107	USA	*Coleoptera*	–	–	EU248855	EU248907	EU248935	KC178691	EU248855	Bischoff *et al.* (2009)
	ARSEF 4152	Australia	Soil	–	–	–	–	–	–	EU248853	Bischoff *et al.* (2009)
	ARSEF 4179	Australia	Soil	–	–	–	–	–	–	EU248854	Bischoff *et al.* (2009)
	CBS 316.51	USA	*Coleoptera*: *Elateridae*	**MT078875**	**MT078860**	**MT078852**	–	–	**MT078888**	**MT078927**	This study
M. candelabrum	BCC29224^{T}	Thailand	*Hemiptera*: leafhopper	**MN781952**	**MN781853**	**MN781708**	**MN781755**	**MN781804**	**MN781881**	–	This study
M. cercopidarum	BCC31660^{T}	Thailand	*Hemiptera*: leafhopper	**MN781953**	**BCC31660**	**MN781709**	**MN781756**	**MN781805**	**MN781880**	–	This study
M. chaiyaphumense	BCC28241	Thailand	*Hemiptera*: *Cicadidae*	**MN781932**	**MN781831**	**MN781684**	**MN781740**	**MN781784**	**MN781884**	–	This study
	BCC78198	Thailand	*Hemiptera*: *Cicadidae*	KX369596	KX369593	KX369592	KX369594	KX369595	**MT078881**	–	Luangsa-ard *et al.* (2017)
M. cicadae	BCC48696	Thailand	*Hemiptera*: *Cicadidae*	**MN781948**	**MN781848**	**MN781703**	–	**MN781800**	**MN781885**	–	This study
	BCC48881^{T}	Thailand	*Hemiptera*: *Cicadidae*	**MN781949**	**MN781849**	**MN781704**	**MN781752**	–	–	–	This study
M. clavatum	BCC84543^{T}	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**	**MN781887**	–	This study
	BCC7600^{T}	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	–	–
	RCEF 3632	China	*Hemiptera*: *Cicadidae*	JF415964	JF415987	JF416022	–	–	JN049872	–	Kepler *et al.* (2012a)

Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5'*tef*	References
M. cylindrosporae	TNS-16371	Japan	*Hemiptera*: *Cicadidae*	JF415963	JF415986	JF416027	JN049902	–	–	–	Kepler *et al.* (2012a)
M. eburneum	BCC79252^{T}	Thailand	*Lepidoptera* pupa	–	**MN781829**	**MN781682**	**MN781736**	–	**MN781914**	–	This study
	BCC79267	Thailand	*Lepidoptera* pupa	–	**MN781826**	–	**MN781735**	–	**MN781915**	–	This study
M. ellipsoideum	BCC12847	Thailand	*Hemiptera* adult	**MN781959**	**MN781860**	**MN781715**	**MN781761**	**MN781810**	**MN781925**	–	This study
	BCC49285^{T}	Thailand	*Hemiptera* adult	**MN781957**	**MN781858**	**MN781713**	**MN781759**	**MN781808**	**MT078876**	–	This study
	BCC53509	Thailand	*Hemiptera* adult	**MN781958**	**MN781859**	**MN781714**	**MN781760**	**MN781809**	**MT078877**	–	This study
M. flavoviride	CBS 700.74	USA	–	**MT078870**	**MT078855**	**MT078847**	**MT078863**	**MT078920**	–	**MT078925**	This study
	ARSEF 2133	Czech Republic	*Coleoptera*	–	–	–	–	–	NR131992	DQ463988	Bischoff *et al.* (2006)
	CBS 125.65	USA	–	**MT078869**	**MT078854**	**MT078846**	**MT078862**	**MT078919**	**MT078885**	**MT078926**	This study
	CBS 218.56	Czech Republic	*Coleoptera*	–	–	KJ398787	KJ398598	–	–	–	Kepler *et al.* (2014)
M. flavum	BCC90870^{T}	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. fusoideum	BCC28246^{T}	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*	–	–	EU248846	EU248898	EU248926	NR132020	–	Bischoff *et al.* (2009)
M. granulomatis	UAMH 11028	Denmark	*Chamaeleo calyptratus*	HM635076	HM195304	KJ398781	–	–	NR132013	–	Sigler *et al.* (2010)
	UAMH 11176	Denmark	*Chamaeleo calyptratus*	–	HM635078	KJ398781	KJ398593	–	HM195306	–	Sigler *et al.* (2010)
M. gryllidicola	BCC22353	Thailand	*Orthoptera*: *Gryllidae*: adult cricket	–	–	–	–	–	–	**MT078890**	Thanakitpipattana *et al.* (2020)
	BCC37915	Thailand	*Orthoptera*: *Gryllidae*: adult cricket	–	–	–	–	–	MN781896	–	Thanakitpipattana *et al.* (2020)
	BCC37918	Thailand	*Orthoptera*: *Gryllidae*	**MN781935**	**MN781836**	**MN781691**	**MN781743**	**MN781790**	**MN781897**	–	Thanakitpipattana *et al.* (2020)
	BCC53857	Thailand	*Orthoptera*: *Gryllidae*	–	–	–	–	–	–	**MT078889**	Thanakitpipattana *et al.* (2020)
	BCC82988	Thailand	*Orthoptera*: *Gryllidae*	MK632117	MK632091	MK632062	MK632166	MK632143	–	**MT078891**	Thanakitpipattana *et al.* (2020)
M. guizhouense	ARSEF 4303	Australia	Soil	–	–	–	–	–	–	EU248859	Bischoff *et al.* (2009)
	ARSEF 4321	Australia	Soil	–	–	–	–	–	–	EU248860	Bischoff *et al.* (2009)
	ARSEF 6238	China	*Lepidoptera*	–	–	EU248857	EU248909	EU248937	–	EU248857	Bischoff *et al.* (2009)
	CBS 258.90	China	*Lepidoptera*	–	–	EU248862	EU248914	EU248942	HQ331448	EU248862	Bischoff *et al.* (2009)
M. huainamdangense	BCC32190	Thailand	*Hemiptera*: leafhopper	**MN781954**	**MN781855**	**MN781710**	**MN781757**	–	**MN781899**	–	This study
	BCC44270^{T}	Thailand	*Hemiptera*: leafhopper	**MN781956**	**MN781857**	**MN781712**	–	**MN781807**	**MN781898**	–	This study
	BCC7672	Thailand	*Hemiptera*: leafhopper	**MN781955**	**MN781856**	**MN781711**	**MN781758**	**MN781806**	**MN781901**	–	This study
M. humberi	IP46	Brazil	Soil	–	–	MH837574	MH837556	MH837565	–	JQ061205	Luz *et al.* (2019)

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Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5'*tef*	References
M. indigoticum	NBRC 100684	Japan	*Lepidoptera*	–	–	–	–	–	–	KJ398784	Kepler *et al.* (2014)
M. kalasinense	BCC53581	Thailand	*Coleoptera* larva	–	–	–	–	–	–	KX823944	Luangsa-ard *et al.* (2017)
	BCC53582	Thailand	*Coleoptera* larva	KC011175	KC011183	KC011189	–	–	KC011179	KX823945	Luangsa-ard *et al.* (2017)
M. khaoyaiense	BCC1376	Thailand	*Lepidoptera* larva	KX983468	KX983462	KX983457	–	KX983465	–	–	Luangsa-ard *et al.* (2017)
M. koreanum	BCC27998	Thailand	*Hemiptera*: *Fulgoromorpha*	**MN781945**	**MN781845**	**MN781700**	–	**MN781797**	**MN781903**	–	This study
	BCC30455	Thailand	*Hemiptera*: *Fulgoromorpha*	**MN781946**	**MN781846**	**MN781701**	**MN781750**	**MN781798**	**MN781904**	–	This study
M. lepidiotae	ARSEF 7412	Australia	*Coleoptera*	–	–	–	–	–	–	EU248864	Bischoff *et al.* (2009)
	ARSEF 4628	Australia	Soil	–	–	–	–	–	–	EU248863	Bischoff *et al.* (2009)
	ARSEF 7488	Australia	*Coleoptera*	–	–	EU248865	EU248917	EU248945	HQ331456	EU248865	Bischoff *et al.* (2009)
M. majus	ARSEF 1015	Japan	*Lepidoptera*	–	–	EU248866	EU248918	EU248946	HQ331444	EU248866	Bischoff *et al.* (2009)
	ARSEF 1914	Philippines	*Coleoptera*	–	–	EU248868	EU248920	EU248948	HQ331445	EU248868	Bischoff *et al.* (2009)
	ARSEF 1946	Philippines	*Coleoptera*	–	–	–	–	–	–	EU248867	Bischoff *et al.* (2009)
M. megapomponiae	BCC25100^{T}	Thailand	*Hemiptera*: *Megopomponia*	**MN781947**	**MN781847**	**MN781702**	**MN781751**	**MN781799**	**MN781906**	–	This study
M. minus	ARSEF 2037	Philippines	*Hemiptera*	AF339580	AF339531	DQ522353	DQ522400	DQ522454	AF138271	–	Sung *et al.* (2007)
	ARSEF 1099	Philippines	*Hemiptera*	–	–	KJ398799	KJ398608	KJ398706	–	–	Kepler *et al.* (2014)
M. niveum	BCC52400^{T}	Thailand	*Hemiptera*: *Cicadidae*	**MN781933**	**MN781832**	**MN781685**	–	**MN781785**	**MN781907**	–	This study
M. nornoi	BCC19364	Thailand	*Lepidoptera* larva	**MN781940**	**MN781841**	**MN781696**	**MN781747**	–	**MN781891**	–	This study
	BCC25948^{T}	Thailand	*Coleoptera*: adult beetle	**MN781941**	**MN781842**	**MN781697**	**MN781748**	–	**MN781892**	–	This study
M. novozealandicum	ARSEF 4661	Australia	Soil	–	–	KJ398811	KJ398622	–	–	–	Kepler *et al.* (2014)
	ARSEF 4674	Australia	Soil	–	–	KJ398812	KJ398623	–	–	–	Kepler *et al.* (2014)
M. ovoidosporum	BCC29223	Thailand	*Hemiptera*: *Cercopidae*	**MN781960**	**MN781861**	**MN781716**	**MN781762**	–	**MN781909**	–	This study
	BCC32600^{T}	Thailand	*Hemiptera*: *Eurybrachidae*	**MN781961**	**MN781862**	**MN781717**	**MN781763**	–	**MN781910**	–	This study
	BCC7634	Thailand	*Hemiptera* adult	**MN781962**	**MN781863**	**MN781718**	**MN781764**	**MN781811**	**MN781908**	–	This study
M. pemphigi	ARSEF 6569	United Kingdom	*Hemiptera*	–	–	KJ398813	KJ398624	DQ468378	–	–	Kepler *et al.* (2014)
	ARSEF 7491	United Kingdom	*Hemiptera*	–	–	KJ398819	KJ398629	DQ468379	–	–	Kepler *et al.* (2014)
	BUM1	China	–	–	–	–	–	–	MH143795	–	Chen *et al.* (2018c)
	BUM39.4	China	–	–	–	–	–	–	KY087809	–	Chen *et al.* 2018c
M. phasmatodeae	BCC2841	Thailand	*Orthoptera*: *Phasmatodea*	MN781931	MN781828	MN781681	MN781738	MN781782	MN781911	–	Thanakitpipattana *et al.* 2020
	BCC49272	Thailand	*Orthoptera*: *Phasmatodea*	MK632119	MK632093	MK632064	–	MK632145	MK632035	**MT078893**	Thanakitpipattana *et al.* (2020)
	BCC55003	Thailand	*Orthoptera*: *Phasmatodea*	–	–	–	–	–	–	**MT078892**	Thanakitpipattana *et al.* (2020)
M. phuwiangense	BCC78206	Thailand	*Coleoptera* adult	–	–	**MN781719**	**MN781765**	**MN781812**	**MT078879**	–	This study
	BCC85068	Thailand	*Coleoptera* adult	–	**MN781864**	**MN781720**	**MN781766**	**MN781813**	**MN781912**	–	This study

Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5'*tef*	References
M. phuwiangense	BCC85069^{T}	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*	KC011172	KC011180	KC011186	KC011184	–	KC011176	–	Luangsa-ard *et al.* (2017)
	BCC47979	Thailand	*Lepidoptera*	KC011173	KC011181	KC011187	KC011185	–	KC011177	–	Luangsa-ard *et al.* (2017)
M. purpureonigrum	BCC89247^{T}	Thailand	*Coleoptera* larva	–	–	**MN781725**	**MN781771**	**MN781817**	–	–	This study
	BCC89248	Thailand	*Coleoptera* larva	**MN781964**	**MN781870**	**MN781728**	–	**MN781819**	–	–	This study
	BCC89249	Thailand	*Coleoptera* larva	**MN781963**	**MN781869**	**MN781726**	**MN781772**	**MN781818**	–	–	This study
M. purpureum	BCC82642^{T}	Thailand	*Coleoptera* larva	–	**MN781867**	**MN781723**	**MN781769**	**MN781816**	**MN781918**	–	This study
	BCC83548	Thailand	*Coleoptera* larva	–	**MN781868**	**MN781724**	**MN781770**	–	**MN781920**	–	This study
	BCC82173	Thailand	*Coleoptera* larva	–	**MN781866**	**MN781722**	**MN781768**	**MN781815**	**MN781919**	–	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	–	–	–	–	–	–	–	EU248849	Bischoff *et al.* (2009)
	ARSEF 2575	USA	*Coleoptera*	–	–	–	–	–	NR132011	–	–
	ARSEF 4739	Australia	Soil	–	–	EU248848	EU248900	EU248928	–	EU248848	Bischoff *et al.* (2009)
M. samlanense	BCC17091	Thailand	*Hemiptera* adult	HQ165665	HQ165727	HQ165686	–	HQ165646	HQ165707	–	Luangsa-ard *et al.* (2017)
	BCC39752	Thailand	*Hemiptera* adult	MN781939	MN781840	MN781695	–	MN781794	MT078880	–	Luangsa-ard *et al.* (2017)
Metapochonia sp.	BUM3.5	China	Soil	KY087810	KY087814	KY087818	KY087822	–	KY087806	–	Chen *et al.* (2018c)
	BUM63.4	China	Soil	KY264178	KY264175	KY264170	KY264181	KY264184	KY264173	–	Chen *et al.* (2018a)
	CBS 64867	France	*Coleoptera*	–	–	LC126075	LC125907	LC125923	–	–	Nishi *et al.* (2017)
	CCTCC M 2016588	China	Soil	KY087812	KY087816	KY087820	KY087824	KY087826	KY087808	–	Chen *et al.* (2018c)
	CCTCC M 2016589	China	Soil	KY264177	KY264174	KY264169	KY264180	KY264183	KY264172	–	Chen *et al.* (2018a)
	CEP414	Argentina	*Blaberidae*: *Epilamprinae*	–	–	–	–	–	MF784813	–	Gutierrez *et al.* (2019)
	CG1123	Brazil	Soil	–	–	KY007614	KY007612	KY007613	–	KC520541	Lopes *et al.* (2018)
	GZAC-IFR1006	China	*Lepidoptera*	–	–	KT166031	KT961694	KT166032	–	–	Chen *et al.* (2017)
	MAFF 243305	Japan	Soil	–	AB700552	LC126078	LC125913	LC125920	–	–	Nishi *et al.* (2017)
	MAFF 244762	Japan	Soil	–	–	LC126079	LC125911	LC125922	–	–	Nishi *et al.* (2017)
	NBRC 112661	Japan	*Diptera*	–	–	LC126076	LC125908	LC125924	–	–	Nishi *et al.* (2017)
	RCEF 2001	China	–	–	–	–	–	–	AY913758	–	Li *et al.* (2010)

(*continued on next page*)

Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5'*tef*	References
M. sulphureum	BCC36585	Thailand	*Lepidoptera* larva	–	–	**MN781686**	–	**MN781786**	–	**MT078931**	This study
	BCC36592[T]	Thailand	*Lepidoptera* larva	–	–	**MN781687**	–	**MN781787**	–	–	This study
	BCC39045	Thailand	*Lepidoptera* larva	**MK632120**	**MK632095**	**MK632066**	–	**MK632147**	**MK632037**	**MT078930**	This study
M. takense	BCC30934	Thailand	*Hemiptera*	HQ165658	HQ165720	HQ165679	HQ165740	HQ165639	HQ165698	–	Luangsa-ard *et al.* (2017)
	BCC30939	Thailand	*Hemiptera*	HQ165659	HQ165721	–	HQ165741	HQ165640	HQ165699	–	Luangsa-ard *et al.* (2017)
M. viridulum	ARSEF 6927	Taiwan	*Hemiptera*	–	–	KJ398815	KJ398681	–	–	–	Kepler *et al.* (2014)
	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	–	–	–	–	–	–	–	AF368501	–	Driver *et al.* (2000)
	CBS 806.71	USA	*Trichoplusia ni*	AY526491	–	EF468787	EF468893	EF468937	AY624205	–	Sung *et al.* (2007)
	NBRC 8560	Japan	*Lepidoptera*	HQ165667	HQ165729	HQ165688	–	–	–	–	Luangsa-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	EF468989	EF468842	EF468788	EF468895	EF468939	**MT078887**	–	Spatafora *et al.* (2007)
Pa. gunnii	G845-19	China	–	–	–	–	–	–	AJ309343	–	Chan *et al.* (2011)
Pa. lilacinus	CBS 284.36	USA	Soil	AY6526475	AY624227	EF468792	EF468898	EF468941	–	–	Sung *et al.* (2007)
Pa. marquandii	CBS 182.27	USA	Soil	EF468990	EF468845	EF468793	EF468899	EF468942	AY624193	–	Sung *et al.* (2007)
Pa. reniformis	ARSEF 429	Philippines	*Orthoptera*: *Tettigoniidae*	HQ165671	HQ165733	HQ165690	–	HQ165650	–	–	Luangsa-ard *et al.* (2017)
	IndGH96	Philippines	–	HQ165670	HQ165732	–	–	HQ165649	–	–	Luangsa-ard *et al.* (2017)
Petchia siamensis	BCC68420	Thailand	Ootheca of *Mantidae*	MK632113	MK632087	–	MK632163	MK632140	–	–	Thanakitpipattana *et al.* (2020)
	BCC73636	Thailand	Ootheca of *Mantidae*	MK632115	MK632089	MK632060	–	MK632138	–	–	Thanakitpipattana *et al.* (2020)
Pochonia chlamydosporia	CBS 504.66	Canada	Soil	AF339593	AF339544	EF469069	EF469098	EF469120	AJ292398	–	Sung *et al.* (2007)
Purpureocillium lavendulum	FMR 10376	Venezuela	Soil	–	FR775489	FR775516	FR775512	–	–	–	Perdomo *et al.* (2017)
Pur. lilacinum	CBS 431.87	Philippines	*Meloidogyne* sp.	–	–	–	–	–	HQ842812	–	Luangsa-ard *et al.*(2011)
Pur. takamizusanense	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
	BCC89300[T]	Thailand	*Lepidoptera* larva	–	**MN781876**	**MN781733**	**MN781778**	–	**MN781917**	–	This study
Pu. pyriformis	BCC85074[T]	Thailand	*Lepidoptera* larva	–	**MN781873**	**MN781730**	**MN781775**	**MN781821**	**MN781929**	–	This study
	BCC85348	Thailand	*Lepidoptera* larva	–	**MN781871**	**MN781728**	**MN781773**	**MN781820**	**MN781927**	–	This study
	BCC85349	Thailand	*Lepidoptera* larva	–	**MN781872**	**MN781729**	**MN781774**	–	**MN781928**	–	This study
Regiocrella camerunensis	ARSEF 7682	–	*Hemiptera*	–	DQ118735	DQ118743	DQ127234	–	–	–	Chaverri *et al.* (2005)
Rotiferophthora angustispora	CBS 101437	–	Bdelloid rotifers	AF339584	AF339535	AF543776	DQ522402	DQ522460	AJ292412	–	Sung *et al.* (2007)
Shimizuomyces paradoxus	EFCC 6279	Korea	*Smilax sieboldii*	EF469131	EF469084	EF469071	EF469100	EF469117	JN049847	–	Sung *et al.* (2007)

Table 1. (Continued).

Species	Strains	Locality	Host	SSU	LSU	*tef*	*rpb1*	*rpb2*	ITS	5′*tef*	References
S. paradoxus	EFCC 6564	Korea	*Smilax sieboldii*	EF469130	EF469083	EF469072	EF469101	EF469118	–	–	Sung *et al.* (2007)
Torrubiella luteorostrata	NHJ 11343	Thailand	*Hemiptera*: scale insect	EF468995	EF468850	EF468801	EF468906	–	JN049859	–	Sung *et al.* (2007)
	NHJ 12516	Thailand	*Hemiptera*: scale insect	EF468994	EF468849	EF468800	EF468905	EF468946	JN049860	–	Sung *et al.* (2007)
T. petchii	NHJ 6209	Thailand	*Hemiptera*: scale insect	EU369104	EU369039	EU369023	EU369061	EU369081	JN049861	–	Johnson *et al.* (2009)
	NHJ 6240	Thailand	*Hemiptera*: scale insect	EU369103	EU369038	EU369022	EU369060	EU369082	–	–	Johnson *et al.* (2009)
T. tenuis	NHJ 345.01	Thailand	*Hemiptera*: scale insect	EU369111	EU369045	EU369030	–	EU369088	–	–	Johnson *et al.* (2009)
	NHJ 6293	Thailand	*Hemiptera*: scale insect	EU369112	EU369044	EU369029	EU369068	EU369087	JN049862	–	Johnson *et al.* 2009

T = Type specimen

posterior distribution of trees excluding the initial set of burn-in tree. Maximum likelihood (ML) analyses were performed with RAxML-VI-HPC2 v. 8.2.12 (Stamatakis 2014) on XSEDE in the CIPRES Science Gateway v. 3.3 (https://www.phylo.org/) using a GTRCAT model of evolution (Stamatakis 2006) with 1 000 bootstrap replicates (MLBS).

RESULTS

Molecular phylogeny

We generated 135 ITS, 43 SSU, 58 LSU, 61 *tef*, 50 *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 neogunni* in *Keithomyces*, *M. kusanagiense* 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-

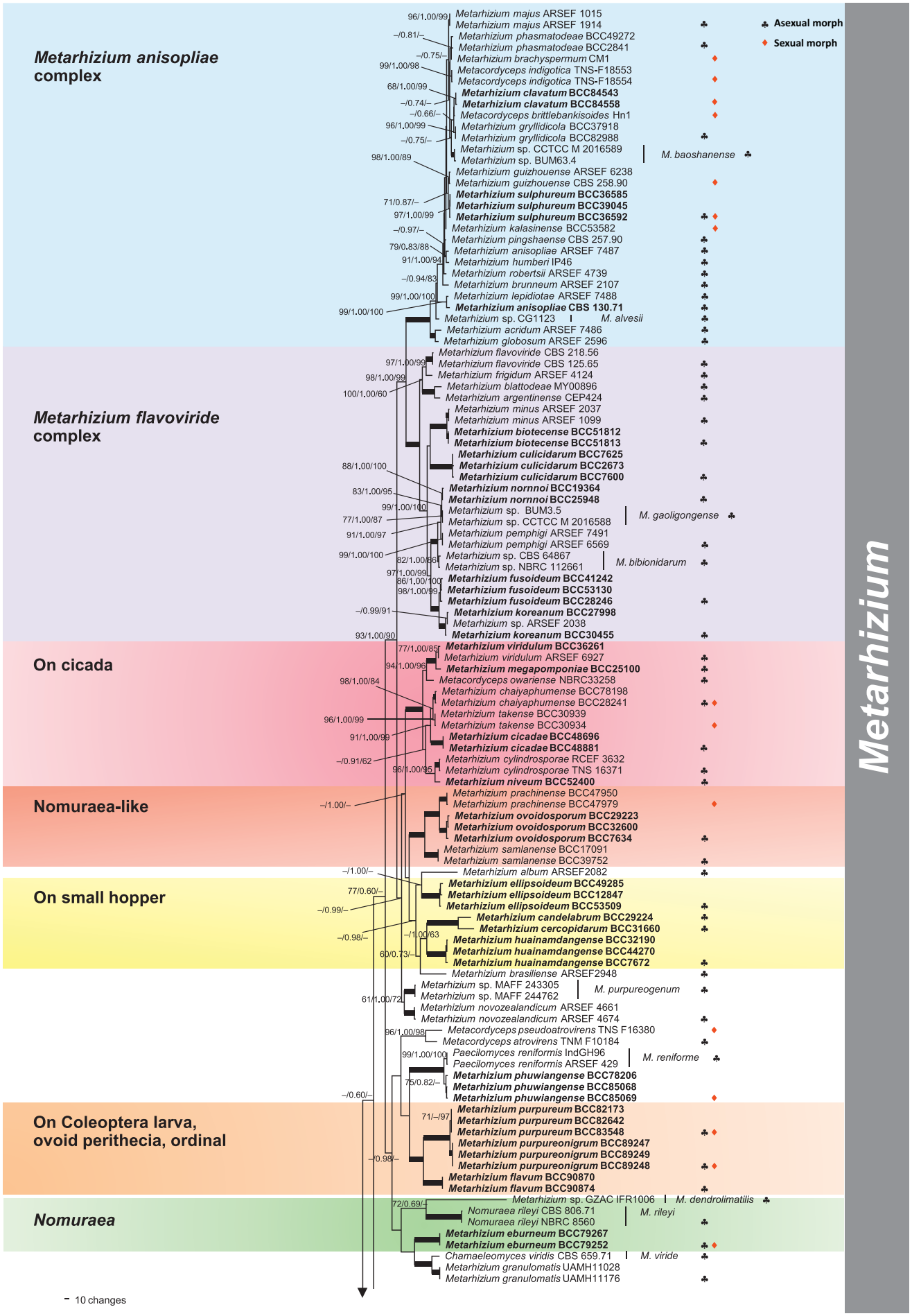

Fig. 1. Phylogenetic reconstruction of *Metarhizium* and related genera in the *Clavicipitaceae* obtained from the combined SSU, LSU, *tef*, *rpb1* and *rpb2* sequences based on Maximum Parsimony, Bayesian analysis and RAxML. Numbers on the nodes are MP bootstrap / Bayesian posterior probability / ML 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).

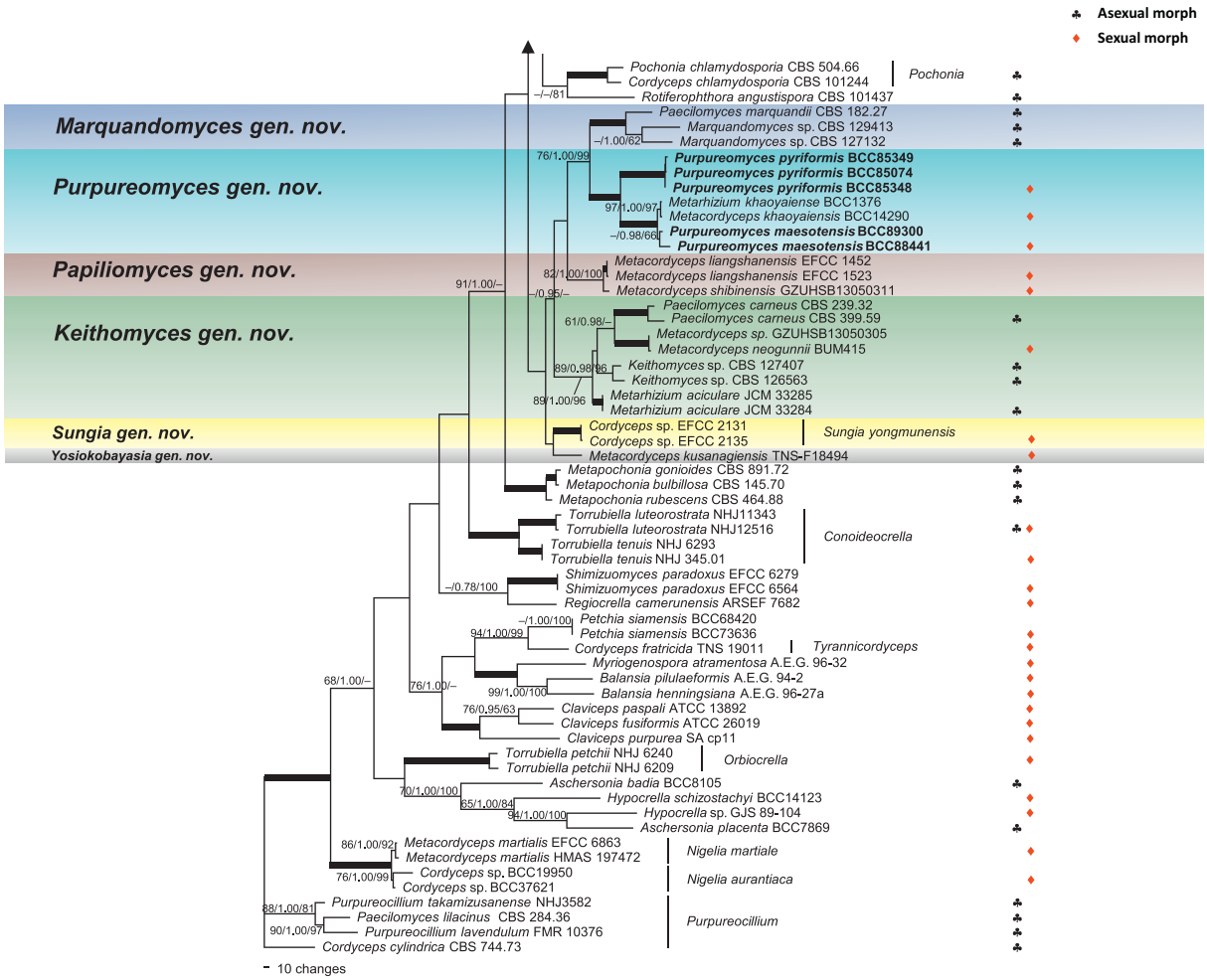

Fig. 1. (Continued).

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 planthoppers 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).

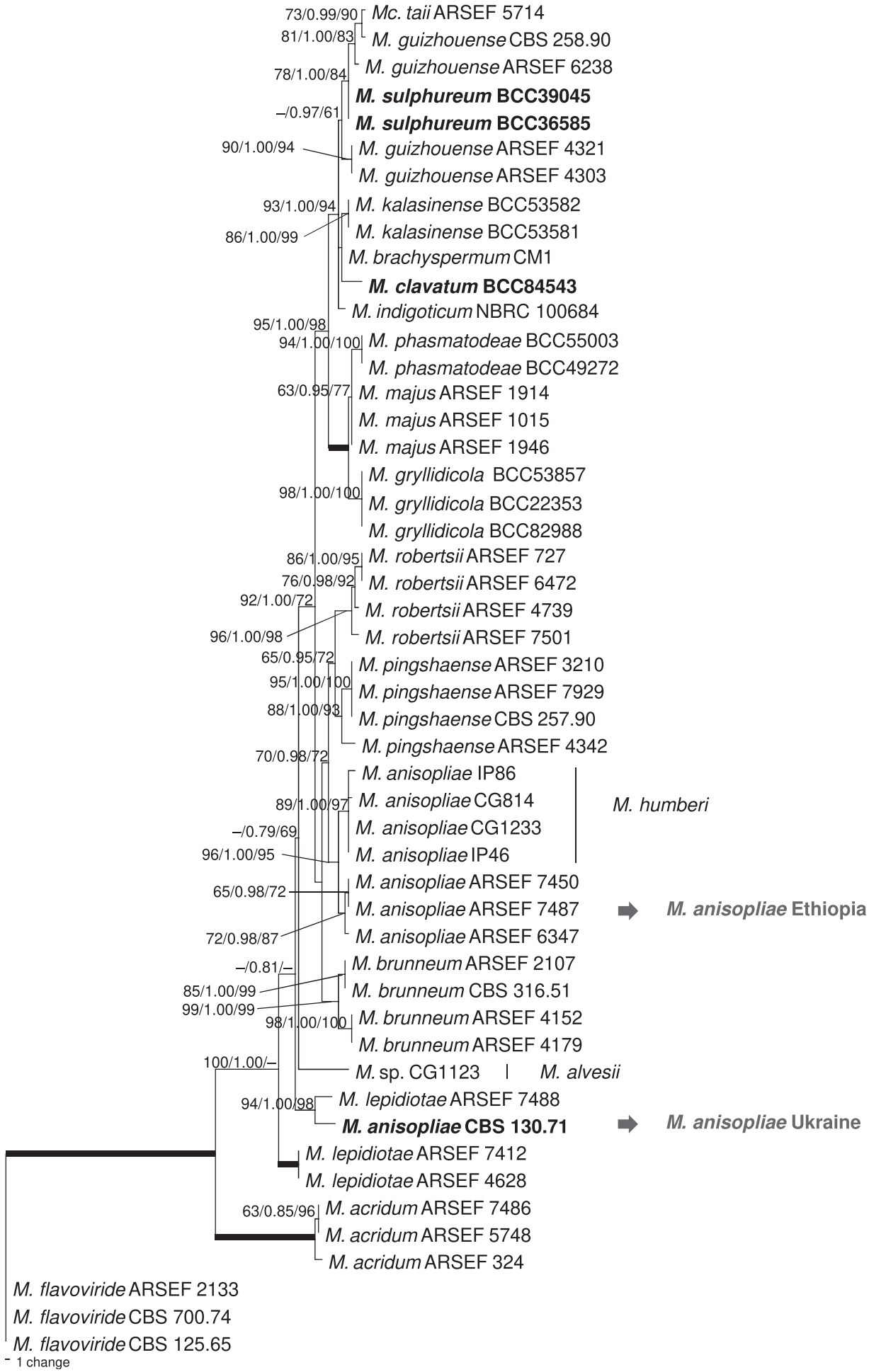

Fig. 2. Phylogenetic reconstruction of *Metarhizium anisopliae* species complex 5′*tef* sequences based on Maximum Parsimony, Bayesian analysis and RAxML. Number on the nodes are MP bootstrap / Bayesian posterior probability / ML bootstrap values above 70 % (MPBS-MLBS) or 0.7 (BPP). Thickened lines mean support for the three analyses was 100 % (MPBS-MLBS) or 1.0 (BPP).

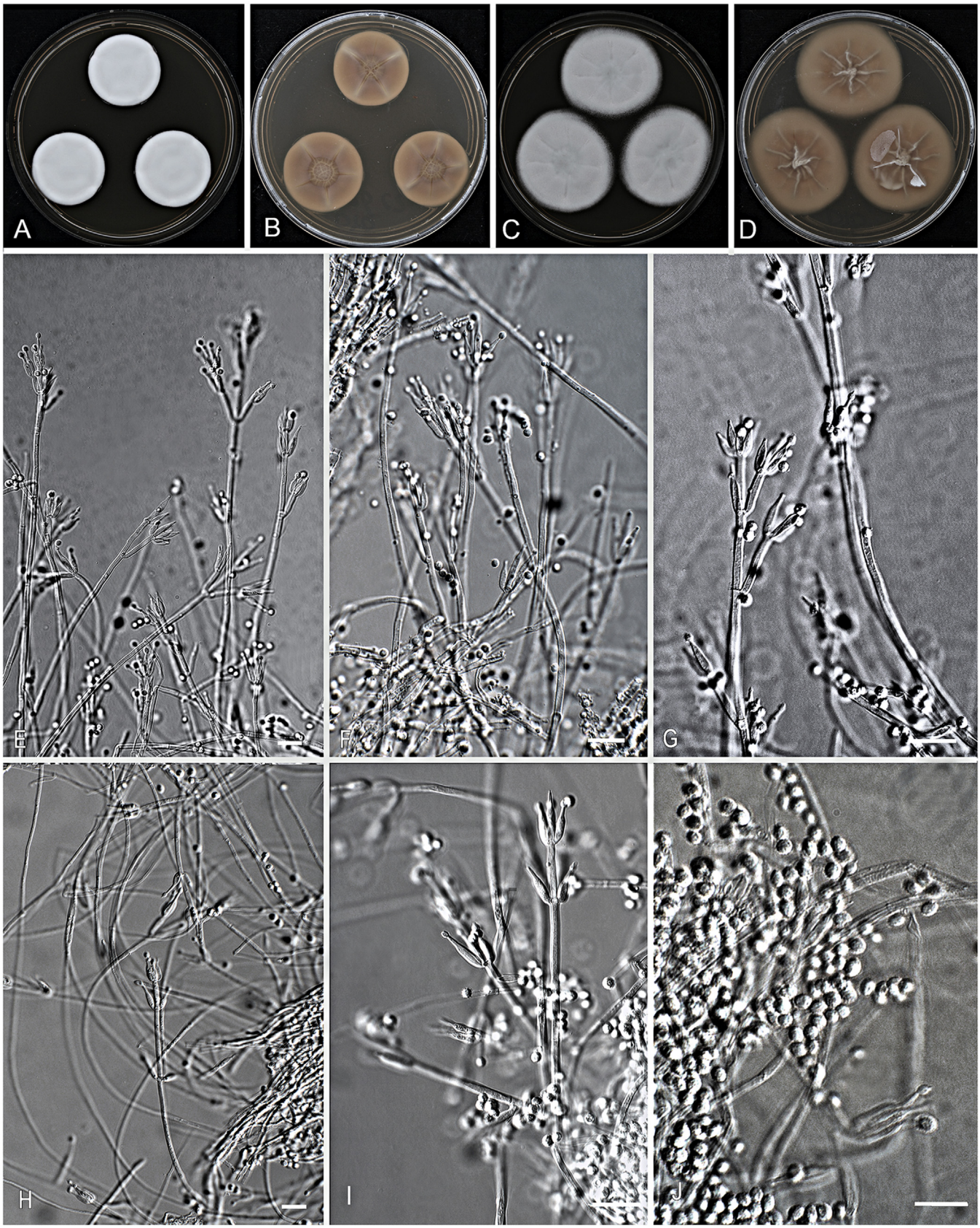

Fig. 3. *Keithomyces carneus.* Colonies after 14 d. **A–B.** CBS 239.32. **A.** On MEA. **B.** On OA. **C–D.** CBS 339.59. **C.** On MEA. **D.** On OA. **E–G.** Conidiophores and conidia on MEA. **H–J.** Conidiophores and conidia on OA. Scale bars = 10 µm.

TAXONOMY

Six new genera (*Keithomyces, Marquandomyces, Papiliomyces, Purpureomyces, Sungia, Yosiokobayasia*) and twenty-one new species are decribed 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.*

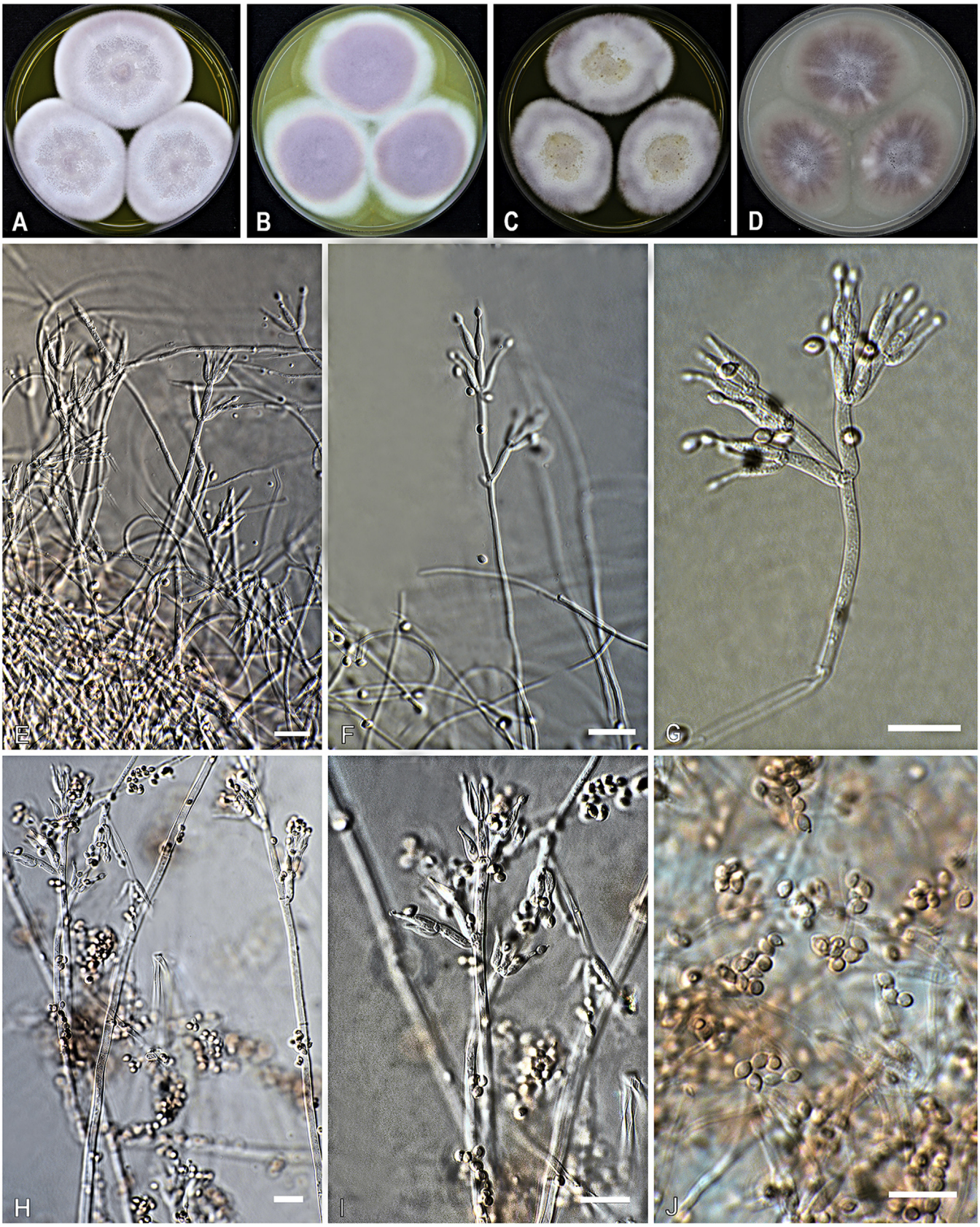

Fig. 4. *Marquandomyces marquandii*. Colonies after 14 d **A–B.** CBS 182.27. **A.** On MEA. **B.** On OA. **C–D.** CBS 282.53. **C.** On MEA. **D.** On OA. **E–G.** Conidiophores and conidia on MEA. **H–J.** Conidiophores and conidia on OA. Scale bars = 10 µm.

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

Table 2. *Metarhizium* hosts, substrates and geographical location.

Species	Substrate	Countries found	References
Metarhizium acridum	*Orthoptera*: *Acrididae*, *Pyrgomorphidae*	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*, *Gryllotalpidae*, *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	Kobayasi & 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. brittlebankisoides	*Coleoptera*: *Scarabaeidae*	China, Japan	Liu *et al.* (2001), Kepler *et al.* (2014), Gutierrez *et al.* (2019)
M. brunneum	*Acari*: *Ixodidae*, *Arneida*, *Coleoptera*: *Cerambycidae*, *Curculionidae*, *Elateridae*, *Scarabaeidae*, *Tenebrionidae*, *Diptera*: *Culicidae*, *Hemiptera*: *Delphacidae*, *Hymenoptera*: *Formicidae*, *Isoptera*: *Rhinotermitidae*, *Termitidae*, *Lepidoptera*: *Bombycidae*, *Hepialidae*, *Lyonetiidae*, *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. campsosterni	*Coleoptera*: *Scarabaeidae*	China	Zhang *et al.* (2004), Kepler *et al.* (2014)
M. cercopidarum	*Hemiptera*: *Cercopidae*	Thailand	This study
M. chaiyaphumense	*Hemiptera*: *Cicadidae* (Cicada nymph)	Thailand	Luangsa-ard *et al.* (2017)
M. cicadae	*Hemiptera*: *Cicadidae*	Thailand	This study
M. clavatum	*Coleoptera* (Larva of *Oxynopterus* sp.)	Thailand	This study
M. culicidarum	*Diptera*: *Culicidae*	Thailand	This study
M. cylindrosporum	*Hemiptera*: *Cicadidae* (Adult cicada)	China, Japan, Taiwan	Guo *et al.* (1986), Tzean *et al.* (1993), Kepler *et al.* (2014), Database of ARSEF
M. dendrolimatilis	*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*)

Table 2. (Continued).

Species	Substrate	Countries found	References
M. flavoviride	*Coleoptera*: *Curculionidae*, *Sacarabaeidae*, *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. fusoideum	*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	*Chameoleo calyptratus*	Denmark	Sigler *et al.* (2010), Kepler *et al.* (2014)
M. gryllidicola	*Orthoptera*: *Gryllidae* (Cricket adult)	Thailand	Thanakitpipattana *et al.* (2020)
M. guizhouense	*Lepidoptera*	China	Guo *et al.* (1986), Bischoff *et al.* (2009)
M. guniujiangense	*Hemiptera* (Cicada nymph)	China	Li *et al.* (2010)
M. huainamdangense	*Hemiptera* (Leafhopper)	Thailand	This study
M. humberi	*Coleoptera, Lepidoptera, Hemiptera,* Soil	Brazil, Mexico	Luz *et al.* (2019)
M. indigoticum	*Lepidoptera* larva (*Cossidae*)	Japan	Kobayasi & Shimizu (1978), Kepler *et al.* (2012a, 2014)
M. kalasinense	*Coleoptera* larva	Thailand	Luangsa-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. nornnoi	*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. pemphigi	*Hemiptera*: *Aphididae*, *Isoptera*: *Rhinotermitidae*, Soil	Canada, China, Georgia, Japan, UK	Guo *et al.* (1986), Kepler *et al.* (2014), Database of ARSEF
M. phasmatodeae	*Orthoptera*: *Phasmatodea*	Thailand	Thanakitpipattana *et al.* (2020)
M. phuwiangense	*Coleoptera* adult	Thailand	This study
M. pingshaense	*Coleoptera*: *Cerambycidae*, *Chrysomelidae*, *Curculionidae*, *Scarabaeidae*, *Diptera*: *Stratiomyidae*, *Hemiptera*: *Cicadidae*, *Cydnidae*, *Delphacidae*, *Pentatomidae*, *Pseudococcidae*, *Isoptera*: *Kalotermitidae*, *Rhinotermitidae*, *Termitidae*, *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	Luangsa-ard *et al.* (2017)
M. pseudoatrovirens	*Coleoptera* larva	Japan	Kobayasi & Shimizu (1982), Kepler *et al.* (2012a, 2014)

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* (*Oxynopterus* sp.)	Thailand	This study
M. reniforme	*Orthoptera*: *Tettigonidae*	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. robertsii	*Coleoptera*: *Carabidae*, *Cerambycidae*, *Chrysomelidae*, *Curculionidae*, *Elateridae*, *Scarabaeidae*, *Tenebrionidae*, *Hemiptera*: *Cicadidae*, *Cydnidae*, *Hymenoptera*: *Formicidae*, *Isoptera*: *Kalotermitidae*, *Rhinotermitidae*, *Termitidae*, *Lepidoptera*: *Nymphalidae*, *Plutellidae*, *Pyralidae*, *Orthoptera*: *Tettigoniidae*, Soil	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	Luangsa-ard *et al.* (2017)
M. sulphureum	*Lepidoptera* larva	Thailand	This study
M. takense	*Hemiptera*: *Cicadidae* (Cicada nymph)	Thailand	Luangsa-ard *et al.* (2017)
M. viride	*Chameoleo 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)

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 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. bibionidarum*, *M. biotecense*, *M. blattodeae*, *M. brachyspermum*[1], *M. brasiliense*, *M. brittlebankisoides*[1], *M. brunneum*, *M. candelabrum*, *M. campsosterni*[1], *M. cercopidarum*, *M. clavatum*[1], *M. culicidarum*, *M. ellipsoideum*, *M. flavoviride*, *M. flavum*[1], *M. frigidum*, *M. fusoideum*, *M. gaoligongense*, *M. globosum*, *M. gryllidicola*, *M. guizhouense*[1], *M. guniujiangense*[1], *M. huainamdangense*, *M. humberi*, *M. indigoticum*[1], *M. kalasinense*[1], *M. koreanum*, *M. lepidiotae*, *M. majus*, *M. minus*, *M. nornnoi*, *M. novozealandicum*, *M. pemphigi*, *M. phasmatodeae*, *M. pingshaense*, *M. purpureogenum*, *M. purpureonigrum*[1], *M. purpureum*[1], *M. robertsii*, *M. sulphureum*[1]
Nomuraea-like	*M. chaiyaphumense*[1], *M. cicadae*, *M. cylindrosporum*, *M. dendrolimatilis*, *M. megapomponiae*, *M. niveum*, *M. ovoidosporum*, *M. owariense*[1], *M. prachinense*[1], *M. rileyi*, *M. samlanense*, *M. takense*[1], *M. viridulum*
Paecilomyces-like	*M. granulomatis*, *M. phuwiangense*[1,2], *M. reniforme*, *M. viride*
Unknown	*M. atrovirens*[1], *M. eburneum*[1], *M. pseudoatrovirens*[1]

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 synnematous, 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.
Basionym: *Spicaria carnea* Duché & R. Heim, Recl. Trav. Cryptogam. Dédiés à Louis Mangin: 454. 1931.
Synonyms: *Paecilomyces carneus* (Duché & R. Heim) A.H.S. Br. & G. Sm., Trans. Br. Mycol. Soc. 40: 70.1957.

Table 4. Comparison between the sexual morphs in *Metarhizium* and closely related species.

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. brittlebankisoides	Multiple, cylindrical, pale green, 100 mm long	Ordinally immersed, flask-shaped, 406–531 × 170–200	Cylindrical, 188–313 × 3–3.2	Cylindrical, 180–300 × 0.94, part-spores, 5.7–8.1 × 0.94	Metarhizium-like
M. campsosterni	Simple, cylindrical, greenish yellow, 160 mm long	Ordinally immersed, pyriform, obovoid, 275–433 × 165–276	Cylindrical, 175–349 × 3.9	Part-spores, 2.9–5.9 × 1	Metarhizium-like
M. chaiyaphumense	Solitary, cylindrical, simple, or 2–3 branched, greyish yellow, 30–35 mm long	Obliquely immersed, ovoid to obpyriform, 550–670 × 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	Ordinally 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,	Ordinally semi-immersed, ovoid, 500–650 × 270–330	Cylindrical, 280–320 × 5–6	Filiform, 200–315 × 1.5–2	Metarhizium-like
M. guizhouense (M. taii)	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. guniujiangense	Multiple, dark green, 40.3–42.5 mm long, confluent at base, apically subulate with acute, yellow and glabrous tip.	Obliquely immersed, ampullaceous, 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, ampullaceous, 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 × 200–400	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	Ordinally 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	Ordinally immersed, elongate ovoid, 600–870 × 250–500	Cylindrical, 245–280 × 6–8	Filiform, 200–275 × 1.5–2	Metarhizium-like
M. purpureum	Multiple, clavate, branched, dark purple, up to 40 mm long, 2.5–3 mm wide	Ordinally immersed, ovoid, 370–520 × 210–300	Cylindrical, 150–250 × 5–8	Filiform, 160–240 × 1.5–2	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

Table 4. (Continued).

Species	Stromata	Perithecia (µm)	Asci (µm)	Ascospores (µm)	Asexual morph
M. takense	Simple, greyish green to dark green, 70–130 mm long, 0.6–1.8 mm wide	Obliquely immersed, flask-shaped, 510–550 × 250–350	Cylindrical, 275– 400 × 5	Filiform, 155–230 × 1.25	Nomuraea-like
Purpureomyces khaoyaiensis	Solitary, white to whitish-purple, 55 mm long, 3–4 mm wide	Obliquely semi-immersed, ovoid, 335–410 × 200–270	Cylindrical, 215–340 × 5–6	Filiform, 160–240 × 1	Lecanicillium-like
Pu. maesotensis	Solitary, cylindrical, purple, 26 mm long 1–1.5 mm wide	Obliquely semi-immersed, ovoid, 360–470 × 260–320	Cylindrical, 100–192.5 × 3–6	Filiform, 107–177.5	Lecanicillium-like
Pu. pyriformis	Solitary, cylindrical, purple, 18 mm long, 3 mm wide	Obliquely immersed, ovoid, 304–350 × 220–250	Cylindrical, 100–182 × 4–5	Filiform, 125–190 × 1	Lecanicillium-like

Metarhizium carneum (Duché & R. Heim) Kepler *et al.*, Mycologia 106: 821. 2014.
Penicillium nopporoense [as '*nopporoensum*'] 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-jinma, from soil under *Angelica keiskei,* 13 Mar. 2013, Nonaka (**holotype** JCM 33284, culture ex-type FKI-7236).

Habitat: Soil.

Known distribution: Japan.

Note: *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: *Metacordyceps neogunnii* T.C. Wen & K.D. Hyde, Phytotaxa 302: 33. 2017.
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.*

Table 5. Micromorphologies and colour of *Metarhizium* and *Purpureomyces* species on SDAY/4.

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 × 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, 3.88–6.55 × 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. brachyspermum	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. brunneum	Argentina, Australia, Austria, Canada, Denmark, Finland, France, Germany, Indonesia, Italy, Japan, Mexico, Myanmar, New Zealand, Norway, Philippines, Portugal, Republic of Geogia, 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. cercopidarum	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. ellipsoideum	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	Pyrifrom, renifrom, 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. fusoideum	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. guizhouense	China	7–12 × 2–3	7–10 × 2–3	Olive

Table 5. (Continued).

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	Obpyriform, 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. pingshaense	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. robertsii	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

(*continued on next page*)

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 khaoyaiensis	Thailand	Lecanicillium-like, tapering gradually towards the apex, 7–18 × 1–3	Ovoid, 2–3 × 1.5–3	White to cream
Pu. maesotensis	Thailand	Lecanicillium-like, tapering gradually towards the apex, 4–21 × 1.5–2	Ovoid, 3 × 1–2.5	White to lilac
Pu. pyriformis	Thailand	Lecanicillium-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 *Metacordyceps* 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* (= *Metarhizium carneum).*

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

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

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

Description (based on Samson, 1974): *Macromorphology*: Colonies on malt-agar growing moderately fast, attaining a diameter of 5–7 cm within 2 wk at 25 °C, consisting of a dense felt with a floccose overgrowth of aerial mycelium, in fresh isolates sometimes producing short erect loose synnemata; at first white, becoming pale vinaceous to vinaceous near dark vinaceous brown, changing with age to brown shades. Colony reverse usually bright yellow to orange-yellow, exudate usually diffusing into the surrounding agar, with age becoming yellow-brown.

Micromorphology: *Vegetative hyphae* hyaline, smooth-walled, 2.5–3.2 μm wide. *Conidial structures* variable, mostly verticillate, sometimes loosely synnematous, especially in fresh isolates. *Conidiophores* hyaline, smooth-walled, 50–300 × 2.5–3 μm, arising from submerged hyphae or formed as side branches on the aerial hyphae, consisting of verticillate branches with whorls of 2–4 phialides. *Phialides* 8–15 × 1.5–2 μm, consisting of a short cylindrical to ellipsoidal basal portion, tapering into a distinct neck, about 1 μm wide. *Conidia* in dry divergent chains, ellipsoidal to fusiform, smooth-walled to finely roughened, hyaline, pale vinaceous *en masse*, 3–3.5 × 2–2.2 μm. *Chlamydospore-like structures* usually present in the submerged mycelium, consisting of solitary, thin-walled, globose to ellipsoidal cells, about 3.5 μm in diameter.

Marquandomyces marquandii (Massee) Samson, Houbraken & Luangsa-ard, ***comb. nov.*** MycoBank MB834880. Fig. 4.
Basionym: *Verticillium marquandii* Massee, Trans. Br. Mycol. Soc. 1: 24. 1898.
Synonyms: *Paecilomyces marquandii* (Massee) S. Hughes, Mycol. Pap. 45: 30. 1951.
Spicaria violacea E.V. Abbott, Iowa St. Coll. J. Sci.: 15. 1926.
Metarhizium marquandii (Massee) Kepler *et al.*, Mycologia 106: 823. 2014.

Description and illustration: See Samson (1974).

Habitat: On mushrooms, soil.

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

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

Metarhizium Sorokīn, Veg. Parasitenk. Mensch Tieren: 268. 1879.

Synonyms: *Chamaeleomyces* Sigler, J. Clin. Microbiol. 48: 3186. 2010.
Metacordyceps G.H. Sung *et al.*, Stud. Mycol. 57: 27. 2007.
Nomuraea Maubl., Bull. Soc. Mycol. France 19: 296. 1903.

Type species: *Metarhizium anisopliae* (Metschn.) Sorokīn, 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 conidiogenesis 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. Conidiogenous 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

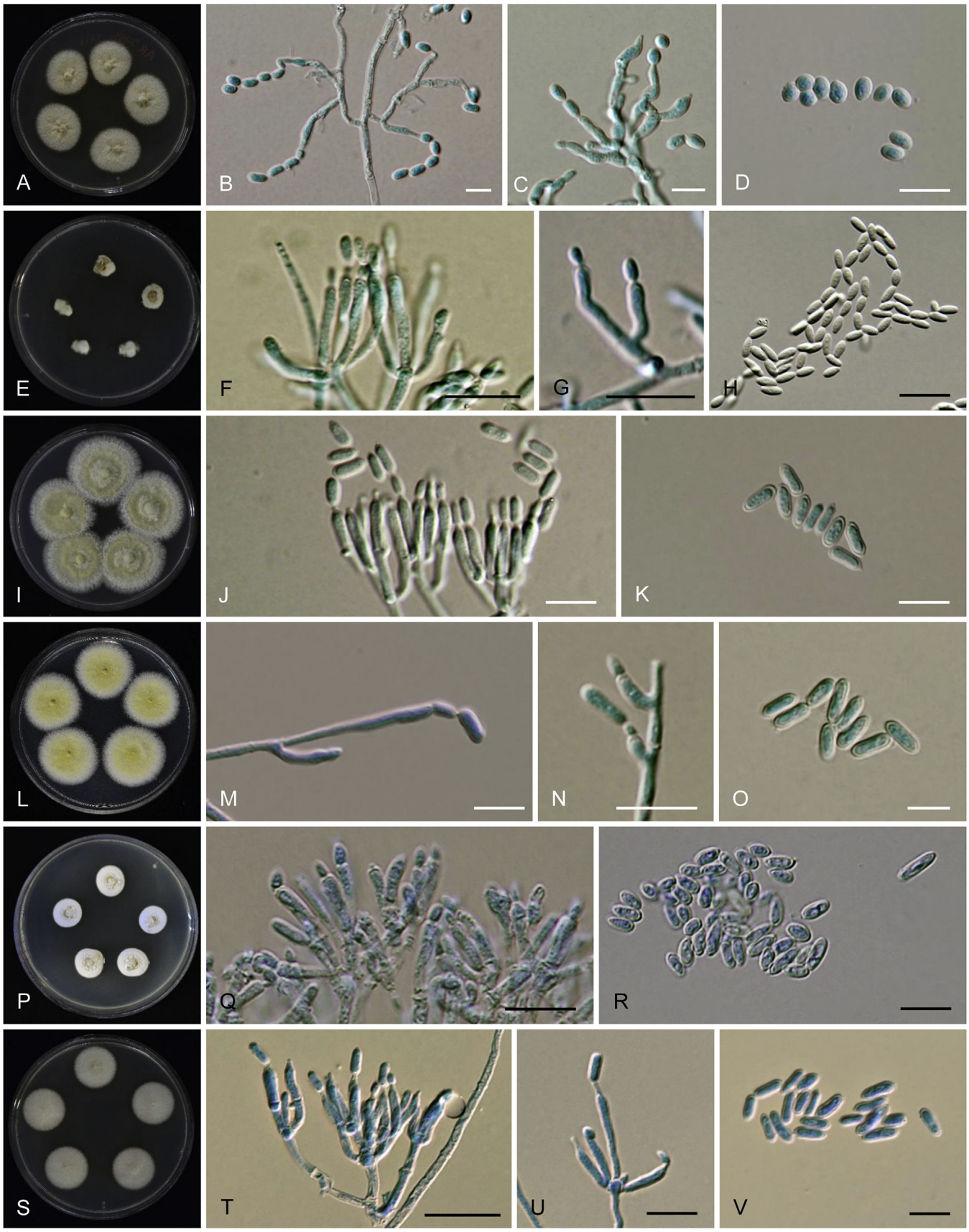

Fig. 5. Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–D.** *M. acridum* ARSEF 7486. **E–H.** *M. album* ARSEF 1942. **I–K.** *M. anisopliae* ARSEF 7487. **L–O.** *M. blattodeae* BCC 20250. **P–R.** *M. brasiliense* ARSEF 2948. **S–V.** *M. brunneum* ARSEF 2107.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

both PDA and SDAY/4 are fast as well as the sporulation, but in SDAY/4 sporulation is less compared to PDA making it is 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.*

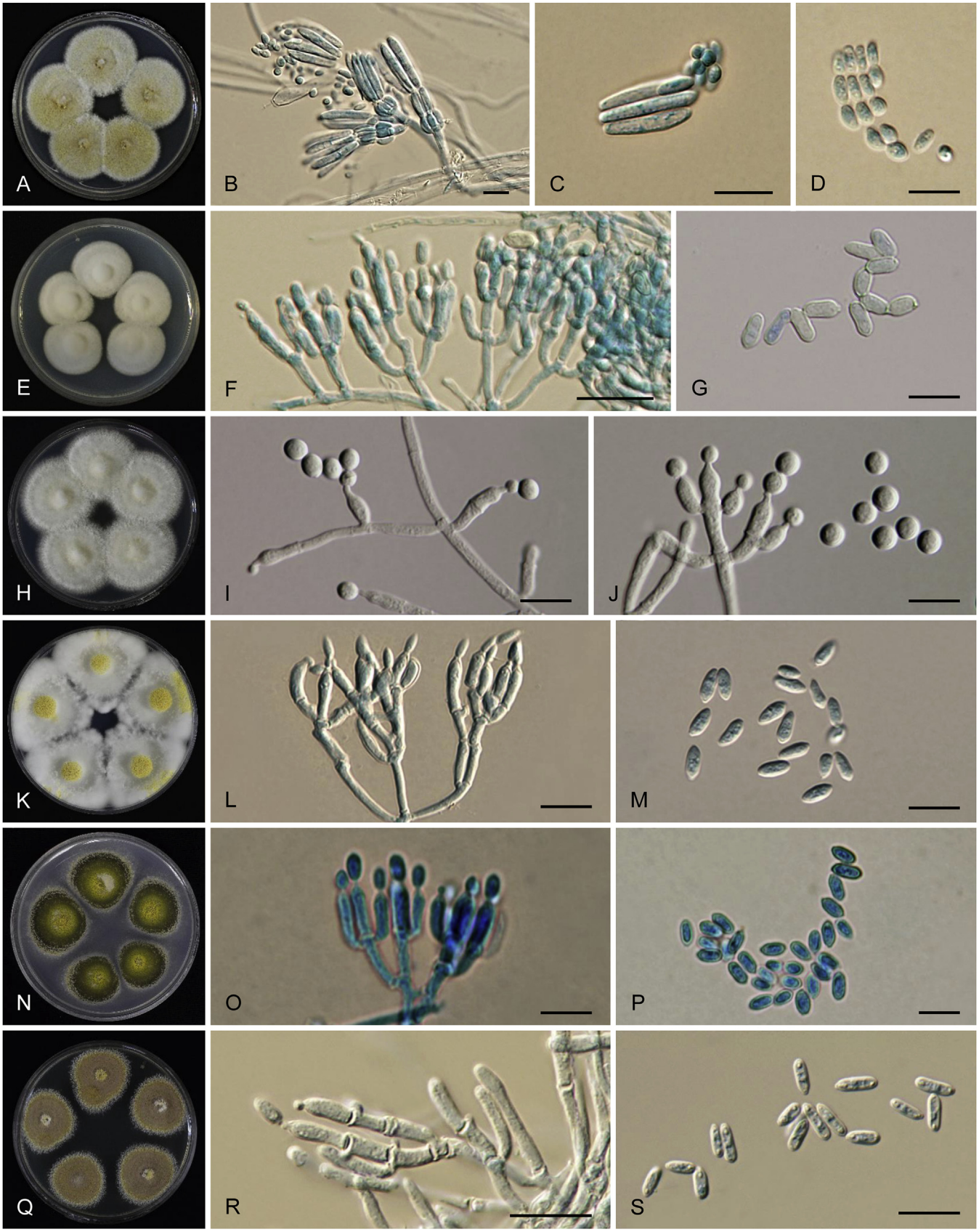

Fig. 6. Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–D.** *M. cylindrosporum* ARSEF 6926. **E–G.** *M. frigidum* ARSEF 4124. **H–J.** *M. globosum* ARSEF 2596. **K–M.** *M. gryllidicola* BCC 82988. **N–P.** *M. kalasinense* BCC 53582. **Q–S.** *M. koreanum*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

Metarhizium anisopliae (Metsch.) Sorokīn, 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.

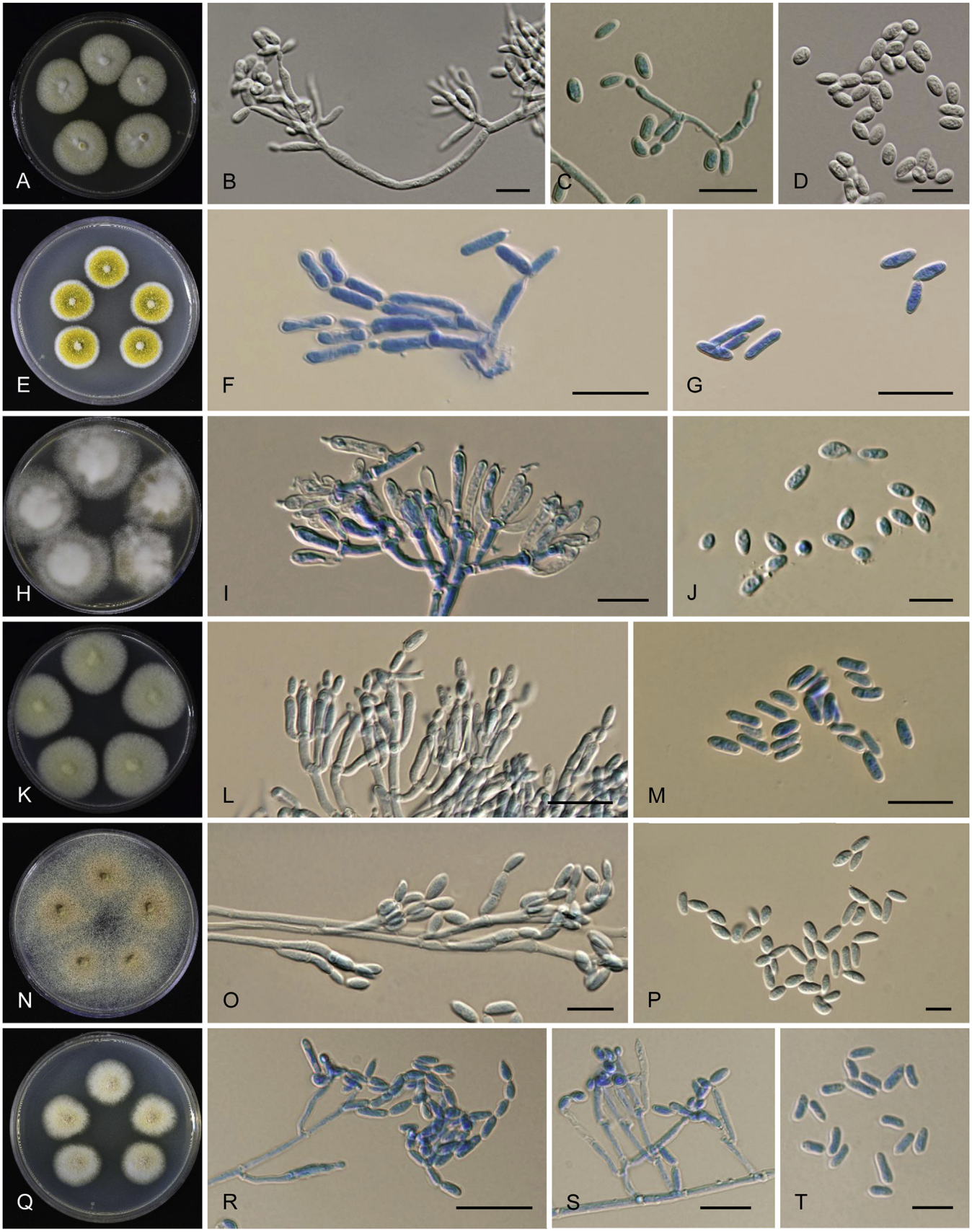

Fig. 7. Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–D.** *M. lepidiotae* ARSEF 7488. **E–G.** *M. majus* ARSEF 1914. **H–J.** *M. minus* ARSEF 2037. **K–M.** *M. novozealandicum* ARSEF 8214. **N–P.** *M. owariense* NBRC 33258. **Q–T.** *M. pemphigi* ARSEF 7491. 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.

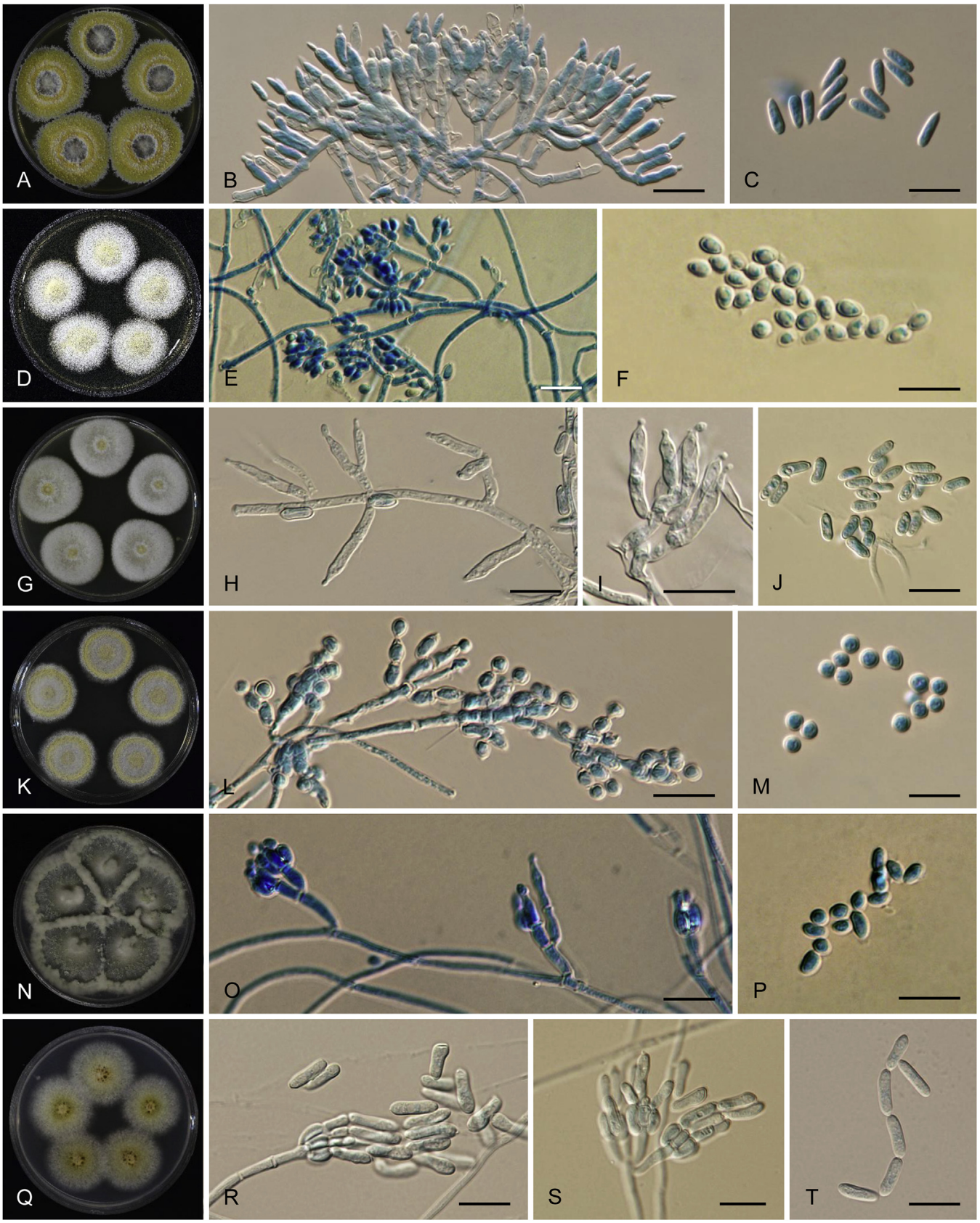

Fig. 8. Colonies on SDAY/4 after 7 d, phialides and conidia of known *Metarhizium* species: **A–C.** *M. phasmatodeae* BCC 47272. **D–F.** *M. prachinense* BCC 47979. **G–J.** *M. robertsii* ARSEF 8820. **K–M.** *M. samlanense* BCC 17091. **N–P.** *M. takense* BCC 30939. **Q–T.** *M. viridulum* ARSEF 6927. Scale bars = 10 µm.

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

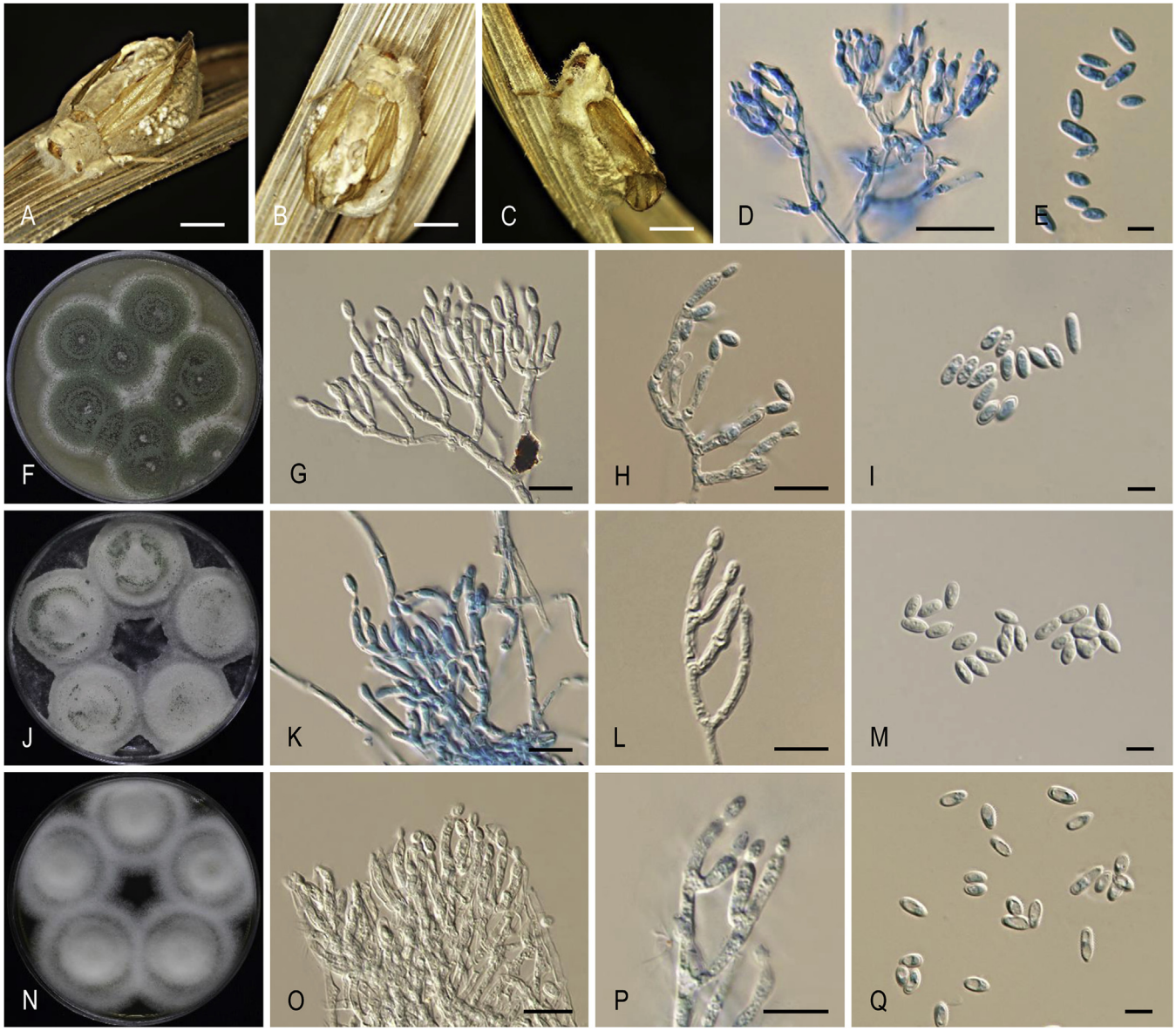

Fig. 9. *Metarhizium biotecense* (BBH 32704, culture ex-type BCC 51812). **A–C.** Fungus on adult brown planthopper (*Nilaparvata lugens*). **D**. Phialides and conidia on host. **E.** Conidia on insect host. **F.** Colonies on OA after 14 d. **G–H.** Conidiophores bearing phialides and conidia on OA. **I.** Conidia on OA. **J.** Colonies on PDA after 20 d. **K–L.** Conidiophores bearing phialides and conidia on PDA. **M.** Conidia on PDA. **N.** Colonies on SDAY/4 after 20 d. **O–P.** Conidiophores bearing phialides and conidia on SDAY/4. **Q.** Conidia on SDAY/4. Scale bars: A–C = 1 mm; D, G, H, K, L, O, P = 10 µm; E, I, M, Q = 5 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. taii*. 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. robertsii*, *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 scarabs (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 FI-

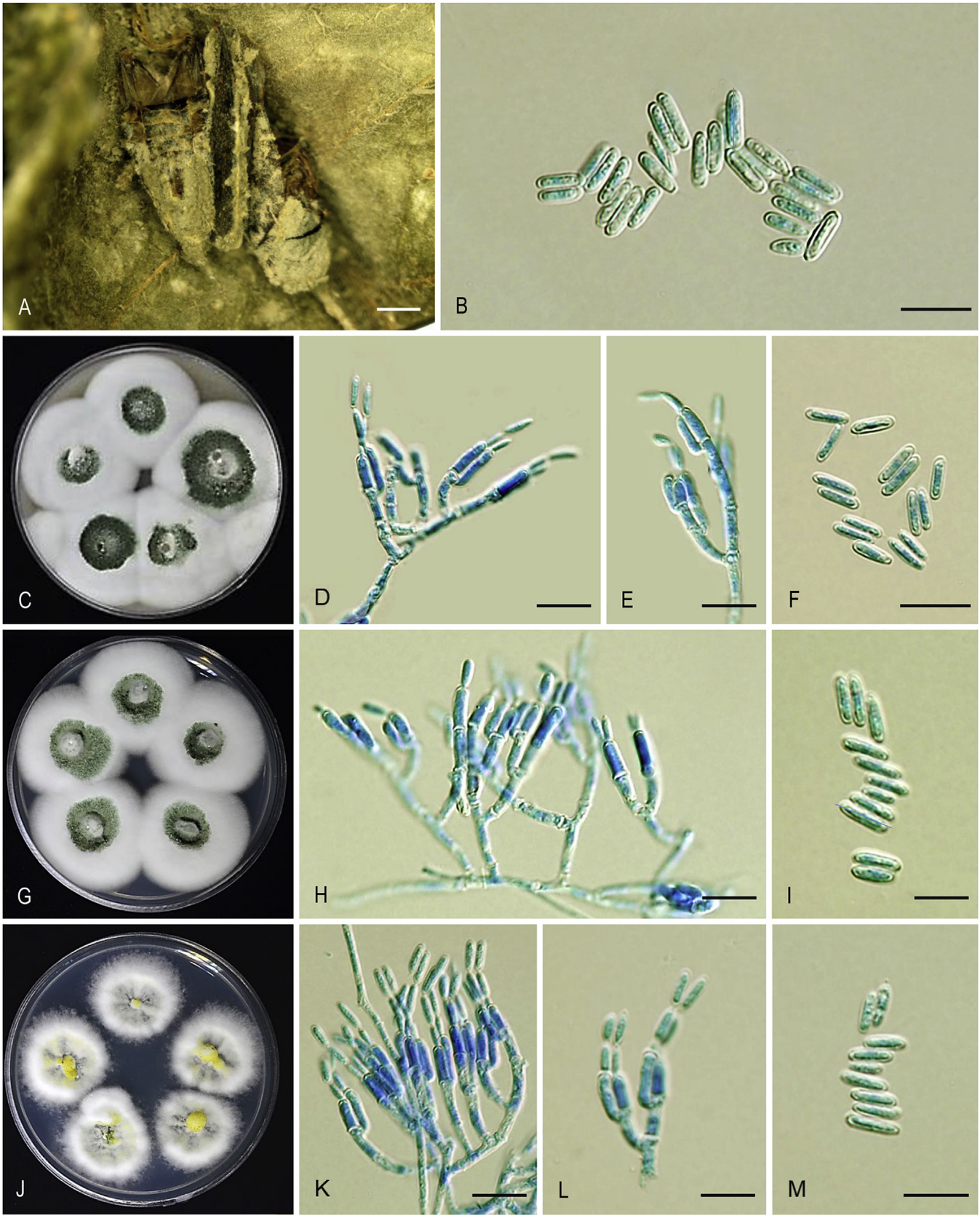

Fig. 10. *Metarhizium candelabrum* (BBH 22654, culture ex-type BCC 29224). **A.** Fungus on adult leafhopper (*Hemiptera*). **B.** Conidia on insect host. **C.** Colonies on OA. **D–F.** Phialides and conidia on OA. **G.** Colonies on PDA. **H–I.** Phialides and conidia on PDA. **J.** Colonies on SDAY/4. **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.

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.

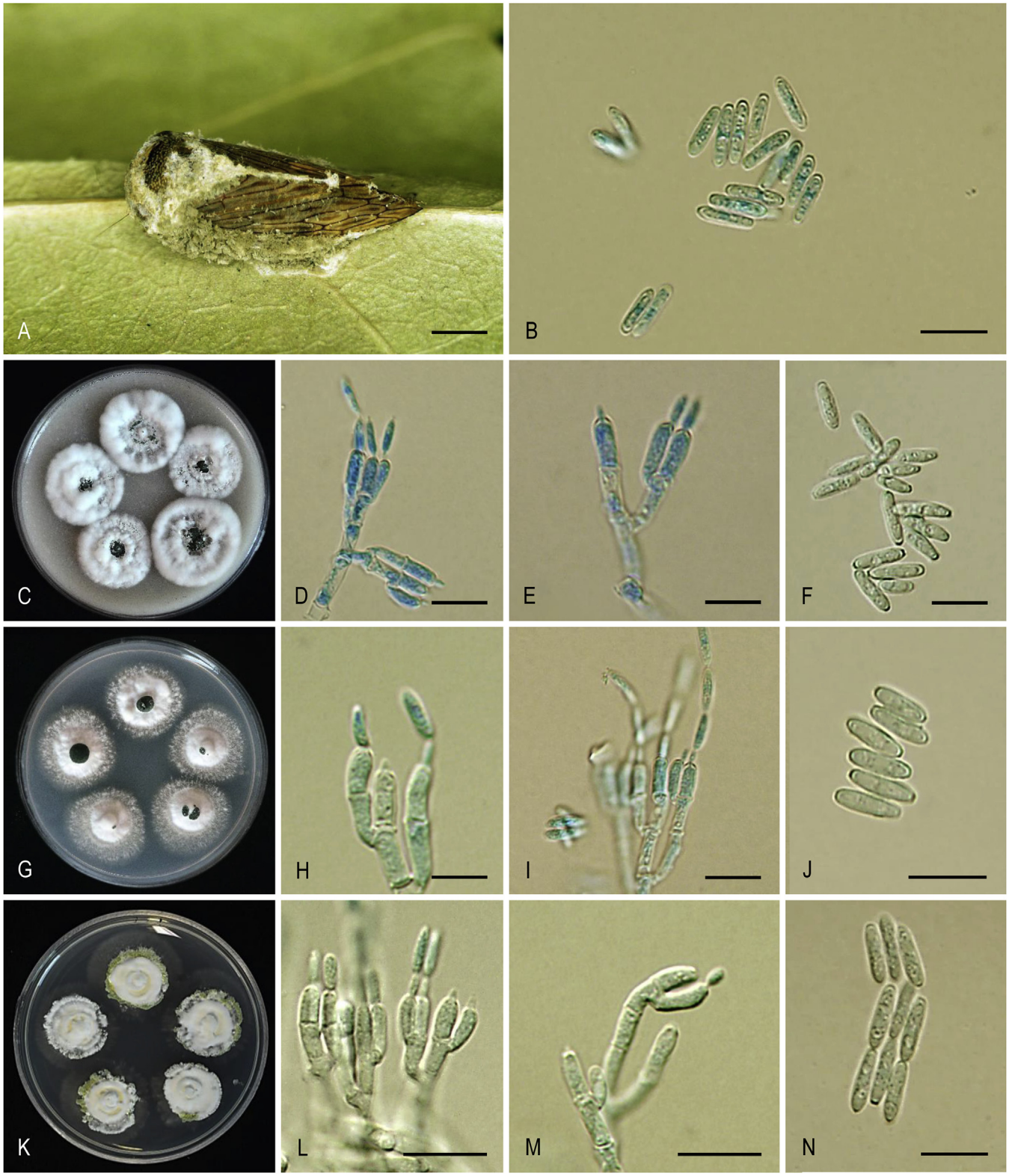

Fig. 11. *Metarhizium cercopidarum* (BBH 24005, culture ex-type BCC 31660). **A.** Fungus on adult leafhopper (*Hemiptera*). **B.** Conidia on insect host. **C.** Colonies on OA. **D–F.** Phialides and conidia on OA. **G.** Colonies on PDA. **H–J.** Phialides and conidia on PDA. **K.** Colonies on SDAY/4. **L–N**. Phialides and conidia on SDAY/4. Scale bars: A = 1 mm; B, D, E, H, I, J, L–M = 10 µm; F = 8 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. *acridum* were originally identified as *M. anisopliae* var. *minus* and *M. anisopliae* var. *anisopliae* (Driver *et al.* 2000) and were only known from grasshoppers and locusts in Africa, Asia, South America and Australia. Unlike most species in the *M. anisopliae* complex having cylindrical conidia, *M. acridum* 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. acridum* and is closest to *M. lepidiotae.* Both *M. acridum* and *M. lepidiotae* 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. bibionidarum, M. biotecense, M. blattodeae, M. culicidarum, M. flavoviride, M. frigidum, M. gaoligongense, M. koreanum, M. fusoideum, M. minus, M. nornnoi,* and *M. pemphigi.* 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, Purpureomyces khaoyaiensis, Metarhizium phuwiangense*, and some species of *Ophiocordyceps* (*Ophiocordyceps unilateralis sensu stricto*, *Ophiocordyceps pseudocommunis*). *Metarhizium atrovirens* differs from *M. pseudoatrovirens* in the oblique arrangement of the perithecia and protruding ostioles. *Metarhizium pseudoatrovirens* has ordinally 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.

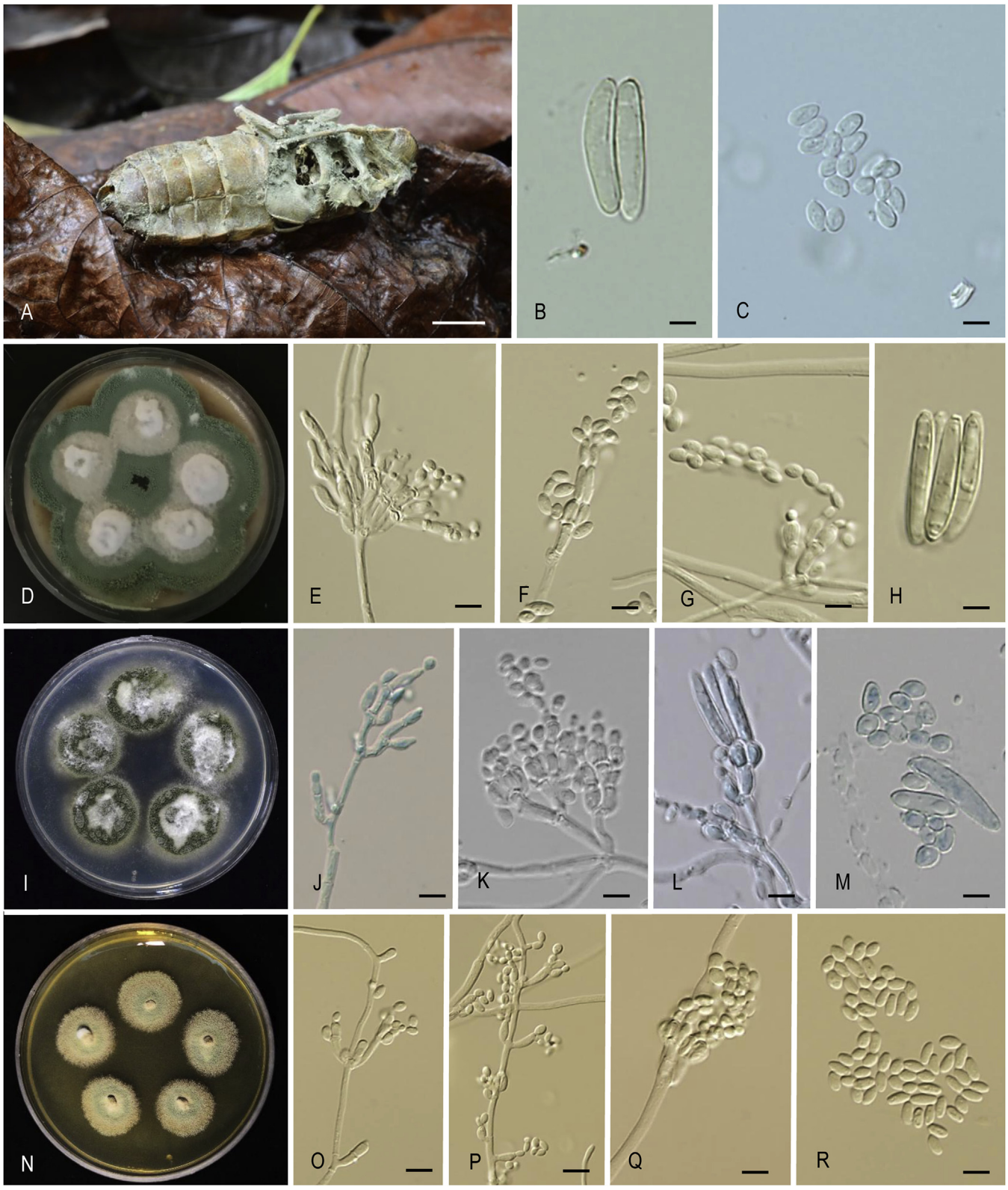

Fig. 12. *Metarhizium cicadae* (BBH 30616, culture ex-type BCC 48881). **A.** Fungus on adult cicada. **B.** Macroconidia on insect host. **C.** Microconidia on insect host. **D.** Colonies on OA. **E–G.** Conidiophores bearing phialides and conidia on OA. **H.** Macroconidia on OA. **I.** Colonies on PDA. **J–L.** Conidiophores bearing phialides and conidia on PDA. **M.** Macro and Microconidia on PDA. **N.** Colonies on SDAY/4. **O–Q.** Conidiophores bearing phialides and conidia on SDAY/4. **R.** Microconidia on SDAY/4. Scale bars: A = 10 mm; B, H = 4 µm; C, E–G, J–M, R = 5 µm; O, Q = 8 µm.

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 bibionidarum* is a member of the *M. flavoviride* complex and is closely related to *M. pemphigi, M. gaoligongense* and *M. nornnoi. Metarhizium gaoligongense* was isolated from soil, *M. pemphigi* was found predominantly on *Hemiptera* while *M. nornnoi* 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, Thanakitpipattana & 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 closely appressed, flat, white at the margins turning to peacock-green (No.162C), powdery while sporulating. Sporulation starts 5 d after inoculation, reverse olive-yellow (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 PDA 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 citrine (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. Suriyachadkun (**holotype** BBH 32704 preserved in a metabolically inactive state, culture ex-type BCC 51812).

Habitat: On adult brown planthopper, *Nilaparvata lugens* (*Hemiptera*: *Delphacidae*) 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, 14.078383 N, 100.601442 E, on adult of *Nilaparvata lugens*, 2 Mar. 2012, C. Suriyachadkun (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, 12.866756 N 99.400444 E, on adult cockroach (*Blattodea*: *Blattellidae*), 24 Aug. 2001, R. Nasit, G. Samuels & R. Reblova (NHJ 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.

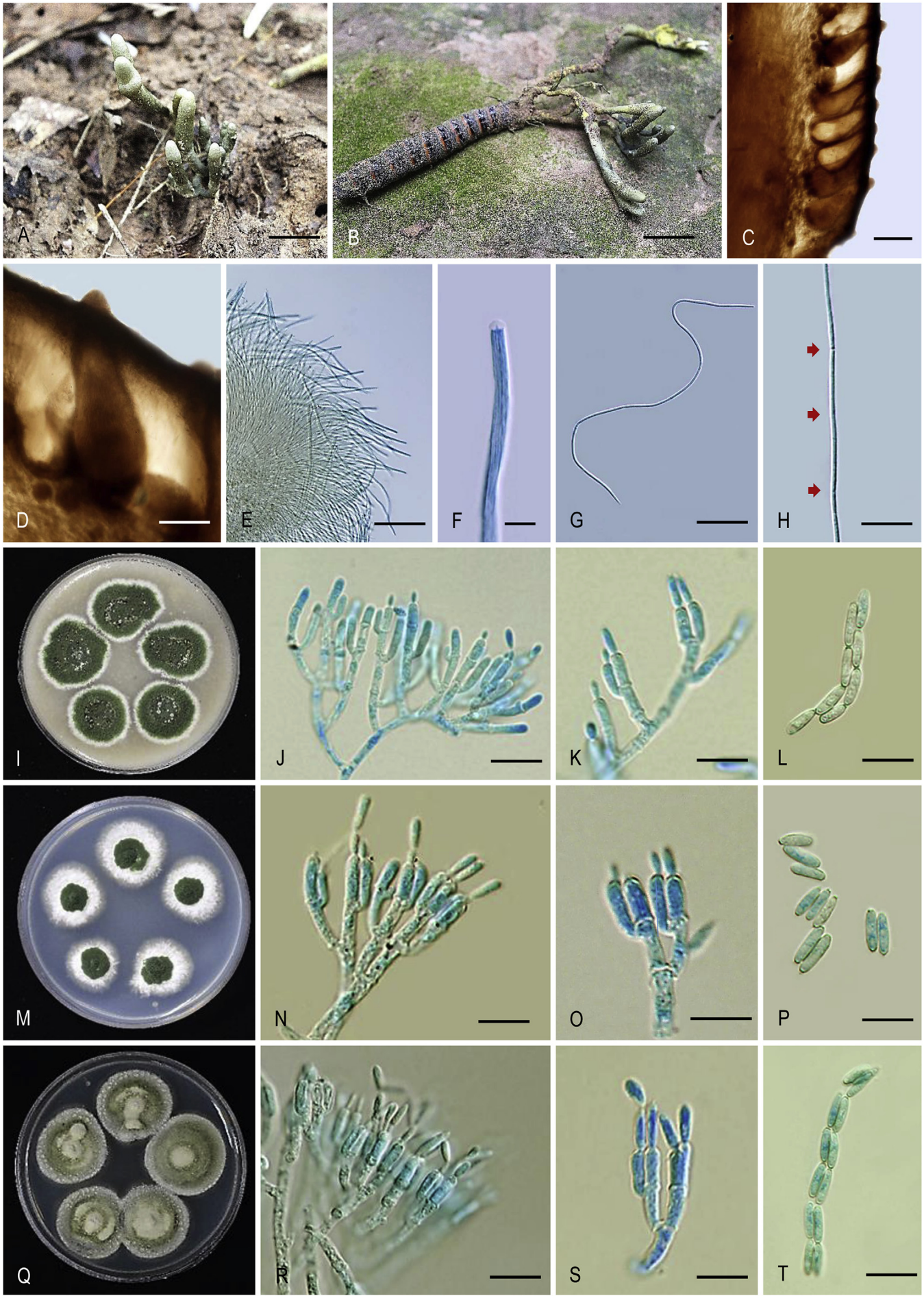

Fig. 13. *Metarhizium clavatum* (BBH 43330, culture ex-type BCC 84543). **A–B.** Stromata arising from host. **C–D.** Oblique perithecial orientation. **E.** Asci. **F.** Ascus tip. **G.** Ascospore. **H.** Whole ascospore showing septa (arrows). **I.** Colonies on OA. **J–L.** Phialides and conidia 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.

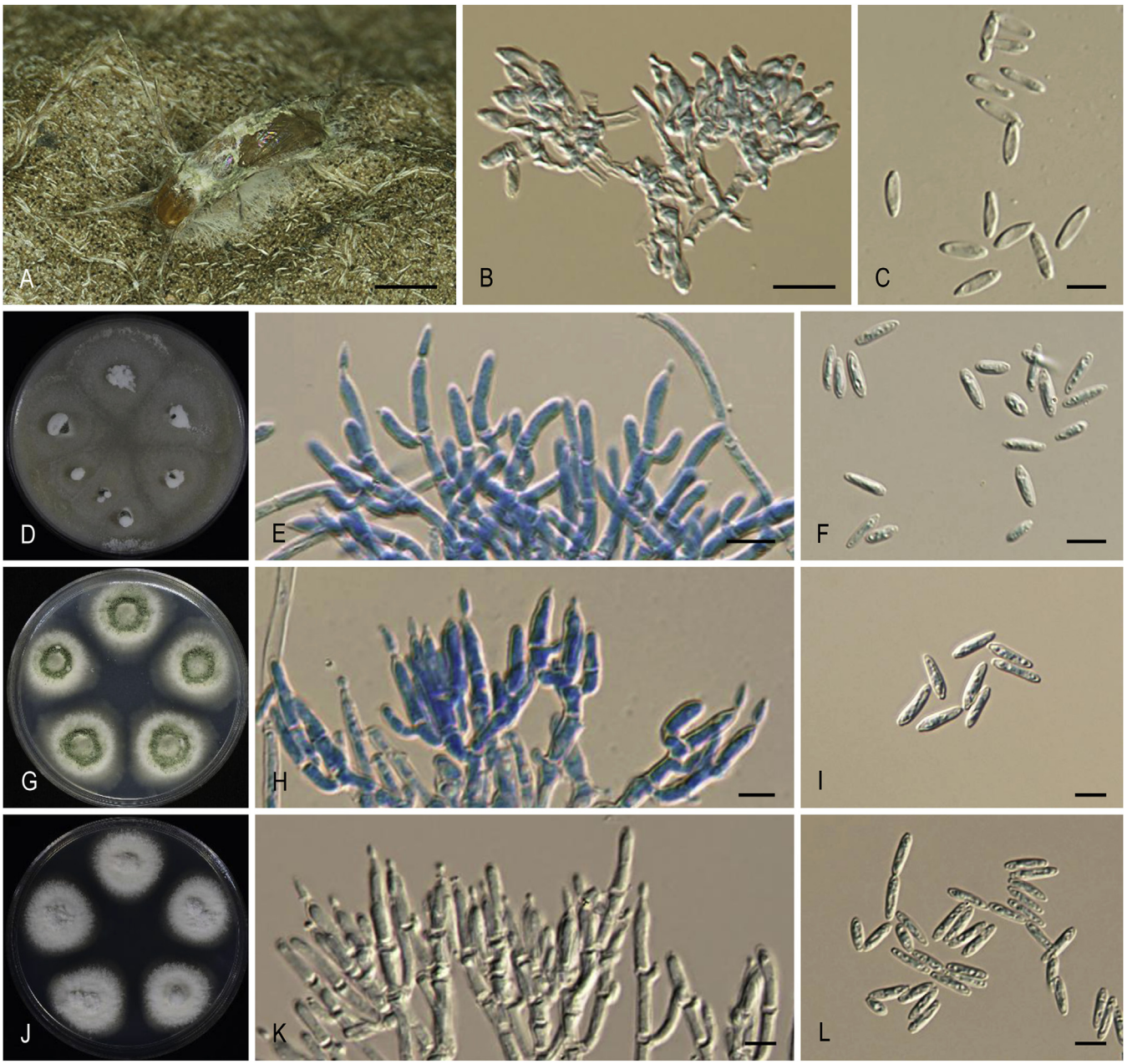

Fig. 14. *Metarhizium culicidarum* (BBH 8129, culture ex-type BCC 7600). **A.** Fungus on adult mosquito (*Diptera*: *Culicidae*). **B.** Phialides and conidia on insect host. **C.** Conidia on host. **D.** Colonies on OA. **E.** Conidiophores bearing phialides and conidia on OA. **F.** Conidia on OA. **G.** Colonies on PDA. **H.** Conidiophores bearing phialides and conidia on PDA. **I.** Conidia on PDA. **J.** Colonies on SDAY/4. **K.** Conidiophores bearing phialides and conidia on SDAY/4. **L.** Conidia on SDAY/4. Scale bars: A = 1 mm; B = 10 µm; C, E, F, H, I, K, L = 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 campsosterni* 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. campsosterni* 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* (9–10.2 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 originally was considered by Driver *et al.* (2000) to be the *M. flavoviride* "Type E" clade. However, this species shows a sister relationship *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, 5–7(–8) × 2 µm. *Conidia* smooth-walled, pale green (oac103-104), cylindrical with rounded apices, (6–)7–8(–9) × 1.5–2 µm.

Colonies on SDAY/4 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–)6–8.5(–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.

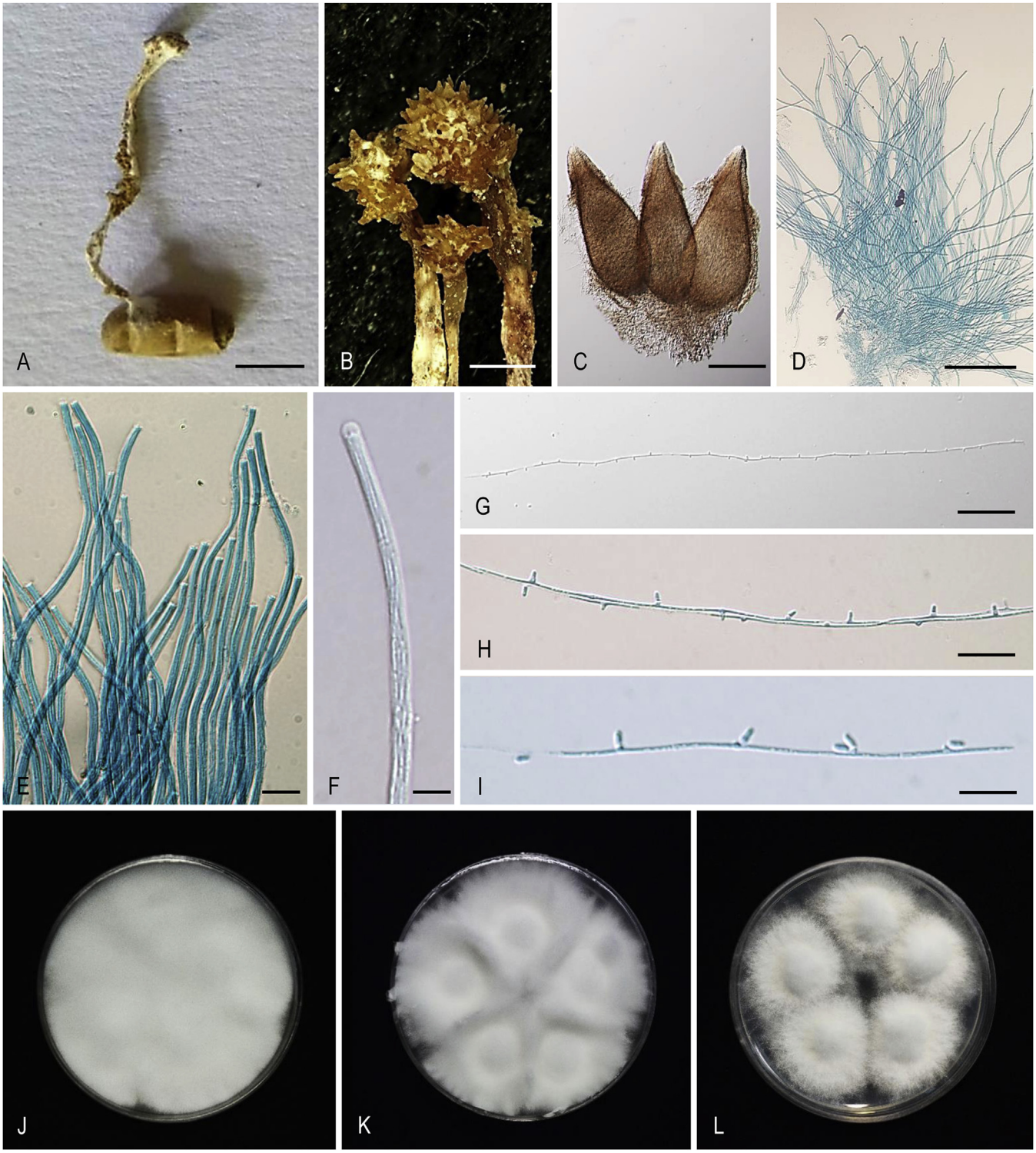

Fig. 15. *Metarhizium eburneum* (BBH 42744, culture ex-type BCC79252). **A.** Fungus on *Lepidoptera* pupa. **B.** Part of stroma showing semi-immersed perithecia. **C.** Perithecia. **D–F.** Asci. **G–I.** Germination and microcyclic sporulation of the ascospores on slide. **J.** Colonies on OA. **K.** Colonies on PDA. **L.** Colonies on SDAY/4. Scale bars: A = 5 mm; B = 1 mm; C = 200 µm; D = 50 µm; E, I = 10 µm; F = 5 µm; G = 30 µm; H = 20 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.

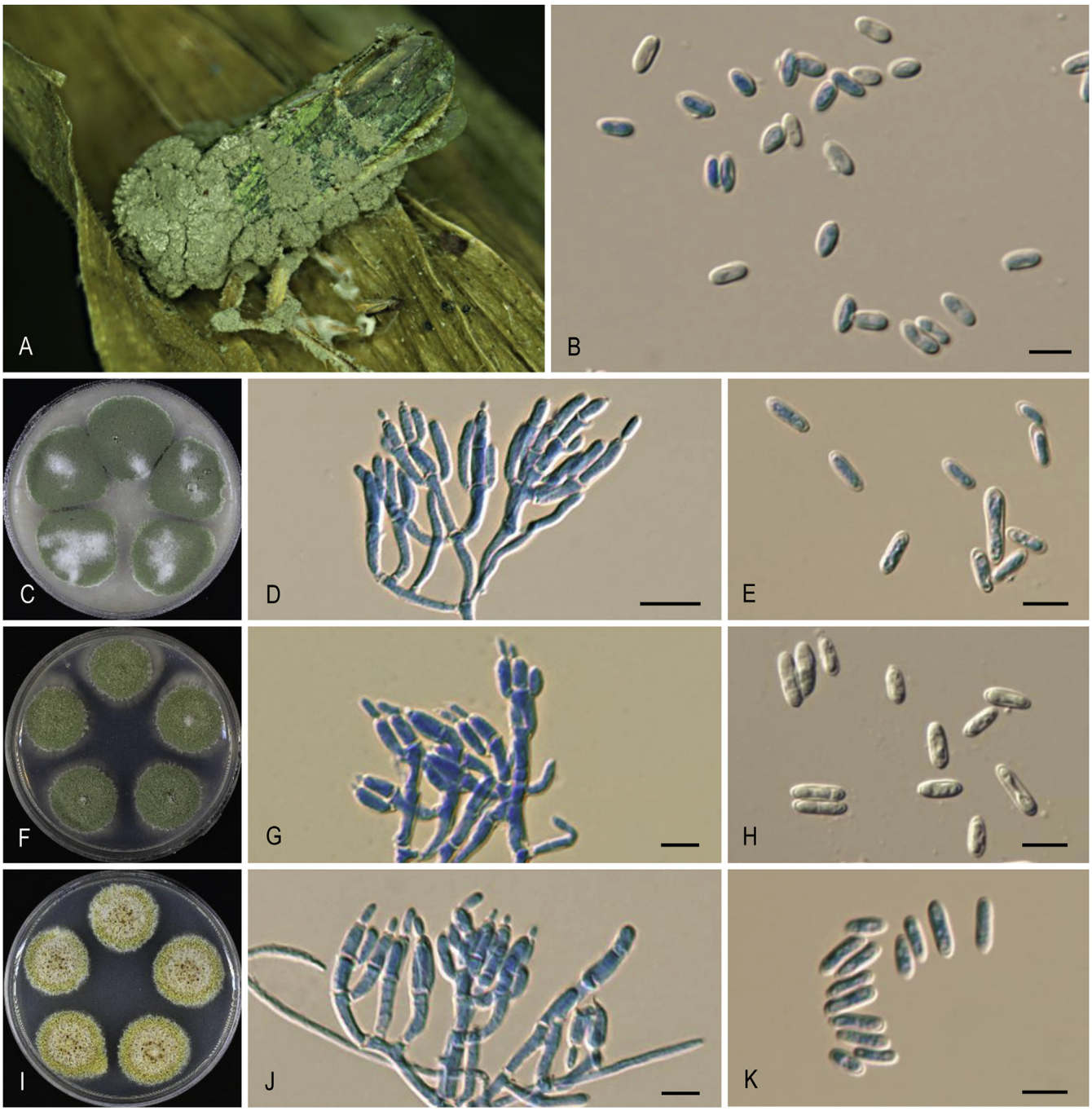

Fig. 16. *Metarhizium ellipsoideum* (BBH 30724, culture ex-type BCC 49285). **A.** Fungus on adult leafhoppers (*Hemiptera*). **B.** Conidia on insect host. **C.** Colonies on OA. **D.** Conidiophores bearing phialides and conidia on OA. **E.** Conidia on OA. **F.** Colonies on PDA. **G.** Conidiophores bearing phialides and conidia on PDA. **H.** Conidia on PDA. **I.** Colonies on SDAY/4. **J.** Conidiophores bearing phialides and conidia on SDAY/4. **K.** Conidia on SDAY/4. Scale bars: A = 1 mm; B, D, E, G, H, J, K = 5 µm.

Metarhizium campsosterni (W.M. Zhang & T.H. Li) Kepler *et al.*, Mycologia 106: 821. 2014.
Basionym: *Cordyceps campsosterni* [as '*campsosterna*'] W.M. Zhang & T.H. Li, Fungal Diversity 17: 240. 2004.
Synonym: *Metacordyceps campsosterni* (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. campsosterni* 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 Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834883. Fig. 11.

Etymology: 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.

Typus: **Thailand**, Loei Province, Phu Suan Sai National Park, on adult leafhopper (*Hemiptera*), 15 Jul. 2008, K. Tasanathai, B. Thongnuch, S. Mongkolsamrit, P. Srikitikulchai & 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).

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

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).

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, filiform, 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 *Platypleura* (*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.

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

Habitat: *Hemiptera*: *Cidadidae.*

Known distribution: Thailand.

Notes: *Metarhizium chaiyaphumense* is closely related to *M. takense*, as well as *M. cicadae, M. cylindrosporum, M. megapomponiae*, *M. niveum*, and *M. viridulum.* All species

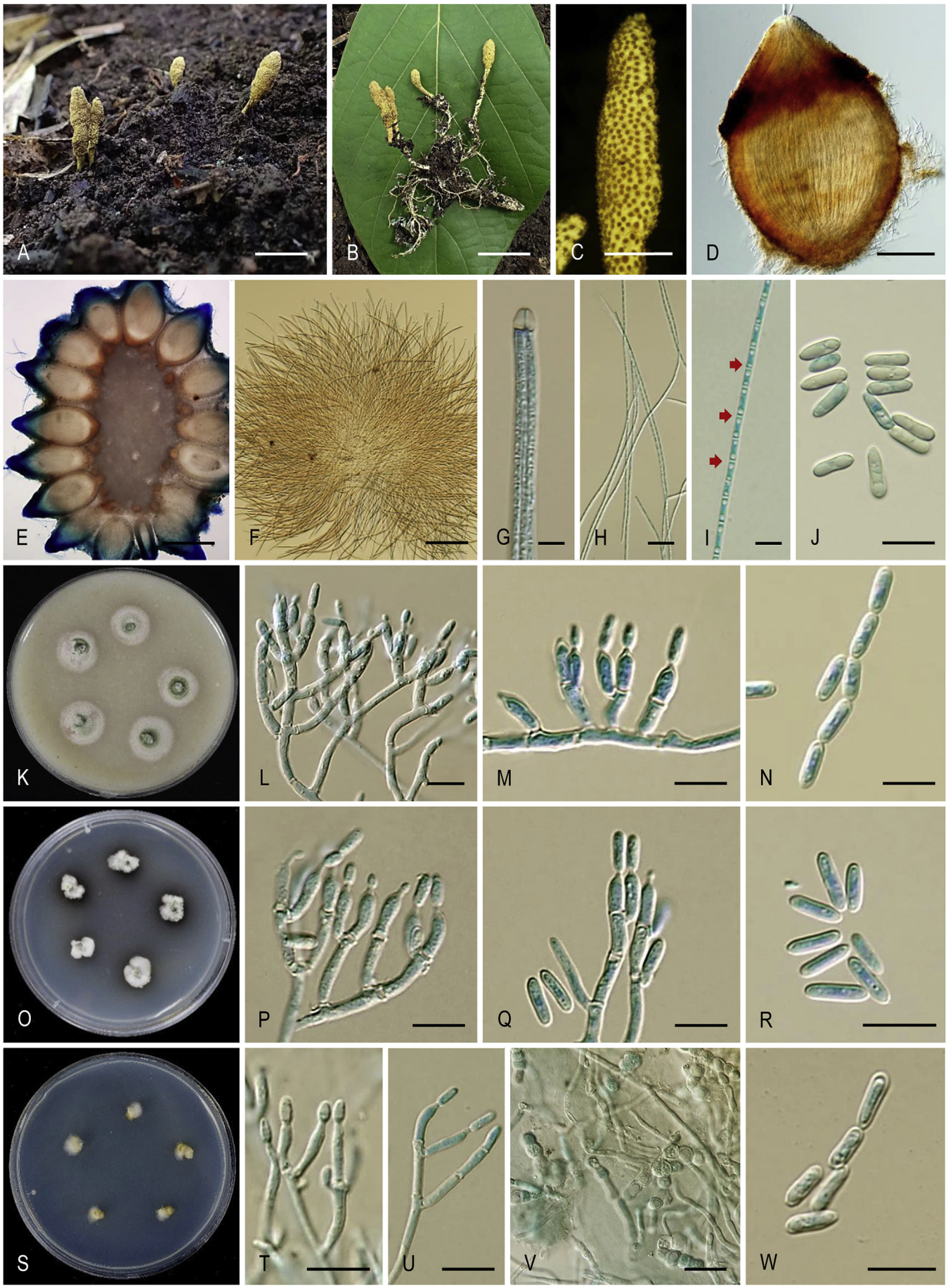

Fig. 17. *Metarhizium flavum* (BBH 47499, culture ex-type BCC 90870). **A–B.** Stromata arising from host. **C–E.** Ordinal perithecial orientation. **F.** Asci. **G.** Ascus tip. **H.** Ascospores. **I.** Whole ascospore showing septa (arrows). **J.** Conidia on insect host. **K.** Colonies on OA. **L–M.** 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. chaiyaphumense,* a characteristic also seen in *M. takense, M. cicadae* and *M. cylindrosporum.*

Metarhizium cicadae Luangsa-ard, Tasanathai, Thanakitpipattana, & 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. *Conidia* 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–)13–18.5(–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. Tasanathai, 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. Tasanathai, P. Srikitikulchai, A. Khonsanit, K. Sansatchanon & W. Noisripoom (BCC 48696).

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

Metarhizium clavatum Luangsa-ard, Mongkolsamrit, Lamlertthon, Thanakitpipattana & 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) × 1–1.5 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) × 2–2.5(–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 Phaothai 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 Phaothai Community Forest, Phitsanulok Province.

Additional materials examined: **Thailand**, Phitsanulok Province, Ban Phaothai Community Forest, 16.735031 N, 100.659606 E, on larva of *Oxynopterus* sp.

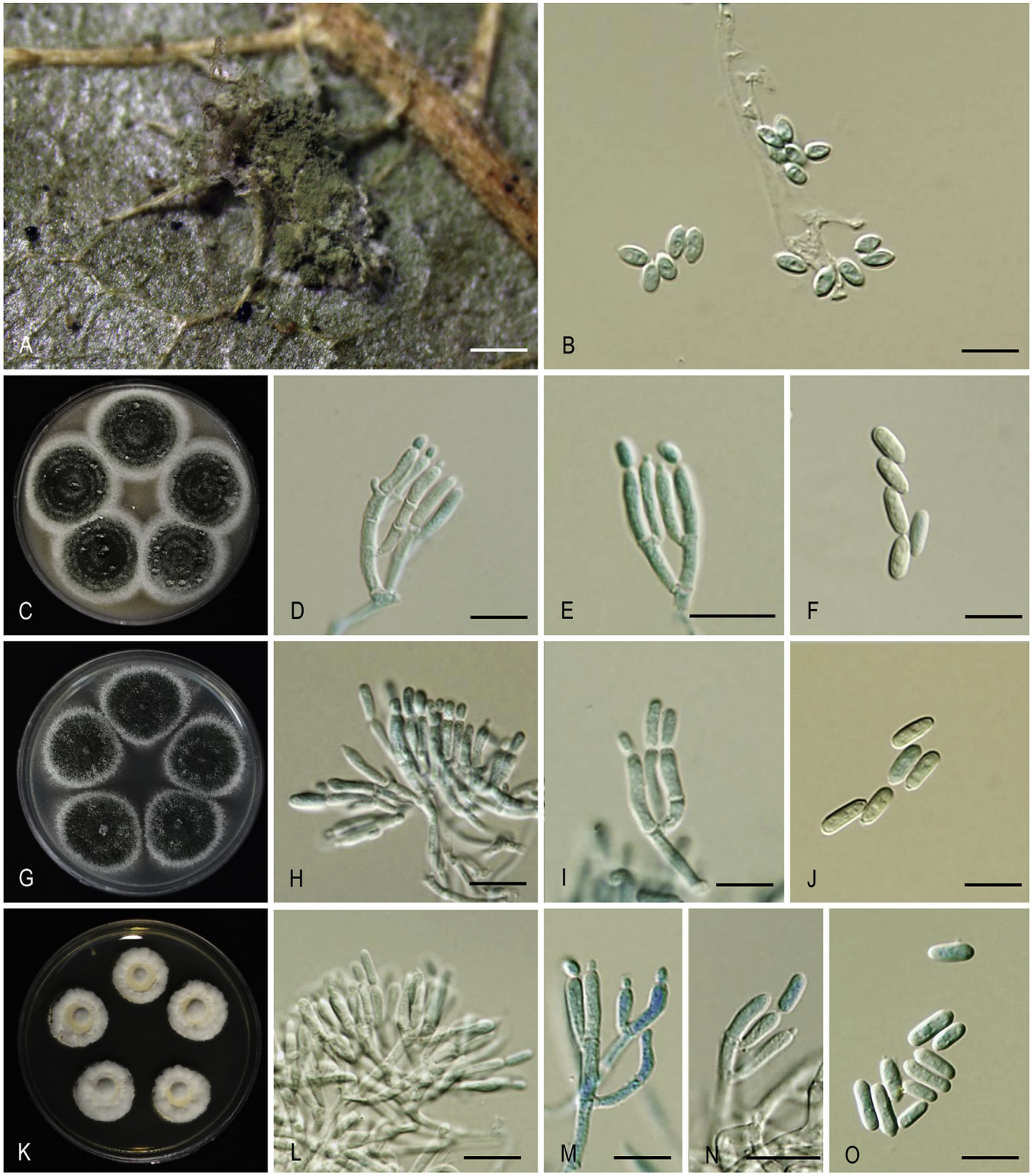

Fig. 18. *Metarhizium fusoideum* (BBH 22698, culture ex-type BCC 28246). **A.** Fungus on adult leaf moth (*Lepidoptera*). **B.** Conidia on insect host. **C.** Colonies on OA. **D–F.** Phialides and conidia on OA. **G.** Colonies on PDA. **H–J.** Phialides and conidia on PDA. **K.** Colonies on SDAY/4. **L–O.** Phialides and conidia on SDAY/4. Scale bars: A = 1 mm; B, D, E, F, H, J, L–O = 10 µm; I = 5 µm.

(*Coleoptera*), 25 Jun. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom, U. Pinruan & S. Lamlertthon (BBH 42806, BCC 84558).

Notes: The macromorphologies of the natural samples of *M. clavatum* are most similar to *M. kalasinense* (Luangsa-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, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834889. 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, white 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 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, white. 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.

Typus: **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 '*cylindrosporae*'] 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).

Typus: **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 dendrolimatilis Z.Q. Liang *et al.*, Mycosphere 8: 33. 2017.

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

Typus: **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, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834890. Fig. 15.

Etymology: Named after the Latin "*eburneus*", meaning white as ivory. Refers to the colour of the stroma and the colonies in culture.

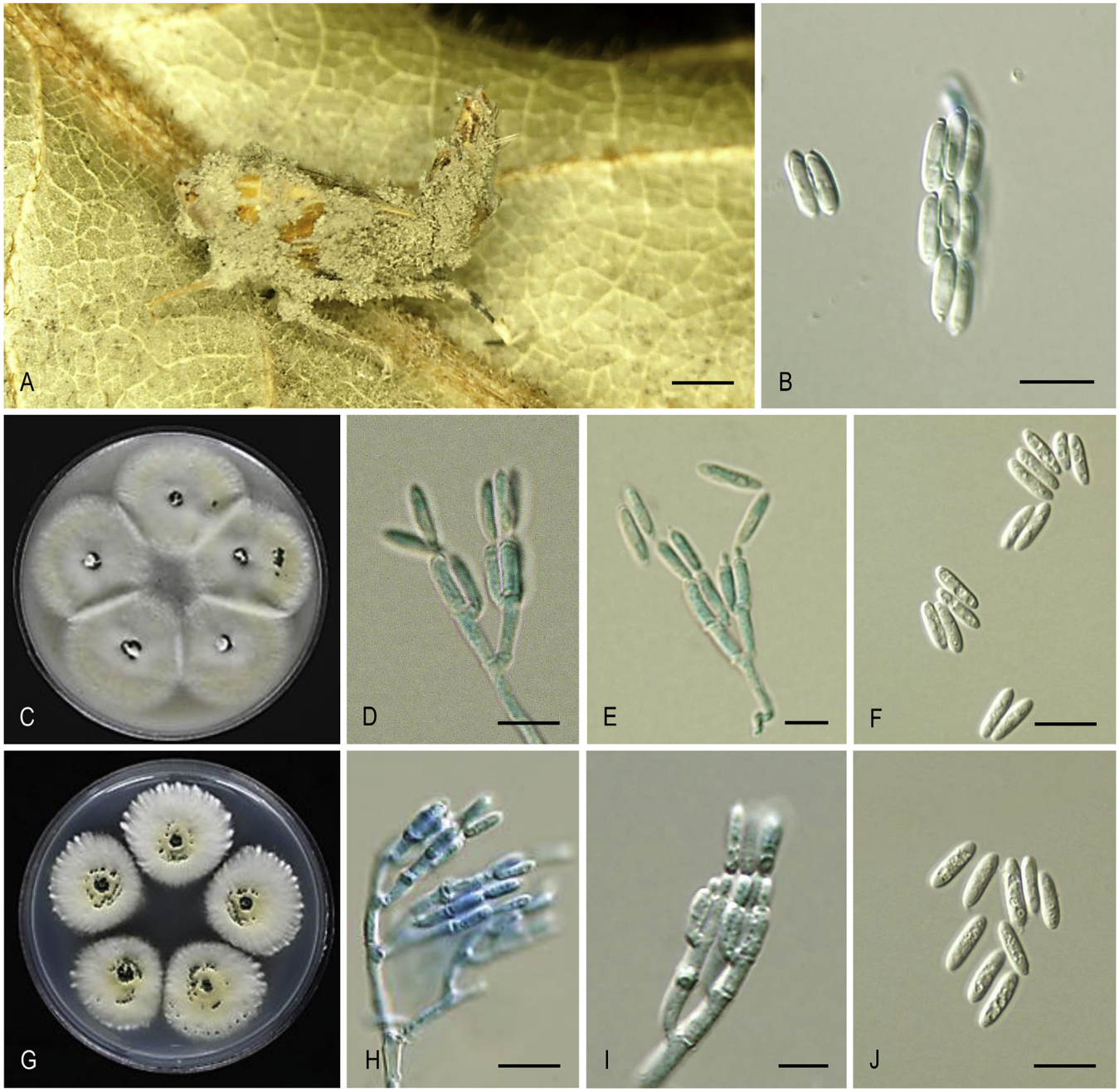

Fig. 19. *Metarhizium huainamdangense* (BBH 29715, culture ex-type BCC 44270). **A.** Fungus on adult leafhopper (*Hemiptera*). **B.** Conidia on insect host. **C.** Colonies on OA. **D–F.** Phialides and conidia on OA. **G.** Colonies on PDA. **H–J.** Phialides and conidia on PDA. Scale bars: A = 1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

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, multiseptate, (222.5–)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 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 SDAY/4 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.

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

Additional materials examined: **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 (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. dendromatilis* (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 eburneum* differs from species on *Coleoptera* such as *M. atrovirens*, *M. flavum, M. phuwiangense, M. pseudoatrovirens, 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 Luangsa-ard, Khonsanit, Thanakitpipattana & 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 PDA 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) with 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 SDAY/4 attaining a diam of 16–18 mm in 20 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. Srikitikulchai & 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, Khao Soi Dao Wildlife Sanctuary, Khao Yai National Park and Phlu Kaeng Waterfall.

Additional materials examined: **Thailand**, Chanthaburi Province, Khao Soi Dao Wildlife Sanctuary, 13.103906 N, 102.194322 E, on adult leafhopper (*Hemiptera*), 26 Mar. 2000, R. Nasit (BBH 2566, BCC 7590); Nakhon Ratchasima Province, Khao Yai 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. Chaygate (BBH 12847, BCC 8687); on adult leafhopper (*Hemiptera*), 10 Dec. 2009, A. Khonsanit, K. Tasanathai, M. Sudhadham, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & T. Chohmee (BBH 27327, BCC 40161); on adult leafhopper (*Hemiptera*), 16 May 2012, A. Khonsanit, K. Tasanathai, M. Sudhadham, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & T. Chohmee (BBH 32448, BCC 53509); Chiang Rai Province, Phlu Kaeng Waterfall nature trail, on adult leafhopper (*Hemiptera*), 17 Jan. 2009, A. Khonsanit, K. Tasanathai, P. Srikitikulchai, R. Promharn, S. Mongkolsamrit & T. Chohmee (BBH 26421, BCC 34770).

Notes: *Metarhizium ellipsoideum* shares similarity with *M. album, M. brasiliense, M. candelabrum, M. cercopidarum,* 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. cercopidarum* 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. cercopidarum* 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 *'Metarrhizium 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 macula-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 Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834892. Fig. 17.

Etymology: Name refers to the yellow colour of stromata.

Stromata two to several, simple, clavate to irregularly shaped, branched, up to 4.5 cm long, 1.5–2 mm wide. *Rhizoids* flexuous, 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. *Perithecia* semi-immersed, ordinal in arrangement with slightly protuberant ostioles, ovoid, (500–)545–640(–650) × (270–)280–320(–330) µm. *Asci* 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). *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 dark 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 SDAY/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–)8–10.5(–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. Srikitikulchai, U. Pinruan, P. Khamsuntorn & 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, found at San Pa Pao Community Forest and San Buak Wai Community Forest, Chiang Mai Province.

Additional materials examined: **Thailand**, Chiang Mai Province, San Pa Pao Community Forest, 19.005714 N, 98.813153 E, on *Coleoptera* larva, 20 Aug. 2019, S. Mongkolsamrit, N. Kobmoo, P. Srikitikulchai, U. Pinruan, P. Khamsuntorn & S. Sommai (BBH 47502, BCC 90874).

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 *Adoryphorus* 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 SDAY/4.

Metarhizium fusoideum Luangsa-ard, Mongkolsamrit, Thanakitpipattana & 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 SDAY/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

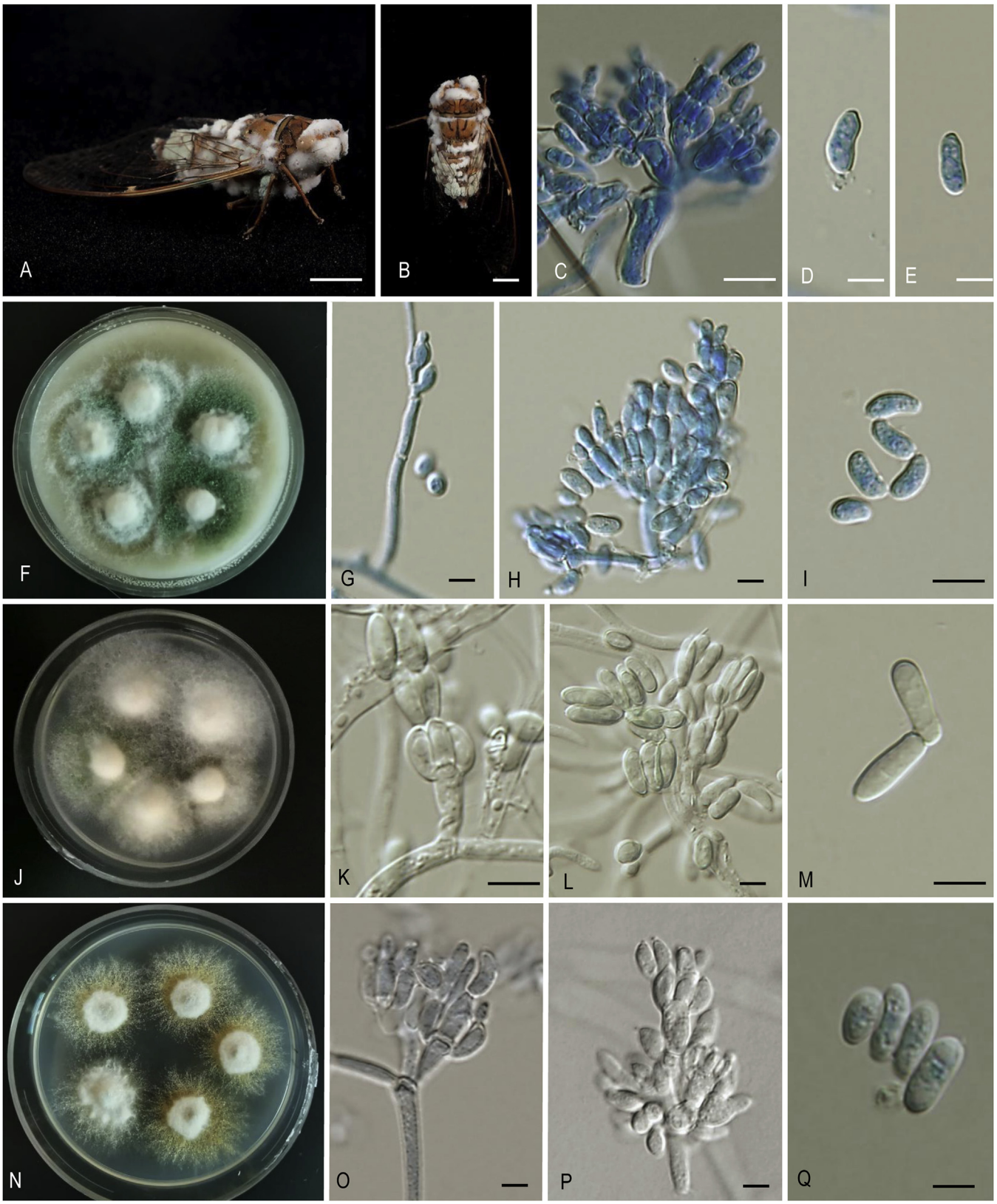

Fig. 20. *Metarhizium megapomponiae* (BBH 19860, culture ex-type BCC 25100). **A–B.** Fungus on adult cicada. **C.** Phialides and conidia on host. **D–E.** Conidium on insect host. **F.** Colonies on OA. **G–H.** Phialides and conidia on OA. **I.** Conidia on OA. **J.** Colonies on PDA. **K–L.** Phialides 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.

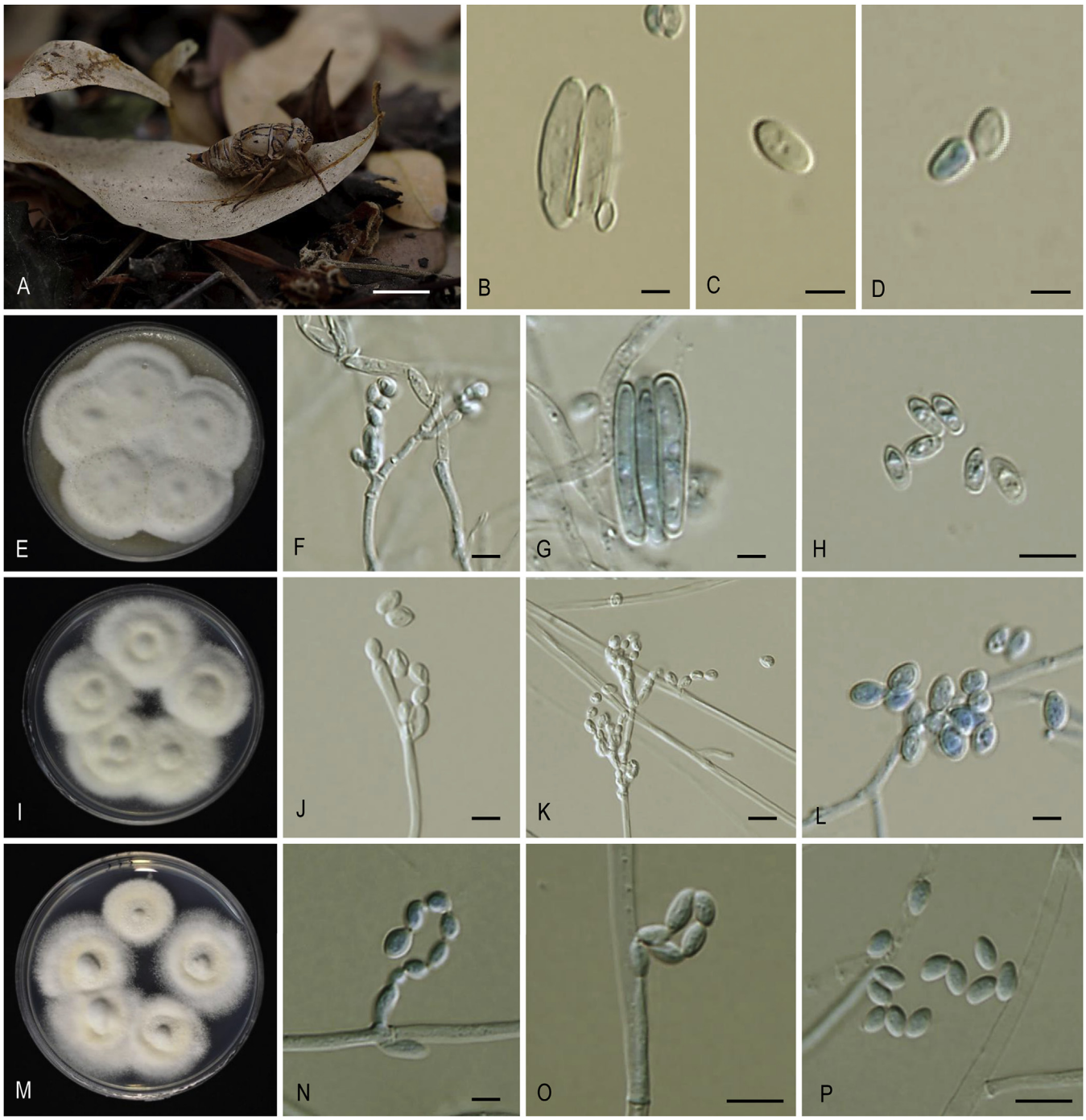

Fig. 21. *Metarhizium niveum* (BBH 35742, culture ex-type BCC 52400). **A.** Fungus on adult cicada. **B.** Macroconidia on insect host. **C–D.** Microconidia on insect host. **E.** Colonies on OA. **F.** Phialides and conidia on OA. **G.** Macroconidia on OA. **H.** Microconidia on OA. **I.** Colonies on PDA. **J–K.** Phialides and conidia on PDA. **L.** Conidia on PDA. **M.** Colonies on SDAY/4. **N–O.** Phialides and conidia on SDAY/4. **P.** Conidia on SDAY/4. Scale bars: A = 10 mm; B–D = 3 µm; F = 8 µm; G, H, K, N–P = 4 µm; J = 5 µm; L = 3 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

phialides are cylindrical and conidia are ellipsoidal to cylindrical with rounded apices.

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. nornnoi, M. pemphigi* 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 machaeralis* (*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: *Chamaeleomyces 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. Promharn, R. Ridkaew, S. Mongkolsamrit & W. Chaygate (BBH 23876, BCC 30917); *idem.*, 14 Aug. 2009, K. Tasanathai, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & T. Chohmee (BBH 26529, BCC 37915), (BBH 26533, BCC 37918); *idem.*, 11 Jul. 2012, A. Khonsanit, K. Sansatchanon, K. Tasanathai, P. Srikitikulchai, R. Somnuk, S. Mongkolsamrit & W. Noisripoom (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. Srikitikulchai, S. Mongkolsamrit & W. Chaygate (BBH 18647, BCC 22353).

Notes: *Metarhizium gryllidicola* is a member of the *M. anisopliae* complex and is close to *M. brittlebankisoides* and *M. clavatum.* It is only found occurring on adult crickets (*Gryllidae*), while *M. brittlebankisoides* 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.

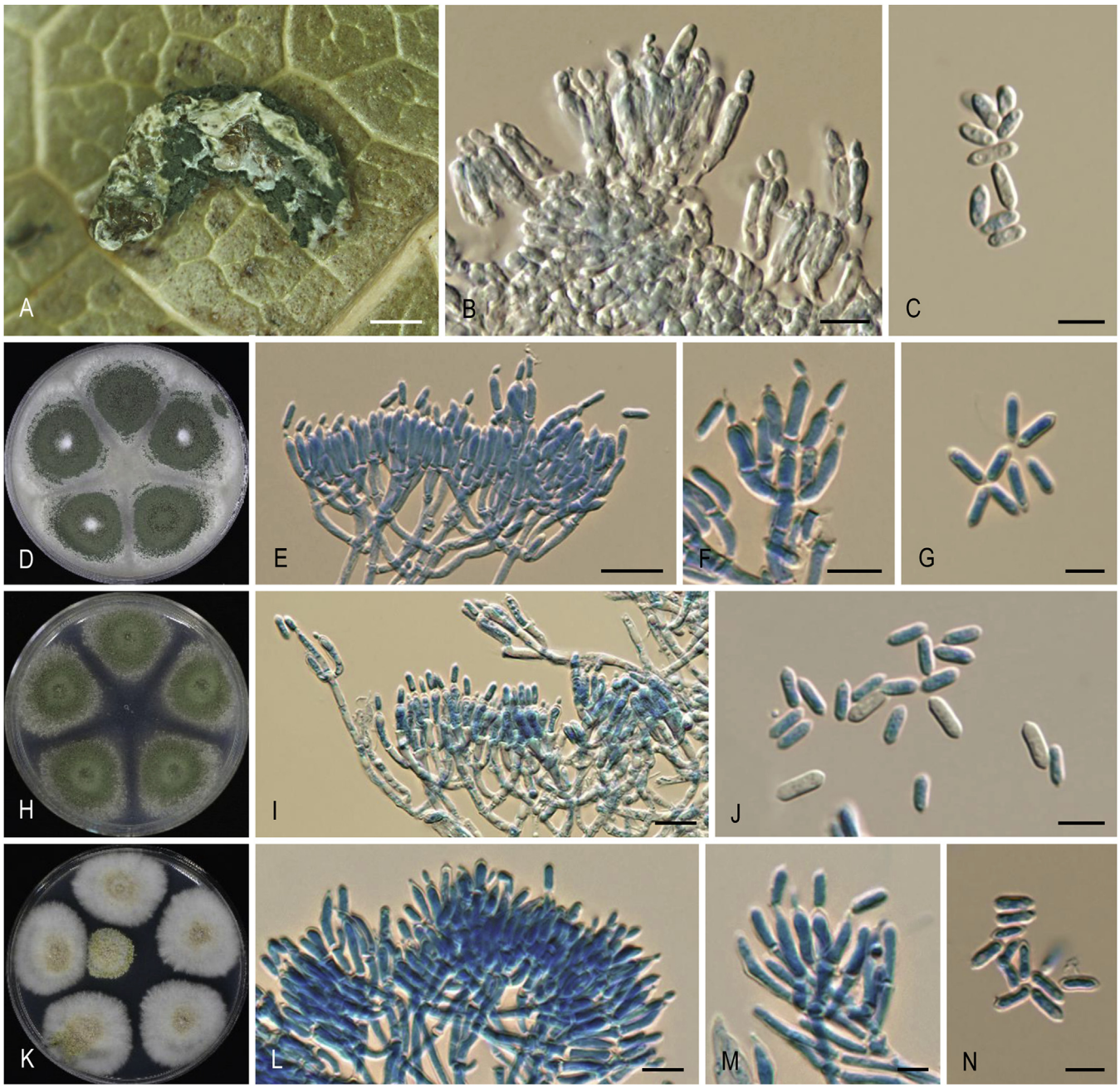

Fig. 22. *Metarhizium nornoi* (BBH 14938, culture ex-type BCC 19364). **A.** Fungus on *Lepidoptera* larva. **B.** Phialides and conidia on insect host. **C.** Conidia on insect host. **D.** Colonies on OA. **E–F.** Conidiophores bearing phialides and conidia on OA. **G.** Conidia on OA. **H.** Colonies on PDA. **I.** Conidiophores bearing phialides and conidia on PDA. **J.** Conidia on PDA. **K.** Colonies on SDAY/4. **L–M.** Conidiophores bearing phialides and conidia on SDAY/4. **N.** Conidia on SDAY/4. Scale bars: A = 1 mm; B, C, F, G, J, M, N = 5 µm; E, I, L = 10 µm.

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 guniujiangense (C.R. Li *et al.*) Kepler *et al.*, Mycologia 106: 822. 2014.
Basionym: *Metacordyceps guniujiangensis* C.R. Li *et al.*, Mycotaxon 111: 223. 2010.

Description and illustration: See Li *et al.* (2010).

Typus: **China**, southern Anhui, Shitai county, National Natural Reserve of Guniujiang, on nymph of cicada (*Hemiptera, Cicadidae*), 27 May 2002, C.R. Li (**holotype** RCEF, Li GNJ020527-04).

Habitat: Cicada nymph (*Hemiptera*).

Known distribution: China.

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 is closely related to *M. cylindrosporum, M. niveum* and *M. viridulum. Metarhizium guniujiangense* 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 stromata. Furthermore, the sizes of perithecia and asci of *M. guniujiangense* (640–770 × 240–320 µm and 310–380 × 4–4.8 µm) are longer than those of *M. owariense* f. *viridiscens* (440–640 × 180–320 µm and 180–300 × 5–6.5 µm, respectively).

Metarhizium huainamdangense Luangsa-ard, Mongkolsamrit, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834894. 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 with rounded apices, 5–7(–8) × 2–2.5(–3) µm.

Cultural characteristics: Colonies on OA attaining a diam of 18 mm in 14 d, pale cream, floccose, entire edge, velvety to woolly, dark green in the centre of colonies due to production of conidia. Sporulation starts at 14 d after inoculation, reverse uncoloured. *Conidiophores* terminating in branches, with 2–3 phialides per branch. *Phialides* cylindrical with semi-papillate apices, 5–7.5(–10) × 2–2.5 µm. *Conidia* smooth-walled, dark green (162A), cylindrical with rounded apices, (5–) 6–9.5(–10) × 2–3 µm.

Colonies on PDA 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 colonies due to production of conidia. Sporulation starts at 14 d after inoculation, reverse uncoloured. *Conidiophores* terminating in branches, with 2–3 phialides per branch. *Phialides* cylindrical with semi-papillate apices, 5–8(–10) × 2–3 µm. *Conidia* smooth-walled, dark green (162A), cylindrical with rounded apices, (5–) 5.5–8.5(–10) × 2–3 µm.

Colonies on SDAY/4 attaining a diam of 10 mm in 14 d, grey pink, fluffy, entire edge, reverse uncoloured. *Conidia* and reproductive structures not observed.

Typus: **Thailand**, Chiang Mai Province, Huai Nam Dang National Park, on leafhopper (*Hemiptera*), 22 Sep. 2010, K. Tasanathai, P. Srikitikulchai & A. Khonsanit (**holotype** BBH 29715 preserved in a metabolically inactive state, culture ex-type BCC 44270).

Habitat: On leafhopper (*Hemiptera*), on the underside of dicotyledonous plants and bamboos in the forest.

Known distribution: Thailand, known from Huai Nam Dang National Park and Namtok Samlan National Park.

Additional materials examined: **Thailand**, Chiang Mai Province, Huai Nam Dang National Park, 19.303919 N, 98.598831 E, on leafhopper (*Hemiptera*), 22 Sep. 2010, K. Tasanathai, P. Srikitikulchai & A. Khonsanit, (BBH 29368, BCC 44271); *idem.*, 25 Sep. 2008, K. Tasanathai, W. Chaygate, P. Srikitikulchai, A. Khonsanit & S. Mongkolsamrit (BBH 24622, BCC 32190); Saraburi Province, Namtok Samlan National Park, 14.440100 N, 100.960308 E, on leafhopper (*Hemiptera*), 30 Aug. 2000, N. Hywel-Jones, S. Sivichai & K. Tasanathai (BBH 8064, BCC 7672).

Notes: *Metarhizium huainamdangense* is closely related to *M. candelabrum* and *M. cercopidarum* that are known to infect leafhoppers (*Hemiptera*) and the production of cylindrical conidia with rounded apices but differs in its growth on SDAY/4. In *M. huainamdangense,* no sporulation could be observed but is abundant in both *M. candelabrum* and *M. cercopidarum.*

Metarhizium humberi Luz *et al.*, J. Invertebr. Pathol. 166: 107216. 2019.

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

Typus: **Brazil**, on soil, 14 Sep. 2001, C. Luz, L.F.N. Rocha, R.O. Silva, M. Unterseher (**holotype** UFG 50751, culture ex-type IP 46 = CG620 = ARSEF 12874).

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

Known distribution: Brazil, Mexico.

Notes: Multi-gene phylogenetic analyses supported the recognition of this species in the *M. anisopliae* complex, close to *M. anisoplae, M. pingshaense* and *M. robertsii.* First reported from soil, *M. humberi* 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 106: 823. 2014.
Basionym: *Cordyceps indigotica* Kobayasi & Shimiz, Bull. Nat. Sci. Mus. Tokyo, Ser. B. 4: 52. 1978.
Synonym: *Metacordyceps indigotica* (Kobayasi & Shimizu) Kepler *et al.*, Mycologia 104: 85. 2012.

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

Typus: **Japan**, Mt. Osuzu-yama, Koyu,gun, Miyazaki Prefecture, on larva of *Holcocerus vicarious,* (*Cossidae, Lepidoptera*), 20 Mar. 1955, G. Imoto & D. Shimizu (**holotype** in TNS).

Habitat: *Lepidoptera* larva (*Cossidae*).

Known distribution: Japan.

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.*

Metarhizium kalasinense Tasanathai *et al.*, Mycol. Prog. 16: 382. 2017.

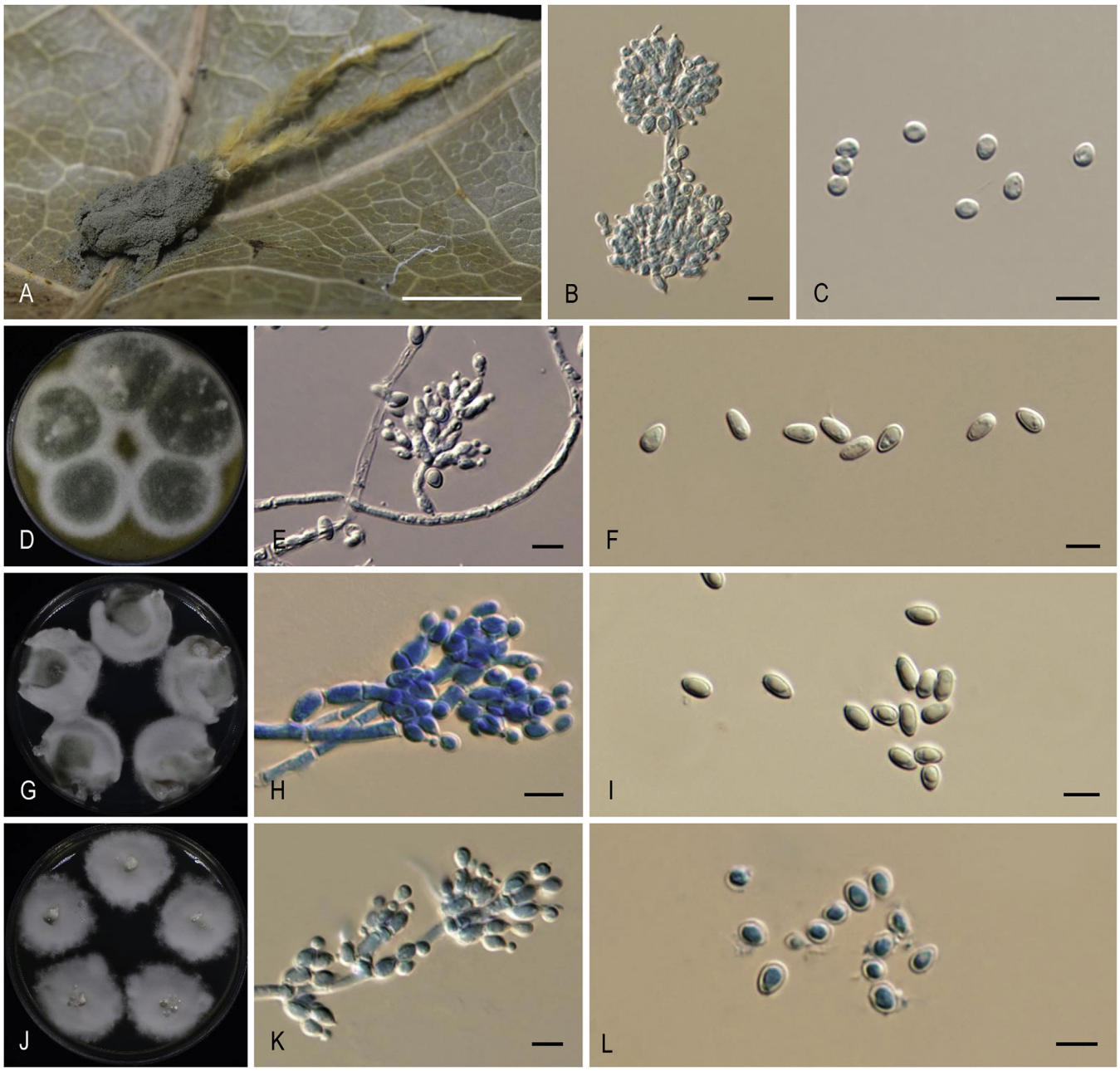

Fig. 23. *Metarhizium ovoidosporum* (BBH 25358, culture ex-type BCC 32600). **A.** Fungus on adult Lophopid planthopper. **B.** Phialides and conidia on insect host. **C.** Conidia on insect host. **D.** Colonies on OA in 14 d. **E.** Conidiophores bearing phialides and conidia on OA. **F.** Conidia 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.

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 funiculose, 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.

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. Noisripoom (**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. Noisripoom (BBH 34584, BCC 53581); *idem.*, 26 Jun. 2012, A. Khonsanit & W. Noisripoom (BBH 32209, BCC 53629); *idem.*, 19 Jul. 2012, K. Tasanathai, A. Khonsanit & W. Noisripoom (BBH 34586, BCC 53874), (BBH 34590, BCC 53876), (BBH 34592, BCC 53877).

Notes: This species is morphologically very similar to *M. campsosterni* but differs not only in having 8-spored asci but also in the size of the perithecia, asci 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 planthopper (*Fulgoromorpha, Hemiptera*) on the underside of leaves. Host'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 light drab (No.119C) in the middle of colony and lime green (No.59) at the margin. *Conidiophores* arising from aerial mycelia, erect, smooth-walled, cylindrical. *Phialides* smooth, cylindrical, (5–)6.5–8.5(–11) × 2–2.5(–3) µm. *Conidia* smooth-walled, olive-green (No.47), cylindrical with rounded apices, ellipsoidal, (6–)6.5–10(–13) × 2–3 µm.

Colonies on PDA attaining a diam of 16 mm in 14 d, flat, closely appressed to the agar surface, at first white turning to olive-green (No.47) with olive-grey (No.42), powdery while sporulating, smoke grey (No. 42) with white mycelia at the margin. Sporulation starts at 5 d after inoculation, reverse olive yellow (No.52), sulphur yellow (No.57) 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–)6–7.5(–8) × 2–2.5 µm. *Conidia* smooth-walled, olive-green (No.47) with olive-grey (No.42), cylindrical with rounded apices, ellipsoidal, (5–)6–7(–8) × 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 planthoppers (*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. Srikitikulchai, R. Ridkaew & S. Mongkolsamrit (BBH 22655, BCC 27998); Saraburi Province, Namtok Samlan National Park, 14.440100 N, 100.960308 E, on adult planthopper, 15 Jul. 2004, K. Tasanathai, N. Boonyuen, P. Puyngain, 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 *Lepidiota consobrina* (*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 *Metarhiziun anisopliae* var. *lepidiotum*, **paratypes** DAR 74303–74306).

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

Known distribution: Australia, Japan, Papua New Guinea.

Notes: *Metarhizium lepidiotae* is morphologically indistinguishable from *M. anisopliae* except in molecular data (Bischoff *et al.* 2009). Our multi-gene analyses show *M. lepidiotae* nested together with *M. anisopliae* CBS 130.71 from Ukraine but not with *M. anisopliae* ARSEF 7487, which was Tulloch's neotype (1979). Our 5′*tef* analysis (Fig. 2) supports this result but also shows other species identified as *M. lepidiotae* (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.

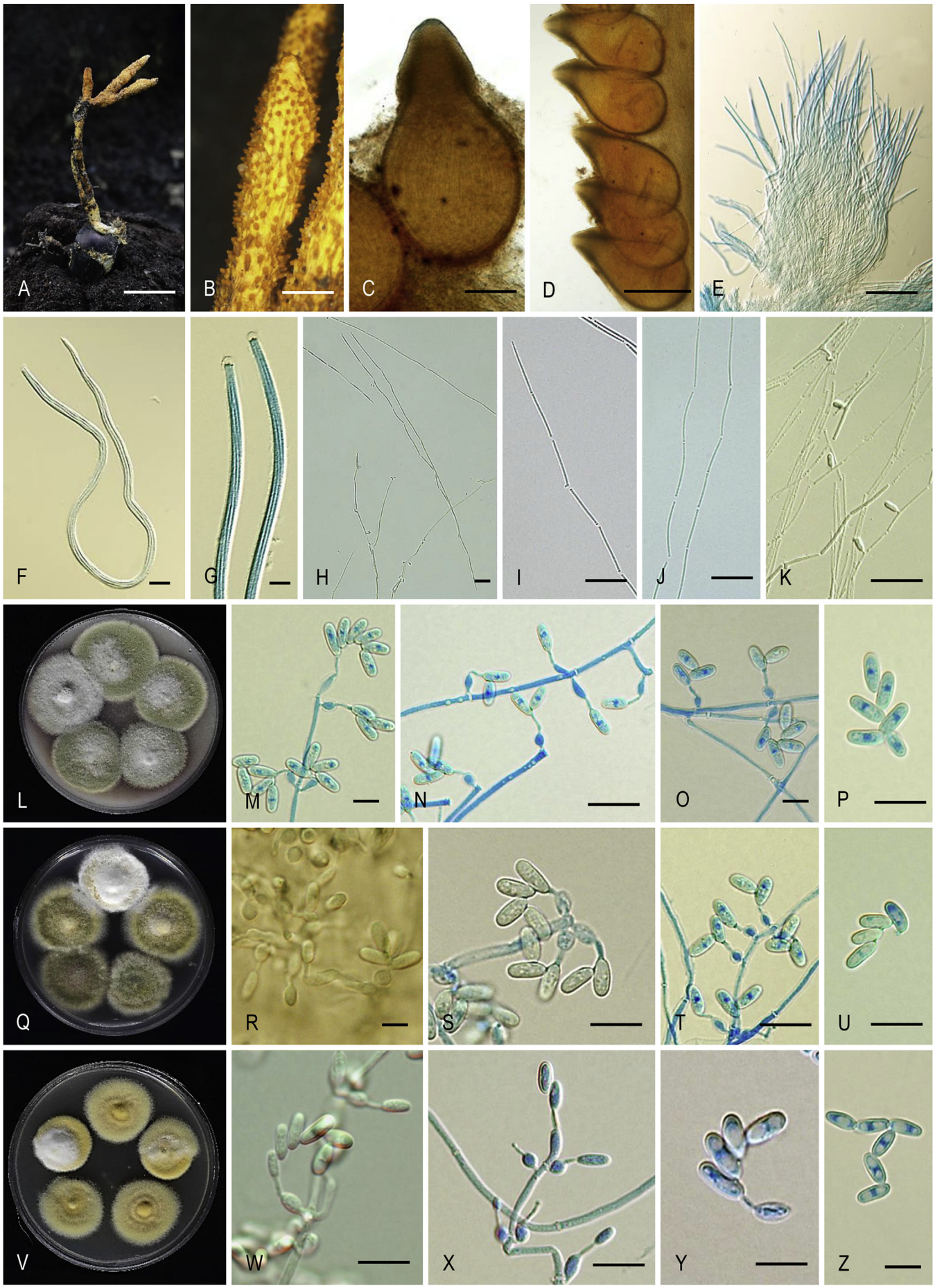

Fig. 24. *Metarhizium phuwiangense* (BBH 47443, culture ex-type BCC 85069). **A.** Stromata arising from host. **B–D.** Oblique perithecial orientation. **E.** Asci. **F.** Ascus. **G.** Asci tips. **H–J.** Ascospores showing part ascospores. **K.** microcyclic sporulation of ascospores. **L.** Colonies 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 anisopliae* f. *major* J.R. Johnst., Entomogenous Fungi of Porto Rico: 27. 1915.
Synonyms: *Metarhizium anisopliae* f. *oryctophagum* Friederichs, Die Grundfragen und Gesetzmassigkeiten der Land-und Forstwirtschäflichen Zoologie: 199. 1930.
Metarhizium anisopliae 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. anisopliae* 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, septate, 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 diam 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. *Phialides* solitary borne directly on the hyphae or on conidiophores, nomuraea-like, smooth-walled, cylindrical, (5–)5.5–7.5(–9) × 3–4 µm. *Conidia* aseptate, smooth-walled, cylindrical, ellipsoidal, usually slightly curved or allantoid, (6–)7–9(–10) × 2–3 µm.

Colonies on PDA attaining a diam of 15 mm in 14 d, mycelium floccose, cottony greyish green to dark green, margin floccose, white, reverse centre yellow to yellow brown, 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.

Typus: **Thailand**, Trang Province, Khao Ban That Wildlife Sanctuary, on adult cicada, *Megapomponia* sp., 19 Mar. 2007, K. Tasanathai, S. Mongkolsamrit, P. Srikitikulchai, R. Promharn & 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 × 3.8–4.4 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).

Typus: **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. biotecense*, 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 ovoid, 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* nomuraea-like, hyaline, smooth-walled. *Conidia* smooth-walled, dimorphic: microconidia ovoid, ellipsoidal, (3–)3.5–5(–6) × 2–3 µm; macroconidia cylindrical, (10–)12.5–18.5(–25) × 3–4 µm.

Colonies on PDA attaining a diam of 18 mm in 14 d, 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, 5 × 2 µm. *Conidia* smooth-walled, ovoid, ellipsoidal, 2–4(–5) × 2–3 µm.

Colonies on SDAY/4 attaining a diam of 15 mm in 14 d, floccose, cottony, white to cream, green edge due to production of conidia. Sporulation starts at 20 d after inoculation, reverse uncoloured. *Phialides* solitary borne directly on the conidiophores, smooth-walled, cylindrical, 4 × 2 µm. *Conidia* smooth-walled, ovoid, ellipsoidal, (2–)2.5–4(–5) × 2–3 µm.

Typus: **Thailand**, Narathiwat Province, Hala Bala Wildlife Sanctuary, on adult cicada (*Hemiptera, Cicadidae*), 9 Apr. 2012, K. Tasanathai, A. Khonsanit & W. Noisripoom (**holotype** BBH 35742 preserved in a metabolically inactive state, culture ex-type BCC 52400).

Habitat: On adult cicada (*Hemiptera*).

Known distribution: Thailand, found at Hala Bala Wildlife Sanctuary, Narathiwat Province.

Notes: *Metarhizium niveum* is closely related to *M. cylindrosporum* occurring on adult cicada and are in a cicada clade comprising *M. chaiyaphumense, M. cicadae, M. megapomponiae, M. owariense*, *M. takense* and *M. viridulum*.

Metarhizium nornnoi Luangsa-ard, Khonsanit, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834897. Fig. 22.

Etymology: Refers to the character of the host, from the Thai "nornnoi", meaning small worm.

Specimens found on *Lepidoptera* larva and *Coleoptera* adult on the leaf litter. The host's body was covered with parrot-green (No.60) powdery conidia. *Phialides* smooth-walled, cylindrical, 6–12 × 1.5–2.5 µm. *Conidia* smooth-walled, parrot-green (No.60), cylindrical, occasionally ellipsoidal, (4–)5–6.5(–8) × 1.5–2 µm.

Cultural characteristics: Colonies on OA attaining 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, parrot-green (No.60), cylindrical with rounded apices, (4–)4.5–6(–7) × 1.5–2 µm.

Colonies on PDA attaining 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 × 1.5–2 µm.

Colonies on SDAY/4 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–)5–7(–9) × 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. Thongnuch, K. Tasanathai, P. Srikitikulchai, R. Choeyklin, 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. nornnoi,* and *M. pemphigi.* This clade is subtended by *M. bibionidarum.* On PDA *M. gaoligonense, M. nornnoi* 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 nornnoi* 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 waisted conidia in *M. novozealandicum.*

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

Etymology: In reference to the predominantly ovoid shape of conidia.

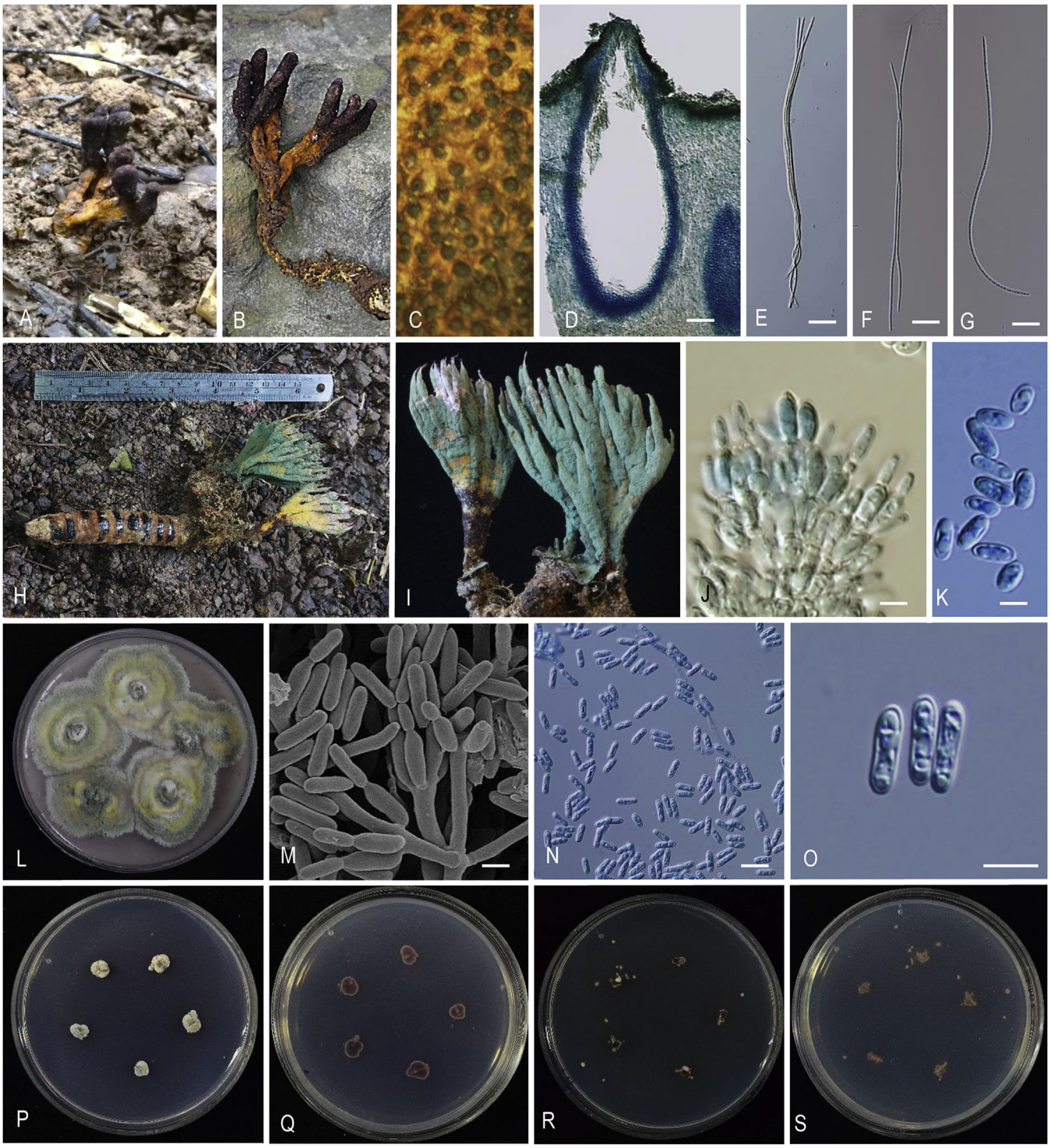

Fig. 25. *Metarhizium purpureonigrum* (BBH 47504, culture ex-type BCC 89247). **A–B.** Stromata arising from host. **C.** Part of perithecial. **D.** Immerse perithecium. Ascus. **E–G.** Ascospores. **H.** Synnemata arising from host. **I.** Green spores on synnemata. **J.** Phialides and conidia on host. **K.** Conidia on host. **L.** Colonies on OA. **M.** SEM of phialides and conidia. **N–O.** Conidia on OA. **P–Q.** Colonies on PDA. **R–S.** Colonies on SDAY/4. Scale bars: D = 70 µm; E–G = 25 µm; J, K, M, O = 5 µm; N = 10 µm.

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,

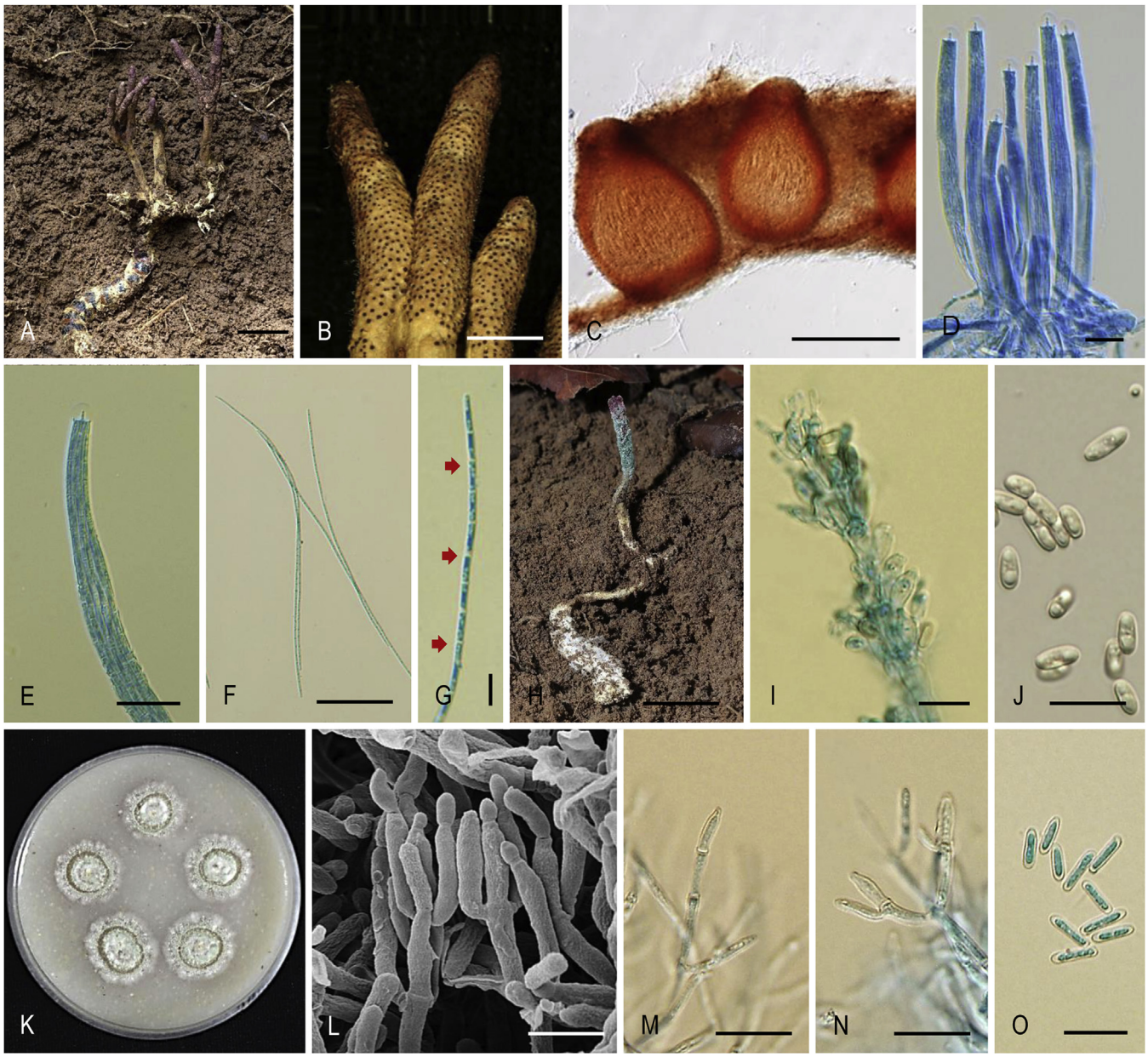

Fig. 26. *Metarhizium purpureum* (BBH 42769, culture ex-type BCC 82642). **A.** Stromata arising from *Coleoptera* larva. **B–C** Ordinal perithecial orientation. **D.** Asci. **E.** Ascus tip. **F.** Ascospores. **G.** Whole ascospore showing septa (arrows). **H.** Synnema arising from *Coleoptera* larva. **I–J.** Phialides and conidia on insect host. **K.** Colonies on OA. **L–O.** Phialides and conidia on OA. Scale bars: A, H = 2 cm; B = 2.5 mm; C = 200 µm; D = 12 µm; E, G, J, M–O = 10 µm; F = 40 µm; I, L = 5 µm.

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. Nasit & W. Chaygate (BBH8126, 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. Mongkolsamrit (BBH 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 froghoppers (*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 subglobose 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: *Cordyceps owariensis* Kobayasi, Bull. Biogeogr. Soc. Jpn. 9: 166. 1939.
Synonyms: *Ophiocordyceps owariensis* (Kobayasi) G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora, Stud. Mycol. 57: 45. 2007.
Cordyceps owariensis f. *viridescens* Uchiy. & Udagawa, Mycoscience 43: 136. 2002.
Ophiocordyceps owariensis f. *viridescens* (Uchiy. & Udagawa) G.H. Sung *et al.*, Stud. Mycol. 57: 45. 2007.
Metacordyceps owariensis f. *viridescens* (Uchiy. & Udagawa) Kepler *et al.*, Mycologia, 104: 185. 2012.
Nomuraea owariensis Uchiy. & Udagawa, 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 *Platypleura 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 (*Platypleura kuroiwae*) 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 part-spores 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. *pemphigum* Driver & R.J. Milner, Mycol. Res. 104: 144. 2000.

Typus: **UK**, Norfolk, 1975, Foster (**holotype** laboratory infected *Pemphigus bursarius* DAR 74295, culture ex-type FI-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 (*Pemphigus trehernei*), 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. nornoi.*

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 conidia. *Phialides* smooth-walled, ovoid with semi-papillate apices, cylindrical, (8–)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. *Conidia* 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. *Conidia* 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

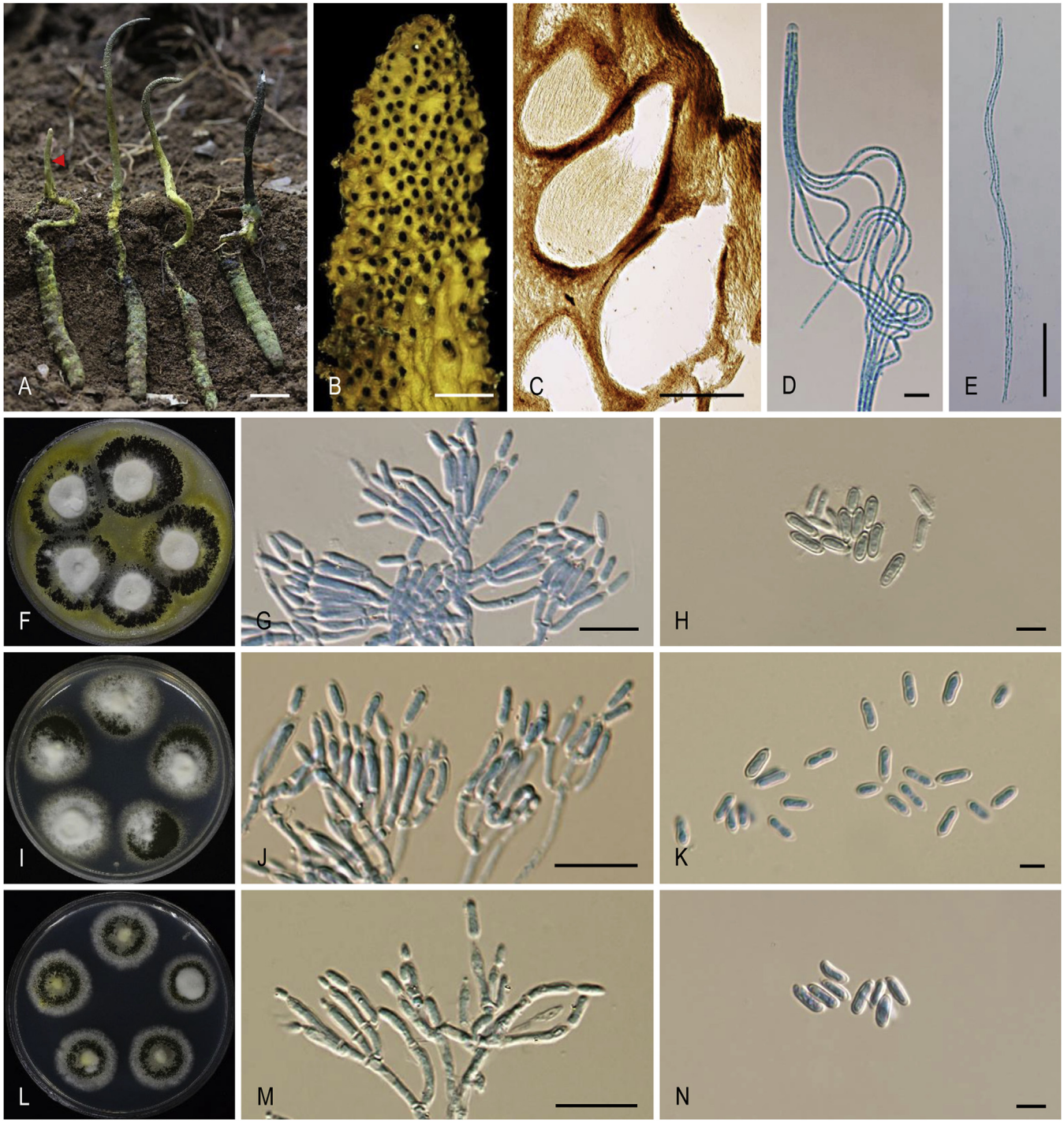

Fig. 27. *Metarhizium sulphureum* (BBH 29463, culture ex-type BCC 36592). **A.** Immature stroma (arrow) with developing and mature stromata on *Lepidoptera* larvae. **B.** Fertile head. **C.** Perithecia. **D.** Ascus and ascus cap showing ascospores inside. **E.** Ascospores. **F.** Colonies on OA 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.

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. Srikitikulchai & 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.

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. Srikitikulchai, S. Watcharapayungkit & W. Noisripoom (BBH 37785, BCC 68409); Nong Khai Province, Wat Hin Mak Peng, 17.983328 N, 102.428481 E, on stick insects, on the leaf litter, 30 Aug. 2009, K. Tasanathai, N.T. Thanh, N.T. Toan, P. Srikitikulchai & T. Chohmee (BBH 27078); Saraburi Province, Khao Yai National Park, 14.439089 N, 101.372228 E, on stick insects, on the leaf litter, 27 Aug. 2012, A. Khonsanit, D. Thanakitpipattana, J. Luangsa-ard, S. Mongkolsamrit & W. Noisripoom (BBH 32525, BCC 55003).

Notes: *Metarhizium phasmatodeae* is in a clade with *M. brachyspermum, M. indigoticum* and *M. majus. Metarhizium phasmatodeae* 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.

Etymology: 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). *Rhizoids* flexuous, 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 (oac686-687), 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 × 1–1.5 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 (oac668-669) in media. Sporulation starts at 14 d after inoculation. *Phialides* produced singly along the hyphae, not in whorls, with swollen globose basal portion, paecilomyces-like, 5–7.5(–10) × 2–3 µm, and distinct necks, (1–)1.5–3(–4) × 1 µm. *Conidia* smooth-walled, hyaline, ellipsoidal to cylindrical with rounded apices, in imbricate chains, 6–7.5(–8) × 3–3.5 µm.

Colonies on PDA attaining a diam of 20 mm in 14 d, pale green (oac874-875) to white mycelium, abundant aerial mycelium, floccose, reverse uncoloured, sporulation starts 14 d after inoculation. *Phialides* produced singly along the hyphae, not in whorls, paecilomyces-like, with swollen globose basal portion, 5–7(–10) × (2–)2.5–3(–4) µm, and distinct necks, (1–)2–3.5(–4) × 1 µm. *Conidia* smooth-walled, hyaline, ellipsoidal to cylindrical with rounded apices, in imbricate chains, (6–)6.5–8(–10) × 3–4 µm.

Colonies on SDAY/4 attaining a diam of 15 mm in 14 d, brown-orange (oac790-791) mycelium with slightly white, abundant aerial mycelium, fluffy, flat, reverse uncoloured. *Phialides* produced singly along on hyphae, not in whorls, paecilomyces-like, swollen globose basal portion, 5–8(–12) × (2–)2.5–3 µm, and distinct necks, (2–)2.5–4(–5) × 1 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. Noisripoom, W. Himaman, P. Jangsantear & B. Sakolrak (**holotype** BBH 47443 preserved in a metabolically inactive state, culture ex-type BCC 85069).

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

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

Additional materials examined: **Thailand**, Khon Kaen Province, Phu Wiang National Park, 16.681017 N, 102.237089 E, on *Coleoptera* adult, 19 Jul. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom, W. Himaman, P. Jangsantear & B. Sakolrak (BBH 47442, BCC 85068); Chaiyaphum Province, Phu Khiao Wildlife Sanctuary, 16.335569 N, 101.550539 E, on *Coleoptera* adult, 14 Aug. 2015, S. Mongkolsamrit, A. Khonsanit, W. Noisripoom, D. Thanakitpipattana, N. Kobmoo, P. Srikitikulchai, S. Wongkanoun & R. Promharn (BBH 41190, BCC 78206).

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 tettigoniid 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 whorls of 2–3 but in *M. phuwiangense* they occur singly along the mycelium. It produces a unique form of conidiogenesis 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 *Alissonotum,* (*Coleoptera, Scarabaeidae*), collection date and collector unknown (culture ex-type CBS 257.90).

Habitat: *Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Isoptera, 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 *pingshaense, anisopliae, robertsii, 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 Luangsa-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 Luangsa-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. *Asci* hyaline, cylindrical, 100–271 × 3–5 µm, apical cap prominent, 1 × 2 µm. *Ascospores* filiform, 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.

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 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 SDAY/4 attaining a diam of 10 mm in 10 d, at first white turning sulphur yellow (No.57) in center of colony due to the production of conidia. 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. Srikittikulchai, A. Khonsanit & W. Noisripoom (**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, 14.439089 N, 101.372228 E, on *Lepidoptera* larva, 12 May 2011, J. Luangsa-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 Luangsa-ard, Tasanathai, Thanakitpipattana & 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. *Asci* 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. Thanakitpipattana, 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. Thanakitpipattana, B. Sakolrak, R. Somnuk, S. Mongkolsamrit, W. Noisripoom & W. Himaman (BBH 44518, BCC 89248), (BBH 47505, BCC 89324), (BBH 43816, BCC 89249), (BBH 43814, BCC 89250).

Notes: Phylogenetically *M. purpureonigrum* is closely related to *M. purpureum* and *M. flavum* but differs in the colour of its stromata in specimens producing the sexual morph. *Metarhizium purpureonigrum* and *M. purpureum* have purple 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 Luangsa-ard, Mongkolsamrit, Lamlertthon, Thanakitpipattana & Samson, ***sp. nov.*** MycoBank MB834900. Fig. 26.

Etymology: Refers to the purple colour of stromata 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. *Perithecia* 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. *Ascospores* filiform, with septa but do not dissociate into partspores, 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 conidiophores. 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 diam 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. Thanakitpipattana, W. Noisripoom, R. Somnuk, P. Srikitikulchai, S. Wongkanoun & S. Lamlertthon (**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. Thanakitpipattana, W. Noisripoom, R. Somnuk, P. Srikitikulchai, S. Wongkanoun & S. Lamlertthon (BBH 42769, BCC 82642), (BBH 41293, BCC 82173); *idem*., 27 Sep. 2016, J. Luangsa-ard, S. Mongkolsamrit, D. Thanakitpipattana, R. Somnuk, W. Noisripoom & S. Lamlertthon (BBH 41815, BCC 83548).

Notes: In sexual morph specimens found in nature, *M. purpureum* is mostly similar to *M. purpureonigrum* by producing multiple purple stromata and perithecia that are ordinal in arrangement. The perithecia and asci 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) Luangsa-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 conidiogenous 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* (NHJ00855.01, 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.

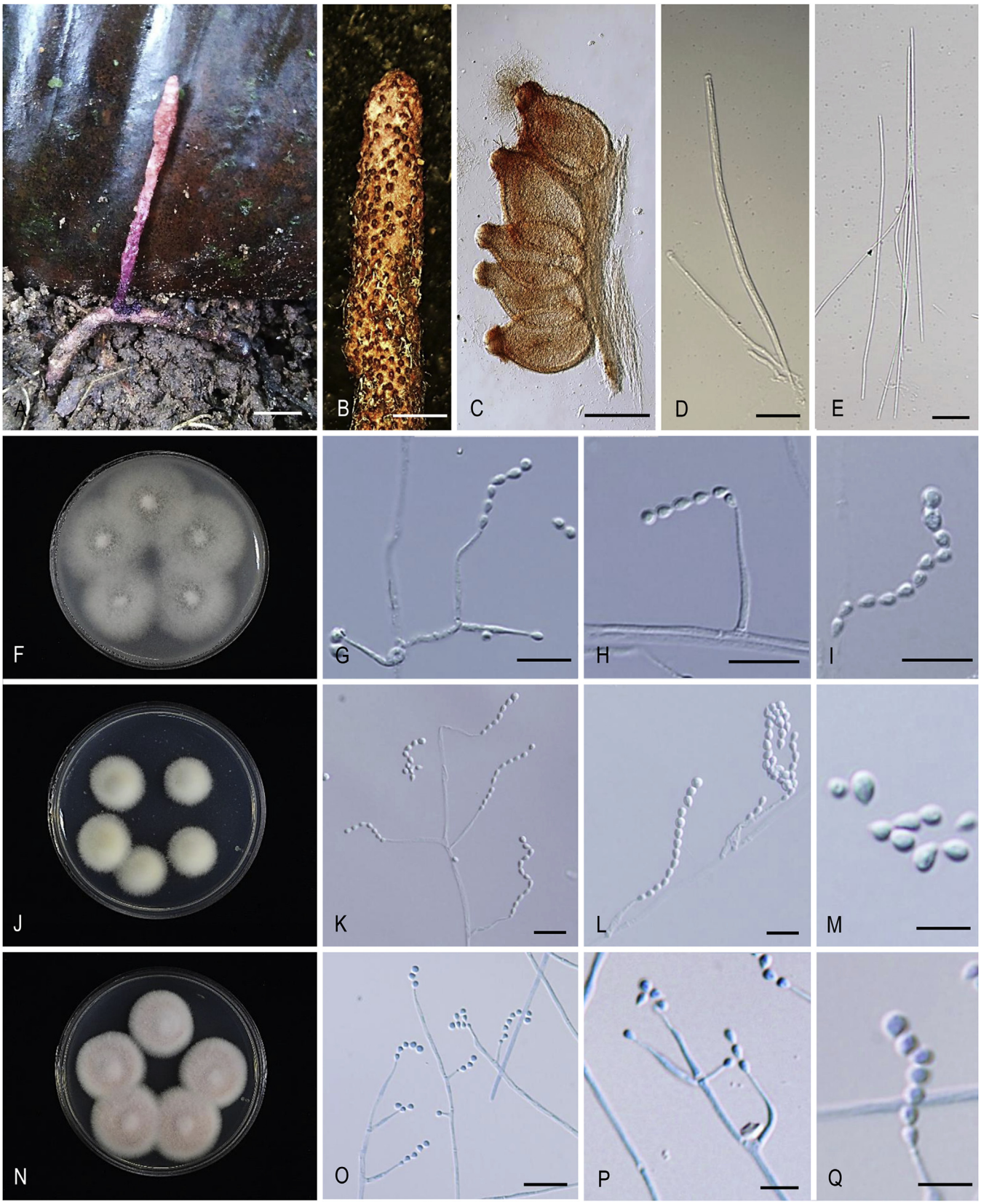

Fig. 29. *Purpureomyces maesotensis* (BBH 44500, culture ex-type BCC 89300). **A–B.** Stroma arising from *Lepidoptera* larva. **C.** Perithecia. **D.** Asci. **E.** Whole ascospores. **F.** Colonies on OA. **G–I.** Phialides and conidia on OA. **J.** Colonies on PDA. **K–M.** Phialides and conidia on 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.

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

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 I91-613).

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). *Conidiophores* arising from aerial mycelia, erect, smooth-walled, cylindrical. *Phialides* smooth-walled, ovoid, occasionally subglobose and cylindrical, (4–)4.2–6(–8) × 2–3.5 µm. *Conidia* smooth-walled, peacock-green (No.162C), globose, (3–)3.4–4(–4.5) µm.

Colonies on PDA attaining a diam of 23–24 mm in 14 d, flat, closely appressed to the agar surface, at first white turning Paris green (No.63), powdery while sporulating, forming a basal felt bearing densely packed, floccose at the margin. Sporulation starts at 3 d after inoculation, reverse yellowish olive-green (No.50), olive yellow (No.52) in the middle of colony and lime green (No.59) 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, Paris green (No.63), globose, 3–4 µm.

Colonies on SDAY/4 attaining a diam of 18 mm in 14 d, flat, closely appressed to the agar surface, at first white turning to sulfur yellow (No.157) 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. Mongkolsamrit (**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. Ridkaew (BBH 27086, BCC 39752), (BBH 27087, BCC 39753), (BBH 27089, 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, Thanakitpipattana & 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,

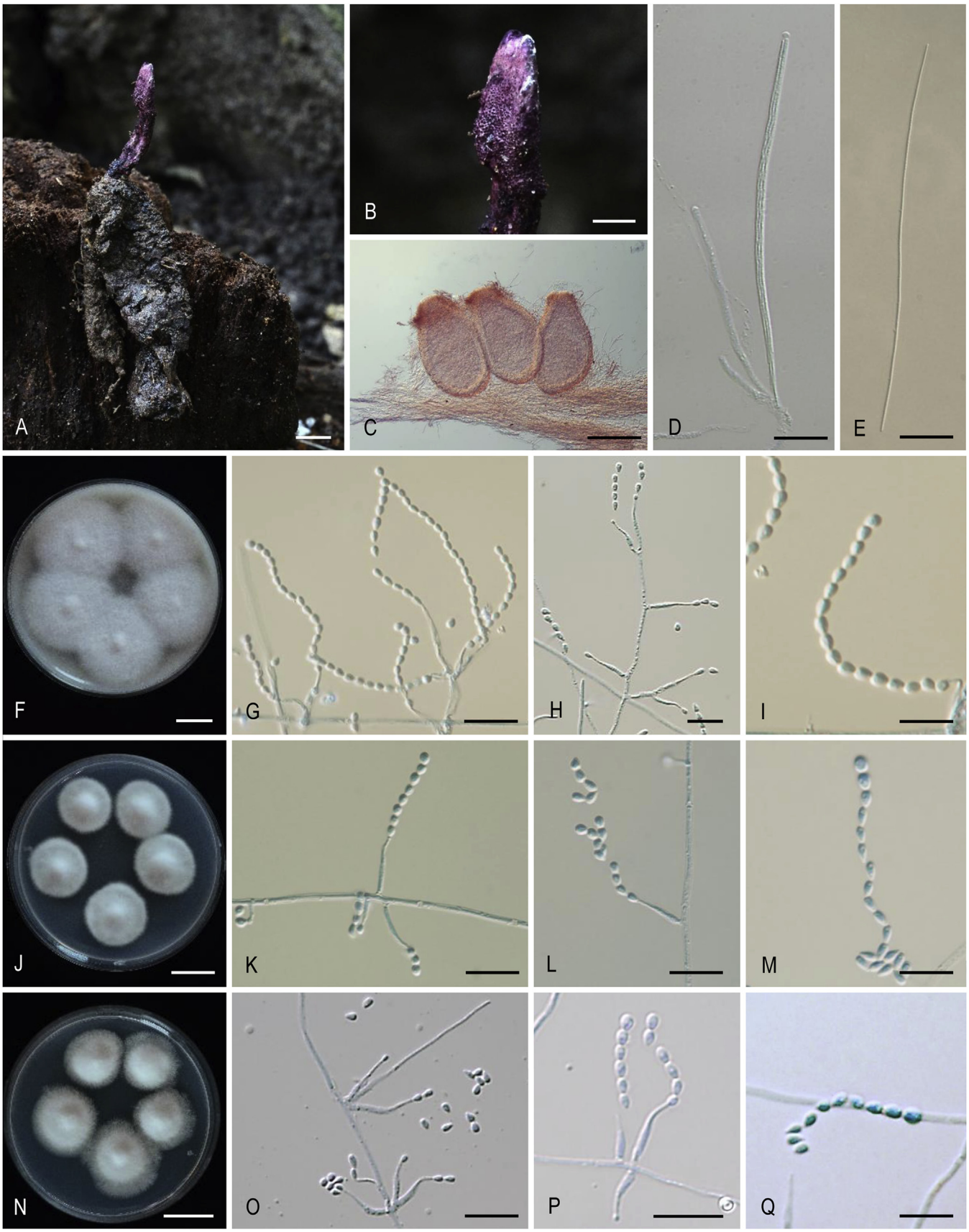

Fig. 30. *Purpureomyces pyriformis* (BBH 43364, culture ex-type BCC 85074). **A–B.** Stroma arising from *Lepidoptera* pupa. **C.** Perithecia. **D.** Asci. **E.** Whole ascospore. **F.** Colonies on OA. **G–I.** Phialides and conidia on OA. **J.** Colonies on PDA. **K–M.** Phialides and conidia on PDA. **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 hosts' bodies were covered with apple-green (No.61), Paris-green (No.63) mycelium. *Perithecia* semi-immersed, oblique in arrangement, ovoid, dark ostioles, 600–700 × 420–450 µm. *Asci* cylindrical, 300–420 × 3–6 µm. *Asci caps* rounded, 5 × 5 µm. *Ascospores* hyaline, filiform, 200–300 × 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, Khao Yai National Park, on *Lepidoptera* larva, 21 May 2009, K. Tasanathai, P. Puyngain, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & T. Chohmee (**holotype** BBH 29463 preserved in a metabolically inactive state, culture ex-type BCC 36592).

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

Known distribution: Thailand, found only in Khao Yai National Park.

Additional materials examined: **Thailand**, Nakhon Ratchasima Province, Khao Yai 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. Mongkolsamrit & T. Chohmee (BBH 26200, BCC 36568); *idem*., 20 May 2009, K. Tasanathai, P. Puyngain, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & T. Chohmee (BBH 26213, BCC 36585); *idem*., 13 Sep. 2009, K. Tasanathai, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit & 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. campsosterni, M. clavatum, M. guizhouense* (*M. taii*), *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. campsosterni, 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 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, 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. Mongkolsamrit, P. Srikittikulchai, 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. Mongkolsamrit, P. Srikittikulchai, 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 grayish 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 (Luangsa-ard *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, Mycosystema 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 diam 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 diam 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 SDAY/4 attaining a diam 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* (*Hemiptera*), 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 Khao Luang National Park.

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

Notes: *Metarhizium viridulum* is closely related to *M. megapomponiae* 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. megapomponiae* (6–11 × 3–5 µm). This is the first report of *M. viridulum* in Thailand.

Papiliomyces Luangsa-ard, 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.*) Luangsa-ard, 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.*) Luangsa-ard, Samson & Thanakitpipattana, ***comb. nov.*** MycoBank MB834903.
Basionym: Cordyceps liangshanensis M. Zang *et al.*, Acta Bot. Yunn. 4: 174. 1982.

Synonym: *Metacordyceps liangshanensis* (M. Zang *et al.*) G.H. Sung *et al.*, Stud. Mycol. 57: 35. 2007.

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

Typus: **China**, Sichuan, Liangshan, on *Lepidoptera* larva in a bamboo forest *Phyllostachydis pubescentibus* 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 part-spores while the latter produces whole filiform 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–)6–13.5(–18) × 1–2 µm. *Conidia* in long chains, hyaline, ovoid, 2–3(–3.5) × (1–)1.5–2 µm.

Colonies on SDAY/4 attaining a diam of 16–20 mm in 7 d, white to creamy, cottony, dense mycelium. Colonies reverse robin 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, Khao Yai National Park, on *Lepidoptera* larva, in leaf litter, 14 Apr. 1997, N.L. Hywel-Jones **(holotype** NHJ 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. Tasanathai, P. Srikitikulchai & A. Khonsanit (BBH 30160, BCC 44287); *idem*., 5 Oct. 2012, K. Tasanathai, A. Khonsanit, W. Noisripoom, P. Srikitikulchai & R. Promharn (BBH 32908, BCC 55765), (BBH 32909, BCC 55766); *idem*., 29 Oct. 2012, K. Tasanathai, A. Khonsanit, W. Noisripoom, D. Thanakitpipattana, P. Srikitikulchai & 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, 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* (stroma 55 mm long, cylindrical asci 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, Himaman, 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 whorls 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 whorls 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 whorls 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, 16.681017 N, 102.237089 E, on *Lepidoptera* pupa, buried in the ground, 19 Jul. 2017, K. Tasanathai, S. Mongkolsamrit, W. Noisripoom, W.

Himaman, P. Jangsantear & B. Sakolrak (MY11732, BCC 85348), (BBH 43359, BCC 85349).

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 olive 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, perithecia, asci 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 asci 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, pochonia-like. *Conidia* in slimy heads, elliptical to oblong, hyaline. *Chlamydospores* present, cylindrical to subglobose, submerged in agar.

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

Notes: This genus 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 chlamydosporia* in the shape of perithecia and the pochonia-like asexual morph.

Typus: **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: *Stroma* 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).

Typus: **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 the 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), Yamamoto *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. khaoyaiense* in *Purpureomyces, M. kusanagiense* in *Yosiokobayasia, M. marquandii* in *Marquandomyces, Mc. liangshanens* and *Mc. 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. chaiyaphumense, 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. campsosterni* (Zhang *et al.* 2004) and *M. phuwiangense* (this study).

Species in *Purpureomyces* whose type species *Purpureomyces khaoyaiensis* 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 *Mc. liangshanensis* and *Mc. shibinensis* to *Papiliomyces*; *M. yongmunense* to *Sungia*; *M. kusanagiense* to *Yosiokobayasia*. 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 barks 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 saprobic 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.

Habitats

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, Luangsa-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 nomuraea-like, paecilomyces-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 (GCPSR) 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. khaoyaiense, 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. brittlebankisoides,* and *M. campsosterni,* as members of the *M. anisopliae* complex on the basis of their asexual morph 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. acridum, M. alvesii, M. anisopliae, M. baoshanense, M. brachyspermum, M. brittlebankisoides, M. brunneum, M. campsosterni, M. clavatum, M. globosum, M. gryllidicola, M. guizhouense, M. humberi, M. indigoticum, 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. brittlebankisoides*, *M. campsosterni, M. clavatum*, *M. guizhouense, M. indigoticum, 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 Metchnikoff's *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 5′*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. biotecense, M. blattodeae, M. culicidarum, M. flavoviride, M. frigidum, M. fusoideum, M. gaoligongense, M. koreanum, M. minus, M. nornnoi* 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. ellipsoideum* and *M. huainamdangense.* Nomuraea-like and paecilomyces-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 paecilomyces-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, Dinidoridae, 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-kingkom host jumps (Nikoh & Fukatsu 2000, Sung *et al.* 2007). In the *Clavipitaceae* 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 (Nourrisson *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. campsosterni*
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. kalasinense*
13. *M. owariense*
14. *M. phuwiangense*
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-spores.

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-spores.....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……2
1b. Ascospores dissociate into part-spores……5

2a. Ascospores lanceolate with tapering ends……3
2b. Ascospores filiform……4

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, ordinally 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, ordinally immersed perithecia, metarhizium-like phialides, on *Coleoptera* larva, stromata 100 –150 mm long……***M. purpureonigrum***
4d. Ascospores 160–240 × 1.5–2 µm, ordinally 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, ordinally semi-immersed perithecia, metarhizium-like phialides, on *Coleoptera* larva, stromata up to 45 mm long……***M. flavum***
4h. Ascospores 222.5–360 × 1 µm, ordinally 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, ordinally immersed perithecia, metarhizium-like phialides, on *Coleoptera* larva (*Scarabaeidae*), stromata 160 mm long……***M. campsosterni***
5b. Part-spores cylindrical, 4.5–5 × 1 µm, obliquely immersed, 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. owariense***
5d. Part-spores cylindrical, 5.7–8.1 × 0.94 µm, ordinally 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……7
(*M. acridum, M. album, M. alvesii, M. anisopliae, M. argentinense, M. baoshanense, M. bibionidarum, M. biotecense, M. blattodeae, M. brasiliense, M. brunneum, M. candelabrum, M. cercopidarum, M. culicidarum, M. ellipsoideum, M. flavoviride, M. frigidum, M. fusoideum, M. gaoligongense, M. globosum, M. gryllidicola, M. huainamdangense, M. humberi, M. koreanum, M. lepidiotae, M. majus, M. minus, M. nornnoi, M. novozealandicum, M. pemphigi, M. phasmatodeae, M. pingshaense, M. purpureogenum, M. robertsii*)
6b. Nomuraea-like phialides……8
(*M. cicadae, M. cylindrosporum, M. dendrolimatilis, M. megapomponiae, M. niveum, M. ovoidosporum, M. rileyi, M. samlanense, M. viridulum*)

6c. Paecilomyces-like phialides……..9
(*M. granulomatis, M. reniforme, M. viride*)

7a. on multiple hosts……..10
(*M. anisopliae, M. bibionidarum, M. brunneum, M. flavoviride, M. frigidum, M. fusoideum, M. humberi, M. lepidiotae, M. majus, M. minus, M. nornnoi, M. novozealandicum, M. pemphigi, M. pingshaense, M. robertsii*)
7b. on cockroaches (*Blattodea*)……11
(*M. argentinense, M. blattodeae*)
7c. on *Diptera*……..12
(*M. culicidarum*)
7d. on *Hemiptera* (small hoppers: *Cicadellidae*, *Cercopidae*, *Delphacidae*)……13
(*M. album, M. biotecense, M. brasiliense, M. candelabrum, M. cercopidarum, M. ellipsoideum, M. huainamdangense, M. koreanum*)
7e. on *Lepidoptera* larva and pupa……..14
(*M. globosum*)
7f. on *Orthoptera*……15
(*M. acridum, M. gryllidicola* on adult crickets, *M. phasmatodeae* on stick insects)
7g. on soil……16
(*M. alvesii, M. baoshanense, M. gaoligongense, M. purpureogenum*)
8a. on *Lepidoptera* larva……17
(*M. dendrolimatilis*)
8b. on *Hemiptera* (cicada nymphs and adults)……..18
(*M. cicadae, M. cylindrosporum, M. megapomponiae, M. niveum, M. viridulum*)
8c. on *Hemiptera* (small hoppers)……19
(*M. ovoidosporum, M. samlanense*)
8d. on *Lepidoptera* larva, mostly from agricultural plots, not from forests……***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 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. fusoideum***
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. nornnoi***
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, olivaceus green colony (on PDA)……***M. argentinense***

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

13a. Conidia ellipsoid, cylindrical, 5–6 × 1.5–2 µm, pale brown colony……***M. album***
13b. Conidia cylindrical, ellipsoid, 5–7 × 2–3 µm, white colony……***M. biotecense***
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. huainamdangense***
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***

16a. Conidia cylindrical, 3.88–6.55 × 2.16–3.25 µm, yellow to greenish colony……***M. alvesii***
16b. Conidia long oval, cylindrical, 6.7–8.5 × 2.6–3.3 µm, greyish green colony (on PDA)……***M. baoshanense***
16c. Conidia cylindrical, 5.4–7.7 × 1.9–2.8 µm, green colony (on PDA)……***M. gaoligongense***
16d. Conidia ovoid to ellipsoid, 4.5–5.5 × 3.5–4 µm, pale ochre or tan colony……***M. purpureogenum***

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

18a. Conidia two types of conidia; ovoid, ellipsoid, 2–6 × 2.5–4 µm; cylindrical, 10–17 × 3–4 µm, dark green colony…***M. cicadae***
18b. Conidia two types of conidia; ovoid, subglobose, 3–8 × 2–3 µm; cylindrical, 14–22 × 3–4 µm, pale yellow colony……***M. cylindrosporum***
18c. Conidia cylindrical, ellipsoid, 7–11 × 3–4 µm, cream to yellow brown colony……***M. megapomponiae***
18d. Conidia ovoid, ellipsoid, 2–5 × 2–3 µm, white to cream colony……***M. niveum***
18e. Conidia cylindrical, 10–16 × 3–4 µm, pale yellow colony……***M. viridulum***

19a. Conidia ovoid, ellipsoid, subglobose, 3–5 × 2–4 µm, olive yellow colony……***M. ovoidosporum***
19b. Conidia globose, 3–5 µm, sulphur yellow to straw yellow colony……***M. samlanense***

ACKNOWLEDGEMENTS

This work is dedicated to Keith A. Seifert 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 Biotechnology (BIOTEC), Grant No. P19-50231 for their support of the 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 Samret Phusaensri (Head of Phu Wiang National Park), Sangaon Veeraping (Village headman of Banphao Thai community forest, Phitsanulok Province) for their cooperation and support of our project research. We thank Thayarat Chaitika, Aundaman Moulchoo for their help in generating molecular data and Kewarin Klamchao for insect identification. We thank USDA ARSEF (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.

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