

Five New Species of *Moelleriella* With *Aschersonia*-like Anamorphs Infecting Scale Insects (Coccidae) in Thailand

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Abstract

The genus *Moelleriella* and its aschersonia-like anamorph mostly occur on scale insects and whiteflies. It is characterized by producing brightly colored stromata, obpyriform to subglobose perithecia, cylindrical asci, disarticulating ascospores inside the ascus and fusiform conidia, predominantly found in tropical and occasionally subtropical regions. From our surveys and collections of entomopathogenic fungi, scale insects and whiteflies pathogens were found. Investigations of morphological characters and multi-locus phylogenetic analyses based on partial sequences of LSU, *TEF* and *RPB1* were made. Five new species of *Moelleriella* and their aschersonia-like anamorphs are described here, including *M. chiangmaiensis*, *M. flava*, *M. kanchanaburiensis*, *M. nanensis* and *M. nivea*. They were found on scale insects, mostly with flat to thin, umbonate, whitish stromata. Their anamorphic and teleomorphic states were mostly found on the same stroma, possessing obpyriform perithecia, cylindrical asci with disarticulating ascospores. Their conidiomata are widely open with several locules per stroma, containing cylindrical phialides and fusiform conidia. However, some specimens of *M. chiangmaiensis* produce hat-shaped stromata apart from the commonly found umbonate stromata, while *M. flava* had yellow stromata with one conidioma per stroma, and *M. kanchanaburiensis* was found only in its anamorphic state. Furthermore, the perithecia of *M. nanensis* were completely embedded in stromata as opposed to other species with semi-immersed perithecia. We also found a teleomorph link to *M. sinensis*, an anamorphic species reported from southeastern China.

Introduction

The entomopathogenic genus *Moelleriella* Bres. (Clavicipitaceae, Hypocreales, Ascomycota) was separated from allied genera of *Aschersonia* Montagne, *Conoideocrella* D. Johnson, G.H. Sung, Hywel-Jones & Spatafora, *Helicocollum* Luangsa-ard, Mongkolsamrit, Noisripoom & Thanakitpipattana, *Orbiocrella* D. Johnson, G.H. Sung, Hywel-Jones & Spatafora, *Regiocrella* P. Chaverri & K.T. Hodge and *Samuelsia* P. Chaverri & K.T. Hodge (Montagne 1848, Chaverri et al. 2005a, Chaverri et al. 2008; Johnson et al. 2009; Luangsa-ard et al. 2017). *Moelleriella* and *Samuelsia* produce aschersonia-like anamorphs (Chaverri et al. 2008; Tadych et al. 2009; Mongkolsamrit et al. 2015). *Moelleriella* species can be recognized with teleomorphs having ascospores disarticulating into part-spores (Chaverri et al. 2008; Mongkolsamrit et al. 2015), whereas *Samuelsia* produce filiform with multiseptate ascospores. The anamorph in *Moelleriella* produce fusiform conidia while in *Samuelsia* only small allantoid conidia are found (Chaverri et al. 2008; Tadych et al. 2009; Mongkolsamrit et al. 2011a, b). Species found in teleomorphs state of *Aschersonia* (*Hypocrella*) producing whole ascospores, apart from its conidial state (Montagne 1848; Saccardo 1878; Petch 1921; Hywel-Jones and Evans 1993; Hywel-Jones and Samuels 1998; Chaverri et al. 2008; Mongkolsamrit et al. 2009, 2015).

The genus *Moelleriella* is recognized by the brightly colored stromata on scale insects (Coccidae, Lecaniidae) and whiteflies (Aleyrodidae) (Chaverri et al. 2008; Tadych et al. 2009; Mongkolsamrit et al. 2011b, 2015). Its species were commonly found in tropical and occasionally in subtropical regions (Montagne 1848; Petch 1921, 1925, 1931; Mains 1959a, 1959b; Hywel-Jones and Evans 1993; Hywel-Jones and Samuels 1998; Chaverri et al. 2008; Tadych et al. 2009; Qiu et al. 2009, 2010; Mongkolsamrit et al. 2011a, 2011b, 2015) as biotrophic parasites of plants (Tadych et al. 2009). In Thailand, nine known species were reported, including *M. alba*, *M. chumphonensis*, *M. javanica*, *M. phukhiaoensis*, *M. pongdueatensis*, *M. raciborskii*, *M. reineckeana*, *M. schizostachyi* and *M. thanathonensis* (Hywel-Jones and Samuels 1998; Luangsa-ard et al. 2008, 2012; Mongkolsamrit et al. 2010, 2015, Li et al. 2016, Tibpromma et al. 2017).

From our surveys of entomopathogenic fungi on scale insects and whiteflies in Thailand specimens were mostly found on the underside of leaves (abaxial surface), occasionally found on its upper side (adaxial surface). Eighteen strains of Thai *Moelleriella* species were studied to clarify the relationships of these collections by using morphological characters and multi-locus phylogenetic analyses to known members of Clavicipitaceae and describe the new taxa to accommodate species diversity in *Moelleriella*.

Materials And Methods

Collections and isolation

Moelleriella specimens attached to the upper side and underside of leaves were collected from national parks, wildlife sanctuary in Thailand throughout the year from 2005-2014. The specimens were separated and placed in plastic boxes (3×6 cm or 6×10 cm) before returning to the laboratory for isolation. Fresh materials were examined and isolated in pure cultures from both the teleomorph and anamorph following the techniques described by Mongkolsamrit et al. (2009).

Morphological observations

For morphological observations, the samples were photographed in the field by using a digital Nikon D5100 camera, or in the laboratory using an Olympus DP70 Digital Camera installed on an Olympus SZX12 stereo microscope. Pure cultures on PDA were photographed using a digital Nikon D5100 camera. The Sixth Royal Horticultural Society (R.H.S.) color chart was used to characterize the colors of fresh specimens and cultures. To observe internal characteristics of the stromata, such as conidiomata and perithecia, sections were made using a cryostat rotary microtome (SLEE.MEV). The micro-morphological characteristics such as phialides, paraphyses, conidia, asci, asci caps and part-spores were mounted with lactophenol or lactophenol cotton blue solution and observed using an Olympus CH40 compound microscope for measurements, measuring the size with a minimum sampling size 5-10 (for conidiomata and perithecia) to 50–100 (for phialides, conidia, asci, asci caps and part-spores), and the average size was calculated to mean ± standard deviation values. Photographs of the micro-morphological characters were done using a DP70 digital camera installed on an Olympus BX51 compound microscope.

DNA extraction, PCR amplification and sequencing

Total DNA was extracted from mycelial mass harvested on PDA using a modified cetyltrimethyl-ammonium bromide (CTAB) method as previously described in Khonsanit et al. (2020). Four nuclear loci, including the nuclear ribosomal internal transcribed spacer (ITS),

the large subunit of the ribosomal DNA (LSU), translation elongation factor-1 α gene (*TEF*) and the partial regions of the RNA polymerase II largest (*RPB1*), were sequenced. The primer pairs and thermocycler conditions for PCR amplifications used in this study followed the protocol described in Mongkolsamrit et al. (2018). The purified PCR products were sequenced with PCR amplification primers for Sanger dideoxy sequencing.

Phylogenetic analyses

The generated DNA sequences in this study were checked for ambiguous bases using BioEdit (Hall 2013) and then submitted to GenBank. Sequences of ITS, LSU, *TEF* and *RPB1* of other taxa for the analyses were taken from previous studies as shown in Table 1. ITS sequences were considered only for barcoding purposes and not included in the multigene analyses. The phylogenetic analyses were performed using Maximum likelihood (ML) and Bayesian inference (BI). The ML analysis was performed with RAxML v. 8.2.12 (Stamatakis 2014) using GTR-GAMMA model of evolution with 1000 bootstrap replicates. The BI analysis was performed using MrBayes v.3.2.7a (Ronquist et al. 2012) with GTR model. Four Markov chains were run from random starting trees for five million generations using sampled frequency of 100 generations and a burn-in of 10% from the total run. RAxML and BI were run on XSEDE in CIPRES portal (www.phylo.org). Phylogenetic trees were visualized in TreeView v.1.6.6 (Page 1996).

Results

Phylogenetic analyses

The strains of *Moelleriella* (18 strains for LSU, 17 strains for *TEF* and 15 strains from *RPB1*) were included in the phylogenetic analyses. A phylogenetic tree using a combined dataset of seventy specimens including allied genera, such as *Aschersonia*, *Conoideocrella*, *Helicocollum*, *Orbiocrella*, *Regiocrella* and *Samuelsia* with *Purpureocillium lilacinum* (CBS 431.87), *P. lilacinum* (CBS 284.36) as outgroup is shown in Fig. 1.

The numbers on the branches represent bootstrap values from the RAxML analysis and posterior probability from the Bayesian inference. The results revealed that seven major clades representing various genera found in Clavicipitaceae, such as *Aschersonia*, *Conoideocrella*, *Helicocollum*, *Moelleriella*, *Orbiocrella*, *Regiocrella* and *Samuelsia* are independently formed. The *Moelleriella* clade segregated into two distinct clades, Clade A and Clade B. Clade A segregated into two sister clades, subclade I and subclade II. Clade A subclade I includes five new species, namely *M. chiangmaiensis*, *M. flava*, *M. Kanchanaburiensis*, *M. nanensis* and *M. nivea*, and seven known species, viz. *M. gracilispora*, *M. mollii*, *M. ochracea*, *M. phukhiaoensis*, *M. pongdueatensis*, *M. sinensis* and *M. zhongdongii*. Most of the species in subclade I were from the Old World (OW), except *M. ochracea* and *M. zhongdongii* that were found from the New World (NW). Clade A subclade I species have mostly flattened stromata, except for *M. pongdueatensis* and *M. zhongdongii* with stud-shaped and thick-pulvinate stromata, respectively. Most species in subclade I have whitish stromata, except *M. flava*, *M. phukhiaoensis* and *M. pongdueatensis* which have pale yellow to yellow stromata. Subclade II includes ten known species, seven of which were found in the NW, namely *M. basicystis*, *M. disjuncta*, *M. evansii*, *M. libera*, *M. phyllogena*, *M. rhombispora* and *M. umbospora*. Only three were found from the OW, such as *M. alba*, *M. chumphonensis* and *M. raciborskii*. Five species in subclade II produce perithecia in tubercles, viz. *M. alba*, *M. chumphonensis*, *M. evansii*, *M. libera* and *M. raciborskii*, while other species have semi-immersed to immersed perithecia in stromata, such as *M. basicystis*, *M. disjuncta*, *M. phyllogena*, *M. rhombispora* and *M. umbospora*. Furthermore, most of the species in this subclade II have pale yellow to yellow stromata, except for *M. alba* with whitish stromata. Clade B includes nine known species with fully embedded perithecia, the species in this clade can be found both in the OW (*M. africana*, *M. insperata*, *M. reineckiana*, *M. schizostachyi*) and the NW (*M. boliviensis*, *M. epiphylla*, *M. macrostroma*, *M. sloanae*, *M. turbinata*). Additionally, the phylogenetic analyses of our study revealed that the species in each clade show no correlation to the different geographic areas.

Taxonomy

Moelleriella chiangmaiensis Khonsanit, Noisripoom, Phosrithong & Luangsa-ard, **sp. nov.** Fig. 2

MycoBank. MB835903

Anamorph. *Aschersonia*-like.

Etymology. Refers to the locality where the type specimen was found, Chiang Mai Province.

Typification. THAILAND. Chiang Mai Province, Doi Inthanon National Park, KM. 25 Nature Trail; 18°35'15.66"N, 98°29'11.69"E; on scale insect (Coccidae) found on the underside of dicotyledonous leaves; 30 Jun. 2005; B. Thongnuch, K. Tسانathai, N. Boonyuen, P. Srikikulchai, R. Ridkaew, S. Mongkolsamrit, W. Chaygate (holotype BBH13024, ex-type living culture BCC18029)

Description. *Anamorphic stromata* convex, flattened, globose to subglobose, hat-shaped, raised, 1-7 mm in diam, white, pale greenish yellow (160C) to moderate yellow (160A) conidial masses. *Conidiomata* scattered, irregularly in shaped, widely open orifice, rim around the orifice thick and raised, 400-500 × 150-270 µm. *Phialides* hyaline, cylindrical, (8-)9.5-15(-20) × 1-2 µm. *Conidia* hyaline, (7-)8-10(-11) × 1.5-2 µm. *Paraphyses* present, hyaline, filiform, up to 130 µm long, 1-1.5 µm wide. *Teleomorphic stromata* thin-umbonate, raised, with globose to subglobose base, 4-7 mm diam, white to moderate yellow (162A). *Perithecia* semi-embedded in stromata, most perithecia fused together, occasionally developing singly in stromata, numerous perithecia per stroma (≤10), obpyriform, 450-500 × 260-360 µm. *Ostioles* deep orange yellow (163A). *Asci* hyaline, cylindrical, (102-)120-167(-220) × (4-)4.5-6.5(-7) µm. *Asci caps* convex, 2 × 4 µm. *Ascospores* hyaline,

disarticulating into part-spores, cylindrical with rounded ends, (7-)9-11(-12) × 1-2 µm. The teleomorph and anamorph could be present in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, convex to pulvinate, attaining a diam of 8-10 mm in 2 wk, white, pale yellow green (155A) conidial masses covering stromatic colonies. Colony reverse brownish orange (164A), pale yellow (164D) at the margins.

Habitat. On scale insects (Coccidae) found on the underside of dicotyledonous leaves.

Additional specimens examined. THAILAND, Chiang Mai Province, Doi Inthanon National Park, KM. 25 Nature Trail; 18°35'15.66"N, 98°29'11.69"E; on scale insects (Coccidae) found on the underside of dicotyledonous leaves; 30 Jun. 2005; B. Thongnuch, K. Tasanathai, N. Boonyuen, P. Srikitikulchai, R. Ridkaew, S. Mongkolsamrit, W. Chaygate (BBH13024, BCC18030, BCC18031, BCC18064); Krabi Province, Jiranan Techaprasan's house (Thap Prik); 8°10'53.31"N, 98°52'38.66"E; on scale insects (Coccidae), found on the underside of plant leaves (Poaceae); 12 Dec. 2012; J. Techaprasan (BBH33051); on scale insect (Coccidae) found on the underside of dicotyledonous leaves; 1 Jan. 2013; J. Techaprasan (BBH33697); Nakhon Ratchasima Province, Khao Yai National Park, Pha Kluaimai Waterfall Nature Trail; 14°26'21.46"N, 101°22'20.20"E; on scale insects (Coccidae) found on the underside of dicotyledonous leaves; 10 Jan. 2013; D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai (BBH33709, BCC60941)

Notes. Phylogenetically, *M. chiangmaiensis* is closely related to *M. nanensis*, *M. nivea*, *M. mollii*, *M. ochracea*, and *M. sinensis* (Fig. 1). Morphologically, *M. chiangmaiensis* is similar to *M. ochracea* in having flattened, globose to subglobose base, white stromata, widely open orifices. However, some specimens containing the anamorphic stromata of *M. chiangmaiensis* are hat-shaped, producing pale yellow conidial masses (Fig. 2 a), while *M. ochracea* produces yellowish orange to orange conidial masses (Chaverri et al. 2008). Additionally, the perithecia in *M. chiangmaiensis* are slightly wider than those reported for other species (Table 3) and have various shapes and position of the conidiomata in the stromata (Fig. 2 a-d). It distinctly produces cream masses of conidia on the colonies on PDA (Fig. 2 n).

Moelleriellaflava Khonsanit, Noisripoom, Phosrithong & Luangsa-ard, **sp. nov.** Fig. 3

MycoBank. MB835904

Anamorph. Aschersonia-like.

Etymology. From the Latin '*flava*' meaning yellow. Refers to the yellow stromata of the specimens.

Typification. THAILAND. Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail; 14°26'21.46"N, 101°22'20.20"E; on scale insects (Coccidae), found on the underside of *Ardisia sanguinolenta* leaves; 9 Jan. 2013; A. Khonsanit, S. Mongkolsamrit, W. Noisripoom (holotype BBH33722, ex-type living culture BCC60924).

Description. *Anamorphic stromata* flat to umbonate, globose to subglobose, 1-4.5 mm in diam, pale greenish yellow (2D) to brilliant greenish yellow (1A), strong orange yellow conidial masses (163B). Only one *conidioma* per stroma, narrowly U-shaped, widely open orifice, 370-600 × 100-300 µm. *Phialides* hyaline, cylindrical, (10-)13-20(-22) × 1.5 µm. *Conidia* hyaline, fusiform, (9-)10.5-12.5(-14) × (1-)1.5-2 µm. *Paraphyses* present, hyaline, filiform, up to 173 µm long, 1-1.5 µm wide. *Teleomorphic stromata* flat to umbonate, globose to subglobose, 2.5-4.5 mm in diam, pale greenish yellow (1D) to brilliant greenish yellow (1A). *Perithecia* scattered or fused together, semi-embedded, numerous perithecia per stroma (≈10), occasionally developing singly in stroma, obpyriform, 260-430 × 90-170 µm. *Ostioles* strong orange (N136B) to dark orange (N163A). *Asci* hyaline, cylindrical, (138-)158-206(-250) × 5-7 µm. *Ascicaps* convex, 3-5 × 4-7 µm. *Ascospores* hyaline, disarticulating into part-spores, cylindrical with truncated ends (6-)7-10.5(-11) × 1-1.5 µm. The teleomorph and anamorph are rarely found in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, pulvinate, wrinkled surface, attaining a diam of 8.5-11 mm in 2 wk, white, pale yellow green (4D) conidial masses. Colony reverse moderate yellow (160A), pale yellow in the margins (160D).

Habitat. On scale insects (Coccidae), found only on underside of *Ardisia sanguinolenta* leaves.

Additional specimens examined. THAILAND, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail; 14°26'21.46"N, 101°22'20.20"E; on scale insects (Coccidae), found on the underside of *Ardisia sanguinolenta* leaves; 9 Jan. 2013; A. Khonsanit, S. Mongkolsamrit, W. Noisripoom (BBH33722, BCC60925; BBH33723, BCC60926; BBH33724, BCC60927, BCC60928; BBH38474, BCC60929, BCC60930).

Notes. *Moelleriella flava* differs from other related species in producing yellow stromata (Fig. 3 a-d) and found only one side of conidioma on the stromata (Fig. 3 a-b, e-f). *Moelleriella flava* produces narrow obpyriform perithecia (Fig. 3 j-k) and longer asci than other species (Table 3). It is found on scale insects feeding only on *Ardisia sanguinolenta* leaves.

Moelleriella kanchanaburiensis Khonsanit, Mongkolsamrit, Noisripoom, Phosrithong Luangsa-ard **sp. nov.** Fig. 4

MycoBank. MB835906

Anamorph. Aschersonia-like.

Etymology. Refers to the place where the type specimen was found, Kanchanaburi Province.

Typification. THAILAND .Kanchanaburi Province, Takhian Thong Waterfall Nature Trail; 15.314651°N, 98.442993°E; on scale insects (Coccidae), found on the underside of bamboo leaves; 20 Nov. 2014; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, .R Promharn, S. Mongkolsamrit, S. Wongkanoun, W. Noisripoom (holotype BBH40814, ex-type living culture BCC75981)

Description. *Anamorphic stromata* flat to umbonate, globose to subglobose, 1–7 in diam, 1–1.5 mm in thick, white, light yellow (17D) to strong orange yellow (17A) conidial masses. *Conidiomata* scattered around the center of stromata, widely open orifice, irregular or U-shaped, 200-350 × 150-250 µm. *Phialides* hyaline, cylindrical, (10-)11.5-36.5(-50) × 1-1.5 µm. *Conidia* hyaline, narrowly fusiform with thickened wall at ends, 10-12.5(-14) × 1.5-2 µm. *Paraphyses* present, hyaline, filiform, up to 110 µm long, 1-1.5 µm wide. *Teleomorphic stromata* raised, 2–3 mm in diam, white. *Perithecia* scattered, semi-embedded, numerous perithecia per stroma (35). *Ostioles* pale green (151D). The teleomorph of *M. kanchanaburiensis* is immature, we could not observe the size and shape of perithecia, asci, asci caps and ascospores. The teleomorph and anamorph are occasionally found in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, convex to pulvinate, flat in the margins, attaining a diam of 9.5-11 mm in 2 wk, white with brilliant greenish yellow (1B) conidial masses. Colony reverse brilliant greenish yellow (1B), white in the margins.

Habitat. On scale insects (Coccidae), found on the underside of bamboo and dicotyledonous leaves.

Additional specimens examined. THAILAND. Kanchanaburi Province, Takhian Thong Waterfall Nature Trail; 15°18'1.21"N, 98°26'54.90"E; on scale insect (Coccidae), found on dicotyledonous leaves; 20 Nov. 2014; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, R. Promharn, S. Mongkolsamrit, S. Wongkanoun, W. Noisripoom (BBH40813, BCC75979, BCC75980).

Notes. *Moelleriella kanchanaburiensis* is found occurring on scale insects on the underside of bamboo and dicotyledonous leaves. The anamorph produces narrowly fusiform conidia with thickened ends appearing as yellow conidial masses in culture. This species can be easily distinguished from other *Moelleriella* species in producing multiple conidiomatal orifices

on around the center of stromata surrounding the scale insects. Additionally, the phialides in *M. kanchanaburiensis* are longer than other *Moelleriella* species (Table 2).

Moelleriella nanensis Khonsanit, Noisripoom, Phosrithong & Luangsa-ard, **sp. nov.** Fig. 5

MycoBank. MB835907

Anamorph. Aschersonia-like.

Etymology. Refers to the locality where the type specimen was found, Nan Province.

Typification. THAILAND. Nan Province, Doi Mongkhon Nature Trail; 18°46'32.27"N, 100°46'22.95"E; on scale insects (Coccidae), found on the upper side of dicotyledonous leaves; 25 Jul. 2013; A. Khonsanit (holotype BBH36571, ex-type living culture BCC66303).

Description. *Anamorphic stromata* flattened to raised, globose to subglobose, 2-6 mm in diam, white, pale greenish yellow conidial masses (160C). *Conidiomata* scattered around the margins of stromata, irregular in shape, widely open orifices, 350-600 × 160-500 µm. *Phialides* hyaline, cylindrical, (9-)10-13.5(-19) × 1-1.5 µm. *Conidia* hyaline, fusiform, (8-)8.5-10.5(-11) × (1-)1.5-2 µm. *Paraphyses* present, hyaline, filiform, up to 110 µm long. 1-1.5 µm wide. *Teleomorphic stromata* raised to convex, globose to subglobose, 3-6 mm in diam, white. *Perithecia* scattered, semi-embedded, perithecia fused together, numerous perithecia per stroma (≈20), obpyriform, 310-550 × 110-180 µm. *Ostioles* moderate yellow (160A) to strong greenish yellow (151A). *Asci* hyaline, cylindrical, (105-)161.5-224.5(-238) × (5-)5.5-9.5(-12) µm. *Asci caps* umbonate, 2-4 × 3.5-6 µm. *Ascospores* hyaline, disarticulating into part-spores, cylindrical with rounded ends, slightly indented in the middle, (7-)8-13(-18) × (1-)1.5-2 µm. The teleomorph and anamorph are present in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, convex, surface wrinkled and flat in the margins, attaining a diam of 8-9 mm in 3 wk, white, pale yellow (160D) conidial masses. Colony reverse light greyish olive (197C), greyish yellow green (197D) at the margins.

Habitat. On scale insects (Coccidae), found on the upper side of dicotyledonous leaves.

Additional specimens examined. THAILAND. Nan Province, Doi Mongkhon Nature Trail; 18°46'32.27"N, 100°46'22.95"E; on scale insects (Coccidae), found on the upper side of dicotyledonous leaves; 25 July 2013; A. Khonsanit (BBH36571, BCC66304, BCC66305).

Notes. Phylogenetically, *M. nanensis* is closely related to *M. nivea* (Fig. 1) and is found on the upper side of dicotyledonous leaves. It differs from *M. nivea* and other species in producing longer obpyriform perithecia (Fig. 5 j), umbonate asci caps (Fig. 5 l) and ascospores that are slightly indented in the center (Fig. 5 m). The conidiomatal orifice in *M. nanensis* could be found surrounding the outer parts of the stroma (Fig. 5 b-c) while in most species the orifices are situated in the center of stromata.

Moelleriella nivea Khonsanit, Mongkolsamrit, Noisripoom, Phosrithong & Luangsa-ard, **sp. nov.** Fig. 6

MycoBank. MB835908

Anamorph. Aschersonia-like.

Etymology. From the Latin '*nivea*' meaning white. Refers to the white stromata of the specimens.

Typification. THAILAND. Surat Thani Province, Khao Sok National Park, Wing Hin Waterfall Nature Trail; 8°54'55.64"N, 98°31'42.25"E, on scale insects (Coccidae), found on dicotyledonous leaves; 28 Nov. 2012; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, W. Noisripoom (holotype BBH33037, ex-type living culture, BCC60891).

Description. *Anamorphic stromata* flat to umbonate, subglobose, 1-5 mm in diam, 1–1.5 mm in thick, white, brilliant yellow (14C) conidial masses. *Conidiomata* aggregated on the center of stromata, few conidiomata per stromata (2–5), U-shaped, rim around the orifice thick, narrow widely open orifices, 280–420 × 120–300 µm. *Phialides* hyaline, cylindrical, 11–15 × 1 µm. *Conidia* hyaline, fusiform, (7–)8–9.5(–10) × (1–)1.5–2 µm. *Paraphyses* present, hyaline, filiform, up to 57 µm long, 1–1.5 µm wide. *Teleomorphic stromata* flat to umbonate, subglobose, 3-3.5 mm in diam, white. *Perithecia* scattered, semi-embedded, occasionally developing singly in stromata, numerous perithecia per stroma (3⁵), obpyriform, 260–420 × 110–230 µm. *Ostioles* vivid yellow (13A). *Asci* hyaline, cylindrical, 130–185 × 5–7 µm. *Asci caps* hemispherical, 4–5 × 5–7 µm. *Ascospores* hyaline, disarticulating into part-spores, cylindrical with rounded ends, (5–)7–10(–10.5) × 1–1.5(–2) µm. The teleomorph and anamorph are present in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, convex to pulvinate, flat in the margins, attaining a diam of 8-9 mm in 2 wk, white, yellowish white (N155A) conidial masses. Colony reverse pale yellow (162D) with white at the margins.

Habitat. On scale insects (Coccidae), found on dicotyledonous leaves.

Additional specimens examined. THAILAND. Surat Thani Province, Khao Sok National Park, Wing Hin Waterfall Nature Trail; 8°54'55.64"N, 98°31'42.25"E, on scale insect (Coccidae), found on dicotyledonous leaves; 28 Nov. 2012; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, W. Noisripoom (BBH33037, BCC58525; BBH33046, BCC58543, BCC58544)

Notes. *Moelleriella nivea* and *M. nanensis* are phylogenetically close but *M. nivea* differs from *M. nanensis* in having smaller stromata. The perithecia, asci and part-spores of *M. nivea* are also shorter than reported in *M. nanensis* (Table 3). In *M. nanensis*, the perithecia are fused together in the stromata (Fig. 5 d) while in *M. nivea* the perithecium develops singly in stromata (Fig. 6 c-d). *M. nivea* produces hemispherical asci caps (Fig. 6 k), while in *M. nanensis* it is umbonate (Fig. 5 k-l). The conidiomata in *M. nivea* are aggregated in the center of stromata (Fig. 6 a-b), almost like a bended tubercle with a cylindrical cavity and a narrow orifice while in *M. nanensis* the conidiomata are scattered around the margins with irregular in shape (Fig. 5 b-c).

Moelleriellasinensis Qiu & Chen, Phytotaxa 429(4): 289-296 (2020). Fig. 7

The description below is based on Thai materials.

Description. *Anamorphic stromata* flat to umbonate, cottony, globose to subglobose, slightly convex with wide base, 2-6 mm in diam, white with vivid yellow (17C) conidial masses. *Conidiomata* scattered in the middle of stromata, elongate flask shaped, narrow orifices, 180-300 × 100-160 µm. *Phialides* hyaline, cylindrical, 11-21 × 1-1.5 µm. *Conidia* hyaline, fusiform, (6.5-)7.5-10(-12) × (1-)1.5-2 µm. *Paraphyses* present, hyaline, filiform, up to 100 µm long, 1-1.5 µm wide. *Teleomorphic stromata* flat to umbonate, globose to subglobose, slightly convex with wide base, 3-6 mm in diam, white to pale yellow (8D). *Perithecia* scattered, semi-embedded, most perithecia fused together, occasionally developing singly in stromata, numerous perithecia per stroma (3¹⁵), obpyriform, 270-480 × 130-260 µm. *Ostioles* white greenish yellow (7D) to brilliant yellow (20A). *Asci* hyaline, cylindrical, (161-)178.5-211.5(-238) × (6-)6.5-9(-11) µm. *Asci caps* hemispherical, 3-5 × 4-6.5 µm. *Ascospores* hyaline, disarticulating into part-spores, cylindrical with rounded ends, (7-)8-14.5(-26) × 1-2 µm. The teleomorph and anamorph are present in the same stroma.

Culture characteristics. Colonies on PDA forming a compact mycelium, convex to pulvinate, flat in the margins, wrinkled surface, attaining a diam of 9-10 mm in 2 wk, white, light greenish yellow (5D) conidial masses. Colony reverse pale yellow (160A), pale greenish yellow (160C) at the margins.

Habitat. On scale insects (Coccidae), found on the upper side of dicotyledonous leaves.

Specimens examined. THAILAND, Nakhon Ratchasima Province, Khao Yai National Park, Mo Sing To Nature Trail, 14°26'21.46"N, 101°22'20.20"E; on scale insects (Coccidae), found on the underside of dicotyledonous leaves; 9 Jan. 2013; D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, R. Promharn (BBH33725, BCC 60931, BCC 60932); Chiang Mai Province, Doi Inthanon National Park, Mae Chaem Junction (KM.38) Nature Trail; 18°35'15.66"N, 98°29'11.69"E; on scale insects (Coccidae), found in the underside of dicotyledonous leaves; 28 Oct. 2013; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, W. Noisriboom (BBH38467, BCC69128; BBH38468, BCC69129); Kanchanaburi Province, Thung Yai Naresuan Wildlife Sanctuary (West), Krathon Ruesi Nature Trail, 15°20'0.11"N, 98°54'59.34"E; on scale insects (Coccidae), found on the underside of dicotyledonous leaves; 18 Nov. 2014; A. Khonsanit, D. Thanakitpipattana, K. Tasanathai, P. Srikitikulchai, R. Promharn, S. Mongkolsamrit, S. Wongkanoun, W. Noisriboom (BBH40812, BCC75977)

Notes. *Moelleriellasinensis* was first proposed by Chen et al. (2020) on whitefly nymphs (Hemiptera) found from Wu Yi Mountain, Fujian province, southeastern China. Only the anamorphic state was described and illustrated therein. This species was nested in a group in *Moelleriella* clade A subclade I (Fig. 1). In our study, we describe and illustrate the teleomorphic state of *M. sinensis* found on scale insects (Coccidae). Phylogenetically, *M. sinensis* is closely related to *M. nivea*, *M. nanensis*, *M. ochracea* and *M. mollii*. *Moelleriellasinensis* differs from other closely related species in producing longer part spores (see Table 3) and elongate flask-shaped conidiomata with narrow orifices in the center of stromata, while in the other species the orifices are widely open.

Discussion

The genus *Moelleriella* was divided into two, Effuse and Globose, clades by Chaverri et al. (2005b, 2008). The Effuse clade comprises species with effuse to thin, pulvinate, mostly white, occasionally pale yellow to orange stromata, occasionally large conidia and produces small part-spores. The Globose clade comprises species with globose, darker yellow to brownish stromata, small conidia and occasionally large part-spores. However, these characters are not unique for each group and can be found overlapping between clades (Chaverri et al. 2008).

In our multigene phylogenetic analyses based on large subunit of the ribosomal DNA (LSU), translation elongation factor-1 α (*TEF*) and the largest subunit of RNA polymerase II (*RPB1*) combined with morphological observations of 18 Thai samples of *Moelleriella* with aschersonia-like anamorphs, five new species in *Moelleriella* in Clade A subclade I were proposed, namely *M. chiangmaiensis* (Fig. 2), *M. flava* (Fig. 3), *M. kanchanaburiensis* (Fig. 4), *M. nanensis* (Fig. 5) and *M. nivea* (Fig. 6). These new species are morphologically and genetically distinct from closely related species such as *M. mollii*, *M. ochracea*, *M. phukhiaoensis*, *M. pongdueatensis* and *M. zhongdongii*. Furthermore, we describe and illustrate for the first time the teleomorphic state of *M. sinensis* in Thailand. These *Moelleriella* species in subclade I (Fig.1) mostly have flat to umbonate, globose to subglobose stromata of its anamorphic state. The teleomorphs have mostly semi-embedded perithecia, except for *M. phukhiaoensis* and *M. zhongdongii* which have completely embedded perithecia. *Moelleriella pongdueatensis* and *M. kanchanaburiensis* were described only based on the anamorphic state. *Moelleriella zhongdongii* has thick pulvinate stromata with constricted base (Liu and Hodge 2005). Furthermore, most of the species in this clade have whitish stromata, except for *M. flava*, *M. phukhiaoensis* and *M. pongdueatensis* which possess pale-yellow to yellow stromata. *Moelleriellasinensis* was first reported only for the anamorphic state from China (Chen et al. 2020), and was described as having whitish to pale yellow, pulvinate stroma, and pale brown conidial mass. However, the Thai specimen containing the anamorphic state of *M. sinensis* has white, flat to umbonate stromata, and vivid yellow conidial masses (Fig. 7).

Subclade II includes 10 known species viz. *M. alba*, *M. basicystis*, *M. chumphonensis*, *M. disjuncta*, *M. evansii*, *M. libera*, *M. phyllogena*, *M. raciborskii*, *M. rhombispora* and *M. umbospora*. The shape of anamorphic stromata in this subclade are mostly flat to thin-pulvinate. The teleomorphic stromata produce two kinds of perithecial arrangement. They are produced single tubercles in the stromata for *M. alba*, *M. chumphonensis*, *M. evansii*, *M. libera* and *M. raciborskii*, while in *M. basicystis*, *M. disjuncta*, *M. phyllogena*, *M. rhombispora* and *M. umbospora* the perithecia are completely embedded in the

thick-pulvinate or stud-shaped stromata. All members of this subclade II produce yellow stromata except for *M. alba* which has whitish stromata.

Clade B includes nine known species viz. *M. africana*, *M. boliviensis*, *M. epiphylla*, *M. insperata*, *M. macrostroma*, *M. reineckiana*, *M. schizostachyi*, *M. sloaneae* and *M. turbinata*. All species in this clade are found in the Globose clade after Chaverri et al. (2008); they have globose, large, hard and tuberculate stromata, compact tissue, except *M. sloaneae* which has effuse or thin pulvinate stromata. All species have fully embedded perithecia in the teleomorphic state, except for *M. insperata* which the teleomorphic state has not been discovered yet. The stromatal colors in this clade are in darker shades, except for *M. sloaneae* which is white. In this paper, we found that the position of conidiomata and shape of its orifices are good diagnostic characters in species delimitation for Thai *Moelleriella* species in the clade A subclade I. The conidiomata of *M. Chiangmaiensis* are scattered, irregular in shaped, having widely open orifices with thick rims (Fig. 2). *Moelleriella flava* has only one conidioma on the stromata, narrowly U-shaped, widely open orifices with thin edges (Fig. 3). *Moelleriella kanchanaburiensis* has scattered conidiomata in the center and effused in the margins of stromata, irregularly shaped, with widely open orifices (Fig. 4). *Moelleriella nanensis* has scattered conidiomata around the margins of stromata, irregularly shaped, with widely open orifices (Fig. 5). The conidiomata of *M. nivea* were aggregated in the middle of stromata (2–5 conidiomata per stroma), prominent from stromatal surfaces with irregular edges, cylindrical in shape, narrow orifices (Fig. 6). *Moelleriellasinensis* has scattered conidiomata in the middle of stromata, elongate flask shaped, with narrow orifices (Fig.7). Thus, we consider the position of conidiomata and its orifices useful in differentiating Thai *Moelleriella* species. Similarly, in *Aschersonia andropogonis* and *A. incrassata* the presence or absence of a rim around the orifice can be used in differentiating species (Liu et al. 2006). *Moelleriella turbinata* has a unique character of having pezizoid conidiomata and small orifices (Liu et al. 2006, Chaverri et al. 2008).

The insect hosts in this genus are found in two hemipteran families, Aleyrodidae and Coccidae (Hemiptera) (Petch 1921; Petch 1932; Liu and Hodge 2005; Liu et al. 2006, Chaverri et al. 2008; Tadych et al. 2009; Mongkolsamrit et al. 2011b; Mongkolsamrit et al. 2015; Li et al. 2016; Chen et al. 2020). However, in the study presented here we only found the hosts as scale insects (Coccidae).

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Data availability All sequence data generated in this study (see Table 1) are available in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>).

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Authors' contribution

The samples in this study were collected by A. Khonsanit, J.J. Luangsa-ard, S. Mongkolsamrit, W. Noisriboom and APMT members. Morphological investigations were observed and illustrated by A. Khonsanit. The insect hosts were identified by N. Phosrithong. Description of the new and known species were described by A. Khonsanit and S. Mongkolsamrit. Molecular data and phylogenetic analyses were performed by W. Noisriboom. A. Khonsanit and S. Mongkolsamrit wrote the original draft, review and editing were performed by A. Khonsanit, S. Mongkolsamrit and J.J. Luangsa-ard. All authors have read and approved the manuscript.

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Tables

Table 1 List of species and GenBank accession numbers of sequences used in this study.

| Species | Strain | Origin | GenBank Accession no. | | |
|---|-----------------|-----------------|-----------------------|-----------------------|-----------------------|
| | | | nrLSU | <i>TEF</i> | <i>RPB1</i> |
| <i>Aschersonia discoidea</i> | BCC2097 | Thailand | - | AY986945 ¹ | DQ000346 ¹ |
| <i>Aschersonia cf. discoidea</i> | I93-901d | Ivory Coast | EU392567 ² | EU392646 ² | EU392700 ² |
| <i>Aschersonia disciformis</i> | P.C. 655 | Honduras | EU392560 ² | EU392643 ² | EU392697 ² |
| <i>Aschersonia disciformis</i> | P.C. 676 | Honduras | EU392566 ² | EU392645 ² | EU392699 ² |
| <i>Conoideocrella luteorostrata</i> | NHJ11343 | Thailand | EF468850 ³ | EF46880 ³ | EF468906 ³ |
| <i>Conoideocrella luteorostrata</i> | NHJ12516 | Thailand | EF468849 ³ | EF468800 ³ | EF468905 ³ |
| <i>Conoideocrella tenuis</i> | NHJ6293 | Thailand | EU369044 ⁴ | EU369029 ⁴ | EU369068 ⁴ |
| <i>Conoideocrella tenuis</i> | NHJ6791 | Thailand | EU369046 ⁴ | EU369028 ⁴ | EU369069 ⁴ |
| <i>Helicocollum surathaniensis</i> | BCC34463 | Thailand | KT222328 ⁵ | KT222336 ⁵ | - |
| <i>Helicocollum surathaniensis</i> | BCC34464 | Thailand | KT222329 ⁵ | KT222337 ⁵ | - |
| <i>Moelleriella africana</i> | P.C. 736 | Ghana | AY986917 ² | AY986943 ² | DQ000344 ² |
| <i>Moelleriella alba</i> | BCC49492 | Thailand | JQ269645 ⁶ | KX254424 ⁶ | JQ256905 ⁶ |
| <i>Moelleriella alba</i> | BCC49409 | Thailand | JQ269646 ⁶ | KX254423 ⁶ | JQ256906 ⁶ |
| <i>Moelleriella basicystis</i> | P.C. 374 | Costa Rica | AY986903 ² | AY986928 ² | DQ000329 ² |
| <i>Moelleriella boliviensis</i> | P.C. 603 | Bolivia | AY986923 ² | AY986950 ² | DQ000351 ² |
| <i>Moelleriella chiangmaiensis</i> | BCC18029 | Thailand | MT659360 | MW091560 | - |
| <i>Moelleriella chiangmaiensis</i> | BBH33051 | Thailand | MT659362 | MT672277 | MT672269 |
| <i>Moelleriella chiangmaiensis</i> | BCC60941 | Thailand | MT659361 | MT672278 | MT672270 |
| <i>Moelleriella chumphoensis</i> | BCC47575 | Thailand | JQ269648 ⁶ | KX254422 ⁶ | JQ256908 ⁶ |
| <i>Moelleriella chumphoensis</i> | BCC47574 | Thailand | JQ269647 ⁶ | KX254421 ⁶ | JQ256907 ⁶ |
| <i>Moelleriella disjuncta</i> | J.B. 205 | Panama | EU392578 ² | EU392654 ² | - |
| <i>Moelleriella epiphylla</i> | P.C. 545 | Bolivia | EU392585 ² | EU392660 ² | EU392711 ² |
| <i>Moelleriella epiphylla</i> | I93-813 | Guiana | EU392583 ² | EU392656 ² | EU392707 ² |
| <i>Moelleriella evansii</i> | P.C. 627 | Ecuador | AY986916 ² | AY986942 ² | DQ000343 ² |
| <i>Moelleriella flava</i> | BCC60924 | Thailand | KF951146 | KX254430 | MT672271 |
| <i>Moelleriella flava</i> | BCC60925 | Thailand | KF951147 | KX254431 | MT672272 |
| <i>Moelleriella flava</i> | BCC60929 | Thailand | KX298238 | KX254432 | MT672273 |
| <i>Moelleriella flava</i> | BCC60930 | Thailand | KX298237 | KX254429 | - |
| <i>Moelleriella gracilispora</i> | CGMCC 3.18989 | China | KC964202 ⁷ | KC964191 ⁷ | KC964179 ⁷ |

| | | | | | |
|--|-----------------|-----------------|-----------------------|-----------------------|-----------------------|
| <i>Moelleriella gracilispora</i> | CGMCC 3.18990 | China | KC964203 ⁷ | KC964192 ⁷ | KC964180 ⁷ |
| <i>Moelleriella insperata</i> | ARSEF 2396 | Philippines | AY518374 ² | DQ070029 ² | EU392713 ² |
| <i>Moelleriella kanchanaburiensis</i> | BCC75979 | Thailand | MT659363 | MT672279 | MT843900 |
| <i>Moelleriella kanchanaburiensis</i> | BCC75980 | Thailand | MT659364 | MT672280 | MT843901 |
| <i>Moelleriella kanchanaburiensis</i> | BCC75981 | Thailand | MT659365 | MT672281 | - |
| <i>Moelleriella libera</i> | P.C. 444 | Mexico | EU392591 ² | EU392662 ² | EU392714 ² |
| <i>Moelleriella libera</i> | P.C. 445 | Mexico | AY986900 ² | AY986925 ² | DQ000326 ² |
| <i>Moelleriella macrostroma</i> | P.C. 605 | Bolivia | DQ000347 ² | AY986946 ² | AY986919 ² |
| <i>Moelleriella macrostroma</i> | J.B. 115 | Costa Rica | AY986920 ² | AY986947 ² | DQ000348 ² |
| <i>Moelleriella mollii</i> | I93-901a | Ivory Coast | EU392599 ² | EU392667 ² | EU392719 ² |
| <i>Moelleriella mollii</i> | I93-901c | Ivory Coast | EU392600 ² | EU392668 ² | EU392720 ² |
| <i>Moelleriella nanensis</i> | BCC66303 | Thailand | KX298236 | KX254427 | MW085940 |
| <i>Moelleriella nanensis</i> | BCC66305 | Thailand | MW080317 | KX254428 | MW085941 |
| <i>Moelleriella nivea</i> | BCC60891 | Thailand | MW080318 | MT672282 | MW085942 |
| <i>Moelleriella nivea</i> | BCC58543 | Thailand | MT659366 | MT672283 | MT672274 |
| <i>Moelleriella nivea</i> | BCC58544 | Thailand | MT659367 | MT672284 | MT843898 |
| <i>Moelleriella ochracea</i> | IE 1308 | Mexico | EU392601 ² | EU392669 ² | EU392721 ² |
| <i>Moelleriella ochracea</i> | P.C. 648 | Honduras | EU392605 ² | EU392671 ² | EU392723 ² |
| <i>Moelleriella phukhiaoensis</i> | BCC19769 | Thailand | KT880502 ⁸ | - | KT880506 ⁸ |
| <i>Moelleriella phukhiaoensis</i> | BCC19773 | Thailand | KT880503 ⁸ | - | KT880507 ⁸ |
| <i>Moelleriella phyllogena</i> | P.C. 555 | Bolivia | EU392610 ² | EU392674 ² | EU392726 ² |
| <i>Moelleriella phyllogena</i> | J.B. 130 | Panama | EU392608 ² | EU392672 ² | EU392724 ² |
| <i>Moelleriella pongdueatensis</i> | BCC31787 | Thailand | KT880500 ⁸ | KX254433 ⁸ | KT880504 ⁸ |
| <i>Moelleriella pongdueatensis</i> | BCC31788 | Thailand | KT880501 ⁸ | KX254434 ⁸ | KT880505 ⁸ |
| <i>Moelleriella raciborskii</i> | BCC48745 | Thailand | - | KX254420 ⁶ | JQ269642 ⁶ |
| <i>Moelleriella raciborskii</i> | Afr 28 | Ghana | DQ070113 ² | EU392675 ² | EU392727 ² |
| <i>Moelleriella raciborskii</i> | P.C. 533 | Vietnam | AY986911 ² | AY986937 ² | DQ000338 ² |
| <i>Moelleriella raciborskii</i> | BCC47597 | Thailand | - | KX254418 ⁶ | JQ269644 ⁶ |
| <i>Moelleriella raciborskii</i> | BCC49361 | Thailand | - | KX254419 ⁶ | JQ269643 ⁶ |
| <i>Moelleriella raciborskii</i> | I93-901b | Ivory Coast | EU392611 ² | EU392676 ² | EU392728 ² |
| <i>Moelleriella reineckiana</i> | BCC1713 | Thailand | - | DQ384968 ⁶ | DQ385008 ⁶ |

| | | | | | |
|-------------------------------------|-----------------|-----------------|-----------------------|-----------------------|-----------------------|
| <i>Moelleriella reineckiana</i> | BCC1765 | Thailand | - | DQ384958 ⁶ | DQ385010 ⁶ |
| <i>Moelleriella rhombispora</i> | P.C. 467 | Costa Rica | AY986908 ² | AY986933 ² | DQ000334 ² |
| <i>Moelleriella rhombispora</i> | P.C. 696 | Honduras | EU392618 ² | EU392680 ² | EU392732 ² |
| <i>Moelleriella schizostachyi</i> | CBS 100067 | Thailand | AY986921 ² | AY986948 ² | DQ000349 ² |
| <i>Moelleriella sloaneae</i> | I94-920 | Guatemala | EU392621 ² | EU392682 ² | EU392734 ² |
| <i>Moelleriella sloaneae</i> | I94-922c | Belize | EU392622 ² | EU392683 ² | EU392735 ² |
| <i>Moelleriella turbinata</i> | P.C. 678 | Honduras | EU392627 ² | EU392687 ² | EU392739 ² |
| <i>Moelleriella turbinata</i> | IMI 352838 | Mexico | EU392625 ² | EU392685 ² | EU392737 ² |
| <i>Moelleriella sinensis</i> | CGMCC3.18911 | China | MK412091 ⁹ | MK393868 ⁹ | MK412101 ⁹ |
| <i>Moelleriella sinensis</i> | BCC60932 | Thailand | MT659368 | - | MT672275 |
| <i>Moelleriella sinensis</i> | BCC69128 | Thailand | KX298234 | KX254425 | MT843899 |
| <i>Moelleriella sinensis</i> | BCC69129 | Thailand | KX298235 | KX254426 | MT672275 |
| <i>Moelleriella umbospora</i> | P.C. 457 | Mexico | AY986904 ² | AY986929 ² | DQ000330 ² |
| <i>Moelleriella umbospora</i> | P.C. 461 | Mexico | EU392628 ² | EU392688 ² | EU392740 ² |
| <i>Moelleriella zhongdongii</i> | P.C. 504 | Costa Rica | EU392631 ² | EU392689 ² | EU392741 ² |
| <i>Moelleriella zhongdongii</i> | P.C. 549 | Bolivia | EU392632 ² | EU392690 ² | EU392742 ² |
| <i>Orbiocrella petchii</i> | NHJ6240 | Thailand | EU369038 ⁴ | EU369060 ⁴ | EU369022 ⁴ |
| <i>Orbiocrella petchii</i> | NHJ6209 | Thailand | EU369039 ⁴ | EU369061 ⁴ | EU369023 ⁴ |
| <i>Purpureocillium lilacinum</i> | CBS 284.36 | - | AY624227 ³ | EF468792 ³ | EF468898 ³ |
| <i>Purpureocillium lilacinum</i> | CBS 431.87 | - | EF468844 ³ | EF468791 ³ | EF468897 ³ |
| <i>Regiocrella camerunensis</i> | CUP 67512 | Cameroon | DQ118735 ¹ | DQ118743 ¹ | DQ127234 ¹ |
| <i>Regiocrella sinensis</i> | CUP CH-2640 | China | DQ118736 ¹ | DQ118744 ¹ | DQ127235 ¹ |
| <i>Samuelsia chalalensis</i> | P.C. 560 | Bolivia | EU392637 ² | EU392691 ² | EU392743 ² |
| <i>Samuelsia geonomis</i> | P.C. 614 | Bolivia | EU392638 ² | EU392692 ² | EU392744 ² |
| <i>Samuelsia mundiveteris</i> | BCC40021 | Thailand | GU552152 ¹ | GU552145 ¹ | - |
| <i>Samuelsia mundiveteris</i> | BCC40022 | Thailand | GU552153 ¹ | GU552146 ¹ | - |
| <i>Samuelsia rufobrunnea</i> | P.C. 613 | Bolivia | EU392638 ² | AY986944 ² | DQ000345 ² |

The accession numbers marked in bold font refer to sequences new in this study

References: ¹Chaverri et al. 2005a, ²Chaverri et al. 2008, ³Sung et al. 2007, ⁴Johnson et al. 2009 ⁵ Luangsa-ard et al. 2017, ⁶Mongkolsamrit et al. 2015, ⁷Yuan et al. 2020, ⁸Li et al. 2016, ⁹Chen et al 2020.

Table 2 Morphological comparisons between the anamorphs of *Moelleriella* species.

| Species | Conidiomata (μm) | Phialides (μm) | Conidia (μm) | Paraphyses | References |
|-----------------------------|----------------------------------|--------------------------------|--|----------------------------------|-------------------------------|
| <i>Moelleriella alba</i> | 140-200 \times 150-180 | $\leq 22 \times 1-4$ | Fusiform, 8-12 \times 1.5-3 | Absent | Mongkolsamrit et al. (2015) |
| <i>M. basicystis</i> | - | 5.5-13.5 \times 2-3 | Ventricose, 11-15.5 \times 3-5 | Absent | Chaverri et al. (2008) |
| <i>M. castanea</i> | - | 7-17.5 \times 1.5-2 | Fusiform, 5-6.7 \times 1.5-2 | Absent | Petch (1932) |
| <i>M. chiangmaiensis</i> | 450-500 \times 150-270 | 8-20 \times 1.5-2 | Fusiform, 7-11 \times 1.5-2 | Present, $\leq 130 \times 1-1.5$ | This study |
| <i>M. chumphonensis</i> | 180-300 \times 130-170 | $\leq 22 \times 1-2$ | Fusiform, 16-22 \times 2-3 | Present | Mongkolsamrit et al. (2015) |
| <i>M. disjuncta</i> | - | 9.5-16 \times 1.5-2.5 | Fusiform, 6.8-9.3 \times 2.3-3 | Absent | Chaverri et al. (2008) |
| <i>M. epiphylla</i> | - | 8-12.7 \times 2.5-3.5 | Ovoid, 9-13.5 \times 3.5-6.5 | Absent | Chaverri et al. (2008) |
| <i>M. evansii</i> | - | 10-17 \times 1.5-2 | Fusiform, 11.2-15 \times 2.5-3.2 | Absent | Chaverri et al. (2008) |
| <i>M. flava</i> | 370-600 \times 100-300 | 10-22 \times 1.5 | Fusiform, 9-14 \times 1-2 | Present, $\leq 173 \times 1-1.5$ | This study |
| <i>M. globosa</i> | - | - | Ovoid, 11.5-14.3 \times 4.5-6 | Absent | Chaverri et al. (2008) |
| <i>M. gracilispora</i> | 166-236 \times 53-136 | 6-12 \times 0.8-1.3 | Fusiform, 11-12 \times 1-2 | Present, 36-103 \times 0.4-0.8 | Yuan et al. (2020) |
| <i>M. guaranitica</i> | - | 14.2-25.2 \times 2-3 | Fusiform, 9-13.5 \times 3-4 | Absent | Chaverri et al. (2008) |
| <i>M. kanchanaburiensis</i> | 200-350 \times 150-250 | 10-50 \times 1-1.5 | Narrowly fusiform, 9-14 \times 1-2 | Present, $\leq 110 \times 1-1.5$ | This study |
| <i>M. libera</i> | - | 10-20 \times 1-1.5 | Fusiform, 9-18 \times 1.5-2.5 | Present, 50-113 \times 1-1.5 | Chaverri et al. (2008) |
| <i>M. macrostroma</i> | - | - | Fusiform, 10.7-14.5 \times 2-3 | Absent | Chaverri et al. (2005b) |
| <i>M. madidiensis</i> | - | 10-20 \times 2.5-3 | Fusiform, 8.5-10.5 \times 2-2.5 | Absent | Chaverri et al. (2008) |
| <i>M. mollii</i> | $\leq 300 \times \leq 160$ | - | Fusiform, 8-14 \times 1-1.5 | Present, ≤ 60 | Hennings (1900), Petch (1921) |
| <i>M. nanensis</i> | 350-600 \times 160-500 | 9-19 \times 1-1.5 | Fusiform, 8-11 \times 1-2 | Present, $\leq 110 \times 1-1.5$ | This study |
| <i>M. nivea</i> | 280-420 \times 120-300 | 11-15 \times 11-1.5 | Fusiform, 7-10 \times 1-2 | Present, $\leq 110 \times 1-1.6$ | This study |
| <i>M. ochracea</i> | 100-600 diam | 7-16 \times 1-1.5 | Fusiform, 8-14 \times 1.5-2 | Present | Chaverri et al. (2008) |
| <i>M. phukhiaoensis</i> | $\leq 430 \times \leq 100$ | $\leq 25 \times 1-2$ | Cylindrical narrow, 16-17 \times 2.5-3.5 | Present, $\leq 90 \times 1-2$ | Li et al. (2016) |
| <i>M. phyllogena</i> | - | 8-10.7 \times | Ventricose, 12-18.5 \times | Absent | Chaverri et al. |

| | | 2-3 | 3.2-5 | | (2008) |
|--------------------------|---------------------------------|---------------------------|-------------------------------------|-------------------------------------|-----------------------------|
| <i>M. pongdueatensis</i> | - | $\leq 23 \times 1-2$ | Fusiform, $9-12.5 \times 1.5-2.5$ | Present, $\leq 110 \times 1-2$ | Li et al. (2016) |
| <i>M. pumatensis</i> | $250-280 \times 90-100$ | ≤ 25 long | Fusiform, $12-15 \times 2-2.5$ | Present, $\leq 180 \times 1.5$ | Mongkolsamrit et al. (2011) |
| <i>M. rhombispora</i> | - | $8-12 \times 1.5-2$ | $9-14 \times 2.5-3$ | Present | Liu et al. (2006) |
| <i>M. sinensis</i> | $103.6-279.6 \times 83.1-145.5$ | $\leq 30 \times 0.8-1.3$ | Fusiform, $6.7-11 \times 1.3-1.8$ | Present, $43.2-68.9 \times 0.6-0.8$ | Chen et al. (2020) |
| <i>M. sinensis</i> | $180-300 \times 100-160$ | $11-21 \times 1-1.5$ | Fusiform, $6.5-12 \times 1-2$ | Present, $\leq 100 \times 1-1.5$ | This study |
| <i>M. sloaneae</i> | - | $5.2-19.7 \times 1.3-2.5$ | Fusiform, $6.3-14.7 \times 1.8-2.8$ | Present | Chaverri et al. (2008) |
| <i>M. turbinata</i> | - | $9-18 \times 2.7-6.3$ | Ovoid, $8-13.5 \times 3.8-6.2$ | Absent | Chaverri et al. (2008) |
| <i>M. umbospora</i> | - | $8.5-10 \times 2-2.5$ | Ventricose, $11-15.5 \times 3-5$ | Absent | Chaverri et al. (2008) |
| <i>M. zhongdongii</i> | - | $10-70 \times 1.5-2$ | Fusiform, $10-15 \times 1-2.5$ | Present | Liu and Hodge (2005) |

Table 3 Morphological comparisons between the teleomorphs of *Moelleriella* species.

| Species | Countries | Host | Stromata | Perithecia | Asci | Asci-caps | Part-spores | References |
|--------------------------|---|---------------------------|---------------|---|--------------------|-----------------------------|--------------------|-----------------------------|
| | found | | (mm) | (μm) | (μm) | (μm) | (μm) | |
| <i>M. alba</i> | Thailand | Scale insects, whiteflies | 3-6 × 1-1.5 | Flask-shaped, 300-550 × 250-300 | 152-280 × 6-10 | 4 μm thick | 11-16 × 1.5-2.5 | Mongkolsamrit et al. (2015) |
| <i>M. basicystis</i> | Caribbean Islands, Costa Rica, Cuba, Panama, Southern Central America | Scale insects, whiteflies | 1-2 mm diam | Flask-shaped, 300-450 × 160-250 | 190-298 × 9.3-18 | 3.2-5.3 μm thick | 11.5-26 × 2.7-4.5 | Chaverri et al. (2008) |
| <i>M. boliviensis</i> | Bolivia, Brazil | Whiteflies | 0.8-3 mm diam | Subglobose to ovoid, 300-400 × 250-300 | 134-150 × 8-8.5 | 0.8-1.7 μm thick | 4.5-7.5 × 2-2.5 | Chaverri et al. (2008) |
| <i>M. castanea</i> | Trinidad | Scale insects | 1-2 mm diam | Flask-shaped, 200-250 × 110-130 | - | - | 4.5-6.3 × 1.5-2.2 | Chaverri et al. (2008) |
| <i>M. Chiangmaiensis</i> | Thailand | Scale insects | 4-7 mm diam | Obpyriform, 450-500 × 260-360 | 102-220 × 4-7 | 4 μm thick | 7-12 × 1-2 | This study |
| <i>M. chumphonensis</i> | Thailand | Scale insects, whiteflies | 2-8 × 0.5-0.8 | Flask-shaped, 580-600 × 340-400 | 290-380 × 14-16 | 5-7 μm thick | 6-12.5 × 1.5-4 | Mongkolsamrit et al. (2015) |
| <i>M. colliculosa</i> | Brazil | Scale insects, whiteflies | 1.5-2 mm diam | Flask-shaped, subglobose, 250-300 × 150 | | 1.5-2 μm thick | 10.2-13.7 × 3.5-5 | Chaverri et al. (2008) |
| <i>M. comuta</i> | Brazil | Scale insects, whiteflies | 1-3 × 2-9 | Flask-shaped, 275-430 × 135-180 | 175-196 × 8.5-12.2 | 4.5-6 μm thick | 7.8-10.5 × 2-2.5 | Chaverri et al. (2008) |
| <i>M. disjuncta</i> | French Guiana, Guyana, Panama, Puerto Rico, Trinidad | Scale insects, whiteflies | 1-3 × 0.5-1.5 | Flask-shaped, 350-400 × 200-250 | 145-231 × 9.5-18.3 | 1.8-3.3 μm thick | 6.8-11.5 × 2.5-3.5 | Chaverri et al. (2008) |
| <i>M. epiphylla</i> | Bolivia, Colombia, Costa Rica, Cuba, Ecuador, Guyana, Honduras, Mexico, Saint Vincent | Scale insects, whiteflies | 0.8-3 mm diam | Flask-shaped, 400-550 × 200 | - | - | 7.8-12 × 3.5-4.5 | Chaverri et al. (2008) |
| <i>M. evansii</i> | Ecuador | Scale | 7-10 mm | Subglobose | 121- | 4.5 | 6-17.2 | Chaverri et al. |

| | | | | | | | | |
|------------------------|--|--|-----------------------|--|----------------------------------|--------------------------|------------------------------|-------------------------------------|
| | | insects, whiteflies | diam | to ovoid, 300-400 × 350-500 | 325 × 8.5- 13.7 | µm thick | × 1.8- 4.2 | (2008) |
| <i>M. flava</i> | Thailand | Scale insects | 2.5-4.5 mm diam | Obpyriform, 260-430 × 90-170 | 138- 250 × 5-7 | 4-7 µm thick | 6-11 × 1-1.5 | This study |
| <i>M. gaertneriana</i> | Brazil, French Guiana, Venezuela. | Scale insects | 6-30 × 6- 20 | Flask- shaped, 247-378 × 142-378 | 120- 178 × 4- 6.5 | 3.3- 4 µm thick | 4-8 × 1.5-2 | Chaverri et al. (2008) |
| <i>M. globosa</i> | Brazil, Trinidad | Scale insects, whiteflies | 1-5.5 mm diam | Flask- shaped, 300-400 × 200-250 | 150- 160 × 8- 10 | - | 6.5-9 × 2-3 | Chaverri et al. (2008) |
| <i>M. guaranitica</i> | Brazil, Paraguay | Insects | 1-4 mm diam | Flask- shaped, 400-450 × 200-250 | 150- 200 × 7.5- 10 | - | 5.5- 8.2 × 2-3 | Chaverri et al. (2008) |
| <i>M. libera</i> | Neotropical | Scale insects, whiteflies | 0.7-2 mm diam | Globose to ovoid, 300- 400 × 300- 600 | 5 µm thick | - | 13-16 × 2.5- 3 | Chaverri et al. (2008) |
| <i>M. macrostroma</i> | Bolivia | Scale insects, whiteflies | 3-22 mm diam | Obpyriform, 377-451 × 137-152 | 140- 197 × 5.2-7 | 3-4 µm thick | 8.7-18 × 2.2- 3 | Chaverri et al. (2005b) |
| <i>M. mollii</i> | Indonesia | Whitefly (<i>Aleyrodes</i> sp.) | 2-4 mm diam | Flask- shaped, ≤500 × ≤200 | 170- 180 × 6-8 | - | 8-17 × 1.5-2 | Koorders (1907), Petch (1921) |
| <i>M. nanensis</i> | Thailand | Scale insects | 3-6 mm diam | Obpyriform, 310-550 × 110-180 | 105- 238 × 5- 12 | 3.5- 6 µm thick | 7-18 × 1-2 | This study |
| <i>M. nivea</i> | Thailand | Scale insects | 3-3.5 mm diam | Obpyriform, 260-420 × 110-230 | 130- 185 × 5-7 | 5-7 µm thick | 5-0.5 × 1-2 | This study |
| <i>M. ochracea</i> | Neotropical | Scale insects, whiteflies | 1-3 mm diam | Flask- shaped, 250-450 × 160-300 | 138- 180 × 5-8 | 3- 3.5 µm thick | 12-15 × 1.5- 2 | Chaverri et al. (2008) |
| <i>M. palmae</i> | Brazil, Peru, Surinam | Scale insects, whiteflies | 0.6-6.5 mm diam | Flask- shaped, 400-450 × 200-250 | 160- 200 × 7- 9.5 | 1 µm thick | 8-11.2 × 2.2- 3 | Chaverri et al. (2008) |
| <i>M. phukhiaensis</i> | Thailand | Scale insects | ≤ 5 mm diam | Flask- shaped, 400-520 × 150-200 | 195- 220 × 8- 12 | 4-6 µm thick | 12.5- 17.5 × 2-3 | Li et al. (2016) |
| <i>M. phyllogena</i> | Argentina, Bolivia, Brazil, Colombia, Ecuador, French | Scale insects, whiteflies | 1-3 mm diam | Flask- shaped, 300-450 × 160-250 | 190- 300 × 9.5- 21.5 | 2- 6.5 µm thick | 13.7- 25 × 2.5- 4.5 | Chaverri et al. (2008) |

| | | | | | | | | |
|-----------------------|---|---------------------------------|-----------------------|--|-----------------------------------|----------------------------|--------------------------|---------------------------|
| | Guiana, Panama, Peru, Venezuela | | | | | | | |
| <i>M. rhombispora</i> | Costa Rica, Guatemala, Honduras, Mexico, Puerto Rico. | Scale insects, whiteflies | 2-2.5 mm diam | 300-450 × 210-300 | 148- 296 × 6- 14 | 5-8 µm thick | 10-14 × 2-3 | Chaverri et al. (2008) |
| <i>M. sinensis</i> | Thailand | Scale insects | 2-6 mm diam | Obpyriform, 270-480 × 130-260 | 161- 238 × 6- 11 | 4- 6.5 µm thick | 7-26 × 1-2 | This study |
| <i>M. sloaneae</i> | Belize, Bolivia, Brazil, Ecuador, Guadeloupe, Guatemala, Guyana, Honduras, Peru, Venezuela | Scale insects, whiteflies | 1.5-2.2 mm diam | Flask- shaped, 400-500 × 250-300 | 163- 248 × 7.2- 10.5 | 3.3- 6.3 µm thick | 9-18.3 × 2-4 | Chaverri et al. (2008) |
| <i>M. turbinata</i> | Neotropics | Scale insects, whiteflies | 1-5 mm diam | Flask- shaped to Obpyriform, 264-320 × 116-130 | 210- 275 × 8- 14 | 2.8- 4.5 µm thick | 13-21 × 2.8- 4.2 | Chaverri et al. (2008) |
| <i>M. umbospora</i> | Honduras, Mexico | Scale insects, whiteflies | 0.5-2.5 mm diam | Flask- shaped, 375-500 × 200-280 | 274- 340 × 21.2- 31.5 | 3-4 µm thick | 21.5- 30.1 × 4-5.5 | Chaverri et al. (2008) |
| <i>M. zhongdongii</i> | Bolivia, Costa Rica, Puerto Rico. | Scale insects, whiteflies | | Flask- shaped, 350-450 × 125-200 | 300 × 6- 10 | 4-5 µm thick | 5-10 × 1-2 | Liu and Hodge (2008) |

Figures

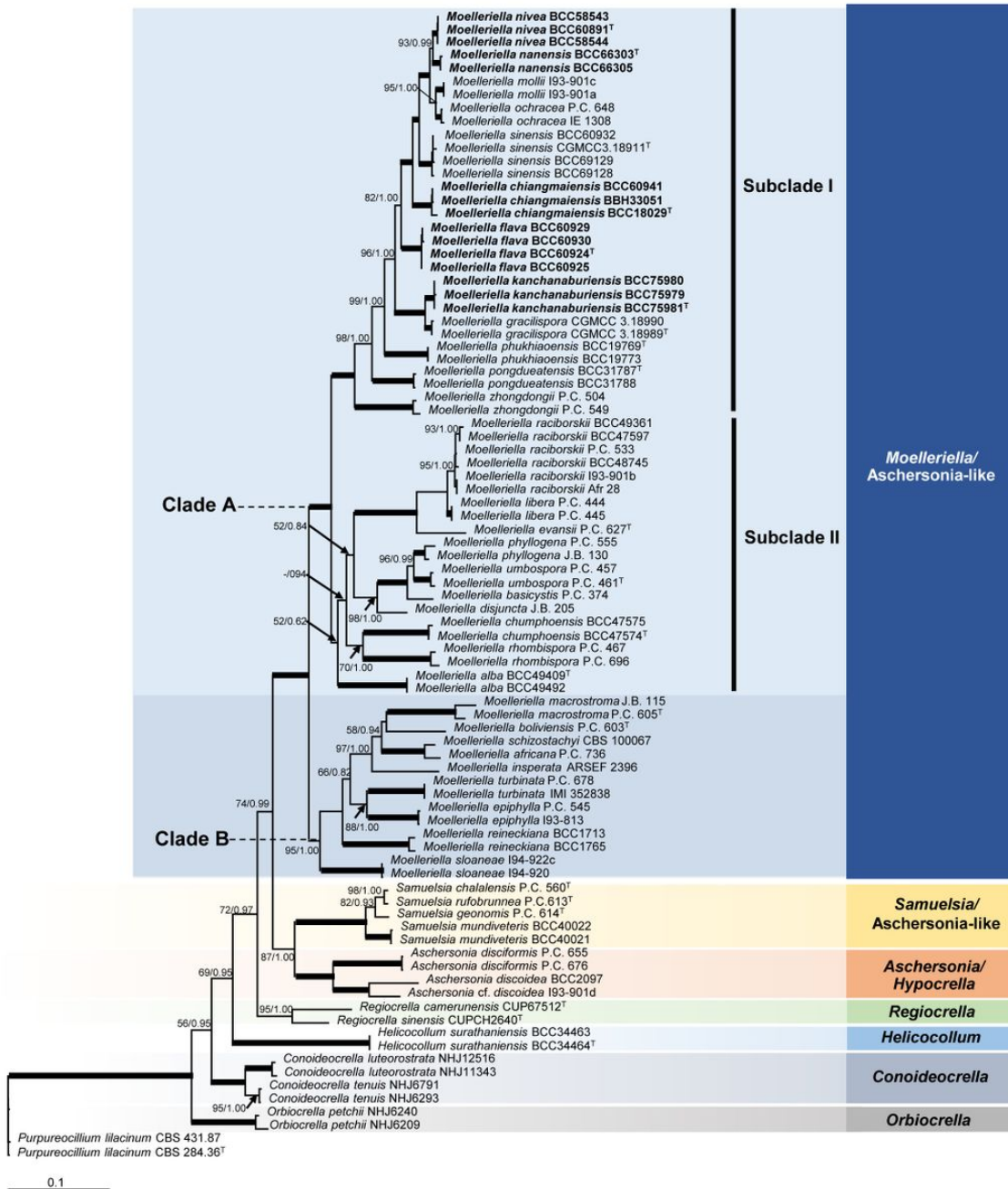


Figure 1

Phylogenetic relationships of *Moelleriella* (Clavicipitaceae) from a multigene dataset (LSU, TEF and RPB1) based on maximum likelihood (RAxML) and Bayesian inference. Numbers along branches are ML bootstrap values and bayesian posterior probabilities (bold branches show strong support, 99-100%)

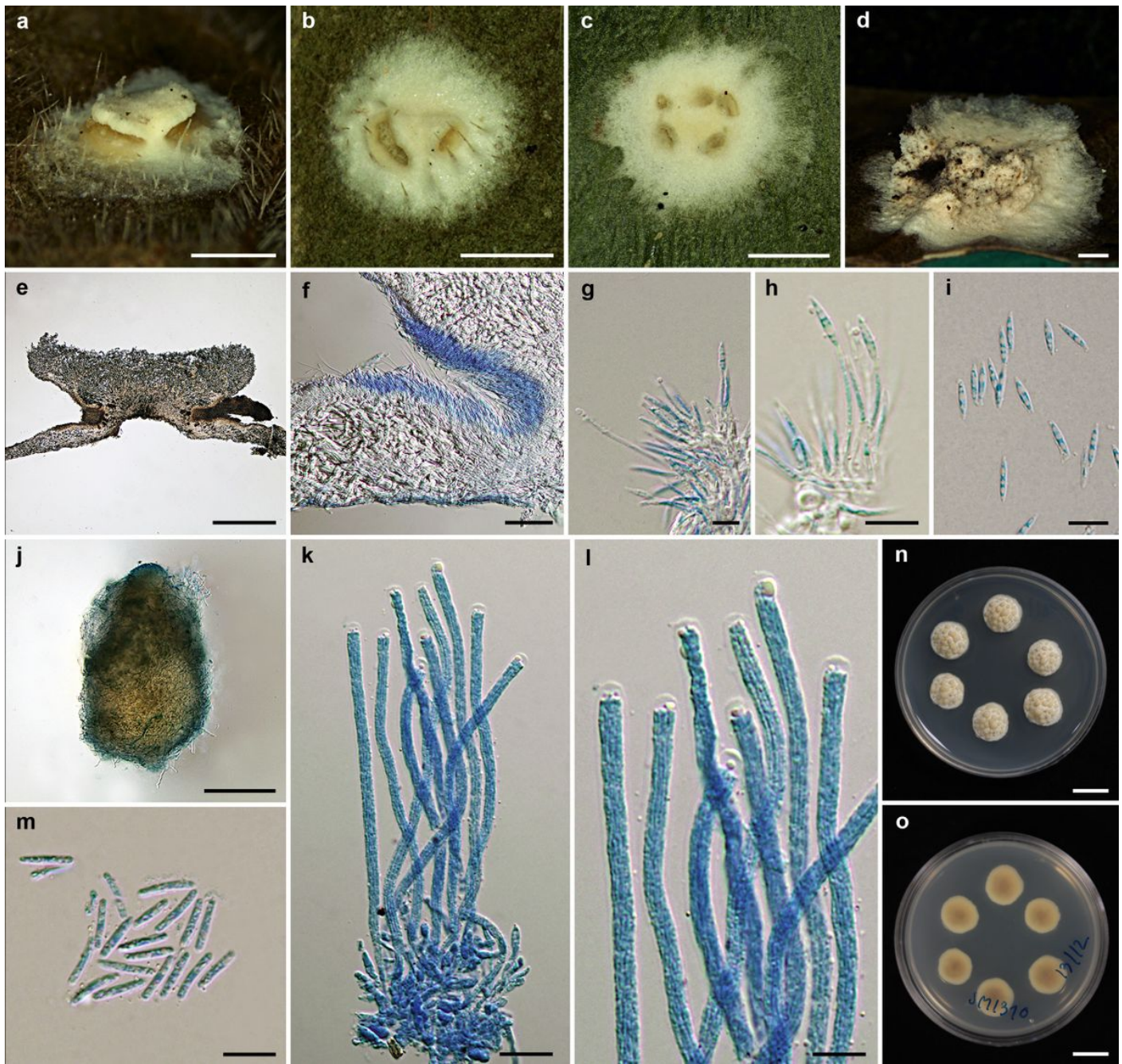


Figure 2

Moelleriella chiangmaiensis. a-c Anamorphic stroma containing conidiomata. d Telomorphic stroma containing conidiomata and perithecia. e-f Section of stroma showing conidiomata. g Phialide and conidium at the tips with papaphyses. h Phialide with conidia at the tips. i Conidia. j Perithecium. k-l. Asci and caps. m Part-spores. n Colony obverse on PDA at 25 °C after 2 wk. o. Colony reverse on PDA at 25 °C after 2 wk. Scale bars: n, o = 10 mm; a-d = 1 mm. e = 500 μ m. j = 200 μ m. f = 100 μ m. k = 20 μ m. g-i, l, m = 20 μ m.

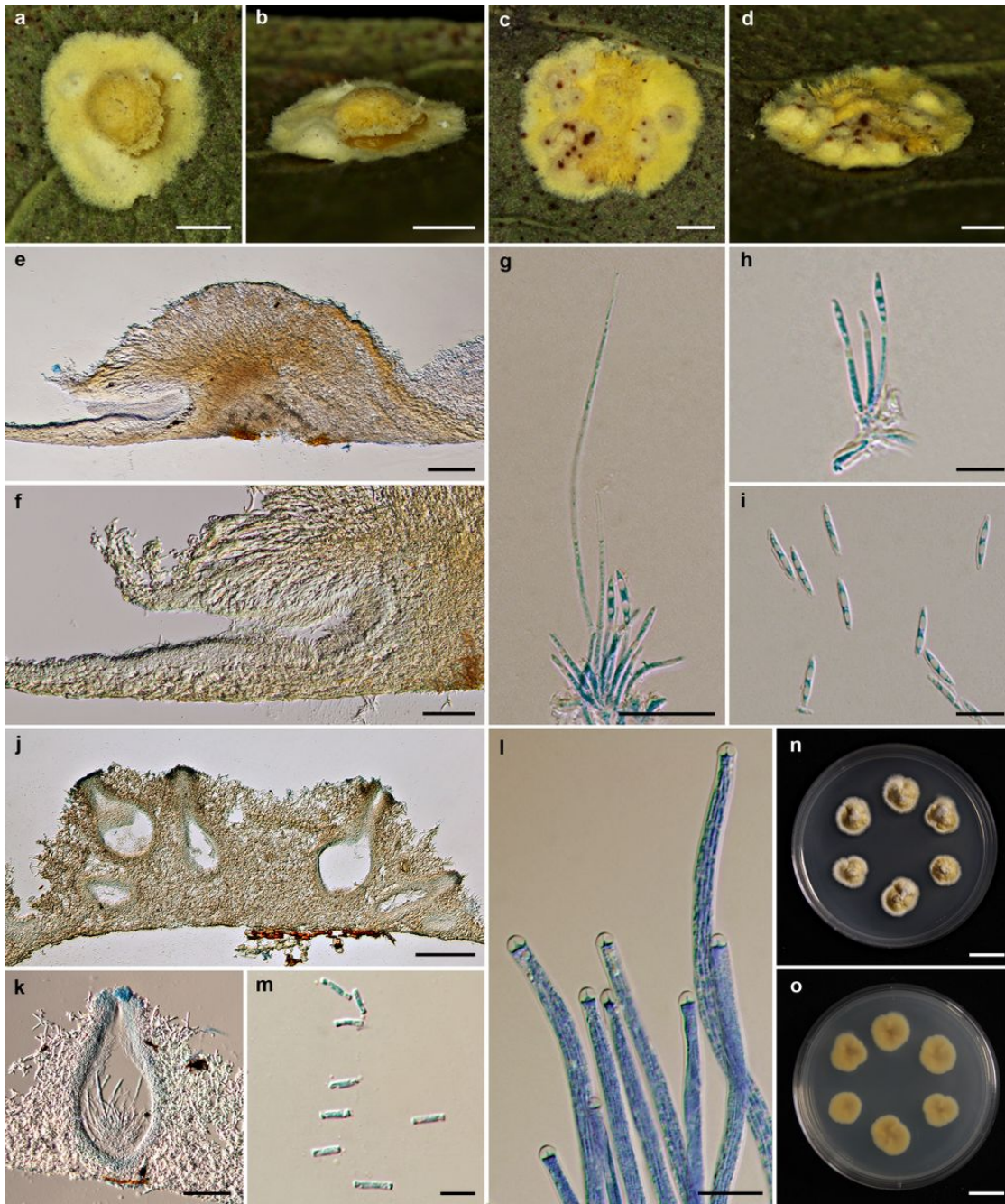


Figure 3

Moelleriella flava. a, b Anamorphic stroma. c, d Telomorphic stroma. e, f Section of stroma showing conidioma. g Phialide and conidia at the tips with papaphyses. h Phialide with conidia at the tips. i Conidia. j Section of stroma showing perithecia. k Perithecium. l Asci and caps. m Part-spores. n Colony obverse on PDA at 25 °C after 2 wk. o Colony reverse on PDA at 25 °C after 2 wk. Scale bars: n, o = 10 mm. a-d = 1 mm. e, j = 200 μm. f, k = 100 μm. g, l = 20 μm. h, i, m = 10 μm.



Figure 4

Moelleriella kanchanaburiensis. a-d Anamorphic stromata containing conidiomata with conidial masses. e-g Section of stroma showing conidiomata. h Phialide and conidium at the tips with papaphyses. i-k. Phialide and conidia at the tips. l Conidia. m Colony obverse on PDA at 25 °C after 2wk. n Colony reverse on PDA at 25 °C after 2 wk. Scale bars: m, n, = 10 mm. a = 5 mm. b-d = 1 mm. e = 200 μ m. f, g = 100 μ m. h = 20 μ m. i-l = 10 μ m.

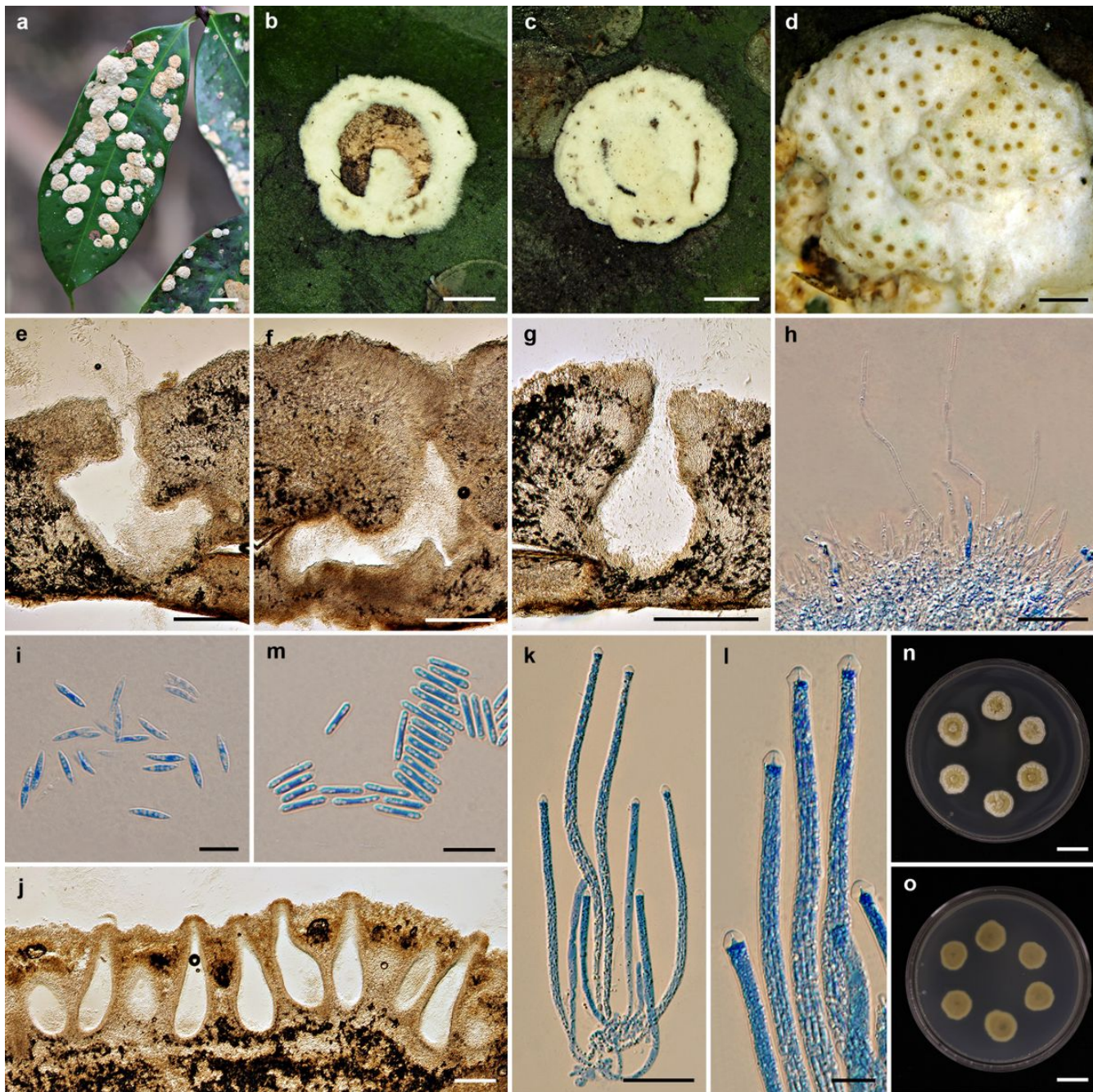


Figure 5

Moelleriella nanensis. a Stromata on upper side of dicotyledonous leaves. b-c Anamorphic stroma containing conidiomata. d Telemorphic stroma. e-g. Section of stroma showing conidioma. h Phialide and conidium at the tips with papaphyses. i conidia. j Perithecia. k Mature asci and developing asci. l Asci and caps. m Part-spores. n Colony obverse on PDA at 25 °C after 3 wk. n Colony reverse on PDA at 25 °C after 3 wk. Scale bars: a, n, o = 10 mm. b-d = 1 mm. e-g, j = 200 μ m. k = 50 μ m. h = 20 μ m. i, l, m = 10 μ m.

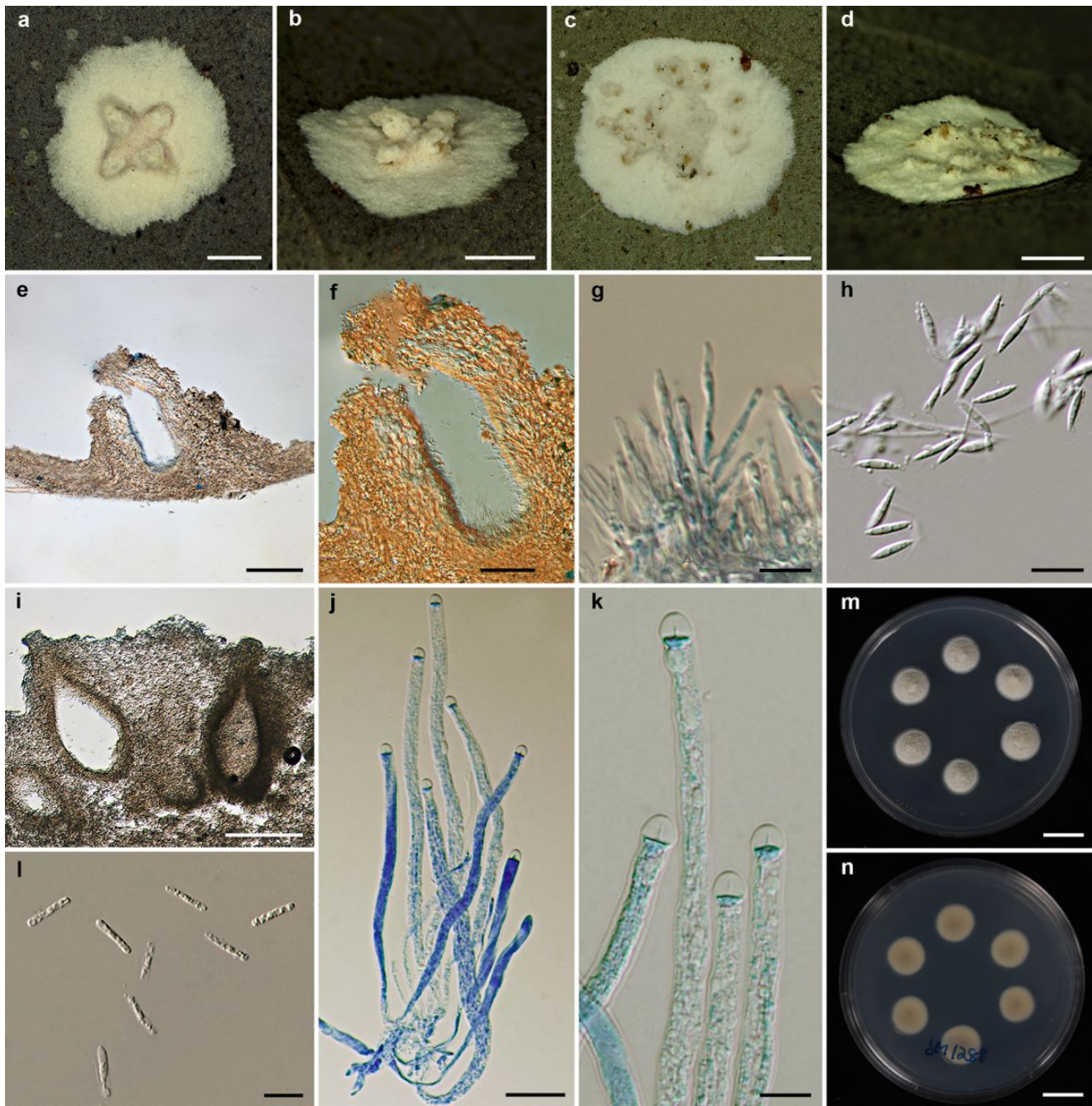


Figure 6

Moelleriella nivea. a, b Anamorphic stroma containing conidiomata. c, d Telomorphic stroma. e-f Section of stroma showing conidioma. g Phialide with conidia at the tips. h conidia. i Perithecia. j Mature asci with developing asci. k Asci and caps. l Part-spores. m Colony obverse on PDA at 25 °C after 1 wk. n Colony reverse on PDA at 25 °C after 1 wk. Scale bars: m, n = 10 mm. a-d = 1 mm. e, i = 200 μ m. f = 100 μ m. j = 20 μ m. g, h, k, l = 10 μ m.

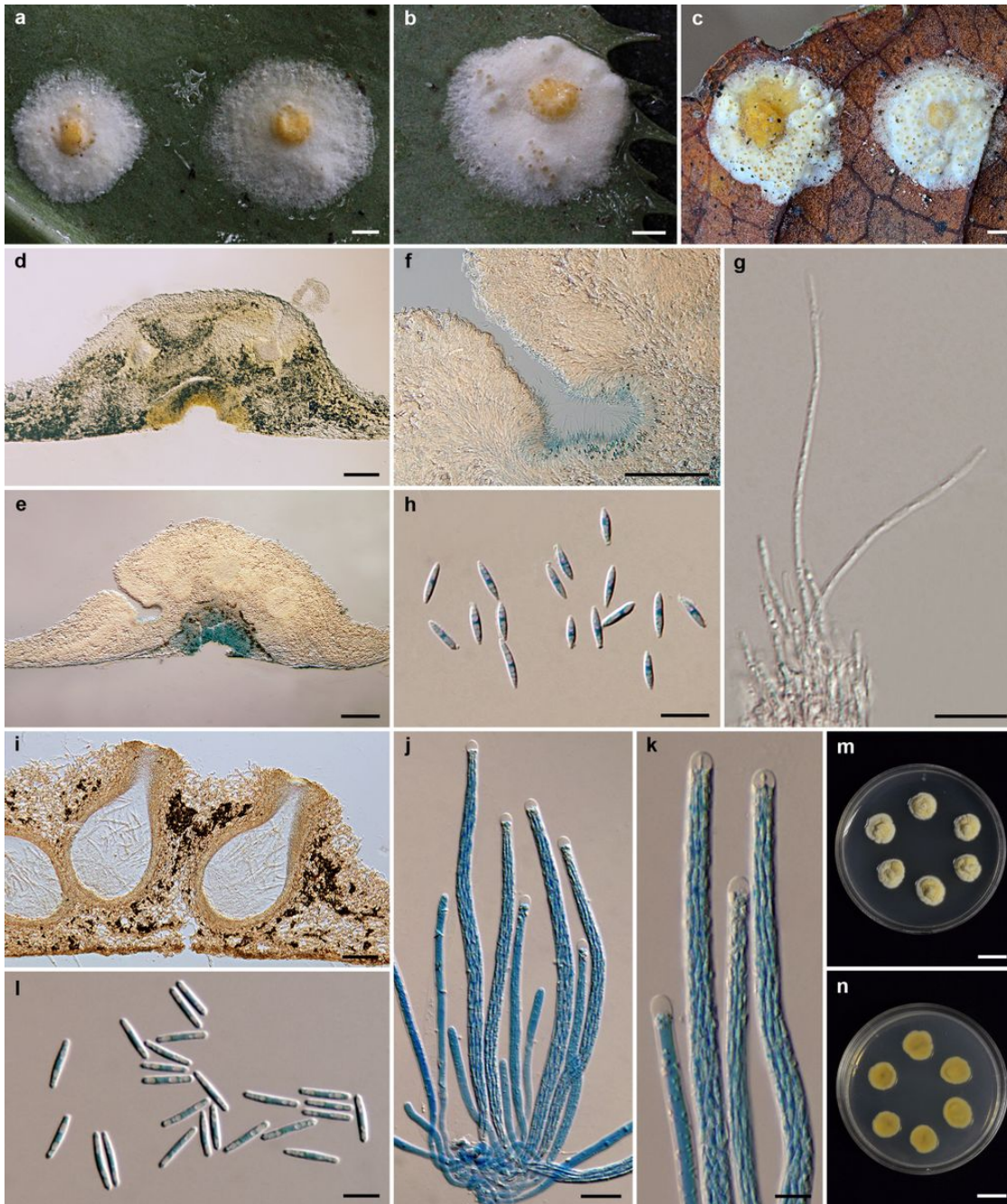


Figure 7

Moelleriella sinensis. a Anamorphic stromata. b, c Anamorphic and telomorphic stromata containing conidiomata. d-f Section of stroma showing conidioma. g Phialide and conidium at the tips with papaphyses. h conidia. i Perithecia. j Mature asci with developing asci. k Asci and caps. l Part-spores. m Colony obverse on PDA at 25 °C after 2 wk. n Colony reverse on PDA at 25 °C after 2 wk. Scale bars: m, n = 10 mm. a-c = 1 mm. d, e = 200 μ m. f, i = 100 μ m. j = 20 μ m. g, h, k, l = 10 μ m.