Novel saprobic *Hermatomyces* species (Hermatomycetaceae, Pleosporales) from China (Yunnan Province) and Thailand

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Abstract

During our survey of the diversity of woody litter fungi in China and Thailand, three *Hermatomyces* species were collected from dead woody twigs of *Dipterocarpus* sp. (Dipterocarpaceae) and *Ehretia acuminata* (Boraginaceae). Both morphology and multigene analyses revealed two taxa as new species (*Hermatomyces turbinatus* and *H. jinghaensis*) and the remaining collections as new records of *H. sphaericus*. *Hermatomyces turbinatus* is characterized by 1) dimorphic conidia, having circular to oval lenticular conidia and 2) turbinate conidia consisting of two columns with two septa composed of 2–3 cells in each column. *Hermatomyces jinghaensis* is characterized by dimorphic conidia, having circular to oval lenticular conidia and clavate or subcylindrical to cylindrical conidia and consisting of one or two columns with 6–8 cells in each column. Phylogenetic analyses of combined LSU, ITS, *tub2*, *tef1*-α and *rpb2* sequence data supports the placement of these new taxa within Hermatomycetaceae with high statistical support.

Keywords

2 new species, hyphomycetes, phylogeny, taxonomy, woody litter fungi
Introduction

Over the past few decades, the number of studies using a molecular-based approach to study microfungal diversity in the greater Mekong subregion (GMS) has increased rapidly, especially on freshwater and woody litter fungi from China (Yunnan Province) and Thailand (Hapuarachchi et al. 2019; Dong et al. 2020; Li et al. 2020; Monkai et al. 2020; Wanasinghe et al. 2020, 2021; Mortimer et al. 2021). Hyde et al. (2018) reported that about 96% of fungi from Thailand are new to science. Feng and Yang (2018) estimated 104,000 fungal species currently exist in Yunnan Province, China; however, only about 6,000 are extant. Therefore, further studies need to be conducted to fill gaps in knowledge regarding the diversity, taxonomy and phylogeny of microfungi in the GMS. Supporting this obligation, we have begun to study plant-based ascomycetes in GMS. The current study accounts for hermatomyces-like ascomycetes recovered from the woody litter in China (Yunnan Province) and Thailand.

_Hermatomyces_ was introduced by Spegazzini (1911) with _H. tucumanensis_ as the type species. Doilom et al. (2017) accommodated _Hermatomyces_ in Lophiotremataceae based on combined LSU, SSU, _tefl_1-α and _rpb2_ sequence data. Later, Hashimoto et al. (2017) validated Hermatomyctaceae (Hermatomyctaceae Locq. 1984 was not validly published, Art. 39.1) to accommodate the genus _Hermatomyces_. This genus is known only by its asexual morph that is characterized by sporodochial conidiomata and dimorphic (lenticular or cylindrical) conidia of one or two types. The lenticular conidia are globose to subglobose, hyaline to pale brown peripheral cells with dark brown central cells, and the cylindrical conidia is hyaline, cylindrical to subcylindrical or turbinate and consisting of 1–4 columns of 2–12 cells (Spegazzini 1911; Tibpromma et al. 2016; Hashimoto et al. 2017; Hyde et al. 2019; Pem et al. 2019; Phukhamsakda et al. 2020).

Based on morphological comparisons and phylogenetic affinities, Koukol et al. (2018) revised _Hermatomyces_ species and described five new species (viz. _H. bifurcatus_, _H. constrictus_, _H. megasporus_, _H. sphaericoides_ and _H. verrucosus_) and one new combination, _H. reticulatus_, from Panama. Accordingly, _H. chromolaenae_, _H. saikhuensis_, _H. tectonae_ were treated as _H. sphaericus_ and _H. subiculosus_, _H. chiangmaiensis_, _H. thailandicus_ were synonymized with _H. reticulatus_, _H. krabiensis_ and _H. indicus_, respectively (Koukol et al. 2018). These are probably species complexes that need more detailed study. Subsequent studies introduced _H. baubiniaie_, _H. biconisporus_, _H. clematidis_, _H. trangensis_ and _H. truncates_ into _Hermatomyces_ (Tibpromma et al. 2018; Hyde et al. 2019; Koukol et al. 2019; Nuankaew et al. 2019; Phukhamsakda et al. 2020). Currently, 24 species are recognized in _Hermatomyces_ (Koukol et al. 2018, 2019; Nuankaew et al. 2019; Delgado et al. 2020; Phukhamsakda et al. 2020; Table 2).

Our investigation led to the discovery of three _Hermatomyces_ species, including two novel species, on dead woody-based substrates. Morphological illustrations and multi-gene phylogenetic analyses with ML, MP and BI of combined LSU, ITS, _tub2_, _tefl_1-α and _rpb2_ sequence data are used to confirm the phylogenetic placement of the novel species within _Hermatomyces_.

**Materials and methods**

**Sample collection, examination and isolation**

Woody litter samples were collected from China (Yunnan Province) during the dry season (December 2019) and Thailand (Tak Province) during the wet season (August 2019). Samples were brought to the laboratory using plastic Ziploc bags. Fungal specimens were then examined using a stereomicroscope (Olympus SZ61, China). Pure cultures were obtained via single spore isolation on potato dextrose agar (PDA) following the methods described in Senanayake et al. (2020). Cultures were incubated at 25 °C for three weeks. Micro-morphological structures were photographed using a Nikon compound microscope (Nikon ECLIPSE Ni) fitted with a Canon (EOS 600D) digital camera. Measurements were taken using the Tarosoft (R) Image Frame Work program. Figures were processed using Adobe Photoshop CS6. Type specimens were deposited in the herbarium of Cryptogams Kunming Institute of Botany Academia Sinica (KUN-HKAS). Ex-type living cultures were deposited at the Culture Collection of Mae Fah Luang University (MFLUCC) and Kunming Institute of Botany Culture Collection (KUMCC).

**DNA extraction, amplification and sequencing**

DNA extraction, amplification, sequencing, sequence alignment and phylogenetic analyses follow the methods of Dissanayake et al. (2020) with the following details. Two partial rDNA genes and three protein coding genes were used in our study, including internal transcribed spacer region (ITS) using primer pair ITS5/ITS4 (White et al. 1990), 28S large subunit nuclear ribosomal (LSU) using primer pair LR0R/ LR5 (Vilgalys and Hester 1990), translation elongation factor 1-alpha gene (tef1-α) using primer pair EF1-983F/EF1-2218R (Rehner and Buckley 2005), RNA polymerase II second largest subunit (rpb2) using primer pair fRPB2-5F/fRPB2-7cR (Liu et al. 1999) and β-tubulin (tub2) using primer pair T1/T22 (O’Donnell and Cigelnik 1997). Amplification reactions were performed in a total volume of 25 μL of PCR mixtures containing 8.5 μL ddH$_2$O, 12.5 μL 2× PCR MasterMix (TIANGEN Co., China), 2 μL DNA template and 1 μL of each primer. The PCR thermal cycle program for LSU, ITS, tef1-α and rpb2 were set as described in Tibpromma et al. (2018). The PCR amplification condition of tub2 was set as denaturation at 94 °C for 3 minutes, followed by 35 cycles of denaturation at 94 °C for 45 seconds, annealing at 56 °C for 50 seconds and extension at 72 °C for 1 minute, with a final extension step at 72 °C for 10 minutes. PCR products were sent to the Qingke Company, Kunming City, Yunnan Province, China, for sequencing. Sequences were deposited in GenBank (Table 1).

**Sequence alignment and phylogenetic analyses**

Representative species used in the phylogenetic analyses were selected based on previous publications (Koukol et al. 2018; Nuankaew et al. 2019; Delgado et al. 2020;
| Organism                      | Strain number | GenBank accession numbers | Reference                                |
|------------------------------|---------------|---------------------------|------------------------------------------|
| *Antagallium gloeobum*       | ANM 925       | GQ221879                  | NA                                        |
| *A. parvulum*                | MFLUCC 14-0821| KU922915                  | NA                                        |
| *Hemarthrospermum amphiparum*| CBS           | LRR12664                  | LRR12664                                 |
| *H. amphiparum*              | CBS 146613    | NA                        | LRR12674                                 |
| *H. amphiparum*              | CBS 146612    | NA                        | LRR12675                                 |
| *H. amphiparum*              | CBS 146613    | LRR12662                  | LRR12673                                 |
| *H. amphiparum*              | CBS 146614    | LRR12666                  | LRR12676                                 |
| *H. amphiparum*              | CBS 146615    | LRR12667                  | LRR12677                                 |
| *H. baihiae*                 | MFLUCC 16-0395| MK443378                  | NA                                        |
| *H. indica*                  | KU764693      | MIH20926                  | MIH279063                                |
| *H. keflavicus*              | CCF 5897      | LS398262                  | LS398441                                 |
| *H. keflavicus*              | CCF 5900      | LS398263                  | LS398442                                 |
| *H. lematitis*               | MFLUCC 17-2085| MT214556                  | MT316063                                 |
| *H. convivus*                | CCF 5904      | LS398264                  | LS398443                                 |
| *H. indicus*                 | MFLUCC 14-1143| KU764692                  | KU872754                                 |
| *H. indicus*                 | MFLUCC 14-1144| KU764693                  | KU872755                                 |
| *H. indicus*                 | MFLUCC 14-1145| KU764694                  | KU872756                                 |
| *H. izomatiensis*            | MH 36201      | LC194367                  | LC194483                                 |
| *H. jingbaensis*             | HKAS 112167   | MW989519                  | MW989495                                 |
| *H. krasiensis*              | MFLUCC 16-0249| KX525742                  | KX525758                                 |
| *H. krasiensis* (H. changmaiensis) | MFLUCC 16-2817 | KY555394                  | KY525952                                 |
| *H. megaparum*               | CCF 5897      | NA                        | LS398265                                 |
| *H. megaparum*               | CCF 5908      | LS398266                  | LS398444                                 |
| *H. nanbolensis*             | KUMCC 16-0149 | KY766059                  | KY766061                                 |
| *H. pandanicola*             | MFLUCC 16-0251| KS255743                  | KS255751                                 |
| *H. reticulatus*             | CCF 5893      | LS398267                  | LS398446                                 |
| *H. reticulatus* (H. subiculatus) | MFLUCC 15-0843 | KS255923                 | KS255927                                 |
| *H. phaeoricos*              | CCF 5896      | NA                        | LS398271                                 |
| *H. phaeoricos*              | CCF 5908      | LS398273                  | LS398446                                 |
| *H. phaeoricos*              | CCF 5907      | NA                        | LS398272                                 |
| *H. phaeoricos*              | CCF 5895      | LS398270                  | LS398449                                 |
| *H. phaeoricos*              | PMA 116080    | LS398281                  | LS398454                                 |
| *H. phaeoricos*              | PMA 116081    | NA                        | LS398283                                 |
| *H. phaeoricos*              | PRM 946201    | NA                        | LS398284                                 |
| *H. phaeoricos*              | PRS 4116      | NA                        | LS398275                                 |
| *H. phaeoricos*              | PRS 4105      | NA                        | LS398286                                 |
| *H. phaeoricos*              | PRS 4104      | NA                        | LS398278                                 |
| *H. phaeoricos*              | PRS 4100      | NA                        | LS398277                                 |
| *H. phaeoricos*              | PRS 4106      | NA                        | LS398279                                 |
| *H. phaeoricos*              | PMA 116085    | NA                        | LS398280                                 |
| *H. phaeoricos*              | PMA 116082    | NA                        | LS398285                                 |
| *H. phaeoricos*              | KZP 462       | NA                        | LS398287                                 |
| *H. phaeoricos*              | PRS 4117      | NA                        | LS398276                                 |
| *H. phaeoricos* (H. chromolaenae) | MFLUCC 16-2818 | KY553939                 | NA                                        |
| *H. phaeoricos* (H. saikhuensis) | MFLUCC 16-0266 | KX525740                 | KX525748                                 |
| *H. phaeoricos* (H. saikhuensis) | MFLUCC 16-0267 | KX525374                 | KX525749                                 |
| *H. phaeoricos* (H. teconae) | MFLUCC 14-1140 | KU764695                 | KU764917                                 |
| *H. phaeoricos* (H. teconae) | MFLUCC 14-1141 | KU764696                 | KU764918                                 |
| *H. phaeoricos* (H. teconae) | MFLUCC 14-1142 | KU764697                 | KU764919                                 |

**Table 1.** GenBank accession numbers of sequences used for the phylogenetic analyses.
Phukhamsakda et al. (2020). Sequences were downloaded from GenBank (http://www.ncbi.nlm.nih.gov/), and their accession numbers are listed in Table 1. The newly generated sequences in this study were assembled by BioEdit 7.0.9.0 (Hall 1999). Individual gene regions were separately aligned in MAFFT v.7 web server (http://mafft.cbrc.jp/alignment/server/) (Katoh et al. 2019). The alignments of each gene were improved by manually deleting the ambiguous regions plus gaps and combined using BioEdit 7.2.3. Final alignments containing LSU, ITS, 
tub2, 
tef1-α and 
rpb2 were converted to NEXUS format (.nxs) using CLUSTAL X (2.0) (Thompson et al. 1997) and processed for Bayesian and maximum parsimony analysis. The FASTA format was changed into PHYLIP format via the Alignment Transformation Environment (ALTER) online program (http://www.sing-group.org/ALTER/) and used for maximum likelihood analysis (ML).

ML was carried out in CIPRES Science Gateway v.3.3 (http://www.phylo.org/portal2/; Miller et al. 2010) using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis 2014) with the GTR+GAMMA substitution model and 1,000 bootstrap iterations. Maximum parsimony analysis (MP) was performed in PAUP v. 4.0b10 (Swofford 2002) with the heuristic search option and Tree-Bisection-Reconnection (TBR) of branch-swapping algorithm for 1,000 random replicates. Branches with a minimum branch length of zero were collapsed, and gaps were treated as missing data (Hillis and Bull 1993).

Bayesian analysis was executed in MrBayes v.3.2.2 (Ronquist et al. 2012). The model of evolution was estimated using MrModeltest v. 2.3 (Nylander et al. 2008) via PAUP v. 4.0b10 (Ronquist and Huelsenbeck 2003). The SYM+I+G for LSU and ITS; HKY+I for 
tub2; GTR+I+G for 
tef1-α and 
rpb2 were used in the final command. Markov chain Monte Carlo sampling (MCMC) in MrBayes v.3.2.2 (Ronquist et al. 2012) was used to determine posterior probabilities (PP) (Rannala and Yang 1996; Zhaxybayeva and Gogarten 2002). Bayesian analyses of six simultaneous Markov chains were run for 2,000,000 generations and trees were sampled and printed to output at every 200 generations (resulting in 10,001 total trees). The first 25% of sampled trees were discarded as part of the burn-in procedure, the remaining 7,501 trees were used to create the consensus tree and the average standard deviation of split frequencies was set as 0.01.

Phylogenetic trees were visualized in FigTree v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/; Rambaut 2012), the tree was edited using Microsoft PowerPoint before
### Table 2. Synopsis of the morphological characteristics of *Hermatomyces* species.

| Species                     | Lenticular conidial size (μm) | Cylindrical / turbinate conidial feature | Host | Country | Reference |
|-----------------------------|-------------------------------|-----------------------------------------|------|---------|-----------|
|                             |                               | Shape                                    |      |         |           |
|                             |                               | Length × width (μm)                      |      |         |           |
|                             |                               | Number of columns (cells)                |      |         |           |
| *Hermatomyces amphiporus*   | 27–36(–38) × 18–29(–31)       | Cylindrical, pyriform or turbinate       |      |         |           |
| *H. bahnsiae*               | 25–36 × 15–20                 | Cylindrical                              | 20–28 × 8–11                              | 1 (2–3-septate) | *B. variegata* | Thailand | Hyde et al. (2019) |
| *H. bicornisporus*          | 28–34 × 15–25                 | Cylindrical                              | 32–39 × 14.5–26                           | 1–2 (3–4 cells) | *Pandanus* sp. | China     | Tibpromma et al. (2018) |
| *H. bifurcatus*             | (24–)30–36.5(–41) × (18–)21.5–26(–28) | Cylindrical Apex: 7–16 × 7–12 Basal: 9.4–13.5, 18.5 | 2 (2–3 cells) | Unknown | Panama | Koukol et al. (2018) |
| *H. chromolaenae*           | 9.2–10.4 × 10.2–11.5          | NA                                       | NA  | NA      | *Chromolaena odorata* | Thailand | Tibpromma et al. (2017) |
| *H. clematis*               | 30–45 × 24–31                | Cylindrical                              | 29.5–35 × 12–14                           | 1–2 (5–6 cells) | *Clematis sikkmensis* | Thailand | Phukhamsakda et al. (2020) |
| *H. constrictus*            | (22–)32.5–29.5 × 19.25–23.5(–27.5) | Cylindrical Lower cells: (20–)24–30.5(–37) × 12–17 Upper cells: (16–)20–26(–30) × 8–14 | 1 (2 cells) | *B. variegata* | Panama | Koukol et al. (2018) |
| *H. dimorphus*              | 35–55 × 15–20                 | Cylindrical                              | 15.4– 20 × 10–15                          | 4 (7 cells) | Unknown | India | Rao and de Hoog (1986) |
| *H. indicus*                | 18–30 × 11.5–19               | Turbinate                                | 22.4–35.4 × 13.4–21.6                     | 2 (6–7 cells) | *Phoenix rugosa* | India | Prasher and Prasher (2014) |
| *H. izoumotoensis*          | 30–36 × 20–27                 | Cylindrical                              | 20.5–33 × 7–12.5                         | 1–2 (3–7 cells) | Unknown | Japan | Hashimoto et al. (2017) |
| *H. jingbaensis*            | 30–40 × 25–30                 | Clavate, subcylindrical                   | 33.43 × 11–13                            | 1–2 (6–8 cells) | Unknown | China | This study |
| *H. krubensis*              | 24.3–32.5 × 12.1–21.3         | Cylindrical                              | 20.4–26.4 × 8.6–19.7                     | 1–2 (2–3 cells) | *P. odorifer* | Thailand | Tibpromma et al. (2016) |
| *H. megasporus*             | (45–)49.5 × 56(–59) × (31)–37–46 | Cylindrical (37–)49.5–60.5(67– ) × 18–28–32 | 2 (5–6–7–10 cells) | Unknown | Panama | Koukol et al. (2018) |
| *H. nahanheensis*           | 20.2–25.1 × 16.6–20.7         | Cylindrical                              | 15.5–26.8 × 12.1–18.2                    | 1–2 (2–3 cells) | *P. sp.* | China | Hyde et al. (2017) |
| *H. pandanicola*            | 12–15.7 × 20–30.1             | Cylindrical                              | 13.2–20.6 × 8.9–11.9                     | 2 (2 cells) | *P. odorifer* | Thailand | Tibpromma et al. (2016) |
| *H. reticulatus*            | 3–40(–45) × 25–34(–41)        | NA                                       | NA  | NA      | Unknown | Thailand, Panama | Hyde et al. (2016); Koukol et al. (2018) |
| *H. saikhuensis*            | 14.2–21.4 × 11.2–19.5         | NA                                       | NA  | NA      | *P. odorifer* | Thailand | Tibpromma et al. (2016) |
| *H. sphaericoides*          | (20.5–)24.5–28(–31) × (20–)23–26(–29) | NA                                       | NA  | NA      | Unknown | Panama | Koukol et al. (2018) |
| *H. sphaericus*             | (PMA 116080) (21–)24/29–32.5(–32.5) × (18–)21–27(–31.5) | NA                                       | NA  | NA      | Various host plants | Tropical or subtropical | Koukol et al. (2018) |
| *H. sphaericus*             | 27–29 × 26–28                 | NA                                       | NA  | NA      | *Dipterocarpus sp., Elretia acuminata* | China, Thailand | This study |
| *H. tecoma*                 | (23–)26–29(–33) × (19–)23–25(–28) | Cylindrical (27–)31–32(–35) × (21–)23 | 2 (6 cells) | *Tectona grandis* | Thailand | Doilom et al. (2017) |
| *H. tranigenus*             | 27.5–35 × 25–32.5             | NA                                       | NA  | NA      | *Aegora pinnata* | Thailand | Niuankaew et al. (2019) |
| *H. truncates*              | (26–)31.5–36.5(–37) × 22–27(–30) | Cylindrical Lower cells: 14–22.5(–28) × 8.5–14.5 Upper cells: 12–18–30 × 6–18–12.5 | 1 (2–3 cells) | *A. carambola* | Ghana, Panama | Koukol et al. (2019) |
| *H. tucumanensis*           | (22–)27–35 × 18–25            | Oblclavate or subcylindrical             | (21–)23–26(–28.5) × 7–14                 | 2 (3–6 cells) | Unknown | Panama | Koukol et al. (2018) |
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being saved in PDF format and finally converted to JPG format using Adobe Illustrator CS6 (Adobe Systems, USA). The finalized alignments and trees were deposited in TreeBASE, submission ID: TB2:S28514 (http://purl.org/phylo/treebase/phylows/study/TB2:S28514).

Ex-type strains are indicated with superscript “T”, and newly generated sequence is shown in bold. NA represents sequences that are unavailable in GenBank.

**Abbreviations:**

- ANM: A.N. Miller;
- BCC: BIOTEC Culture Collection, Bangkok, Thailand;
- CBS: Centraal Bureau voor Schimmel cultures, Utrecht, The Netherlands;
- CCF: Culture Collection of Fungi, Charles University, Prague, Czech Republic;
- HKAS: The herbarium of Cryptogams Kunming Institute of Botany Academia Sinica;
- KH: K. Hirayama;
- KUMCC: Culture Collection of Kunming Institute of Botany, Kunming, China;
- KZP: O. Koukol;
- MFLUCC: Mae Fah Luang University Culture Collection, Chiang Rai, Thailand;
- PMA: Herbarium of the University of Panama, Panama City, Panama;
- PRC: Herbarium of the Charles University, Prague, Czech Republic;
- PRM: Herbarium of the National Museum, Prague, Czech Republic.

| Species          | Lenticular conidia size (μm) | Cylindrical / turbinate conidia feature | Host      | Country  | Reference               |
|------------------|------------------------------|----------------------------------------|-----------|----------|-------------------------|
| *H. turbinatus*  | 24–30 x 17–21                | Turbinate 27–36 x 19–28 2 (2–3 cells) | Diploporus sp. | Thailand | This study              |
| *H. uniseriatus* | 27–36 x 15.5–24              | Cylindrical 19–34 x 10–12.5 1 (3–4 cells) | Smilac campestris | Argentina | Leão-Ferreira et al. (2013) |
| *H. verrucosus*  | 23–30(–39) x 21–29.5         | NA NA NA | Unknown | Panama   | Koukol et al. (2018)    |

NA: absent

**Results**

**Phylogenetic analysis**

The phylogenetic analysis was conducted using 57 strains in Hermatomyctaceae, and two outgroup taxa *Anteaglonium globosum* (ANM 925.2) and *A. parvulum* (MFLUCC 14-0821) in Pleosporales (Table 1). The aligned sequence matrix comprised five gene regions (LSU: 887 bp, ITS: 530 bp, *tub2*: 606 bp, *tefl*-α: 952 bp and *rpb2*: 1,028 bp) and a total of 4,003 characters (including gaps), of which 3,207 characters were
Figure 1. Phylogenetic RAxML tree based on analysis of a combined LSU, ITS, tub2, tef1-α and rpb2 and dataset. Bootstrap support values for ML and MP equal to or higher than 75% and Bayesian PP equal to or greater than 0.95 are shown at nodes. Hyphens (--) represent support values less than 75% / 0.95 BYPP. The ex-type strains are in bold and the new isolate in this study is in blue bold. The tree is rooted with Anteaglonium globosum (ANM 925.2) and A. parvulum (MFLUCC 14-0821). The scale bar represents the expected number of nucleotide substitutions per site.
constant, 174 variable characters were parsimony-uninformative and 622 characters were parsimony-informative. The Kishino-Hasegawa test shows length = 1,388 steps with CI = 0.671, RI = 0.884, RC = 0.593 and HI = 0.329. The RAxML analysis of the combined dataset yielded a best scoring tree with a final ML optimization likelihood value of -13406.55506. Estimated base frequencies were as follows: A = 0.241874, C = 0.266701, G = 0.257552, T = 0.233873; substitution rates AC = 1.188604, AG = 4.826453, AT = 1.273226, CG = 0.855218, CT = 11.409386, GT = 1.00; gamma distribution shape parameter $\alpha = 0.16102$.

In the phylogenetic tree obtained from ML, MP and BI analysis (Fig. 1) the maximum likelihood analysis resulted in trees largely with similar topology and clades as in the maximum parsimony and Bayesian analyses. The new species, *Hermatomyces turbinatus*, is sister to *H. nabanheensis* (KUMCC 16-0149) with high support (94% ML, 91% MP and 1.00 BYPP, Fig. 1). *Hermatomyces jinghaensis* is nested between *H. trangensis* and *H. clematidis* with a strongly supported monophyletic group (98% ML, 92% MP, 1.00 PP; Fig. 1). New isolates of *H. sphaericus* (KUMCC 20-0231; MFLUCC 21-0036) clustered with remaining *H. sphaericus* strains as a monophyletic group (Fig. 1). The topology of the phylogenetic tree is in accordance with recent phylogenetic studies discussing species in Hermatomycetaceae (Nuankaew et al. 2019; Phukhamsakda et al. 2020).

**Taxonomy**

*Hermatomyces turbinatus* G.C. Ren & K.D. Hyde, sp. nov.

MycoBank No: 558166
Facesoffungi Number No: FoF09735

Figure 2

**Etymology.** Referring to the turbinate shape of the conidia.

**Holotype.** HKAS 112724.

**Description.** Saprobic on woody litter of *Dipterocarpus* sp. (Dipterocarpaceae)

**Sexual morph** Undetermined. **Asexual morph** Colonies on natural substrate forming sporodochial conidiomata, superficial, scattered, small groups, circular or oval, sterile mycelial outer zone enclosing a black-brown velvety margin, sparse, black sporulating center, shiny, glistening, circular or oval, conidia readily liberated when agitated. *Mycelium* superficial, branched, septate, hyaline to pale brown, 2–3 μm wide. *Conidiophores* 6–8 × 2–3 μm, micronematous, straight or flexuous, smooth, short, pale brown. *Conidiogenous cells* 3–5 × 2–3 μm, monoblastic, integrated, terminal, determinate, often arising directly on the superficial mycelium, subsphefical, ovoid or ampulliform, hyaline to pale brown, smooth finely verruculose. *Conidia* dimorphic, solitary, smooth-walled. *Lenticular conidia* 24–30 × 17–21 μm (x = 27 × 20 μm, n = 20), 12–15 μm thick, thick-walled, circular to oval in front view, smooth, solitary, muriform, central cells dark brown to black, peripheral cells hyaline to pale brown,
forming a weakly ring, sometimes slightly constricted at septa, obovoid or oblong in lateral view, arranged in 2 rows, a row of composed of 4–6 cells, end cells pale brown to hyaline, middle cells dark brown. Turbinate conidia turbinate, pyriform, 27–36 μm
in length, 19–28 μm wide in broadest part of lower cells, (x = 32 × 23 μm, n = 20), asymmetrical with the upper cells smaller than lower cells, thick-walled, smooth, septate, constricted distinct at septa, consisting of two columns with two septa composed of 2–3 rectangular to globose cells in each column, usually upper part of terminal cells dark brown, becoming hyaline towards the lower side, two cells hyaline in the lower cells swollen with oil globules.

**Known host and distribution.** *Dipterocarpus* sp. (Thailand).

**Culture characteristics.** Colonies on PDA, reaching 30–40 mm diam., after 3 weeks at 25–30 °C, circular, convex with papillate and radially furrowed at the center, rough, labate, crenate edge, fluffy, dense, gray black, in reverse darkens at the center, pale brown to gray at edge.

**Material examined.** Thailand, Tak Province. Ban Na Sam Ngao District, on woody litter of *Dipterocarpus* sp. (Dipterocarpaceae), 22 August 2019, G. C. Ren, TSY04 (HKAS 112724, **holotype**), ex-type living culture, MFLUCC 21-0038.

**Notes.** *Hermatomyces turbinatus* is introduced as a new species based on its distinct morphology, which is supported by phylogenetic analyses. In the phylogenetic analyses, *H. turbinatus* is distinct from extant species in this genus and formed a sister clade to *H. nabanheensis* with strong support (94% ML, 91% MP, 1.00 PP; Fig. 1). *Hermatomyces turbinatus* differs from *H. nabanheensis* in having turbinate conidia with two columns, while *H. nabanheensis* has cylindrical conidia with one or two columns. *Hermatomyces turbinatus* has two conidial types, and its lenticular conidia are similar to *H. tectonae* in shape and size. However, the turbinate conidia of *H. turbinatus* have 2 columns of 2–3 cells in each column, while the turbinate conidia of *H. tectonae* have 2 columns of 3 cells in each column. We also compared the morphological characters of *H. turbinatus* to other species of *Hermatomyces* (Table 2). Despite no molecular data being available for the three species viz. *H. dimorphus*, *H. uniseriatus* and *H. truncates*, *H. turbinatus* nonetheless differs from these species in conidial characteristics (Table 2).

**Hermatomyces jinghaensis** G.C. Ren & K.D. Hyde, sp. nov.
MycoBank No: 558165
Facesoffungi Number No: FoF09736
Figure 3

**Etymology.** The species epithet “jinghaensis” refers to the location where the species was collected.

**Holotype.** HKAS 112167.

**Description.** Saprobic on unidentified woody litter. **Sexual morph** Undetermined. **Asexual morph** Colonies on natural substrate forming sporodochial conidiomata, superficial, scattered, small groups, circular, sterile mycelial outer zone enclosing a black velvety margin, dense, thick, black sporulating center, shiny, glistening, circular or oval, conidia readily liberated when agitated. Mycelium superficial, branched, septate,
Figure 3. *Hermatomyces jinghaensis* (HKAS 112167, holotype) **a, b** sporodochia on natural substrate **c** vertical section of sporodochium **d** conidiophores **e, f** conidiogenous cells **g–l** cylindrical conidia **m–s** mature lenticular conidia. Scale bars: 50 μm (**c**); 30 μm (**d**); 20 μm (**e–r**); 30 μm (**s**).

hyaline to pale brown, 2–3 μm wide. *Conidiophores* 30–45 × 2–3 μm, mononematous, cylindrical, straight or flexuous, smooth, pale brown. *Conidiogenous cells* 4–6 × 2–3 μm, monoblastic, integrated, terminal, determinate, often arising directly on the superficial mycelium, cylindrical, ampulliform, hyaline to pale brown, smooth finely verrucose. *Conidia* dimorphic solitary, smooth-walled. *Lenticular conidia* 30–40 × 25–30 μm.
Novel saprobic *Hermatomyces* species from the GMS

(x = 37 x 28 μm, n = 20), 21–25 μm thick, thick-walled, circular to oval in front view, smooth, solitary, muriform, central cells brown to dark brown, peripheral cells hyaline to subhyaline, forming a wide and distinct ring, sometimes slightly constricted at septa, obvoid or oblong in lateral view, central cells brown to dark brown, peripheral cells pale brown to brown. *Cylindrical conidia* 33–43 μm in length, 11–13 μm wide in broadest part of lower cells (x = 39 x 12 μm, n = 20), clavate or subcylindrical, straight or flexuous, septate, constricted distinct at the septa, with large guttules, consisting of one or two columns, each column with 6–8 cells, apical cell rectangular to globose, smooth, hyaline, smooth, basal cells acute, rectangular to cylindrical, pale brown.

**Known host and distribution.** Unidentified woody litter (China)

**Material examined.** China, Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Jinghong, Jingha (21°78.06’N, 101°05.61’E), on unidentified woody litter, 19 December 2019, D.N. Wanasinghe, DW57 (HKAS 112167, holotype), no living culture.

**Notes.** *Hermatomyces jinghaensis* is introduced as a new species based on its distinct morphology and the phylogenetic results of a combined LSU, ITS, *tub2*, *re11-x* and *rpb2* dataset. *Hermatomyces jinghaensis* nested with *H. clematidis* and *H. trangensis* in a strongly supported monophyletic group (99% ML, 100% MP, 1.00 PP; Fig. 1). *Hermatomyces jinghaensis* is characterized by both lenticular and cylindrical conidia. *Hermatomyces jinghaensis* differs from *H. clematidis* in having cylindrical conidia with one or two columns, each of which has 6–8 cells with large guttules, while the latter has 5–6 cells for each column conidia. *Hermatomyces trangensis* differs from *H. jinghaensis* in having only lenticular conidia.

*Hermatomyces sphaericus* (Sacc.) S. Hughes 1953.

Mycobank No: 298410
Facesoffungi Number No: FoF05259
Figure 4

**Description.** Saprobic on woody litter of *Dipterocarpus* sp. (Dipterocarpaceae) and *Ehretia acuminata* (Boraginaceae). **Sexual morph** Undetermined. **Asexual morph** Colonies on natural substrate forming sporodochial conidiomata, superficial, circular or irregular, scattered or crowded, consisting of a velvety, dense, annular, gray brown, sterile mycelial outer zone and a black, glistening, abundantly sporulating granulose center, with conidia readily liberated when agitated. *Mycelium* 2–2.5 μm wide, superficial, composed of a tightly network of branched, separtate, smooth or finely verruculose, hyaline or pale brown hyphae. *Conidiophores* 10–13 x 2–4 μm (x = 12 x 3 μm, n = 10) micronematous, cylindrical or forked, smooth, hyaline or pale brown, often corresponding to conidiogenous cells. *Conidiogenous cells* 5–8 x 3–5 μm (x = 7 x 4 μm, n = 20), monoblastic, integrated, terminal, cylindrical, hyaline to pale brown, smooth or finely verruculose. *Conidia* of one type, 27–29 x 26–28 μm (x = 28 x 27 μm, n = 30) μm, 19–24 μm thick, solitary, lenticular, globose, subglobose in front view, muriform, smooth, central cells brown, dark brown, outer ring of peripheral cells narrow, pale brown to brown, often constricted at septa, disk-shaped in lateral view,
Figure 4. *Hermatomyces sphaericus* (HKAS 112725) a, b colonies on the natural substrate c mycelia d–g young conidia h–k mature conidia (h–j surface view k thickness view) l germinated conidium m, n culture characters on PDA. Scale bars: 1000 μm (a); 200 μm (b); 20 μm (c–i, l); 30 μm (j, k); 3 cm (m, n).

consisting of two rows, each row with 4–6 cells, hyaline to light brown at lower and upper cells, middle cells brown to black brown.

**Known host and distribution.** Tropical and subtropical regions of Central and South America, Africa, Asia, Oceania and North America. The species were found
as saprobes on Acanthaceae, Apocynaceae, Arecaceae, Asteraceae, Dipterocarpaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Leguminosae, Mimosaceae, Nyctaginaceae, Oxalidaceae, Pandanaceae, Pinaceae, Rhamnaceae, and Sterculiaceae (Zhang et al. 2009; Koukol et al. 2018, 2019).

**Culture characteristics.** Colonies on PDA, reaching 35–40 mm diam., after 3 weeks at 25–30 °C, with circular, umbonate, fluffy, velvety, entire edge, a circular raised band, gray white, in reverse dark gray, black toward the center.

**Material examined.** Thailand, Tak Province, Tha Song Yang District, on woody litter of *Dipterocarpus* sp. (Dipterocarpaceae), 22 August 2019, G. C. Ren, T903 (HKAS 112725), living culture, MFLUCC 21-0036; China, Yunnan Province, Xishuangbanna (21°55.19'N, 101°15.24'E), on woody litter of *Ehretia acuminata* (Boraginaceae), 4 August 2020, G. C. Ren, JH39 (HKAS 112166), living culture, KUMCC 20-0231.

**Notes.** The characters of our new strain of *Hermatomyces sphaericus* (KUMCC 20-0231, MFLUCC 21-0036) are similar to the type collection (K(M)–IMI 37763) in having gray black to black sporodochia, mononematous, pale brown, smooth, monoblastic, integrated, terminal, cylindrical, hyaline to pale brown conidiogenous cells and globose to subglobose conidia (Hughes 1953). A multigene phylogeny indicates that novel strains clustered within the *H. sphaericus* clade (Fig. 1). We name our strain (KUMCC 20-0231, MFLUCC 21-0036) as *H. sphaericus*, which has been reported from different plant families and genera (Koukol et al. 2018). However, we consider this might be a species complex that need further detailed studies. Our study provides the new host records of *H. sphaericus* on *Dipterocarpus* sp. (Dipterocarpaceae) and *Ehretia acuminata* (Boraginaceae), and updates sequence data for the new collections of *H. sphaericus*.

**Discussion**

This study introduces two new species of woody-based litter fungi; *Hermatomyces jinghaensis* from Yunnan, China and *Hermatomyces turbinatus* on *Dipterocarpus* sp. from Thailand. We also report for the first time two new records of *H. sphaericus* on *Dipterocarpus* sp. and *Ehretia acuminata* in China and Thailand.

*Hermatomyces* (Hermatomycetaceae) is different from other similar genera in its sporodochial conidiomata and in having one to two (lenticular and cylindrical conidia) unusual conidial types (Spegazzini 1911). All species of *Hermatomyces* have lenticular conidia with similar characteristics, whereas some species have cylindrical and turbinate conidia, which have greater variance in shape, size, number of columns and cells. Koukol et al. (2018, 2019) have reported that multiple species may occur together on a single sample, a phenomenon we observed, which may complicate morphological identification and separation for culturing. Therefore, molecular sequence data are more reliable for the identification of *Hermatomyces* species (Tibpromma et al. 2016, 2017, 2018; Nuankaew et al. 2019; Phukhamsakda et al. 2020).
*Hermatomyces sphaericus* was introduced by Hughes (1953), which may be the most widespread of species in *Hermatomyces* distributed across many subtropical and tropical regions worldwide (Wijayawardene et al. 2014; Doilom et al. 2017; Koukol et al. 2018, 2019; Hyde et al. 2019; Jayasiri et al. 2019; Nuankaew et al. 2019; Phukhamsakda et al. 2020). This species has been reported as saprobic on dead plant tissues of several host families (Tibpromma et al. 2016, 2017; Doilom et al. 2017; Jayasiri et al. 2019). In addition, Koukol et al. (2018) reported that *H. sphaericus* (ARIZ: PS0053) was isolated from seeds of *Apeiba membranacea* (Malvaceae), suggesting this species could be an endophyte. Previous studies have indicated that *H. sphaericus* is not restricted to any single host (Koukol et al. 2018, 2019), whereas other species of *Hermatomyces* are saprobic on a limited number of hosts and are limited to specific regions (Rao and de Hoog 1986; Leão-Ferreira et al. 2013; Prasher and Prasher 2014; Hyde et al. 2016, 2017, 2019; Tibpromma et al. 2016, 2017, 2018; Doilom et al. 2017; Hashimoto et al. 2017; Koukol et al. 2018, 2019; Nuankaew et al. 2019; Delgado et al. 2020; Phukhamsakda et al. 2020; Table 2). In this study, our new strains of *H. sphaericus* had slight morphological differences in lenticular conidia size compared to the type strains and other strains of *H. sphaericus* (Hughes 1953, Table 2). As reported by Koukol et al. (2018), *H. sphaericus* is a plurivorous species, and accordingly the phenotypic variation among strains could be influenced by environmental factors and culture conditions or it could have speciated in isolated populations (Hyde et al. 2020).

Species delineation in *Hermatomyces*, especially in the *H. sphaericus* clade, is subject to much controversy due to species inconsistency in morphological and phylogenetic status. Koukol et al. (2018) synonymized *H. chromolaenae, H. saikh-uensis* and *H. tectonae* under *H. sphaericus* based on morphological and molecular comparisons and suspected that *H. pandanicola* could either be a hybrid species or incorrect sequences were used in the analysis. Koukol et al. (2019) considered that during isolation of *H. biconisporus*, a conidium of *H. sphaericus* might have been taken instead, leading to contamination when extracting DNA and the misinterpretation of its taxonomic placement. Phukhamsakda et al. (2020) further confirmed that *H. biconisporus, H. pandanicola* and *H. sphaericus* should be treated as the same species based on Genealogical Concordance Phylogenetic Species Recognition (GCPSR) analysis.

*Hermatomyces* had long been treated as “incertae sedis” within Ascomycota (Wijayawardene et al. 2012). Doilom et al. (2017) placed *Hermatomyces* in Lophiotremataceae based on phylogenetic analyses, and consequently, Hashimoto et al. (2017) revised the family Lophiotremataceae based on morphological observations and phylogenetic analyses, and *Hermatomyces* was accepted in the family Hermatomycetaceae, as monophyletic. Recent studies and our study indicate *Hermatomyces* to be highly polyphyletic, and *Hermatomyces* morphology has evolved, which is mainly characterized by lenticular and cylindrical conidia (Fig. 1; Koukol et al. 2018, 2019; Hyde
et al. 2019; Phukhamsakda et al. 2020). Support for a single \textit{H. sphaericus} species (Fig. 1) lacks internal statistical support and includes \textit{H. biconisporus}, \textit{H. chromolaenae}, \textit{H. pandanicola}, \textit{H. saikhuensis} and \textit{H. tectonae} and we suspect that this is a species complex. Tibpromma et al. (2018) also noted that \textit{H. sphaericus} could be a species complex including several species and did not accept the synonymy of \textit{H. saikhuensis} and \textit{H. tectonae} in \textit{H. sphaericus} owing to their significant base-pair differences.

In this study, we combined two non-translated loci (LSU, ITS) and three protein-coding regions (\textit{tub2}, \textit{tef1-\alpha} and \textit{rpb2}) to carry out phylogenetic analysis for \textit{Hermatomyces} species in order to validate phylogenetic placement of the taxa within \textit{Hermatomyces}. In our phylogenetic analyses, \textit{H. tectonae}, \textit{H. chromolaenae}, \textit{H. biconisporus}, \textit{H. pandanicola} and \textit{H. saikhuensis} grouped together with strains of \textit{H. sphaericus} (PRC 4100, PRC 4104, PMA 116081). \textit{Hermatomyces saikhuensis} and \textit{H. chromolaenae} are characterized by one conidium type (lenticular) similar to \textit{H. sphaericus}, however, they differ in the shape, color and size of conidia (Tibpromma et al. 2016, 2017; Table 2). \textit{Hermatomyces tectonae}, \textit{H. biconisporus} and \textit{H. pandanicola} are characterized by dimorphic conidia which differ from \textit{H. sphaericus} (Tibpromma et al. 2016, 2018; Doilom et al. 2017; Koukol et al. 2018; Table 2). \textit{Hermatomyces sphaericus} (PRC 4100, PRC 4104, PMA 116081) did not have a morphological description for inter-species comparison (Koukol et al. 2018). Further taxon sampling and more sequence data are needed to elucidate this clade.

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