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Texas microfungi: *Hermatomyces amphisporus* (*Pleosporales*, Dothideomycetes) revisited

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The pleosporalean anamorph *Hermatomyces amphisporus* is recorded for the first time from the U.S.A. based on several specimens collected on *Sabal minor* (*Arecaceae*) during mycological surveys carried out in the state of Texas. Phylogenetic analyses of novel DNA sequence data belonging to four nuclear regions (ITS rDNA, EF1-α, RBP2, β-TUB) revealed its taxonomic position within the monotypic family *Hermatomycetaceae* (*Pleosporales*, Dothideomycetes) in congruence with its morphological features. A description of the fungus in culture is provided here for the first time. Interestingly, apart from the lenticular conidia, also cylindrical conidia were formed together with chlamydosporous structures and pycnidia producing hyaline, nonseptate conidia. Further notes on the morphology on natural substrate, ecology and distribution in the U.S.A. and worldwide of this rare fungus are provided.

The recently introduced species *H. bauhiniae*, which presents morphological characteristics different from the typical *Hermatomyces* spp., is found to be based on a confusing description, thus a different genus should be found to accommodate it.

Key words: anamorphic ascomycete, phylogenetic placement, saprobic, taxonomy, genotypic variability, *Hermatomyces bauhiniae*.

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Pleosporální anamorfní druh *Hermatomyces amphisporus* je poprvé zaznamenán z USA z několika sběrů na *Sabal minor* (*Arecaceae*) získaných během mykologických průzkumů ve státu Texas.

Fylogenetické analýzy nově získaných sekvencí ze čtyř jaderných úseků (ITS rDNA, EF1-α, RBP2, β-TUB) ukázaly jeho pozici v rámci monotypické čeledi *Hermatomycetaceae* (*Pleosporales*, Dothideomycetes) ve shodě s jeho morfologickými znaky. Poprvé je u tohoto druhu podán popis morfologie v kultuře. Je zajímavé, že krom čočkovitých konidií se v kultuře tvořily i válcovité konidie spolu s chlamydosporními strukturami a pyknidami, které produkovaly hyalinní jednobuněčné konidie. Zmíněny jsou i další poznámky k morfologii na přirozeném substrátu, ekologii a rozšíření tohoto vzácného druhu v USA a ve světě.

Nedávno popsaný druh *H. bauhiniae*, který se odlišuje svou morfologií od typických zástupců rodu *Hermatomyces*, je dle našeho zjištění založen na zavádějícím popisu a měl by být přeřazen do jiného rodu.

SHORT TAXONOMIC REPORT

Material and methods. The studied specimens were collected during field trips carried out in forested areas of Harris County, southeastern Texas, in 2019. Plant debris samples such as dead leaves of the palm tree *Sabal minor* (Jacq.) Pers. were examined in the field using a hand lens and those showing fungal colonies were briefly washed off under tap water and incubated at room temperature (23–25 °C) for a few days. Further single-spore isolation and morphological studies were performed according to Koukol et al. (2018). Fungal structures were mounted in lactophenol cotton blue and examined under an Olympus BX45 compound microscope. Minimum, maximum, 5^{th} and 95^{th} percentile values were calculated based on 50 measurements of each structure at 1000× magnification and outliers are given in parenthesis. Line drawings were made using a drawing tube (Carl Zeiss, Oberkochen, Germany) and improved in Inkscape (inkscape.org). Specimens are deposited in ILLS (Illinois Natural History Survey Fungarium, Champaign) and living strains in CBS (Westerdijk Fungal Biodiversity Institute, Utrecht) and CCF (Culture Collection of Fungi, Charles University, Prague) (Tab. 1).

DNA was extracted from 2-week old cultures grown on MEA using a Zymo Research Fungal/Bacterial Kit (Zymo Research, Orange, CA, USA). Primer set ITS1F/NL4 (White et al. 1990, O'Donnell 1993) was used to amplify the complete internal transcribed spacer (ITS) and partial nuclear ribosomal large subunit (LSU) regions. Fragments of the genes encoding the elongation factor 1α (EF1-α), the RNA polymerase II second largest subunit (RPB2) and the β-tubulin (β-TUB) were amplified using the primer sets 983F/2218R (O'Donnell & Cigelnik 1997), fRPB2-5F/fRPB2-7cR (Liu et al. 1999) and T1/T22 (Rehner & Buckley 2005), respectively. Further procedures for purifying and sequencing PCR products were carried out following Koukol et al. (2018), and newly obtained sequences were deposited in GenBank (Tab. 1). They were subjected to BLAST searches to first confirm their identity and then added to the ITS, RPB2, EF1-α and β-TUB datasets previously used in Koukol et al. (2018). Model selection and settings for Maximum likelihood (ML) and Bayesian phylogenetic analyses also followed Koukol

Tab. 1. Sequences of specimens and strains of *Hermatomyces amphisporus* generated in this study and their GenBank accession numbers.

Specimen	Strain	GenBank accession numbers			
		ITS-LSU	EF1-α	RPB2	β-TUB
ILLS 82991	CBS 146613	LR812662	LR812657	LR812668	LR812673
ILLS 82994	CBS 146611	LR812663	LR812658	LR812669	LR812674
ILLS 82996	CBS 146610 = CCF 6394	LR812664	–	–	–
ILLS 82997	CBS 146612	LR812665	LR812659	LR812670	LR812675
ILLS 82998	CBS 146614	LR812666	LR812660	LR812671	LR812676
ILLS 82999	CBS 146615 = CCF 6392	LR812667	LR812661	LR812672	LR812677

et al. (2018). Analyses were performed using RAxML v8.2.10 (Stamatakis 2014) implemented on the CIPRES Science Gateway server (Miller et al. 2010) and MrBayes v3.2.6 (Ronquist et al. 2012), respectively.

Hermatomyces amphisporus R.F. Castañeda & Heredia, Cryptog. Mycol. 21(4): 223, 2000 Figs. 1–3

Description on natural substrate. Colonies forming sporodochial conidiomata, superficial, more or less circular, oval or irregular, often confluent, non-subiculate, brown-black, consisting of an orbicular, brown, flattened outer zone surrounding a glistening, granulose, brownish-black sporulating centre where the cylindrical conidia are spotted among the lenticular ones; subiculum lacking or inconspicuous, 200–750 µm diam. which may reach up to 1500 µm when confluent and form large patches 3–6 mm long. Mycelium mostly superficial, composed of more or less compact network of repent, branched, septate, smooth, anastomosing, pale brown to brown hyphae, 2–4.5 µm wide; subicular hyphae short, ascending or repent, undulate or irregularly flexuous, smooth or sparsely verrucose. Conidiophores micronematous, mononematous, cylindrical, erect, subhyaline or pale brown, smooth or finely verrucose, 7–13 × 3–5 µm, often reduced to conidiogenous cells. Conidiogenous cells monoblastic, integrated, terminal, determinate, subhyaline to pale brown or brown, cylindrical or slightly subulate, often arising directly on the superficial mycelium and closely packed together at the fertile centre, globose, subglobose or ampulliform, 3–7 × 3–5 µm. Conidia dimorphic, solitary, dry; lenticular conidia muriform, smooth, broadly ellipsoidal or disk-shape in front view, central cells brown or dark brown to black, peripheral cells subhyaline to pale brown, forming a wide and distinct ring 3–5 µm wide, slightly constricted at the septa or not, ellipsoidal to narrow ellipsoidal in side view with two distinct adpressed halves, each half seen laterally as a row of 5–8 cells, end cells subhyaline to pale brown, middle cells dark brown to

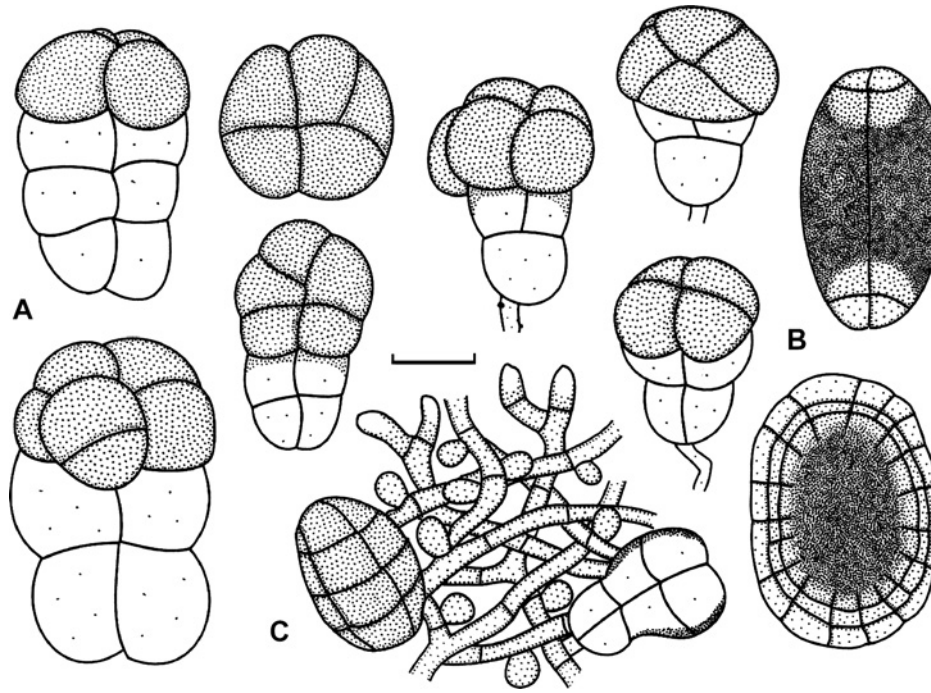


Fig. 1. *Hermatomyces amphisporus* (ILLS 82994). **A** – cylindrical conidia; **B** – lenticular conidia; **C** – young conidia, conidiogenous cells and superficial hyphae. Scale bar = 10 µm. Drawing G. Delgado.

black, 27–36(38) × 18–29(31) µm, 14–20 µm thick; cylindrical conidia turbinate, pyriform, cylindrical or subcylindrical, septate, smooth, 22–38(42) µm long, composed of 6–12 hyaline, cylindrical or swollen cells arranged in two (rarely four) columns, 10–17(21) µm wide, constricted at the septa, sometimes arising from a single basal cell (6)9–13 µm wide at the top; columns ending in a bulbous apex divided into 4 or more apical cells, grey when young, brown when older, 16–23(26) µm wide. Sexual morph unknown.

Description in culture. Colonies on MEA at 25 °C reaching 9–16 mm after 7d, velvety, circular, grey, raised 1–3 mm above the agar surface, margin entire, reverse dull black; sporulation observed after 3 months and only in two (CBS 146611, CBS 146615) out of six strains, conidia similar in size to those on natural substrate but lenticular conidia showing higher variability and distortions. Hyaline multicellular chlamydosporous structures produced intercalary and terminally, potentially originating as strongly distorted lenticular conidia. Coelomycetous synanamorph produced in strains CBS 146610, CBS 146611 and CBS 146615; conidiomata pycnidial, superficial or partially immersed in the agar, solitary or

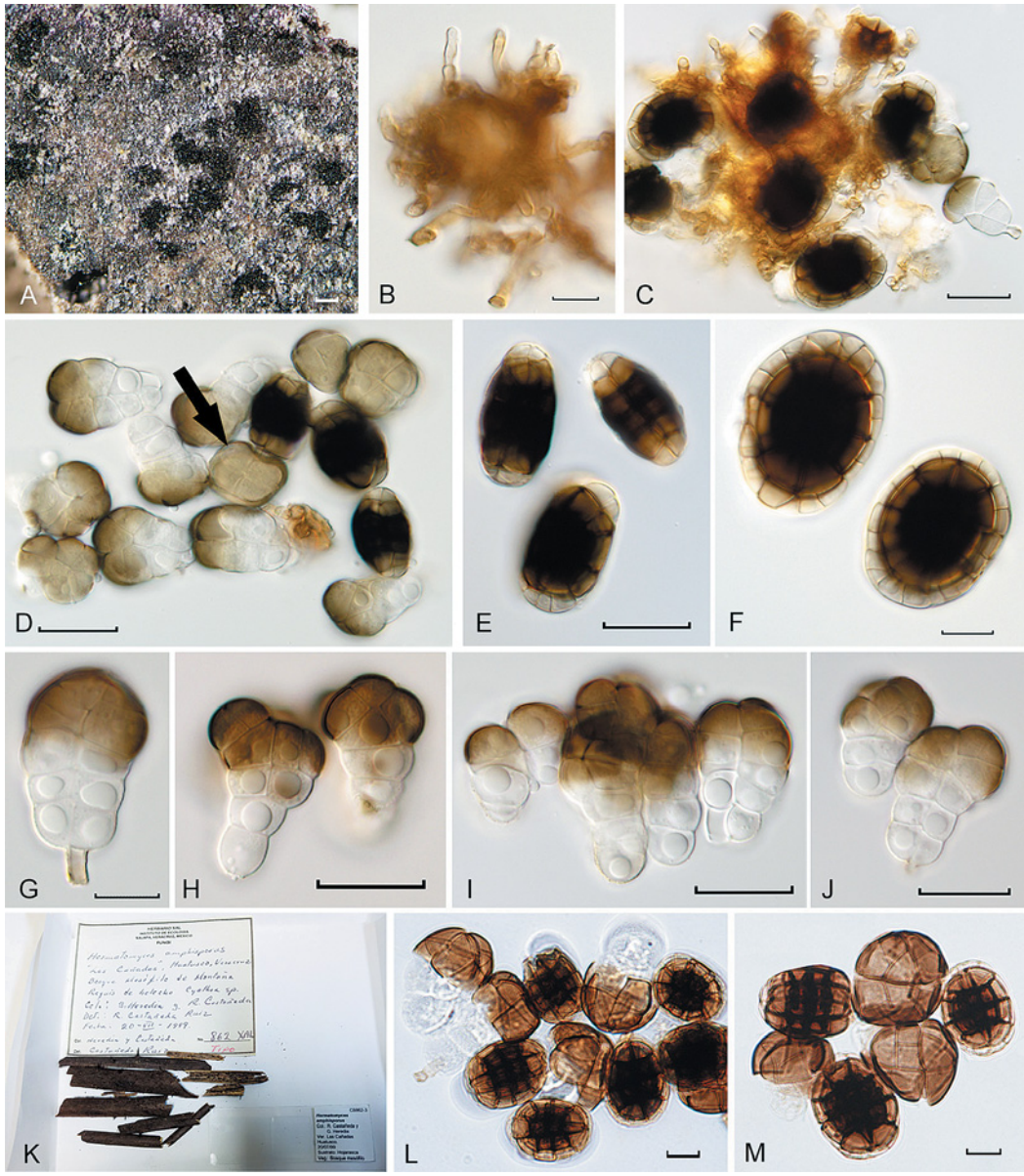


Fig. 2. *Hermatomyces amphisporus* on natural substrate (A–J: ILLS 82996; K–M: XAL 862-2). **A** – colonies on rachides of dead leaves of *Sabal minor*; **B** – subicular hyphae; **C** – fertile part of the sporodochium with both types of conidia; **D** – cylindrical and lenticular conidia, arrow points to a cylindrical conidium with four columns of cells; **E–F** – lenticular conidia; **G–J** – cylindrical conidia in side view; **K** – envelope with holotype of *H. amphisporus*; **L–M** – cylindrical and lenticular conidia in the permanent slide from the holotype. Scale bars: A = 200 µm; B, F = 10 µm; C–E, G–J = 20 µm; L–M = 10 µm. Photos O. Koukol & G. Heredia.

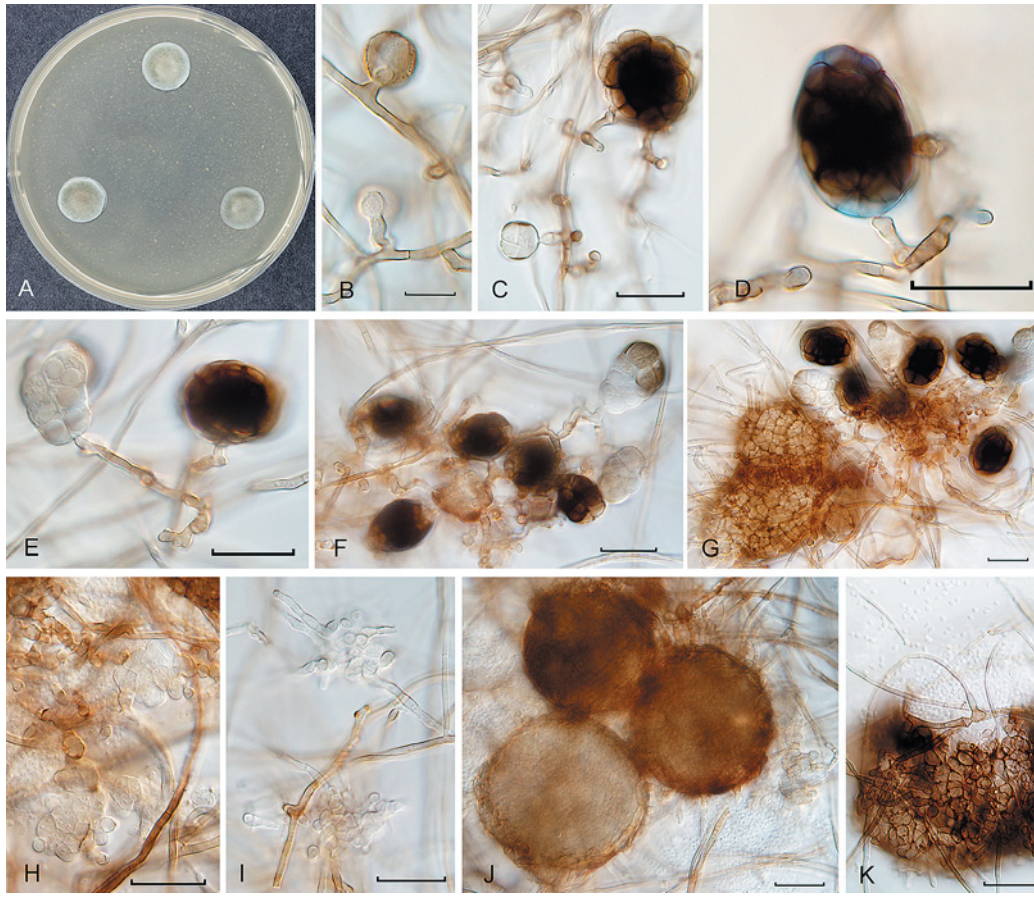


Fig. 3. *Hermatomyces amphisporus* (CBS 146615) in culture. **A** – colonies on MEA; **B–C** – development of lenticular conidia; **D** – lenticular conidium still attached to a conidiogenous cell (mounted in cotton blue); **E–F** – lenticular and cylindrical conidia; **G** – both types of conidia with young pycnidia; **H–I** – chlamydosporous structures; **J–K** – pycnidia with conidia. Scale bars: B = 10 µm; C–K = 20 µm. Photos O. Koukol.

confluent, globose or subglobose, brown, non-ostiolate, 54–72 µm in diam.; pycnidial wall pseudoparenchymatous. Conidia subglobose or oval, thin-walled, smooth, hyaline, aseptate, often produced in white masses covering the tip of pycnidia, 2–3 × 1.5–2 µm.

Notes. A comparison of the Texas specimens with the type material of *H. amphisporus* (Fig. 2 K–M) and the species protologue showed that they agree well in size and shape of cylindrical conidia, the holotype having dimensions of 30–38 × 20–26 µm and 12–13 mm wide at the top of the basal cell (Castañeda &

Heredia 2000). However, colony morphology and lenticular conidia differ in some details from the holotype. The Mexican material has nest-like, olivaceous brown, subiculate sporodochia, apparently with a well-developed, velvety outer zone in contrast with the inconspicuous or almost absent subiculum of the Texas collections (Fig. 2A). Lenticular conidia, on the other hand, are narrower and thinner according to the protologue, being 20–21 µm wide and 12–15 µm thick. Moreover, the cylindrical conidia were originally described as composed of 6–11 cells arranged in four columns. The original drawing and our specimens consistently show mostly two columns of cells, rarely four, which divide into four or more cells at the grey-brown, bulbous apex.

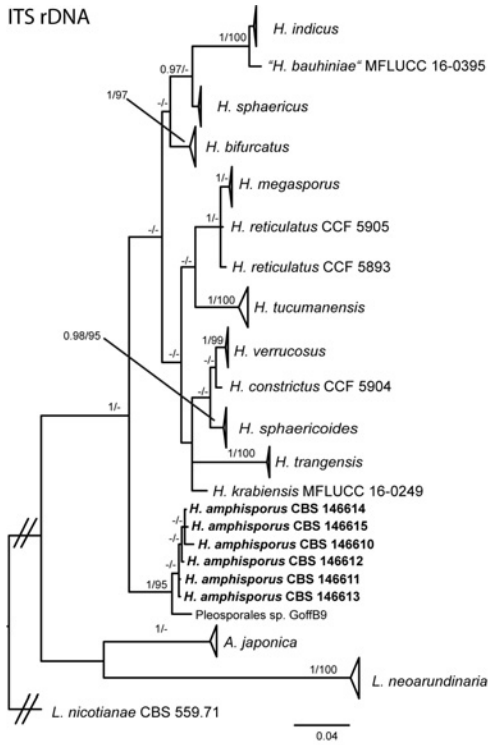
The genus *Hermatomyces* Speg. has been the subject of intense investigation in recent years resulting in the consequent addition of several novelties from Southeast Asia, Panama and Africa together with the introduction of the monotypic family *Hermatomycetaceae* (*Pleosporales*, Dothideomycetes) to accommodate it (Tibpromma et al. 2016, Hashimoto et al. 2017, Koukol et al. 2018, Koukol & Delgado 2019). The species *H. amphisporus* was first described based on a specimen collected on dead decaying branches of *Cyathea* sp. and on setae of an unidentified fungus in a cloud forest in Mexico (Castañeda & Heredia 2000). The fungus is characterised by the presence of dimorphic conidia, the cylindrical ones turbinate to pyriform or globose-campanulate and composed of 6–11 cells arranged in 4 rows, usually with only one cell at the base and the rows increasing toward a grey-brown, leprous apex. Since the original description, it has been rarely collected worldwide with scattered records from Vietnam on a dead branch of an unknown tree (Meľnik et al. 2013) and from another rainforest in Mexico on decaying branches (Martínez et al. 2014). Koukol et al. (2018) considered that the fungus might have a wider distribution range if closely resembling specimens identified as *H. tucumanensis* in the literature are taken into account, in particular a specimen collected on a dead trunk of an unidentified tree in Cuba (Mercado 1984) and another specimen on rachides of dead leaves of the palm tree *Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc. from the state of Florida, U.S.A. (Delgado 2013).

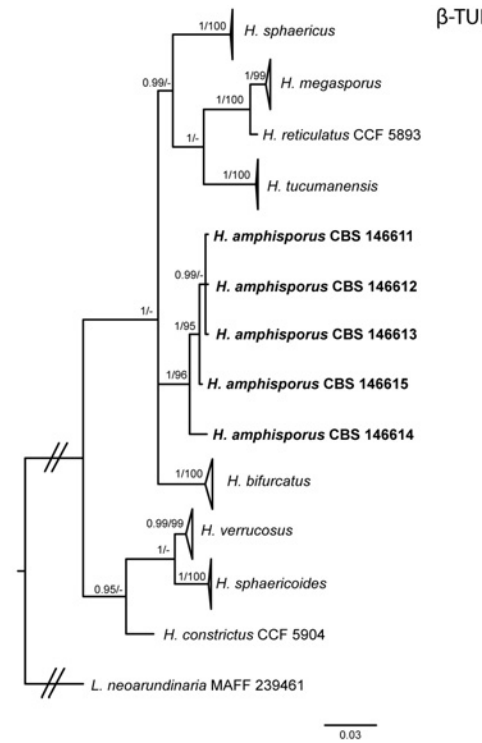
In general, the genus *Hermatomyces* has been poorly documented in the continental United States with only one specimen identified as *H. tucumanensis* (Bates et al. 2018). An online search in Mycoportal (https://mycoportal.org/portal/) showed that the material linked to this name corresponds to the Florida specimen mentioned above (BPI 884154D) but its examination to confirm identity remains pending. However, considering that the fungus was found several times in subtropical Texas, it is likely to occur also in nearby Florida. Its distribution is therefore expanded from Mexico to the north-east where it is probably widespread in other locations across the southeastern United States with abundance of palm tree hosts and similar climate. Examination of Texas specimens

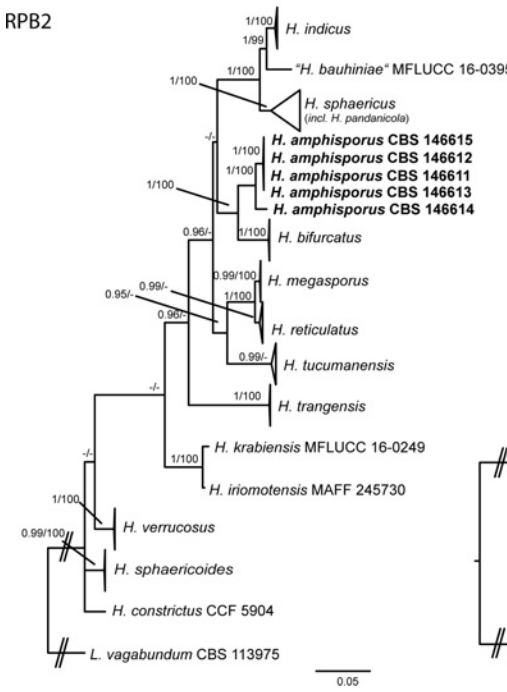
confirmed *H. amphisporus* to be a variable species, particularly concerning the morphology of their cylindrical conidia which range from turbinate or pyriform in the holotype to cylindrical or subcylindrical, often with less distinct bulbous upper cells and one or two swollen basal cells (Figs. 1, 2 G–J). The lack of a distinct subiculum surrounding the fertile sporulating centre of conidiomata is probably due to the influence of very different ecological factors affecting locations in Texas and Mexico. Both collection sites in Texas were lowland floodplain forests adjacent to rivers where the palm host *Sabal minor* tends to occur. They often experience flooding, which partially or totally covers these understory short palm trees for certain periods of time, favouring the dispersal of conidia but reducing the production of subicular hyphae. Interestingly, the regularly changing dry and wet seasons seem to be optimal for *Hermatomyces* species, as observed by Koukol et al. (2018) in the lowland tropical forest of Panama. In contrast, the type locality in the state of Veracruz, Mexico, is in a cloud forest at 1300 m a.s.l. characterised by high moisture and mild temperatures throughout the year, which may enhance the development of subicular hyphae as a protection to the fertile zone of conidiomata.

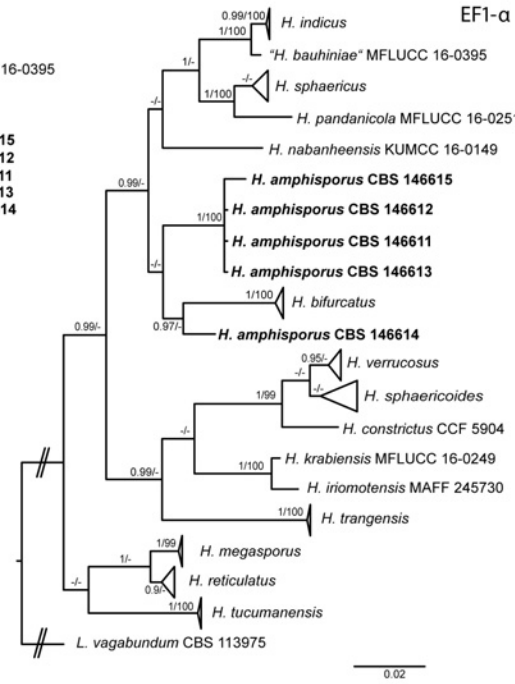
In culture, two (CBS 146611 and CBS 146615) out of the six strains sporulated on MEA and surprisingly produced both cylindrical and lenticular conidia (Fig. 3 B–G). Sporulation in artificial media is rare or intermittent among *Hermatomyces* species and has so far been reported mostly for certain isolates of monomorphic species such as *H. sphaericus* (Sacc.) S. Hughes and *H. sphaericoides* Koukol & G. Delgado (Zhang et al. 2009, Koukol et al. 2018). Only Matsushima (1993) previously reported a dimorphic species which he named '*H. tucumanensis*' from decaying petioles of a palm tree and a twig of a broadleaved tree in Peru which sporulated well on corn meal agar. It produced typical lenticular but also cylindrical conidia composed of two columns of 4–6 inflated, hyaline cells which cannot be referred to *H. tucumanensis* or any other species described to date. Remarkably, the production of a coelomycetous, pycnidial synanamorph in some Texas strains of *H. amphisporus* such as CBS 146610, CBS 146611 and CBS 146615 (Fig. 3 J, K) has never been observed before in the genus. Interestingly, production of similarly looking 'spermatial state' forming globose black spermogonia and hyaline spermatia has been observed in other pleosporalean anamorphs such as *Quadricrura septentrionalis* Kaz. Tanaka, K. Hiray & Sat. Hatak when growing

Fig. 4. Phylogenetic trees inferred from Bayesian and ML analyses showing the position of *Hermatomyces amphisporus* (in bold) within *Hermatomycetaceae* based on ITS, β-TUB, RPB2 and EF1-α. Numbers above branches represent PP > 0.95 and ML bootstrap support values BS > 95%. Sequences of *Aquasubmersa japonica*, *Lophiotrema neoarundinaria*, *L. vagabundum* and *Lepidosphaeria nicotiae* were used as outgroups. Collapsed branches denote multiple sequences of a given species. For strain codes, refer to Koukol et al. (2018). ▶


ITS rDNA
H. indicus
"H. bauhiniae" MFLUCC 16-0395
H. sphaericus
H. bifurcatus
H. megasporus
H. reticulatus CCF 5905
H. reticulatus CCF 5893
H. tucumanensis
H. verrucosus
H. constrictus CCF 5904
H. sphaericoides
H. trangensis
H. krabiensis MFLUCC 16-0249
H. amphisporus CBS 146614
H. amphisporus CBS 146615
H. amphisporus CBS 146610
H. amphisporus CBS 146612
H. amphisporus CBS 146611
H. amphisporus CBS 146613
Pleosporales sp. GoffB9
A. japonica
L. neoarundinaria
L. nicotianae CBS 559.71
0.04


β-TUB
H. sphaericus
H. megasporus
H. reticulatus CCF 5893
H. tucumanensis
H. amphisporus CBS 146611
H. amphisporus CBS 146612
H. amphisporus CBS 146613
H. amphisporus CBS 146615
H. amphisporus CBS 146614
H. bifurcatus
H. verrucosus
H. sphaericoides
H. constrictus CCF 5904
L. neoarundinaria MAFF 239461
0.03


RPB2
H. indicus
"H. bauhiniae" MFLUCC 16-0395
H. sphaericus
(incl. H. pandanicola)
H. amphisporus CBS 146615
H. amphisporus CBS 146612
H. amphisporus CBS 146611
H. amphisporus CBS 146613
H. amphisporus CBS 146614
H. bifurcatus
H. megasporus
H. reticulatus
H. tucumanensis
H. trangensis
H. krabiensis MFLUCC 16-0249
H. iriomotensis MAFF 245730
H. verrucosus
H. sphaericoides
H. constrictus CCF 5904
L. vagabundum CBS 113975
0.05


EF1-α
H. indicus
"H. bauhiniae" MFLUCC 16-0395
H. sphaericus
H. pandanicola MFLUCC 16-0251
H. nabanheensis KUMCC 16-0149
H. amphisporus CBS 146615
H. amphisporus CBS 146612
H. amphisporus CBS 146611
H. amphisporus CBS 146613
H. bifurcatus
H. amphisporus CBS 146614
H. verrucosus
H. sphaericoides
H. constrictus CCF 5904
H. krabiensis MFLUCC 16-0249
H. iriomotensis MAFF 245730
H. trangensis
H. megasporus
H. reticulatus
H. tucumanensis
L. vagabundum CBS 113975
0.02

on PDA (Tanaka et al. 2009). The naming given by these authors implies the existence of a sexual process or at least the capacity to form teleomorphic states. However, teleomorphs are currently unknown for *Hermatomyces* although their discovery in the future is not ruled out considering the numerous pleomorphic families known in *Pleosporales* (Wijayawardene et al. 2017, 2018).

The phylogenetic affinities of the fungus based on the novel DNA sequence data showed that *H. amphisporus* forms a strongly supported monophyletic clade among members of *Hermatomycetaceae* in the ITS, RPB2 and β-TUB phylogenies, although its position within the family was variable (Fig. 4). Moreover, the *H. amphisporus* clade was distant from the morphologically similar *H. pandanicola* Tibpromma, Bhat & K.D. Hyde, which also produces turbinate cylindrical conidia (Tibpromma et al. 2016). They can also be separated on morphological grounds with *H. pandanicola* having smaller conidia, the cylindrical ones having a lower number of cells with 4 arranged in two short columns, and a size of 13.2–20.6 × 8.9–11.9 µm. Our study also showed an interesting pattern in the genotype diversity. The six Texas strains of *H. amphisporus* have almost identical ITS-LSU sequences (differing only in 3 indels out of 1400 bps), but differ to various extent in their coding gene regions. In the case of EF1-α, the strain CBS 146614 deviated in 21 bps from the remaining ones, resulting in the placement of this strain outside the *H. amphisporus* clade (Fig. 4). In the absence of any phenotypic difference, this divergence reflects intraspecific variability and the necessity to consider species boundaries based on evidence from multiple strains and genes.

In the course of the present study, the morphologically atypical species *H. bauhiniae* Phukhams., D.J. Bhat & K.D. Hyde (Hyde et al. 2019) came to our attention and was subject to scrutiny. This dimorphic species was described based on a single specimen collected on a dried branch of *Bauhinia variegata* (L.) Benth. (*Fabaceae*) in Thailand. According to the illustration and description in the protologue, the putative lenticular conidia are muriform, smooth, brown to dark brown, broadly ellipsoidal to oval in front view, often with a distinct subhyaline, inflated basal cell, and they strongly resemble conidia of several *Berkleasmium*-like species (Holubová-Jechová 1987, Qu et al. 2014, Hüseyin et al. 2014). Cylindrical conidia, on the other hand, are composed of one column, 2–3-septate, doliiform, cylindrical or subcylindrical in shape, with rounded apex and clavate or doliiform, verrucose apical cells. However, the germinating conidium illustrated in Fig. 25o strongly resembles the typical lenticular conidia of *Hermatomyces* species and is obviously different from the *Berkleasmium*-like conidia depicted in the rest of the photographic plate. Sporodochial conidiomata as seen in Fig. 25 a–c also lack the outer nest-like subiculum surrounding the fertile centre which is characteristic of *Hermatomyces* species. Further molecular

evidence suggests that sequences attributed to the '*H. bauhiniae*' strain might belong to *H. indicus* Prasher & Sushma (Prasher & Sushma 2014). Hyde et al. (2019) and our ITS, RPB2 and EF1-α phylogenies showed '*H. bauhiniae*' grouped with strains MFLUCC14-1143 and MFLUCC14-1144 of *H. indicus* from Thailand with strong support. Moreover, nucleotide sequence comparisons of their ITS, LSU and EF1-α sequences show that they are almost identical. In contrast, the RPB2 gene exhibited more variation with 21 bp differences, which could be sufficient for a taxonomic novelty but could also reflect intraspecific variability such as in the case of *H. amphisporus* and EF1-α mentioned above. *Hermatomyces indicus* is known from the Paleotropics and has so far been recorded in India, Thailand and Sierra Leone. Co-occurrence of multiple *Hermatomyces* species on the same substrate or together with other sporodochial fungi, e.g. *Dictyosporium hydei* Prasher & R.K. Verma, has been previously observed (Koukol & Delgado 2019) and therefore, special attention is needed during isolation of these anamorphs in pure culture. Apparently, the authors isolated into culture and sequenced *H. indicus*, but described and illustrated a different, probably novel sporodochial *Berkleasmium*-like fungus. A proper genus should be found to accommodate it and a new combination be made. On this basis, a lectotype must be designated for the validly described name *H. bauhiniae*, which must remain attached to the fungus "that corresponds most nearly with the original description or diagnosis" (Art. 9.14, Turland et al. 2018), which obviously in this case is the morphology described in the protologue.

Specimens examined

United States. Texas, Harris County, Spring, Meyer Park, 30°00'15.9" N, 95°31'35.7" W, 33 m a.s.l., on rachides of dead leaves of *Sabal minor*, 29 Sept. 2019 leg. & det. G. Delgado & O. Koukol (ILLS 82994 = CBS 146611); ibid., 3 Nov. 2019 (ILLS 82996 = CBS 146610, CCF 6394; ILLS 82997 = CBS 146612; ILLS 82991 = CBS 146613). – Houston, Bear Creek Pioneers Park, by Langham Creek, 29°50'04.8" N, 95°37'29.0" W, 30 m a.s.l., on rachides of dead leaves of *Sabal minor*, 10 Oct. 2019 leg. & det. G. Delgado & O. Koukol (ILLS 82998 = CBS 146614; ILLS 82999 = CBS 146615, CCF 6392).

Mexico. Veracruz, Huatusco, Las Cañadas cloud forest, on setae of an unidentified fungus on decaying branches of *Cyathea* sp., 20 July 1999 leg. & det. R.F. Castañeda & G. Heredia (XAL 862-2, Holotype).

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