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Morphological and multigene phylogenetic evidence uncovers a new lineage of *Longipedicellataceae* from a native Amazonian floodplain palm

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Abstract. During a mycological survey of microfungi in the Brazilian Amazon, a unique asexual hyphomycete was collected from submerged decaying plants (*Arecaceae*). The establishment of the new genus is primarily justified by its striking and highly specialized morphology. On natural substrate, the taxon forms a complex, three-dimensional network of densely interwoven, multi-branched conidiophores. Furthermore, the verruculose ornamentation on conidia and conidiogenous cells provides a clear diagnostic distinction from all other known genera in the family. While multigene phylogenetic analyses (ITS, LSU, SSU, and *tef1*) place this taxon within *Longipedicellataceae*, the molecular support for its internal position is moderate (MLBS 83%, BPP 0.83). This study emphasizes the priority of stable morphological characters in fungal taxonomy, especially when encountering ambiguous phylogenetic signals in understudied tropical ecosystems, while also demonstrating that the rDNA operon plus a single-copy gene marker are insufficient and that multigene or genomic analyses are needed.

Key words: *Arecaceae*, *Ascomycota*, freshwater fungi, hyphomycetes, molecular biology, palm fungi, systematic, taxonomy

Introduction

Pleosporales is the largest and most ecologically diverse order within *Dothideomycetes*, encompassing a wide range of lifestyles from saprobes to major plant pathogens (Zhang et al. 2012; Hyde et al. 2013). Within this order, the suborder *Massarineae* has undergone recent taxonomic refinement. Previously considered phylogenetically ambiguous, its boundaries have been clarified by several studies aimed at better resolving its evolutionary and biological relationships. (Tanaka et al. 2015; Phukhamsakda et al. 2016; Dong et al. 2020).

Longipedicellataceae, established by Phukhamsakda et al. (2016), is a small, but distinct, lineage within *Massarineae*. The family currently includes three genera, *Longipedicellata*, *Pseudoxylomyces*, and *Submersispora*, comprising approximately six species. Its asexual morphs have been regarded as relatively limited, typically producing chlamydospores, chlamydospore-like conidia, or simple mononematous conidiophores with holoblastic conidiogenesis (Tanaka et al. 2015; Phukhamsakda et al. 2016; Dong et al. 2020). All known taxa are associated with freshwater habitats, indicating adaptation to submerged substrates.

The characteristic of Amazonian environments, within their vast geographic extent and habitat diversity, supports a high diversity of fungi, as evidenced by the numerous new species and genera described in recent years, particularly among asexual ascomycetes (Forzza et al. 2010; Fiuza et al. 2015; Gusmão et al. 2017; Barbosa et al. 2021; Monteiro et al. 2022).

Studies on palm-associated mycobiota in the region have increased in recent decades (Castro et al. 2011, 2012; Miglio & Monteiro 2022; Ferreira et al. 2025).

Euterpe oleracea Mart. (açai palm) is a species native to the Amazon and widely recognized for its economically important fruit, which has experienced growing demand in Brazil and international markets due to its high nutritional and energy value (Souza 2000). However, despite

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the economic importance of *E. oleracea* in Brazil, its mycobiota remains poorly known.

During surveys of Amazonian microfungi, a new hyphomycete was collected from submerged, decaying material of *E. oleracea* in a floodplain. Morphological analysis revealed clear differences from previously described hyphomycetes, supporting the establishment of a new genus.

Materials and methods

Sample processing

Submerged, decaying leaflets of *Euterpe oleracea* Mart. were collected in January 2024 in the Ilha do Combu Environmental Protection Area (EPA), Belém, Pará, Brazil. The area presents typical Amazonian vegetation, including trees, shrubs, lianas, and understory species distributed across low, seasonally flooded areas and higher floodplains less affected by water (Jardim & Vieira 2001).

Leaflets were processed following the washing technique of Castañeda et al. (2016). After washing, samples were placed in Petri dishes with moistened filter paper to establish moist chambers for fungal growth and incubated in a large EPS (expanded polystyrene) box lined with damp paper towels to maintain humidity. The box was opened five times per week for 30 minutes to allow air circulation. Moist chambers were examined under a stereomicroscope (Leica S8APO) after 72 hours and periodically for 30–45 days to detect reproductive structures of microfungi.

Morphological study, illustration and isolation

Reproductive structures were carefully removed from the substrate using fine needles and mounted on permanent slides with polyvinyl alcohol mounting medium, following Waller et al. (2002). Identification was based on morphological analysis and measurement of taxonomically relevant microstructures under a light microscope, with comparisons to the pertinent literature. Illustrations were prepared from photomicrographs captured with a DP25 digital camera attached to a light microscope (Olympus BX51), with or without differential interference contrast (DIC). Scanning electron microscopy (SEM) images were obtained at the SEM Laboratory of the Museu Paraense Emílio Goeldi using a Tescan Mira3 microscope equipped with a field emission gun (FEG). Samples were mounted on 12 mm aluminum stubs with double-sided carbon adhesive tape and sputter-coated with gold (Au) for 2 min 30 s, producing a 10–15 nm conductive layer. Images were acquired using secondary electron (SE) detection at 5 kV, with working distances of 10–15 mm. Reproductive structures of microfungi were isolated on cornmeal carrot agar (CMCA; 30 g cornmeal, 30 g carrot, 13 g agar per liter) and water agar (WA). After confirmation of culture purity, strains were preserved using the water method (Castellani 1939) and mineral oil method (Buell & Weston 1947). The strain was deposited in the Coleção de Culturas de Microrganismos da Bahia (CCMB), and permanent slides were deposited in the Herbarium (HUEFS), both at the State University of Feira de Santana, Bahia, Brazil.

DNA extraction, amplification (PCR) and sequencing

Colonies grown on CMCA and WA for up to 30 days at ~25°C were used for DNA extraction, with mycelium scraped and transferred to extraction tubes. Genomic DNA was extracted using the DNeasy® Plant Mini Kit (Qiagen) following the manufacturer's instructions. Primers and PCR conditions are provided in Table 1, and reactions followed Souza et al. (2025). PCR products were visualized on 1% agarose gel, purified with polyethylene glycol (PEG) (Lis and Schleif 1975), and sequenced at the FIOCRUZ Sequencing Platform, Bahia, Brazil.

Phylogenetic analyses

Consensus DNA sequences were assembled using BioEdit v. 5.0.9 (Hall 1999) and subsequently compared to sequences in the NCBI GenBank database via the BLASTn tool, aiming to identify closely related sequences and determine their taxonomic placement at the order and family levels. Based on the BLASTn results, an LSU dataset was compiled, primarily following Calabon et al. (2021), and focused on species within the suborder *Massarineae*. The sequences were aligned using MAFFT interface (Katoh & Standley 2013). A comprehensive alignment was generated for each locus (ITS, LSU, SSU, *tef1*), including sequences from genera within *Massarineae*. The sequences were aligned in MAFFT using the AUTO option (Katoh et al. 2005) and then concatenated in MEGA v. 7 (Kumar et al. 2016). The final dataset comprised two strains of the studied taxon and 46 related taxa. *Corynespora cassiicola* CBS 100822 and *Corynespora smithii* CABI 5649b were used as outgroups (Table 2).

Table 1. Genes/DNA loci amplified in this study with respective PCR primers and protocols. D – denaturation; Cy – cycles; A – annealing; E – extension; FE – final extension; CD – cool-down.

Gene/loci	PCR primers (forward/reverse)	PCR Protocol	References loci/protocol
ITS	ITS5/ITS4	D: 94°C/5′, 30Cy (A: 52°C/40′, E: 72°C/40′), FE: 72°C/5″, CD: 4°C/forever	White et al. 1990/Barreto et al. 2023
LSU	LR0R/LR5	D: 94°C/5′, 30Cy (A: 52°C/40′, E: 72°C/40′), FE: 72°C/5″, CD: 4°C/forever	Rehner & Samuels 1994; Vilgalys & Hester 1990/Barreto et al. 2023
SSU	NS1/NS4	D: 94°C/5′, 30Cy (A: 48°C/50″, E: 72°C/1′30″), FE: 72°C/7′, CD: 4°C/forever	White et al. 1990/Barreto et al. 2023
tef1	EF1-983F/EF1-2218R	D: 94°C/5′, 30Cy (A: 54°C/50″, E: 72°C/1′30″), FE: 72°C/7′, CD: 4°C/forever	Rehner & Buckley 2005/Barreto et al. 2023

Maximum likelihood (ML) analyses were conducted in IQ-TREE (Nguyen et al. 2015) using a randomized stepwise addition parsimony tree and 100 independent searches. Branch support was estimated with 1,000 ultrafast bootstrap replicates (Hoang et al. 2018). The best-fit substitution models and partitioning scheme were selected with ModelFinder (Kalyaanamoorthy et al. 2017) under the corrected Akaike Information Criterion (AICc), based on six partitions: ITS1, 5.8S, ITS2, LSU, SSU, and *tef1*.

Bayesian inference (BI) was performed in MrBayes v.3.2.7a via the CIPRES Science Gateway (Miller et al. 2010; http://www.phylo.org/), using the same partitioning

Table 2. GenBank Accession numbers of taxa used in this study. New sequences are in bold. [T]Ex-type isolates.

Taxon	Source	GenBank accession number				References
		LSU	SSU	ITS	*tef1*	
Bambusicola bambusae	MFLUCC 11–0614[T]	JX442035	JX442039	NR_121546	KP761722	Dai et al. 2012
Bambusicola irregulispora	MFLUCC 11–0437[T]	JX442036	JX442040	NR_121547	KP761723	Dai et al. 2012
Bambusicola massarinia	MFLUCC 11–0389[T]	JX442037	JX442041	JX442033	KP761725	Dai et al. 2012
Bambusicola splendida	MFLUCC 11–0439[T]	JX442038	JX442042	NR121549	KP761726	Dai et al. 2012
Bimuria novae-zelandiae	CBS 107.79[T]	AY016356	AY016338	NR_159620	DQ471087	Lumbsch & Lindemuth 2001
Byssothecium circinans	CBS 675.92	GU205217	GU205235	–	GU349061	Schoch et al. 2009
Corynespora cassiicola	CBS 100822	GU301808	GU296144	OQ410655.1	GU349052	Schoch et al. 2009
Corynespora smithii	CABI5649b	GU323201	–	FJ852597	GU349018	Schoch et al. 2009
Falciformispora lignatilis	BCC 21117	GU371826	GU371834	KF432942	GU371819	Schoch et al. 2009
Falciformispora lignatilis	BCC 21118	GU371827	GU371835	KF432943	GU371820	Schoch et al. 2009
Helicascus nypae	BCC 36752	GU479789	GU479755	–	GU479855	Suetrong et al. 2009
Karstenula rhodostoma	CBS 690.94	GU301821	GU296154	–	GU349067	Schoch et al. 2009
Latorua caligans	CBS 576.65[T]	MH870362	–	MH858723	–	Vu et al. 2019
Latorua grootfonteinensis	CBS 369.72[T]	NG_058181	–	–	–	Crous et al. 2015
Lentithecium aquaticum	CBS 123099[T]	GU301823	GU296156	NR_160229	GU349068	Schoch et al. 2009
Lentithecium clioninum	KT 1149A[T]	AB807540	AB797250	LC014566	AB808515	Tanaka et al. 2015
Lentithecium clioninum	KT 1220	AB807541	AB797251	LC014567	AB808516	Tanaka et al. 2015
Lentithecium pseudoclioninum	KT 1111	AB807544	AB797254	AB809632	AB808520	Tanaka et al. 2015
Longipedicellata aptrootii	MFLUCC 10–0297	KU238894	KU238895	KU238893	KU238892	Zhang et al. 2016
Longipedicellata aptrootii	MFLUCC 18–0988	MN913744	–	MT627733	–	GenBank
Macrodiplodiopsis desmazieri	CBS 140062[T]	NG_058182	–	NR_132924	–	Crous et al. 2015
Massarina cisti	CBS 266.62[T]	FJ795447	FJ795490	LC014568	AB808514	Tanaka et al. 2009
Massarina eburnea	H 3953	AB521735	AB521718	–	AB808517	Hirayama 2010
Massarina eburnea	CBS 473.64	GU301840	GU296170	AF383959	GU349040	Schoch et al. 2009
Montagnula opulenta	AFTOL-ID 1734	DQ678086	AF164370	AF383966	–	Schoch et al. 2006
Morosphaeria ramunculicola	JK 5304B	GU479794	GU479760	–	–	Suetrong et al. 2009
Multiseptospora thailandica	MFLUCC 11–0183[T]	NG_059554	KP753955	NR_148080	KU705657	Liu et al. 2015
Neokalmusia scabrispora	KT2202	AB524594	AB524453	LC014576	AB539107	Tanaka et al. 2009
Palmiascoma gregariascomum	MFLUCC 11–0175[T]	KP744495	KP753958	KP744452	–	Liu et al. 2015
Parabambusicola thysanolaenae	KUMCC 18–0147[T]	NG_066435	NG_067681	NR_164044	MK098209	GenBank
Parabambusicola thysanolaenae	KUMCC 18–0148	MK098198	MK098202	MK098193	MK098211	GenBank
Paraconiothyrium brasiliense	CBS 100299[T]	JX496124	AY642523	JX496011	–	Verkley et al. 2014
Paraphaeosphaeria michotii	MFLUCC 13–0349[T]	KJ939282	KJ939285	KJ939279	–	GenBank
Paraphaeosphaeria minitans	CBS 122788	EU754173	EU754074	–	GU349083	de Gruyter et al. 2009
Phaeodothis winteri	CBS 182.58	GU301857	GU296183	–	DQ677917	Schoch et al. 2009
Pleohelicoon fagi	MFLUCC 15–0182[T]	NG_066320	NG_065791	NR_163353	–	Jayasiri et al. 2019
Pleomonodictys descalsii	CBS 142298[T]	KY853522	–	KY853461	–	Hernandez-Restrepo et al. 2017
Pseudoxylomyces aquaticus	KUMCC 17-0312[T]	NG_075324	NG_073548	NR_171972	MT954381	Dong et al. 2020
Pseudoxylomyces elegans	KT 2887	AB807598	AB797308	LC014593	AB808576	Tanaka et al. 2015
Pseudoxylomyces elegans	NS-14	KX765281	–	KX765280	–	Prabhugaonkar & Jalmi 2017
Splanchnonema platani	CBS 221.37	MH867404	–	MH855894	DQ677908	Vu et al. 2019
Splanchnonema platani	CBS 222.37	KR909316	KR909318	KR909311	KR909319	Ahmed et al. 2015
Submersispora variabilis	MFLUCC 17-2360[T]	NG_073790	NG_073549	NR_171973	–	Dong et al. 2020
Submersispora variabilis	N-KR15	MZ538561	MZ538575	MZ538527	MZ567103	GenBank
Trematosphaeria pertusa	CBS 122368[T]	FJ201990	FJ201991	KF015668	KF015701	Zhang et al. 2008
Trematosphaeria pertusa	CBS 122371	GU301876	GU348999	KF015669	KF015702	Schoch et al. 2009
Verrucobulbifera globosa	CCMB 782[T]	**PX677378**	**PX677380**	**PX677379**	**PX627880**	This study
Verrucobulbifera globosa	CCMB 784	**PZ295605**	**PZ295587**	**PZ295457**	**PZ311586**	This study

scheme and models as in the ML analysis. Two runs of four chains were executed for 50 million generations, sampling every 1,000 generations, with a stopval of 0.01. A burn-in of 25% was applied, and the remaining trees were used to generate a 50% majority-rule consensus tree and estimate Bayesian posterior probabilities (PP).

Bootstrap support (BS ≥ 80%) and posterior probabilities (PP ≥ 0.80) were mapped onto the phylogeny and considered moderate support (Kress et al. 2002; Hyde et al. 2013). The tree was visualized in FigTree v1.4.4 (Rambaut 2012) and edited in Inkscape v1.1.1. Newly generated sequences were deposited in GenBank.

Results

Phylogenetic analyses

Phylogenetic analyses using Maximum Likelihood (ML) and Bayesian Inference (BI) produced similar topologies based on the concatenated multilocus dataset. The ML topology tree is presented (Fig. 1), with bootstrap support (MLBS ≥ 70) and Bayesian posterior probabilities (BPP ≥ 0.70) indicated at the nodes.

The dataset included 46 terminals representing 11 families of *Massarineae*, plus two outgroup taxa from *Pleosporineae*, totaling 3,227 characters (including gaps: ITS 855 bp; LSU 877 bp; SSU 1,417 bp; *tef1* 962 bp), with 850 parsimony-informative and 2,206 constant sites.

The best-fit models were GTR+F+G4 (General Time Reversible model) for ITS1, SYM+I+G4 (Symmetrical substitution model) for 5.8S, HKY+F+I+G4 (Hasegawa–Kishino–Yano model) for ITS2 and GTR+F+I+G4 for LSU, SSU, *tef1*. The optimal ML tree had a likelihood of −ln = −19500.895, and the BI analysis reached convergence with an average standard deviation of split frequencies of 0.009875 after 1,200,000 generations.

The phylogenetic analysis (Fig. 1) recovered nine well-supported lineages (MLBS 100%, BPP 1.0) corresponding to families within *Massarineae*: *Bambusicolaceae*, *Didymosphaeriaceae*, *Massarinaceae*, *Trematosphaeriaceae*, *Latoruaceae*, *Lentitheciaceae*, *Longipedicellataceae*, *Macrodiplodiopsidaceae*, and *Parabambusicolaceae*. *Morosphaeriaceae* and *Pleomonodictyaceae* were also recovered with support values of MLBS 96%, BPP 0.99 and MLBS 91%, BPP 1, respectively.

Longipedicellata, *Submersispora*, *Pseudoxylomyces*, and *Verrucobulbifera* form a well-supported clade within *Longipedicellataceae* (MLBS 100%, BPP 1.00). Within this family, *Verrucobulbifera* is sister to *Longipedicellata* and *Submersispora* (MLBS 83%, BPP 0.83).

The placement of the new taxon as sister to *Longipedicellata* and *Submersispora* is moderately supported by ML (BS = 83%) and by Bayesian inference (PP = 0.83), indicating phylogenetic uncertainty. Single-locus analyses showed topological incongruence, especially for SSU and *tef1*, likely reflecting limited phylogenetic signal and locus-specific evolutionary patterns. The *tef1* dataset was particularly unstable, placing the new taxon with the outgroup, possibly due to alignment issues or low signal.

Taxonomy

Verrucobulbifera Miglio, J.S. Monteiro, R.F. Castañeda & Gusmão, gen. nov. (Fig. 2)

MycoBank MB 861427

Diagnosis: Differs from every other genera described in the literature due to its bulbil-like appearance in natural substrate, three-dimensional and multi-branched conidiophores and ornamentation of conidiogenous cells and conidia. Forms a distinct lineage within *Longipedicellataceae*, separated from related genera.

Type: *Verrucobulbifera globosa* Miglio, J.S. Monteiro, R.F. Castañeda & Gusmão

Etymology. *Verrucobulbifera* (Ver.ru.co.bul.bi'fe.ra), fem. adj., from Latin *verrūca* (= wart, small protuberance), *bulbus* (= bulb, swollen base), and *-fera* (from *fero*, to bear, to carry). The genus name refers to the ornamentation of the conidia and conidiogenous cells, as well as to the bulbil-like structures formed on the natural substrate.

Asexual morph. Colonies scattered, globose to pulvinate, sessile, brown to olivaceous brown. Mycelium superficial, composed of septate, brown to pale brown hyphae. Conidiophores differentiated, solitary, multi-branched, growing upwards or laterally and forming a very loose and densely interwoven, three-dimensional network. Conidiogenous cells monoblastic or polyblastic, integrate and terminal, mostly verruculose, brown to pale brown. Conidial secession schizolytic. Conidia solitary, globose to pyriform, sub-hemispherical, truncate at the base, unicellular, brown to pale brown, mostly verruculose. Sexual morph: unknown.

Verrucobulbifera globosa Miglio, J.S. Monteiro, R.F. Castañeda & Gusmão, sp. nov. (Fig. 2)

MycoBank MB 861428

Type: Brazil, Pará, Belém, Ilha do Combu, 1°28′33″S, 48°28′06″W, on decaying leaflet submerged of *Euterpe oleracea* Mart. (*Arecaceae*), 21 Jan. 2024, B.V. Miglio Miglio-212 (HUEFS 276555 – holotype; ex-type living culture CCMB 782).

Etymology. *globosa* (glo.bo'sa), fem. adj., from Latin *globōsus* (= spherical, rounded), derived from *globus* (= sphere, ball, globe). Refers to the globose shape of the conidia.

Asexual morph. Colonies on the natural substrate scattered, lobose to pulvinate, sessile, mostly scattered, sometimes coalescent, superficial, brown to olivaceous, brown, 140–210 × 80–150 µm. Mycelium superficial, composed of septate, verruculose, brown to pale brown hyphae, 2.5–6.25 µm wide. Conidiophores differentiated, multi-branched growing upwards or laterally and forming a very loose and densely interwoven, three-dimensional network. Conidiogenous cells mostly polyblastic, sometimes monoblastic, integrate and terminal, verruculose, brown to pale brown, 4–10(–15) × 3–7 µm. Conidial secession schizolytic. Conidia solitary, sometimes in short chains, globose to pyriform, sub-hemispherical, truncate

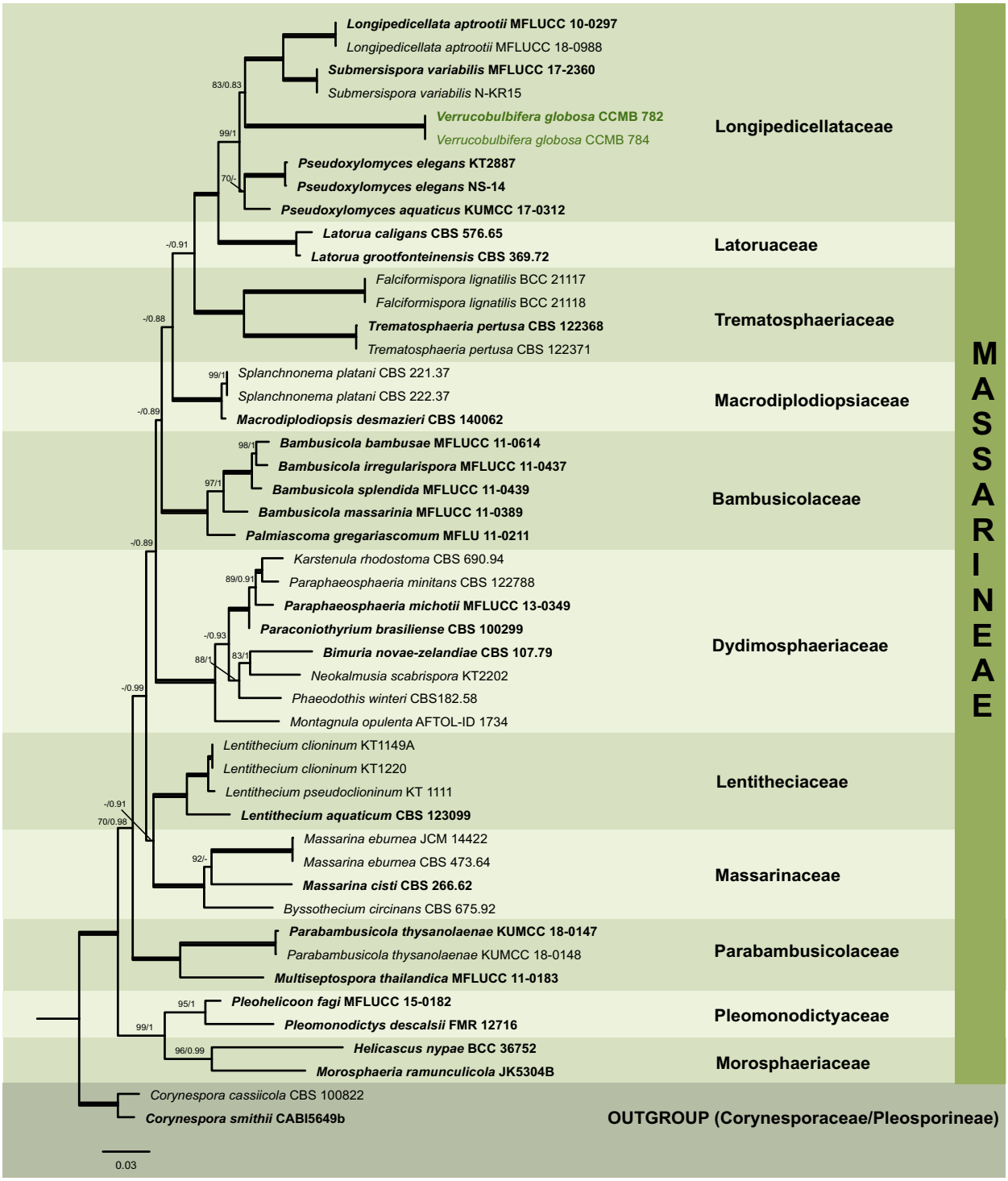


Figure 1. Maximum likelihood phylogenetic tree based on the combined ITS, LSU, SSU, and *tef1* datasets. Bootstrap support values from the maximum likelihood (ML) analysis ≥70% and Bayesian posterior probability (BPP) values ≥0.70 are shown at the nodes, with a dash ('–') indicating lack of statistical support. The scale bar represents the expected number of substitutions per site. Fully supported branches (MLBS = 100% and BPP = 1.0) are indicated by thicker lines. The newly generated sequence is shown in green (gen. et sp. nov.), and ex-type strains are indicated in **bold**. The tree is rooted with *Corynespora cassiicola* CBS 100822 and *Corynespora smithii* CABI5649b (*Corynesporaceae*, *Pleosporineae*).

at the base, unicellular, brown to pale brown, verruculose, dry, 7–12 × 7–9 µm. Sexual morph: unknown.

Culture characteristics. On CMCA, colony subglobose, flat, undulate edge, reaching 15 mm in 20 days at 25°C, dark brown by the center to olivaceous grey by the edge, surface rough (Fig. 3F); the reverse side is dark brown. Hyphae branched, septate, pale brown.

Distribution. Known only from the type locality.

Habitat and ecology. Palmicolous.

Notes. On natural substrates, conidiophores are rarely observed, with only clusters of conidiogenous cells and conidia visible (Fig. 2B). In culture, conidiophores become more evident, and the branching pattern is clearly expressed (Fig. 3A–C). Occasionally, short chains of two conidia are formed in culture, a feature not observed in natura (Fig. 3D, E). Light microscopy revealed conidia

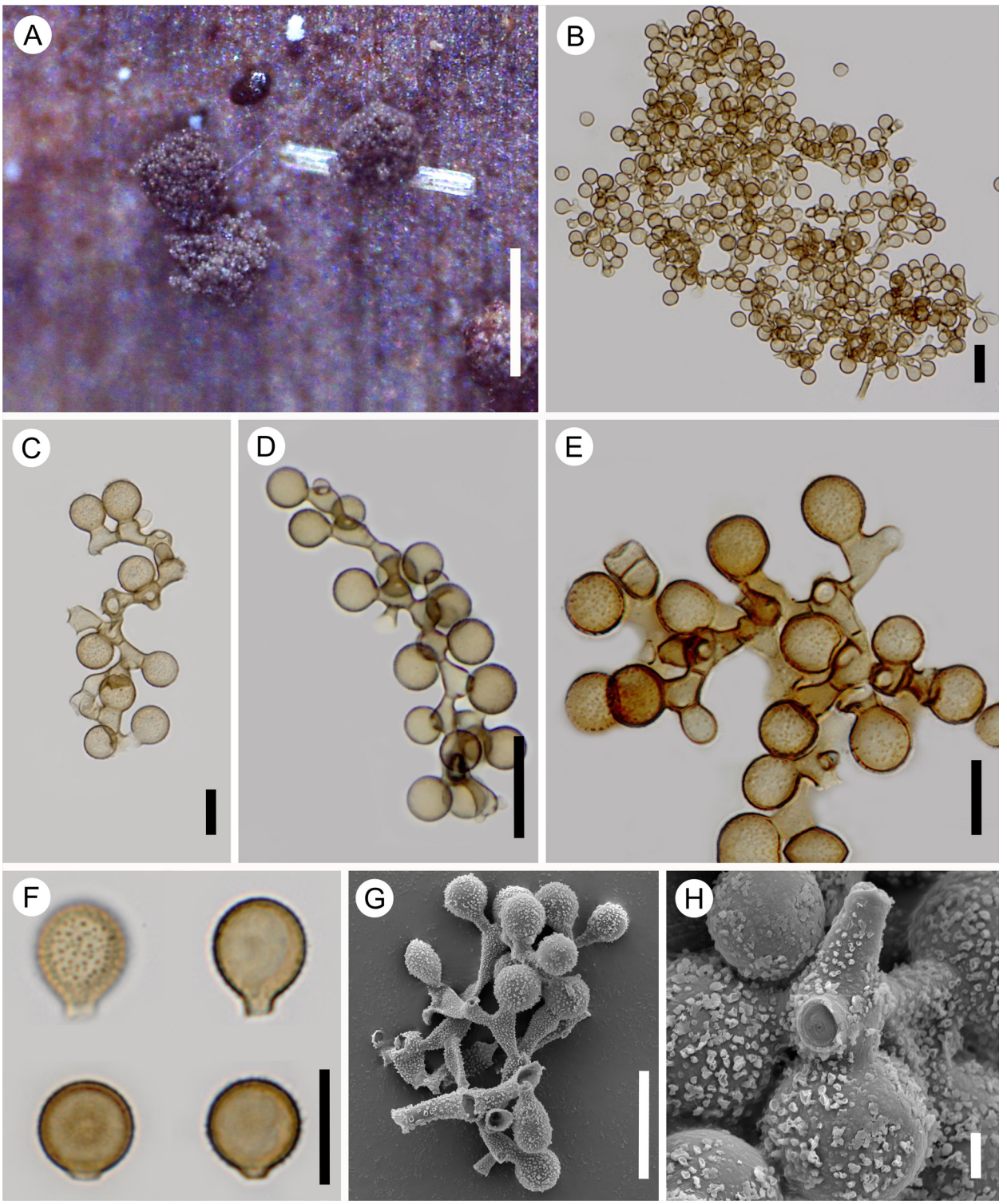


Figure 2. *Verrucobulbifera globosa* (HUEFS 276555 – holotype). A – colonies on the natural substrate; B – general view of conidiophores, conidiogenous cells and conidia; C–E – details of conidiophores, conidigenous cells and conidia; F – detail of conidia; G–H – SEM images of conidiophores, condiogenous cells and conidia. Scales: A = 0.2 mm; B, D, G = 20 µm; C, E, F = 10 µm; H = 2 µm.

with a distinctly verruculose surface, prompting further examination by scanning electron microscopy (SEM). SEM confirmed that both conidia and conidiogenous cells share this ornamentation (Fig. 2F–H). The branching pattern of conidiophores in *V. globosa* resembles that described for the conidia of *Dendroclathra caeruleofusca* Voglmayr & G. Delgado, although this taxon has an uncertain taxonomic placement (*Sordariomycetes*, *Hypocreomycetidae incertae sedis*), is not related phylogenetically to our new genus, as they are assigned to different higher taxonomic levels.

Additional examined material. BRAZIL. Pará, Belém, on decaying leaflet submerged of *Euterpe oleracea* Mart., 14 Aug. 2024, B.V. Miglio Miglio-282 (HUEFS 290746 – paratype; living culture CCMB 784).

Discussion

The multilocus analysis (ITS, LSU, SSU, *tef1*) places *Verrucobulbifera* within *Longipedicellataceae* (MLBS 100%, BPP 1.00), forming a sister clade to *Longipedicellata* and *Submersispora* (MLBS 83%, BPP 0.83). Despite this relationship, the three genera differ markedly in morphology. *Longipedicellata* produce chlamydospores structures as its anamorph (Phukhamsakda et al. 2016), whereas *Submersispora* forms mononematous conidiophores and dark, muriform conidia (Dong et al. 2020).

Topological incongruence among single-locus phylogenies was observed, likely reflecting differences in evolutionary rates and processes such as incomplete lineage sorting (Avise & Robinson 2008; Steenwyk et al. 2023). Although the *tef1* dataset showed an inconsistent placement of the new taxon in single-gene analyses, it contributed to a more stable and biologically coherent topology in the concatenated analysis (Fig. 1). Notably, excluding *tef1* disrupted the monophyly of *Pseudoxylomyces*, indicating that this locus retains important phylogenetic signal despite its individual instability. Ribosomal (ITS, LSU, SSU) and protein-coding (*tef1*) markers may reflect distinct evolutionary histories (Cedeño-Sanchez et al. 2024). Given that only four loci were analyzed, the concatenated dataset was considered to provide the most

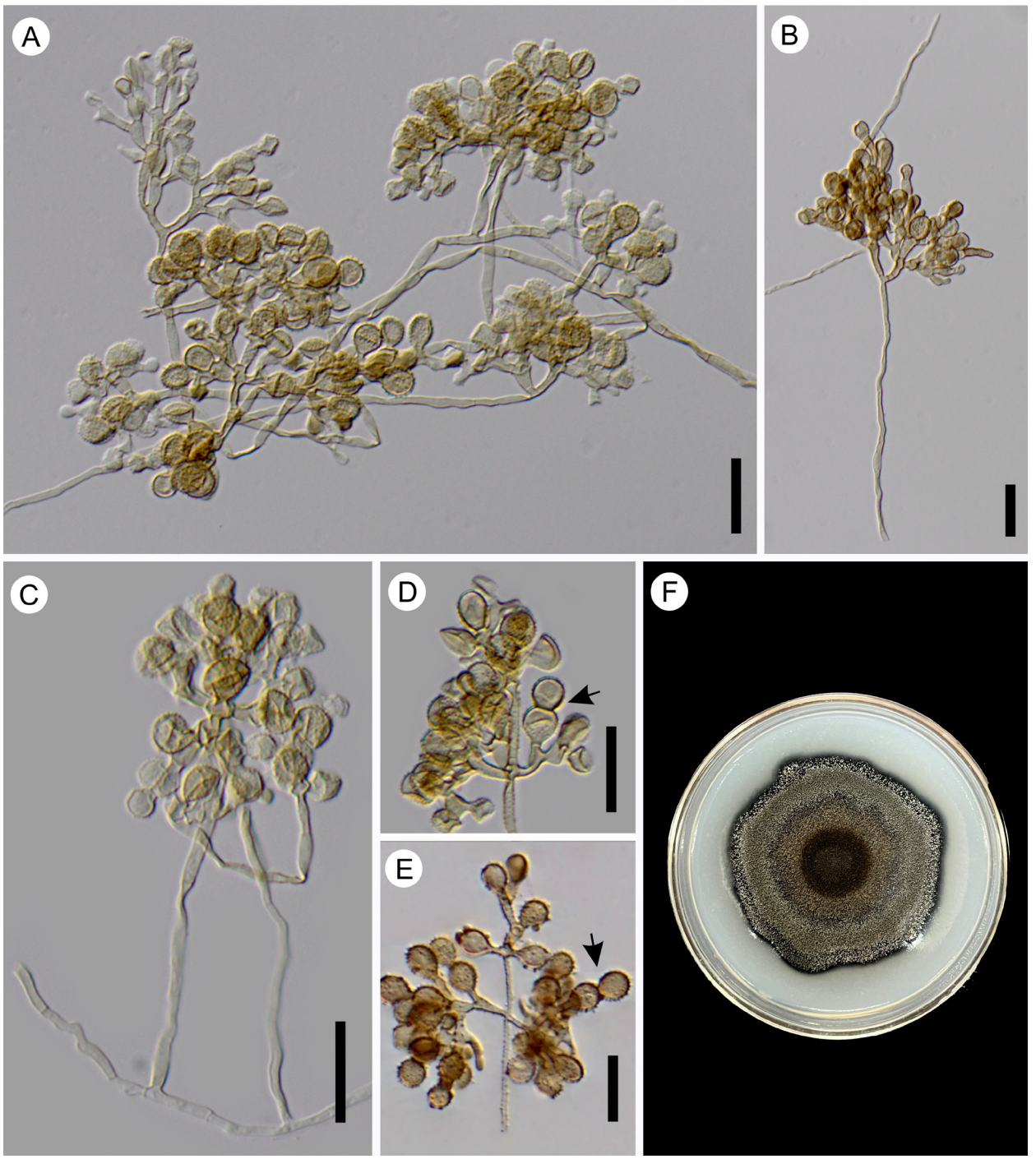


Figure 3. *Verrucobulbifera globosa* (CCMB 782 ex-type culture). A–C – conidiophores, integrated conidiogenous cells and conidia in culture; D–E – arrows indicate the short conidial chains observed only in culture; F – colony on CMCA. Scales: A–E = 20 µm.

robust estimate of the phylogenetic relationships and to improve its inference (Mirarab et al. 2016).

The establishment of *Verrucobulbifera* gen. nov. is supported by its unique conidiophore architecture, previously unknown in *Longipedicellataceae*. On natural substrates, the fungus appears bulbil-like, but microscopy reveals a dense, three-dimensional network of multi-branched conidiophores. This pattern resembles the clathrate development described for *incertae sedis* genera, *Dendroclathra* and *Sympodioclathra* (Voglmayr & Krisai-Greilhuber 1997; Voglmayr & Delgado-Rodriguez 2001). In *Dendroclathra*, conidial growth involves repeated dichotomous branching and frequent fusion of hyphal tips, forming a complex network (Voglmayr & Delgado 2001). A similar organization is observed in *V. globosa*, although anastomoses were not detected. In *Sympodioclathra*, conidia are also dichotomously branched and clathrate (Voglmayr & Krisai-Greilhuber 1997). Clathrate structures are defined as latticed networks (Kirk et al. 2008), but in previously described taxa these are hollow (Seifert et al. 2011). In contrast, *Verrucobulbifera* is non-hollow, being densely filled with conidiogenous cells and conidia, and lacking hyphal anastomoses.

Other morphologically comparable genera, such as *Pseudaegerita* (*Leotiomycetes*, *Helotiales*, *Hyaloscyphaceae*) and *Korunomyces* (*incertae sedis*), produce aggregated or branched structures, particularly in culture. However, *Pseudaegerita* forms daughter cells from conidia (Abdullah et al. 2005), and *Korunomyces zapatensis* has larger conidia (17–28 µm vs. 7–12 × 7–9 µm) and more conspicuous conidiophores (Holubová-Jechová & Castañeda-Ruiz 1986). In contrast, conidiophores in *V. globosa* are subtle and may resemble somatic hyphae (Fig. 3A–C).

The morphology of the genera mentioned above provided a useful framework for interpreting and describing the new genus. However, none of them appears to be phylogenetically related to *V. globosa*. *Dendroclathra* (*Sordariomycetes*, *Hypocreomycetidae incertae sedis*) has sequence data available in public databases, but its placement at a higher taxonomic rank precludes meaningful inclusion in the phylogenetic analysis (GenBank direct submission). The same applies to *Pseudaegerita* (*Leotiomycetes*, *Helotiales*, *Hyaloscyphaceae*) (Vu et al. 2019). Sequence data are also available for some species of *Sympodioclathra* and *Korunomyces*, although both genera remain *incertae sedis* (Vu et al. 2019). If any of these genera were closely related to *V. globosa*, some degree of sequence similarity would be expected in BLAST searches; however, no such relationship was recovered.

A key diagnostic feature of *Verrucobulbifera* is the verruculose ornamentation of the cell walls (Fig. 2F–H), absent in *Pseudoxylomyces*, *Longipedicellata*, and *Submersispora*, which have smooth-walled conidia. This ornamentation resembles the "spikey warts" of *Latorua* (*Latoruaceae*), a sister family to *Longipedicellataceae* (Fig. 1; Crous et al. 2015), suggesting possible ecological or evolutionary convergence.

The moderate support for the placement of *Verrucobulbifera* may reflect the limited sampling within *Longipedicellataceae*. Nonetheless, the morphological divergence from related taxa is clear. The development of a complex, multi-branched conidiophore network and the presence of verruculose ornamentation represent distinctive features within *Massarineae*. These stable morphological traits are therefore considered reliable for generic delimitation, complementing the current molecular evidence.

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Conflicts of interest

The authors declare that they have no conflicts of interest.

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Data availability

The sequencing data were submitted to GenBank under the number provided in Table 2. Herbarium specimens are deposited in Herbário (HUEFS) of the State University of Feira de Santana, Bahia, Brazil and the strains are in Coleção de Culturas e Microrganismos da Bahia (CCMB) of the State University of Feira de Santana, Bahia, Brazil.

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Supplementary electronic materials

Figure S1. ITS individual gene tree ML analysis of *Massarinae* families. Download file

Figure S2. LSU individual gene tree ML analysis of *Massarinae* families. Download file

Figure S3. SSU individual gene tree ML analysis of *Massarinae* families. Download file

Figure S4. *tef1* individual gene tree ML analysis of *Massarinae* families. Download file

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