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Akanthomyces infaproensis sp. nov. (Cordycipitaceae, Hypocreales), a new entomopathogenic fungus from Sabah, Malaysian Borneo

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Abstract

Akanthomyces Lebert belongs to the family Cordycipitaceae (Hypocreales, Sordariomycetes), which is regarded as one of the most important groups of entomopathogenic fungi (EPF). Despite the high fungal diversity in Sabah, Malaysia, the systematics and phylogeny of *Akanthomyces* in this region is still lacking. This study aimed to characterize entomopathogenic fungal specimens collected from Sabah using morphological and molecular phylogenetic approaches to determine their taxonomic status. During surveys of entomopathogenic fungi, two specimens infecting lepidopteran host were collected and examined using morphological characterization and molecular phylogenetic analyses. Five genetic markers, including the internal transcribed spacer (ITS) region, small subunit ribosomal RNA (SSU), translation elongation factor 1-alpha (*TEF1-α*), RNA polymerase II largest subunit (RPB1), and RNA polymerase II second largest subunit (RPB2), were amplified and sequenced to infer phylogenetic relationships. Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) based on individual and concatenated datasets (ITS–SSU–*TEF1-α*-RPB1–RPB2). The analyses consistently recovered the Bornean isolates as a distinct, well-supported lineage. Morphologically, the isolates are distinguished by robust, cream to pale-yellow branched synnemata, smaller perithecia, larger ellipsoidal conidia and filiform, multiseptate ascospores that disarticulate at maturity into cylindrical to slightly barrel-shaped part-spores at maturity compared with closely related species. Based on the combined morphological and phylogenetic evidence, *Akanthomyces infaproensis sp. nov.* is described from Sabah, Malaysia. The discovery of this new species expands the known diversity of *Akanthomyces* and highlights the tropical rainforests of Sabah as reservoirs of undescribed fungal diversity.

Key words: Lepidoptera, molecular phylogeny, Sabah, taxonomy, new taxa

Introduction

The genus *Akanthomyces* belongs to the family Cordycipitaceae (Hypocreales, Sordariomycetes) (Vinit *et al.* 2018, Bu *et al*. 2025). The genus was originally described to accommodate the type species *A. aculeatus* Lebert, which was discovered on a moth in France (Lebert 1858). Major taxonomic revisions were subsequently undertaken by Mains (1950), who amended the genus and provided detailed accounts of its constituent species. Kepler *et al*. (2017) re-evaluated Cordycipitaceae, using multigene phylogenetic data and redefined generic boundaries, resulting in *Torrubiella* and *Lecanicillium* W. Gams & Zare. Being synonymized with *Akanthomyces*, which have nomenclatural priority. Species of *Akanthomyces* are widely distributed and occur in both temperate and tropical ecosystems (Hsieh *et al*. 1997, Wang *et al*. 2024).

Akanthomyces is characterized by synnematous asexual morphs bearing phialides that produce conidia in chains and sexual morphs with superficial perithecia on infected arthropod hosts (Hsieh *et al.* 1997, Mongkolsamrit *et al.*

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2018, Wang *et al*. 2024, Bu *et al*. 2025). Species infect a broad range of arthropods, particularly Lepidoptera, Araneae, Hemiptera, and Coleoptera, and are distributed in both tropical and temperate regions, although their diversity remains insufficiently explored in many biodiversity-rich areas (Vinit *et al.* 2018, Chen *et al*. 2023, Wang *et al.* 2024, Shrestha *et al.* 2019).

According to Index Fungorum (https://www.indexfungorum.org/Names/Names.asp (accessed 8 July 2026), the genus *Akanthomyces* currently consists of 35 accepted species. The highest diversity was reported from subtropical and tropical regions of China and Southeast Asia (Kubátová *et al*. 2024, Wang *et al.* 2024).

Species of *Akanthomyces* are considered promising biological control agents for phloem-sucking plant pests, such as aphids and whiteflies, because their infection process relies on topical contact rather than ingestion (Manfrino *et al*. 2022). Different commercial preparations have already been developed from former *Lecanicillium* species (now *Akanthomyces*) for use in Integrated Pest Management (IPM), especially within greenhouse environments (Caride *et al*. 2024). Taxonomic accuracy is crucial in these applications, as the efficacy and host specificity of a strain depend on accurate identification to ensure both biosafety and successful pest suppression (Manfrino *et al*. 2022, Caride *et al.* 2024). Consequently, discovering and describing indigenous strains is vital for developing adapted biocontrol agents (Caride *et al*. 2024). Although a detailed assessment of microfungal diversity in Northern Borneo caves has been reported by Wasti *et al*. (2024), no species of *Akanthomyces* were documented.

The INFAPRO Rainforest Rehabilitation Project site, located adjacent to the Danum Valley Conservation Area (DVCA) in Lahad Datu, Sabah, Malaysia, was established in 1992 to restore degraded lowland dipterocarp rainforest. As one of the largest rainforest rehabilitation projects in Sabah, the area supports high fungal biodiversity and provides an important habitat for entomopathogenic fungi (Douglas 2022, Silva *et al*. 2019, Reynolds *et al.* 2011).

The objectives of this study were to: (1) collect insects infected by entomopathogenic fungi from the INFAPRO project area adjacent to Danum Valley Conservation Area in Lahad Datu, Sabah, Malaysia; and (2) describe and characterize a novel species of *Akanthomyces* using morphological and molecular phylogenetic data.

Materials and methods

Specimen Collection and Isolation

Fresh specimens of entomopathogenic fungi together with the Lepidoptera host were collected from INFAPRO Project Area (4°58′14.62″ N, 117°41′11.46″ E), Lahad Datu, Sabah, Malaysia, at an elevation of 52 m on 12 March 2024 (FIGURE 1). The specimens were found on leaves in shaded areas of the tropical forest environment, and all relevant collection data were recorded. Fresh specimens were photographed in situ using a digital smartphone camera and carefully placed in sterile plastic containers for transport to the laboratory. To minimize microbial contamination, isolation procedures were performed on the same day of collection. Fungal isolates were obtained by aseptically excising small pieces of stromatal tissue from the infected insect host and transferring them onto Potato dextrose agar (PDA; Merck, Germany) plates using a sterile needle (Luangsa-ard *et al*. 2018, Aini *et al*. 2020). The medium was supplemented with antibiotics streptomycin (50 mg/L) to suppress bacterial contamination (Manfrino *et al*. 2022), and cultures were incubated at room temperature until colonies reached approximately 2–3 cm in diameter. Hyphal tips from actively growing colonies were subcultured onto fresh PDA plates to obtain pure cultures for subsequent analyses. Pure cultures were maintained for further study and preserved under appropriate storage conditions. The collected specimens were subsequently dried using silica gel and deposited in the Borneensis Collection (BORH), Institute for Tropical Biology and Conservation (ITBC), Universiti Malaysia Sabah (UMS), Kota Kinabalu, Sabah, Malaysia.

Morphological Characteristics

Macromorphological features of the host were documented from the collected fresh material. The macromorphological characteristics of fresh specimens, including host type, stroma color and shape, and perithecium orientation, were observed and measured using a stereomicroscope (Bu *et al.* 2025).

Micromorphological features such as perithecia, asci, and ascospores were observed. The fungal structures were mounted on glass slides in 1% (w/v) Congo red solution. These structures were examined and photographed using a compound microscope (Leica DM2500 LED, Germany) equipped with a 100× oil immersion objective lens (total

magnification ×1000 with a 10× eyepiece) (Wang *et al.* 2024). Axenic cultures obtained from fresh specimens were grown on PDA plates at room temperature for 10–14 days, after which the colony characteristics, including size, shape, texture, and color, were recorded. Asexual morphological features from cultures were also examined. Measurements were taken from 20–30 structures to assess the morphological variability (Bu *et al*. 2025).

For scanning electron microscopy (SEM), samples were initially fixed in 2.5% glutaraldehyde prepared in 0.1 M phosphate buffer (pH 7.2) and kept overnight at 4 °C. After fixation, the specimens were rinsed three times in the same buffer and subsequently post-fixed in 1% osmium tetroxide for 1 h at 4 °C. The samples were then dehydrated through a graded ethanol series (30%, 50%, 70%, 90%, and 100% ethanol) and dried using a CO_2 critical-point dryer. The dried materials were mounted onto aluminium stubs with carbon adhesive tape, sputter-coated with an approximately 10 nm thick layer of gold-palladium and observed under a scanning electron microscope at an accelerating voltage of 5–10 kV (Meirelles *et al.* 2023, Subari *et al.* 2025, Shahbaz *et al*. 2026).

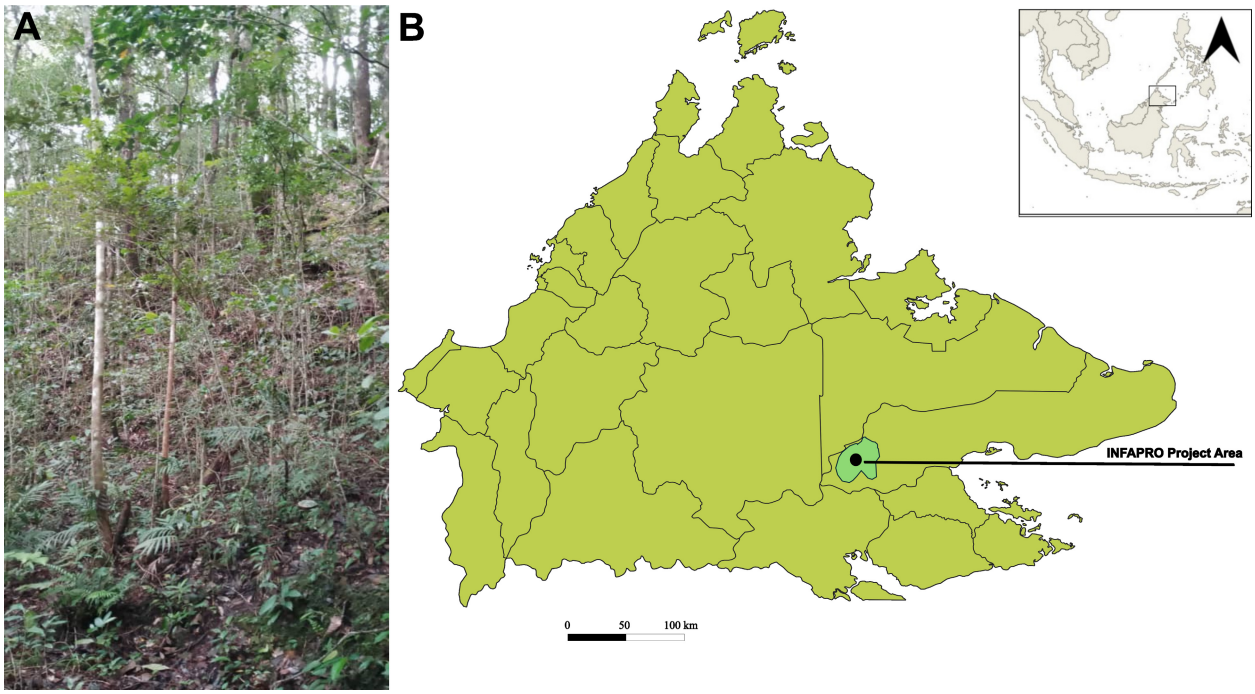

FIGURE 1. Collection site of *Akanthomyces infaproensis* sp. nov (BORH(EF)00008 in Sabah, Malaysia. **(A)** Habitat. **(B)** Sampling location (black dot) in Sabah (green). The study map was created using QGIS 3.44.3 software (https://qgis.org/download/).

DNA extraction, PCR amplification, and sequencing

Total genomic DNA was extracted from fungal stromatal and synnematal tissues carefully removed from fresh and dried infected host specimens using the E.Z.N.A.® Plant & Fungal DNA Kit (Omega Bio-Tek, USA) following the manufacturer's protocol. Phylogenetic analyses were performed using five nuclear gene regions: the Internal Transcribed Spacer (ITS), the nuclear small subunit ribosomal RNA (SSU), the translation elongation factor 1-alpha (*TEF1-α*), the largest subunit of RNA polymerase II (RPB1), and the second largest subunit of RNA polymerase II (RPB2), which are widely recognized as reliable markers for species identification and phylogenetic inference in entomopathogenic fungi (Kepler *et al.* 2017, Aini *et al*. 2020). The primers used to amplify the molecular markers were ITS1 and ITS4 for the ITS region (White *et al.* 1990), SSU-REV475 and SSU-FW105 for the SSU region (White *et al.* 1990), EF1-983F and EF1-2218R for the *TEF1-α* region (Rehner & Buckley, 2005), RPB1-Af and RPB1-Cr for the RPB1 region (Castlebury *et al.* 2004), and fRPB2-5F2 and fRPB2-7cR for the RPB2 region (O'Donnell *et al.* 2007). Amplifications were carried out using a Bio-Rad T100 thermal cycler (Bio-Rad, Singapore) under the following PCR conditions: an initial denaturation at 94 °C for 3 min, followed by 33 cycles of denaturation at 94 °C for 30 s, annealing at 51 °C for 50 s for ITS and RPB1, 55 °C for 50 s for SSU, 58 °C for 50 s for *TEF1-α*, and 54 °C for 50 s for RPB2, followed by extension at 72 °C for 1 min. A final extension was carried out at 72 °C for 10 min (Su *et al.* 2019). After electrophoresis, PCR products were visualized via UV light at 312 nm. For sequencing, successfully amplified products were sent to Apical Scientific Sdn. Bhd., Selangor, Malaysia, for sequencing. The quality of the newly generated sequences was checked, edited, and subsequently deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank; Table 1).

TABLE 1. List of Species and GenBank accession numbers of sequences used in this study.

Species	Voucher Number	Host	ITS	SSU	*TEF1-α*	RPB1	RPB2	References
Akanthomyces aculeatus	BCC17075	Lepidoptera	GQ250011	GQ249958	GQ250033	-	-	Unpublished
A. aculeatus	TS772	Sphingidae	KC519371	KC519368	KC519366	-	-	Sanjuan *et al*. (2014)
A. araneosus	KY11341	spider	ON502826	-	ON525443	-	ON525442	Chen *et al.* (2022)
A. araneosus	KY11342	spider	ON502844	-	ON525445	-	ON525444	Chen *et al*. (2022)
A. attenuatus	ACB30112	-	MW465671	-	-	-	-	Unpublished
A. attenuatus	CBS 170.76^{T}	Hemipteran	MH860970	MH872739	OP762607	OP762611	OP762615	Manfrino *et al.* (2022)
A. attenuatus	SCAUDCL56	Soil	MN736538	-	-	-	-	Du *et al.* (2019)
A. attenuatus	SCAUDCL38	Thripidae	MN736537	-	-	-	-	Du *et al.* (2019)
A. attenuatus	xiajiNamtso20	water	MZ544556	-	-	-	-	Unpublished
A. attenuatus	ZP1	-	OR083384		-		-	Unpublished
A. australiensis	BRIP 72630a^{T}	Insect	NR_191288	OR527516	OR514840	-	OR514848	Unpublished
A. baishanensis	GZAAS 25-0551	-	PX375522	-	PX423129	-	PX423195	Unpublished
A. baishanensis	GZAAS 25-0552		PX375520	PX375644	PX423127	PX423262	PX423194	Unpublished
A. bannaensis	SWFC CLZhao 34016^{T}	-	NR_200677	-	-	-	PP588774	Zhang *et al*. (2024)
A. bannaensis	CLZhao 34017	-	PP571896	-	-	-	-	Zhang *et al*. (2024)
A. buriramensis	BCC 45166	Lepidoptera	ON006537	-	ON013547	-	ON013562	Khonsanit *et al.* (2024)
A. buriramensis	BCC 47936	Lepidoptera	ON006538	-	ON013548	-	ON013563	Khonsanit *et al*. (2024)
A. dipterigenus	CHE-CNRCB 1274	-	PX136049	-	PV435856	PV435859	-	Unpublished
A. dipterigenus	CBS 126.27	Coccids	OP756342	KM283773	KM283820	KM283840	KM283862	Unpublished
A. dipterigenus	SCA17	*Melanaphis sacchari*	OR512362	-	OK216929	-	-	Castrillo *et al*. (2024)
A. dipterigenus	SCA81	*Melanaphis sacchari*	OR512363	-	OK216930	-	-	Castrillo *et al*. (2024)
A. laosensis	YFCC 1910941	spiders	OQ509523	-	OQ506286	OQ511535	OQ511549	Wang *et al*. (2024)
A. laosensis	YFCC 1910942	spiders	OQ509524	-	OQ506287	OQ511536	OQ511550	Wang *et al*. (2024)
A. lecanii	ALL-8	*Saissetia coffeae*	PX471508	-	-	-	-	Unpublished
A. lecanii	CBS 114.25	Scale Insects	PV407399	-	PV414586	-	PV458017	Zhao *et al.* (2025)

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TABLE 1. (Continued)

Species	Voucher Number	Host	ITS	SSU	*TEF1-α*	RPB1	RPB2	References
A. lecanii	CBS 115.25	Coccidae	PV407397	MH854805	PV414584	-	PV458015	Vu *et al.* (2019)
A. lecanii	CBS:221.25	*Coccus viridis*	PV407400	MH854850.1	PV414587	-	PV458018	Vu *et al.* (2019)
A. lecanii	CBS 455.70B	-	PV407398	MH859794	PV414585	-	PV458016	Zhao *et al.* (2025)
A. fusiformis	BCC 40756	Lepidoptera	ON006542	-	ON013552	ON013576	ON013567	Khonsanit *et al.* (2024)
A. muscarius	CBS 101236	Lepidoptera	PV407418	-	PV414603	-	PV458034	Zhao *et al.* (2025)
A. muscarius	CBS:455.70C	-	PV407419	MH859795	PV414604	-	PV458035	Vu *et al.* (2025)
A. muscarius	CBS 340.37	*Puccinia graminis*	PV407420	-	PV414605	-	PV458036	Vu *et al.* (2019)
A. muscarius	CBS 393.49	-	PV407421	-	PV414606	-	PV458037	Zhao *et al.* (2025)
A. muscarius	IMI 068689^{T}	-	NR_111096	-	-	-	-	Schoch *et al.* (2014)
A. muscarius	CBS 126905	soil	PV407402	-	PV414589	-	PV458020	Zhao *et al.* (2025)
A. muscarius	CBS 297.64	*Thaumatopoea pityocampa*	PV407415	-	PV414600	-	PV458031	Zhao *et al.* (2025)
A. muscarius	CBS:576.50	Rhabdophaga rosaria	MH856762	-	PV414599	-	PV458030	Zhao *et al.* (2025)
A. muscarius	CBS 341.66	Tundra soil	PV407412	-	PV414598	-	PV458029	Zhao *et al.* (2025)
A. muscarius	2-Nov-GR29b	*Lycorma delicatula*	-	OR582989	OR602797	OR602846	OR602850	Hajek *et al.* (2023)
A. muscarius	ARSEF 14661	*Lycorma delicatula*	OR577160	-	OR593725	OR593718	OR593721	Hajek *et al.* (2023)
A. niveus	BCC 79887	Lepidoptera	ON006544	-	ON013554	ON013578	-	Khonsanit *et al.* (2024)
A. niveus	BCC 40747	Lepidoptera	ON006543	-	ON013553	ON013568	ON013577	Khonsanit *et al.* (2024)
A. noctuidarum	BBH16595	Lepidoptera	MT356075	-	MT477979	-	-	Aini *et al.* (2020)
A. noctuidarum	BCC36265	Lepidoptera	MT356072	-	MT477978	MT477994	MT477987	Aini *et al.* (2020)
A. noctuidarum	BCC47498	Lepidoptera	MT356074	-	MT477980	MT477996	MT477988	Aini *et al.* (2020)
A. noctuidarum	HKAS 132256	Lepidoptera	PX375521	PX375645	PX423128	PX423263	-	Unpublished
A. noctuidarum	CLZhao 35270	Lepidoptera	OR841531	-	-	-	-	Aini *et al.* (2020)

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TABLE 1. (Continued)

Species	Voucher Number	Host	ITS	SSU	*TEF1-α*	RPB1	RPB2	References
A. noctuidarum	CLZhao 35269	Lepidoptera	OR841532	-	-	-	-	Aini *et al.* (2020)
A. noctuidarum	BCC28571	Lepidoptera	MT356075	-	MT477981	MT478009	. MT478006	Aini *et al.* (2020)
A. phariformis	BCC 76537	Lepidoptera	ON006550	-	ON013560	-	ON013584	Khonsanit *et al.* (2024)
A. phariformis	BCC 45148	Lepidoptera	ON008556		ON013559		ON013583	Khonsanit *et al*. (2024)
A. pseudonoctuidarum	YFCC 1808943	Noctuidae	OQ509525	-	OQ506288	OQ511537	OQ511551	Unpublished
A. pseudonoctuidarum	YFCC 1808944	Noctuidae	OQ509526	-	OQ506289	-	OQ511552	Unpublished
A. pyralidarum	BCC28816	Lepidoptera	MT356080	-	MT477982	MT478000	MT478007	Aini *et al.* (2020)
A. pyralidarum	BCC29197	Lepidoptera	MT356083	-	MT508840	MT478003	MT477991	Aini *et al.* (2020)
A. pyralidarum	BCC40869	Lepidoptera	-	MT356082	MT477984	MT478002	MT477990	Aini *et al.* (2020)
A. pyralidarum	BCC32191	Lepidoptera	MT356081	-	MT477983	MT478001	MT477989	Aini *et al.* (2020)
A. infaproensis	**BORH(EF)00008^{T}**	**Lepidoptera**	**PZ456498**	**PZ742859**	**PZ452110**	**PZ754706**	**PZ754708**	**This study**
A. infaproensis	**BORH(EF)00009**	**Lepidoptera**	**PZ456499**	**PZ742860**	**PZ452111**	**PZ754707**	**PZ754709**	**This study**
A. sabanensis	JCh007	*Parthenolecanium* sp.	KC633242		-		-	Chiriví-Salomón *et al.* (2015)
A. sabanensis	JCh030	*Parthenolecanium* sp.	KC633234		-		-	Chiriví-Salomón *et al.* (2015)
A. sabanensis	JCh021	*Parthenolecanium* sp.	KC633233				-	Chiriví-Salomón *et al.* (2015)
A. taiwanicus	NTUCC 20-060^{T}	Lepidoptera	MT974202	-	MW200213	MW200221	MW200230	Unpublished
A. taiwanicus	NTUPPMCC 20-060-1	Lepidoptera	PP194458	-	-	-	-	Unpublished
A. tortricidarum	BCC28583	Tortricidae	MT356076	-	MT478004	MT477997	MT477992	Aini *et al.* (2020)
A. tortricidarum	BCC41868	Tortricidae	MT356077	-	MT477985	MT477998	MT478008	Aini *et al.* (2020)
A. tortricidarum	BCC72638	Tortricidae	MT356076	-	MT478004	MT477997	MT477992	Aini *et al.* (2020)
A. tuberculatus	BCC16819	-	GQ250005	GQ249962	GQ250037	-	-	Unpublished
A. tuberculatus	NBRC 106949	-	JN943318	-	AB968608	JN992475	AB968569	Schoch *et al.* (2012)
A. tuberculatus	NBRC 106956	-	JN943309	-	-	JN992478	-	Schoch *et al.* (2012)

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TABLE 1. (Continued)

Species	Voucher Number	Host	ITS	SSU	*TEF1-α*	RPB1	RPB2	References
A. tuberculatus	OSC 111002	-	JN049830	DQ522553	DQ522338	-	DQ522435	Kepler *et al.* (2012)
A. uredinophilus	AFHP206	*Hemileia vastatrix*	PX496034	-	PX632754	PX632746	PX632750	Unpublished
A. uredinophilus	AFHP204	*Hemileia vastatrix*	-	PX496033	PX632753	PX632745	PX632749	Unpublished
A. uredinophilus	B1	Myxomycete	PQ590478	-	PQ610578	-	-	Cherepanova *et al*. (2025)
A. uredinophilus	B2	Aphididae	PQ590479	-	PQ610579	-	-	Cherepanova *et al*. (2025)
A. uredinophilus	B4	Tipuloidea	PQ590480	-	PQ610580	-	-	Cherepanova *et al*. (2025)
A. uredinophilus	KUN 101469	Insect	MG948306	-	MG948316	MG948312	MG948314	Wei *et al.* (2018)
A. uredinophilus	KUN 101466	Insect	MG948305	-	MG948315	MG948311	MG948313	Wei *et al.* (2018)
A. uredinophilus	GZCC 24-0142	-	PX375488	PX375623	PX423095	PX423234	PX423167	Unpublished
A. xixiuensis	HKAS 125851 ^{T}	Lepidoptera	NR_191207	OP693479	OP838888	OP838890	OP838892	Liu *et al*. (2024)
A. xixiuensis	XX21081764	Lepidoptera	OP693460	OP693478	OP838887	OP838889	OP838891	Liu *et al*. (2024)
Purpureocillium lilacinum	CMUCDMT02	-	JN038196	-	-	-	-	Mar *et al.* (2012)
P. lilacinum	KUVET M022	-	MT487860	-	-	-	-	Unpublished

Notes: "-" shows no data in GenBank, while the newly generated sequences are in bold, and the type strains are indicated with superscript T.

Sequence alignment and phylogenetic analyses

The newly generated sequences in this study were compared with publicly available sequences using BLASTn analysis (https://www.ncbi.nlm.nih.gov/geo/query/blast.html). Based on BLASTn results and morphological similarities, the relevant sequences were obtained. Five genetic markers (ITS, SSU, *TEF1-α*, RPB1, and RPB2) were used to construct phylogenetic trees. Individual phylogenetic analyses were conducted for each genetic marker separately and analyses were conducted using all available sequences for each locus independently. The ITS, SSU, *TEF1-α*, RPB1 and RPB2 datasets comprised of 501 characters for ITS,490 for SSU, 762 for *TEF1-α*, 689 for RPB1 and 733 for RPB2, respectively. For the concatenated phylogenetic analysis, only taxa with multilocus sequence data available for at least two or more loci were included, and missing loci were treated as missing data in the combined alignment. Two sequences of *Purpureocillium lilacinum* (Thom) Luangsa-ard, Houbraken, Hywel-Jones & Samson (CMUCDMT02 and KUVET M022) were selected as outgroup taxa based on their close phylogenetic affinity yet distinct placement relative to *Akanthomyces* (Aini *et al.* 2020). Details of all sequences used in this study are provided in Table 1. Individual gene datasets, including ITS, SSU, *TEF1-α,* RPB1, and RPB2 (Supplementary Figures S1–S5), as well as a concatenated dataset, were analyzed. The combined dataset (ITS, SSU, *TEF1-α,* RPB1, and RPB2) was selected as the primary phylogenetic framework due to its higher resolution and robustness (Fig. 2).

Sequence alignments were initially performed using MAFFT v7 and further inspected and manually adjusted in AliView to improve alignment accuracy. Raw sequences were edited and assembled using BioEdit v7.1, and ambiguous nucleotides were corrected where necessary. Poorly aligned regions and excessive gaps were trimmed to produce high-quality alignments for downstream analyses (Clewley 1995, Hall *et al*. 2011, Chen *et al*. 2023, Sung *et al.* 2007). The best-fit nucleotide substitution model was determined using ModelFinder and further evaluated using jModelTest2 (Darriba *et al.* 2012), implemented through the CIPRES Science Gateway (https://www.phylo.org/). Maximum

likelihood (ML) phylogenetic analysis was performed using RAxML v8.2.12 (Stamatakis 2014) implemented on the CIPRES Science Gateway platform. The concatenated ITS, SSU, *TEF1-α*, RPB1, and RPB2 dataset was analyzed under the GTR+G substitution model using a single partition scheme, with 1000 rapid bootstrap replicates to estimate branch support. Bootstrap values (BS ≥70%) were considered indicative of strong support.

The ITS alignment consisted of 204 parsimony-informative sites, 6 singleton sites, and 291 constant sites. The SSU alignment consisted of 149 parsimony-informative sites, 4 singleton sites, and 337 constant sites. The *TEF1-α* alignment consisted of 150 parsimony-informative sites, 13 singleton sites, and 599 constant sites. The RPB1 alignment consisted of 251 parsimony-informative sites, 28 singleton sites, and 410 constant sites. The RPB2 alignment consisted of 262 parsimony-informative sites, 11 singleton sites, and 460 constant sites. The final concatenated alignment comprising ITS, SSU, *TEF1-α*, RPB1, and RPB2 sequences consisted of 3175 nucleotide characters, including 1016 constant sites, 62 singleton sites, and 2097 parsimony-informative sites.

Bayesian inference (BI) analysis was conducted using MrBayes v3.2.7a on the CIPRES Science Gateway platform (Miller *et al.* 2010, Ronquist and Huelsenbeck 2003). The concatenated ITS–SSU–*TEF1-α*-RPB1–RPB2 dataset was partitioned according to individual gene regions, and substitution models were selected using jModelTest v2.1.4 (Darriba *et al*. 2012). The GTR + I + G model was applied to the ITS, SSU and *TEF1-α* partitions, whereas the GTR + I model was applied to the RPB1 and RPB2 partitions. Two independent runs, each consisting of four Markov chains (three heated chains and one cold chain), were performed for 5,000,000 generations. Trees were sampled every 1,000 generations, and the first 25% of sampled trees were discarded as burn-in after assessing convergence between runs. Convergence was evaluated based on the average standard deviation of split frequencies (<0.01) and effective sample size (ESS >200) values. Phylogenetic relationships were inferred based on maximum likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP), with BS ≥70% and PP ≥0.95 considered significant support values.

The resulting phylogenetic trees were visualized using FigTree v1.4.4 (https://evomics.org/resources/software/molecular-evolution-software/figtree/) and further edited in Adobe Illustrator v27.6.1. The final sequence alignments were deposited in TreeBASE under submission ID 34567.

Results

Molecular Phylogeny

Maximum Likelihood (ML) and Bayesian Inference (BI) analyses produced broadly similar overall topologies (Figure 2). Therefore, the ML trees are presented, with maximum likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP) indicated at the nodes. The ITS phylogenetic analysis recovered the two Bornean isolates, BORH(EF)00008 and BORH(EF)00009, as a distinct clade with BS = 88% and PP = 0.93. This clade was recovered as sister to *Akanthomyces xixiuensis* represented by HKAS 125851 and XX21081764 from China, support from both analyses (BS = 78%; PP = 1.00). The combined *A. infaproensis—A. xixiuensis* lineage was further related to *Akanthomyces australiensis* (BRIP 72630a) from Australia, with ML bootstrap support but weak Bayesian support (BS = 82% and PP = 0.78, Supplementary Figure 1).

The SSU phylogenetic analysis recovered BORHEF00008 and BORHEF00009 as a distinct lineage representing *Akanthomyces infaproensis sp. nov.* (BS = 97%; PP = 1.00). The new species was recovered as sister to *Akanthomyces xixiuensis* (XX21081764 and HKAS125851) from China, with BS = 80% and PP = 0.78 support values. The *A. infaproensis* lineage was nested within the *Akanthomyces* clade together with *A. pyralidarum, A. baishanensis, A. tuberculatus*, and *A. noctuidarum* (Supplementary Figure 2).

In the *TEF1-α* phylogeny, BORH(EF)00008 and BORH(EF)00009 formed a distinct lineage sister to a clade comprising *Akanthomyces noctuidarum* Aini, Luangsa-ard, Mongkols. & Thanakitp. from Thailand (MT477978–MT477981) and China (PX423128), *A. tuberculatus* from Thailand (GQ250034) and the USA (GQ250035 and MF416490), and *A. aculeatus* from Thailand (GQ250033), with BS = 78% and PP = 0.95 statistical support (Supplementary Figure 3).

The RPB1 phylogenetic analysis showed that BORH(EF)00008 and BORH(EF)00009 formed a distinct clade within *Akanthomyces* (BS = 88%; PP = 0.98). This lineage was recovered as the sister taxon to *Akanthomyces noctuidarum* (Petch) Kepler, B. Shrestha & Spatafora (PX423263, MF416647, MT477994, MT477995, and MT477996) from China, USA, and Thailand, with BS = 90% and PP = 0.90 supports (Supplementary Figure 4).

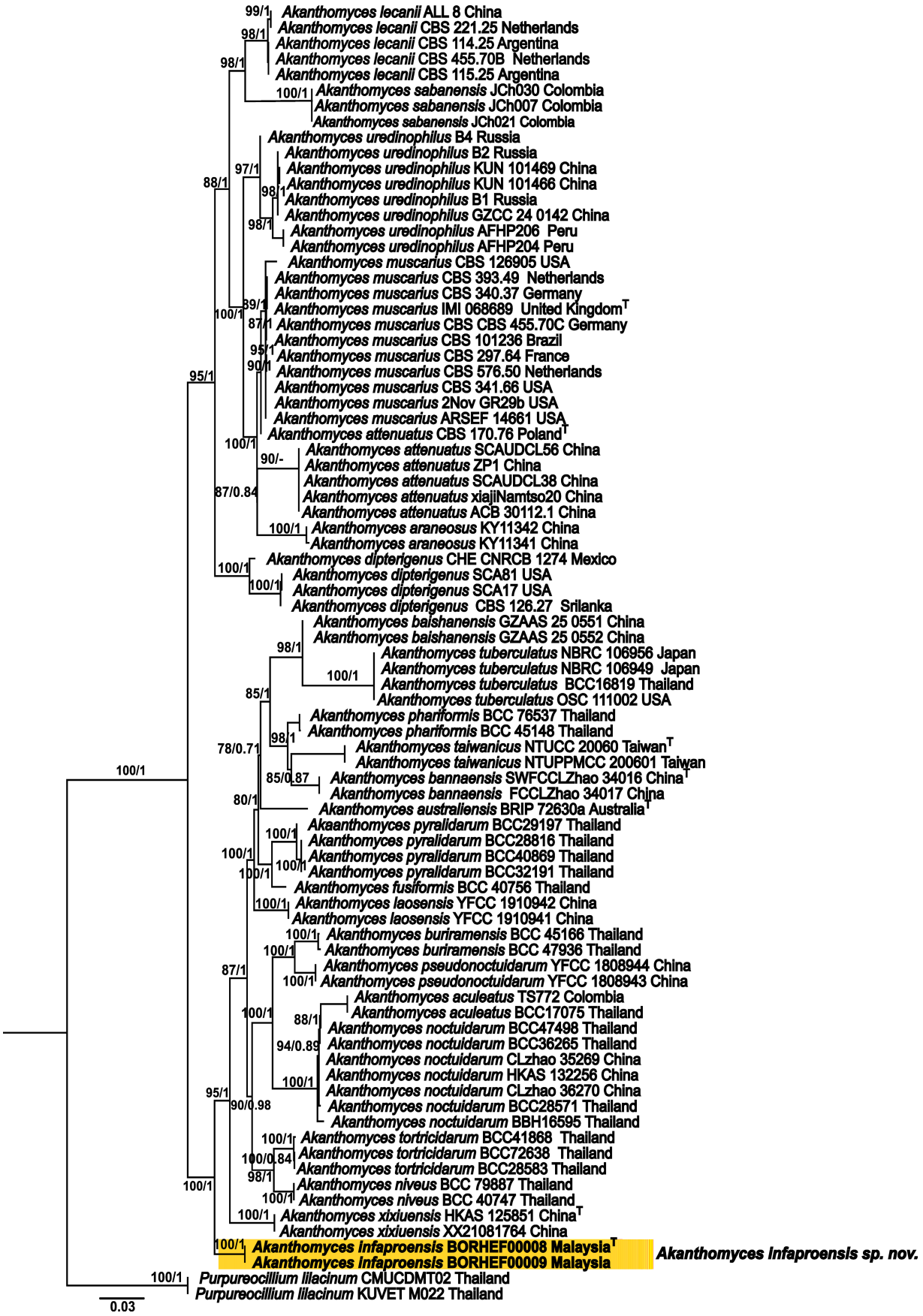

FIGURE 2. Maximum likelihood phylogenetic tree inferred from the concatenated ITS–SSU–*TEF1*-*α*-RPB1–RPB2 dataset using RAxML v8.2.12 implemented on the CIPRES Science Gateway under the GTR+G model with 1000 rapid bootstrap replicates. Values at the nodes represent maximum likelihood bootstrap support (BS) and Bayesian posterior probabilities (PP), respectively. "T" indicates type material. The newly described species is highlighted in bold.

The RPB2 phylogenetic analysis recovered BORHEF00008 and BORHEF00009 as a distinct lineage representing *Akanthomyces infaproensis sp. nov.* (BS = 100%; PP = 1.00). This lineage formed a sister relationship with *Akanthomyces xixiuensis* (OP838892 and OP838891) from China (BS = 82%; PP = 0.71) and was apart from other closely related species, including *A. tortricidarum, A. pyralidarum, A. laosensis, A. bannaensis, A. tuberculatus, A. baishanensis, A. pseudonoctuidarum*, and *A. noctuidarum* within the genus *Akanthomyces* (Supplementary Figure 5).

In the concatenated ITS–SSU–*TEF1-α*-RPB1–RPB2 phylogenetic tree, different species of *Akanthomyces* were included. Species of *Akanthomyces* formed a well-supported distinct lineage. Two Bornean isolates, BORH(EF)00008 and BORH(EF)00009, formed a distinct lineage with BS = 100% and PP = 1.00 statistical support. This lineage was recovered as sister to *Akanthomyces tortricidarum* (BCC28583, BCC41868, and BCC72638) from Thailand with BS = 95% and PP = 1.00 support values. The combined phylogenetic evidence supports the recognition of the Bornean isolates as a distinct species, *Akanthomyces infaproensis sp. nov.* (Figure 2).

Taxonomy

***Akanthomyces infaproensis* Shahbaz & J.S. Sathiya Seelan, *sp. nov.* (Fig. 3)**
MycoBank number: 863832

Etymology:—The species epithet *"infaproensis"* is derived from the Innoprise—FACE Foundation Rainforest Rehabilitation Project (INFAPRO), Danum Valley, Sabah, Malaysia, referring to the rainforest restoration site where the fungus was collected.

Holotype:—MALAYSIA, Sabah, Lahad Datu, INFAPRO Rainforest Rehabilitation Project site, adjacent to the Danum Valley Conservation Area, 4°58′14.62″N, 117°41′11.46″E, 52 m a.s.l., on an adult Lepidoptera attached to the underside of a leaf, 12 March 2024, M. Shahbaz and J.S. Sathiya Seelan BORH(EF)00008 (holotype).

Description: On adult Lepidoptera (moth). Hosts medium-sized, approximately 15–25 mm long, with a light brown (5D5–5D6) to greyish (N4–N5) cuticle. Host attached to the underside of a leaf, with fungal growth emerging predominantly from the dorsal thorax and abdominal segments.

Sexual morph on host: Perithecia were flask-shaped, semi-immersed to superficial, either solitary or clustered on the host cuticle, dark brown (5F4–6F6) to reddish-brown (7D5–8E5), measuring 285–320 × 125–150 µm ($\bar{x}$ = 302.5 × 137.5 µm, n = 20) (Fig. 3C and D). The perithecial centrum was well developed, composed of densely packed, parallel asci, forming a compact hymenial layer. This layer measured approximately 90–120 µm in thickness, with tightly arranged asci embedded in a gelatinous matrix (Fig. 3E). Asci were cylindrical, elongate, thin-walled, measuring 190–220 × 8–12 µm ($\bar{x}$ = 205 × 10 µm, n = 20). The ascus apex was rounded to slightly pointed, lacking a prominent apical cap (Fig. 3F). Ascospores hyaline, filiform, smooth-walled, multiseptate, 120–150 × 2.5–3.5 µm, arranged parallel within the ascus, remaining intact when immature and becoming disarticulated at the septa upon maturity (Fig. 3G). At maturity, each ascospore disarticulates into cylindrical to slightly barrel-shaped part-spores measuring 12–16 × 2–3 µm ($\bar{x}$ = 14 × 2.5 µm, n = 20) (Fig. 3H).

***Asexual morph on host*:** Synnemata were cream (4A3–4A4) to pale yellow (4A3–4A4), erect, branched, arising in clusters from the host body and terminating in dark brown fertile heads (Fig. 3A–B).

Cultural characteristics: The fungus colony on PDA was circular and fast-growing, reaching 35–40 mm in diameter after 14 days at 25°C. The surface colony was white (1A1), cottony to floccose, with a slightly raised surface and entire to slightly irregular margins (Fig. 3I). The reverse colony was pale cream (3A2–4A2) to light beige (4B3–5B4) (Fig. 3J).

Asexual morph in culture: Phialides cylindrical to slender, tapering towards the apex, measuring 20–50 × 2–3 µm ($\bar{x}$ = 35 × 2.5 µm, n = 20) (Fig. 3K–M). Conidia ellipsoid, hyaline, smooth-walled, measuring 5–7 × 2–3 µm ($\bar{x}$ = 6 × 2.5 µm, n = 20) (Fig. 3N).

***Additional specimen examined*:** Malaysia, Sabah, Lahad Datu, Rainforest Rehabilitation Project, Danum Valley Conservation Area, 4°58′14.62″N, 117°41′11.46″E, elevation 52 m a.s.l., on an adult Lepidoptera attached to the underside of a leaf, 12 March 2024, M. Shahbaz & J.S. Sathiya Seelan, BORH(EF)00009.

***Living Culture*:** A living culture derived from BORH(EF)00009 is maintained at the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia.

Distribution: Currently known only from the INFAPRO Rainforest Rehabilitation Project, adjacent to the Danum Valley Conservation Area, Lahad Datu, Sabah, Malaysia.

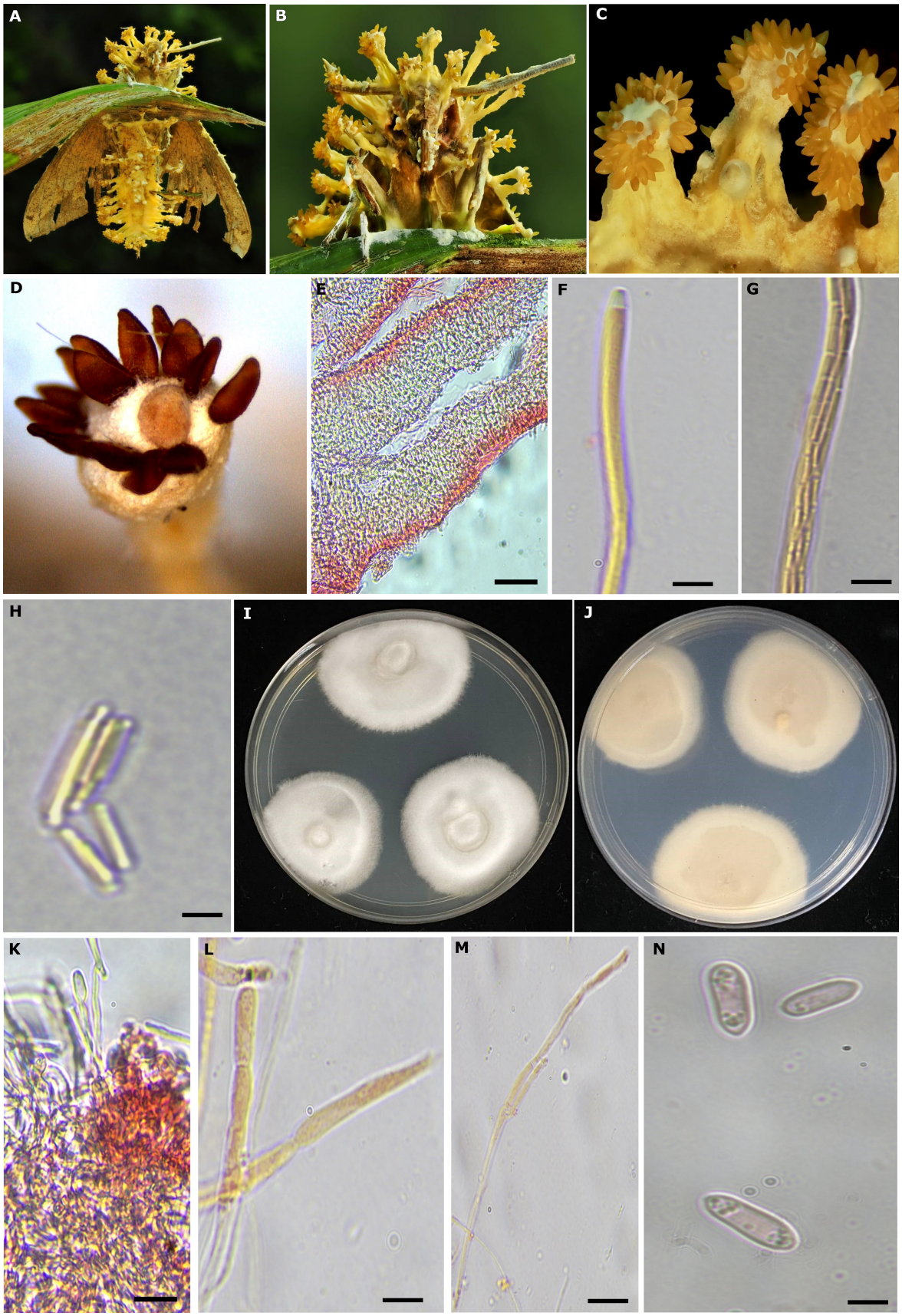

FIGURE 3. ***Akanthomyces infaproensis sp. nov.*** A–H. BORH(EF)00008, holotype specimen. A–B. Fungus on adult moth; C–D. Perithecia; E. Perithecial centrum; F. Ascus tip; G. Asci and ascospores showing septa; H. Ascospores fragmenting into part-spores. I–N. Asexual morph produced in culture derived from BORH(EF)00009. I. Colony on PDA (front view); J. Colony on PDA (reverse view); K–M. Phialides and synnemata; N. Conidia. Scale bars: E = 100 µm; F = 50 µm; G = 20 µm; H = 5 µm; K = 20 µm; L = 10 µm; M = 10 µm; N = 5 µm.

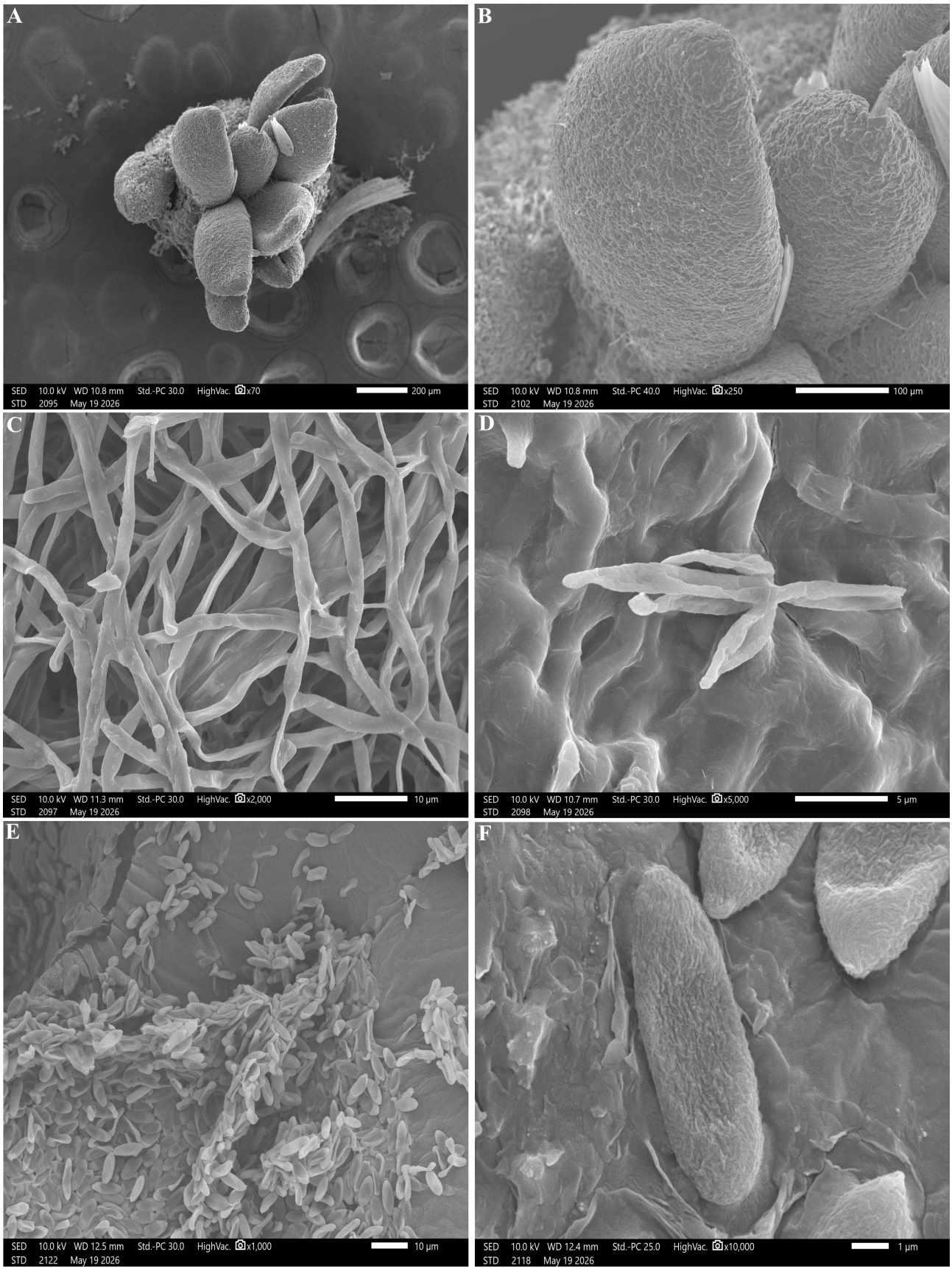

FIGURE 4. Scanning electron microscopy of *Akanthomyces infaproensis sp. nov*. (BORH(EF)00008, holotype). (A and B) Synnema, (C and D) Conidiophore, (E and F) Conidia.

Remarks: Phylogenetic analyses of the individual ITS, SSU, *TEF1-α*, RPB1, and RPB2 datasets as well as the concatenated five-locus dataset consistently recovered BORH(EF)00008 and BORH(EF)00009 as distinct lineage within *Akanthomyces*. Morphologically, *A. infaproensis* is characterized by relatively small perithecia (285–320 × 125–150 µm), filiform multiseptate ascospores that disarticulate at maturity into cylindrical to slightly barrel-shaped part-spores (12–16 × 2–3 µm), and comparatively large ellipsoid conidia (5–7 × 2–3 µm). It differs from *A. tortricidarum* mainly in its larger conidia and from *A. niveus*, *A. noctuidarum*, *A. tuberculatus*, and *A. buriramensis* in the combination of smaller perithecia and larger part-spores. The combined molecular and morphological evidence supports its recognition as *Akanthomyces infaproensis sp. nov.*

Under an electron microscope, the synnemata were densely aggregated and arose directly from the host surface as compact clusters. Individual synnemata appeared clavate to cylindrical, with slightly swollen, rounded apices. The surface of the synnemata was roughened, rugose, with a wrinkled texture (Fig. 4A and B). The conidiophores formed a dense, intertwined hyphal network that was hyaline, smooth-walled, and septate. The conidiophores were slender, elongated, and irregularly branched (Fig. 4C and D). The conidia were produced abundantly in crowded masses over the fertile surfaces that were hyaline, smooth-walled, and ellipsoidal to short cylindrical in shape. The conidia appeared elongated and cylindrical with a rounded end and tapered basal regions (Fig. 4E and F).

TABLE 2. Morphological comparison of *Akanthomyces infaproensis* and related species.

Species	Host	Perithecia (µm)	Asci (µm)	Part-spores (µm)	Phialides (µm)	Conidia (µm)	References
Akanthomyces aculeatus	Lepidoptera (moth)	-	-	-	6–16 × 2.5–4	3–6 × 2–3	Mains (1950)
Akanthomyces buriramensis	Lepidoptera (adult Noctuidae moth)	Fertile region: 500–560 × 200–380	43.5–55 × 4.5–5	Part-spores: 4.6–14.5 × 0.5–1; filiform, multiseptate, breaking into part-spores	4–5 × 2–3.4	3–5 × 2–2.2	Khonsanit *et al.* (2024)
A. infaproensis sp. nov.	**Lepidoptera**	**285–320 × 125–150**	**190–220 × 8–12**	**Part-spores: 12–16 × 2–3; Filiform, multiseptate, breaking into part-spores.**	**20–50 × 2–3**	**5–7 × 2–3**	**This study**
Akanthomyces niveus	Lepidoptera (adult moth)	400–530 × 180–200	273–568 × 4–5	Part-spores: (5–6–14)–22 × 0.5–1	-	-	Khonsanit *et al.* (2024)
Akanthomyces noctuidarum	Lepidoptera (adult moth, Noctuidae)	(530–)623–993(–1000) × (290–)308–413(–425)	(170–)196–423(–550) × (2–)2.7–3.8(–4)	(6–)7–10.7(–13) × 1; filiform, multiseptate, breaking into part-spores	(5–)6.8–9(–10) × (1.8–)2–2.4(–3)	(3–)3.5–4.5(–6) × 1	Aini *et al.* (2020)
Akanthomyces pseudonoctuidarum	Lepidoptera (adult Noctuidae moth)	-	-	-	6.8–26.0 × 2.1–3.6	2.6–6.4 × 1.5–2.2	Wang *et al.* (2024)
Akanthomyces tortricidarum	Lepidoptera (adult moth, Tortricidae)	-	-	-	(5–)6–8(–10) × (1.8–)2–2.7(–3)	Long synnemata: (2–)2.5–3(–3.2) × (0.8–)1–1.4(–2); Short synnemata: (1–)1.8–2.7(–3) × 1–2	Aini *et al.* (2020)
Akanthomyces xixiuensis	Lepidoptera (moth)	-	-	-	6–27 × 2–4	3.5–5.6 × 2.2–3.2	Liu *et al.* (2024)

Discussion

Based on the molecular and morphological evidence, we propose *Akanthomyces infaproensis* as a new species. All five single-locus analyses (ITS, SSU, *TEF1-α*, RPB1, and RPB2) recovered the two Bornean isolates as a distinct lineage within *Akanthomyces*, although their inferred sister-group relationships varied among loci. The ITS, SSU, and RPB2 analyses placed the new species close to *A. xixiuensis*, whereas the *TEF1-α* and RPB1 datasets indicated relationships with *A. noctuidarum*, *A. tuberculatus* and/or *A. aculeatus*. Such topological incongruence among single-locus phylogenies may reflect differences in evolutionary rates, incomplete lineage sorting, or locus-specific phylogenetic signal (Steenwyk *et al.* 2023, James *et al.* 2020). The concatenated five-locus analysis recovered the Bornean isolates as an independent lineage (BS = 100%; PP = 1.00), sister to *A. tortricidarum*. Together with the diagnostic morphological differences, these results support recognition of *A. infaproensis* as a distinct species.

Morphologically, *Akanthomyces infaproensis* belongs to the group of *Akanthomyces* species associated with Lepidoptera hosts and characterized by stromata emerging from insect bodies and a combination of synnematous asexual structures and perithecial sexual morphs. Among these taxa, *A. tortricidarum* is the most morphologically similar species. However, *A. tortricidarum* is distinguished by its markedly smaller, predominantly fusoid conidia (2–3 × 1–1.4 μm), whereas *A. infaproensis* produces larger ellipsoid conidia (5–7 × 2–3 μm), providing a distinct character. *A. xixiuensis*, another Lepidoptera-associated species, differs in smaller fusoid to ovoid conidia (3.5–5.6 × 2.2–3.2 μm). Likewise, *A. aculeatus* differs by forming smaller ellipsoidal to obovoid conidia (3–6 × 2–3 μm), whereas *A. infaproensis* possesses larger ellipsoid conidia and cylindrical tapering phialides.

Another closely related species, *A. niveus*, differs primarily in its sexual morph characteristics. *Akanthomyces niveus* produces larger superficial perithecia and filiform, multiseptate ascospores that disarticulate into cylindrical part-spores. In contrast, *A. infaproensis* produces smaller perithecia and comparatively shorter filiform ascospores (120–150 × 2.5–3.5 μm), which disarticulate into cylindrical to slightly barrel-shaped part-spores (12–16 × 2–3 μm). These differences in perithecial dimensions, ascospore morphology and part-spore dimensions help distinguish the two species. *Akanthomyces noctuidarum* is distinguished by its multiseptate, filiform ascospores that fragment into one-celled part-spores, larger perithecia (623–993 × 308–413 μm) and narrower cylindrical conidia (3.5–4.5 × 1 μm). In contrast, *A. infaproensis* produces smaller perithecia, broader ellipsoid conidia and filiform multiseptate ascospores that disarticulate at maturity into cylindrical to slightly barrel-shaped part-spores. Similarly, *A. buriramensis* differs in having ampulliform to lageniform phialides, smaller ellipsoid to fusoid conidia (3–5 × 2–2.2 μm) and smaller part-spores. The combination of larger ellipsoid conidia, smaller perithecia, and differences in part-spore dimensions distinguishes *A. infaproensis* from these related species.

Regarding host association, *A. infaproensis* was found on an adult moth (Lepidoptera), with stromata emerging from the dorsal thorax and abdominal regions. Association with Lepidoptera is shared with several other species of *Akanthomyces*, including *A. tortricidarum*, *A. xixiuensis*, *A. aculeatus*, *A. niveus*, *A. noctuidarum*, *A. pseudonoctuidarum*, and *A. buriramensis*. Therefore, host association alone is not diagnostic for the new species. Rather, the combination of morphological differences and its distinct phylogenetic placement support recognition of *A. infaproensis* as a novel species.

As an entomopathogenic fungus, *Akanthomyces* species play important ecological roles by naturally regulating insect populations and contributing to ecosystem balance (Di Sora *et al.* 2025, Nicoletti and Becchimanzi 2020). These fungi are also involved in nutrient cycling through the decomposition of infected insect hosts, thereby supporting forest ecosystem functioning (Armand *et al.* 2020). The discovery of *A. infaproensis* represents a new fungal species associated with Lepidoptera and contributes to a better understanding of *Akanthomyces* diversity and host-fungus interactions in tropical rainforest ecosystems.

Although the inferred sister-group relationships varied among the individual loci, all five single-locus analyses consistently recovered BORH(EF)00008 and BORH(EF)00009 as a distinct lineage within *Akanthomyces*. The concatenated ITS–SSU–*TEF1-α*-RPB1–RPB2 analysis further recovered the two Bornean isolates as a strongly supported independent lineage (BS = 100%; PP = 1.00). This consistent separation across the molecular datasets, together with the diagnostic morphological characteristics, provides strong evidence supporting recognition of the Bornean isolates as *Akanthomyces infaproensis sp. nov.*

Importantly, *A. infaproensis* was discovered in the INFAPRO Rainforest Rehabilitation Project site, a regenerating tropical forest established following selective logging. The occurrence of a previously unknown entomopathogenic fungal species in this rehabilitated landscape highlights the conservation value of rainforest restoration programmes, indicating that recovering forests may provide suitable habitats for previously undocumented fungal taxa. This finding

suggests the potential importance of rehabilitated tropical forests as reservoirs of fungal diversity; however, comparative biodiversity assessments with natural forests are required before making conclusions regarding their relative diversity. Therefore, the discovery of *A. infaproensis* should be considered as evidence of the conservation potential of restoration areas rather than a demonstration that rehabilitated forests support fungal diversity comparable to natural forests. Moreover, the discovery reinforces Sabah as a biodiversity hotspot for entomopathogenic fungi and indicates that many undescribed species are likely to remain undiscovered in the forests of Borneo. Given the growing interest in *Akanthomyces* species as sources of environmentally friendly biocontrol agents and biologically active secondary metabolites, the recognition of *A. infaproensis* provides a basis for future investigations into its ecological role and biological properties; however, its insect pathogenicity, host range, virulence, biosafety, and potential applications as a biocontrol agent remain to be experimentally evaluated.

Conclusion

The delimitation of *Akanthomyces infaproensis* is supported by an integrated taxonomic approach combining morphological and multilocus phylogenetic evidence. The species forms a strongly supported independent lineage within *Akanthomyces* and is distinguished from phylogenetically related species by a combination of relatively small perithecia, comparatively large ellipsoid conidia, and filiform multiseptate ascospores that disarticulate into cylindrical to slightly barrel-shaped part-spores. The species was collected from an adult lepidopteran host in the INFAPRO Rainforest Rehabilitation Project site, Sabah, Malaysia. Its discovery expands the known diversity of entomopathogenic fungi in tropical Borneo and highlights rehabilitated tropical forests as potentially important habitats for undocumented fungal diversity.

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CRediT authorship contribution statement

Muhammad Shahbaz, Jaya Seelan Sathiya: Fieldwork and sample collection. Muhammad Shahbaz, Chong Chuan Cheak, and Jaya Seelan Sathiya Seelan: Conceptualization and formal analysis. Muhammad Shahbaz, Chong Chuan Cheak, Ibrahem Ghani Wasti, Yap Sau Wai and Jaya Seelan Sathiya Seelan: Writing–original draft, figures, initial review, and editing. Jaya Seelan Sathiya Seelan: Critical review. Jaya Seelan Sathiya Seelan: Supervision and final validation.

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Data availability: The nucleotide sequences have been deposited in the NCBI GenBank database (https://submit.ncbi.nlm.nih.gov/subs). The accession numbers for *Akanthomyces infaproensis* BORH(EF)00008 are ITS: PZ456498, SSU: PZ742859, *TEF1-α*: PZ452110, RPB1: PZ754706, and RPB2: PZ754708. The accession numbers for BORH(EF)00009 are ITS: PZ456499, SSU: PZ742860, *TEF1-α*: PZ452111, RPB1: PZ754707, and RPB2: PZ754709.

Declarations

Competing interests: The authors declare that they have no conflict of interest.

Ethical approval: The current research work does not require any ethical approval.

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Supplementary Material. The following supporting information can be downloaded at the DOI landing page of this paper:

Supplementary Figure 1. Maximum likelihood phylogenetic tree of *Akanthomyces* inferred from the ITS dataset using RAxML v8.2.12

Supplementary Figure 2. Maximum likelihood phylogenetic tree of *Akanthomyces* inferred from the SSU dataset using RAxML v8.2.12

Supplementary Figure 3. Maximum likelihood phylogenetic tree of *Akanthomyces* inferred from the *TEF1-α* dataset using RAxML v8.2.12

Supplementary Figure 4. Maximum likelihood phylogenetic tree of *Akanthomyces* inferred from the RPB1 dataset using RAxML v8.2.12

Supplementary Figure 5. Maximum likelihood phylogenetic tree of *Akanthomyces* inferred from the RPB2 dataset using RAxML v8.2.12