Polyphyletic genera in Xylariaceae (Xylariales): *Neoxylaria* gen. nov. and *Stilbohypoxylon*

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Abstract

Several genera in Xylariaceae are polyphyletic in phylogenetic trees and represent more than one distinct genus. However, it is challenging to resolve these genera that are often phylogenetically distantly related, because many taxa have never been recollected and sequenced. Those that have been named and sequenced often lack documented characters or herbarium material. In this paper, we use descriptive morphology of fresh collections, and molecular data to resolve some taxonomic problems in Xylariaceae. During the of microfungi on palms in Thailand, we collected several novel xylariaceous taxa. Herein, we introduce a new genus *Neoxylaria* which is distantly related to *Xylaria sensu stricto* and a new species *Stilbohypoxylon elaeidis*. *Neoxylaria* is characterized by relatively small stromata with conspicuously exposed perithecial contours under a narrowly striped outer layer. *Neoxylaria* accommodates a species morphologically similar to *Xylaria juruensis*, which was also collected from palm material in Brazil and *X. queenslandica* collected from *Archontophoenix alexandrae* in Australia. As no molecular data exists for these old collections, we have linked them with morphology to our fresh collection and use both molecular data and morphology to introduce the new genus. *Neoxylaria juruensis* (Henn.) Konta & K.D. Hyde, comb. nov. and *N. queenslandica* (Joanne E. Taylor, K.D. Hyde & E.B.G. Jones) Konta & K.D. Hyde, comb. nov. are therefore established. Multigene phylogenetic analysis shows that our new species (*S. elaeidis*) clusters with *Stilbohypoxylon sensu stricto* (*Stilbohypoxylon* clade II) and

clarifies the nature of the genus. The new species differs from other species in having solitary, smooth stromata and forms synnemata-like structures on the host, but not on the stroma. The novel taxa introduced here are supported by multigene phylogeny and morphology. Comprehensive morphological descriptions, illustrations and a phylogenetic tree to show the placement of new taxa are provided.

Keywords – 3 new taxa – palmicolous fungi – phylogeny – Sordariomycetes – taxonomy – Thai fungi

Introduction

Xylariaceae has a long history of study and is one of the largest and most diverse families of Ascomycota (Fröhlich & Hyde 2000, Tang et al. 2009, Stadler et al. 2013, Koyani et al. 2016, Daranagama et al. 2018). Most xylariaceous species are saprobes or endophytes, while a few are considered to be plant pathogens (Rogers 2000, Okane et al. 2008, Stadler et al. 2013, Husbands & Aime 2018, Pourmoghaddam et al. 2018). Xylariaceous taxa exhibit high diversity in tropical regions and produce a high number of bioactive secondary metabolites (Fröhlich & Hyde 2000, Stadler & Hellwig 2005, Senanayake et al. 2015, Adnan et al. 2018a, Chen et al. 2018, Elias et al. 2018, Cedeño-Sanchez et al. 2020). Over time, several genera have either been included or excluded from Xylariaceae and the family limits remain unstable (Daranagama et al. 2016, 2018, Tibpromma et al. 2017, Fournier et al. 2018a, Voglmayr et al. 2018, Wendt et al. 2018). The evolutionary relationships of Xylariaceae with other related families using molecular clock evidence have been studied by Samarakoon et al. (2016), Hongsanan et al. (2017) and Hyde et al. (2017, 2020). Samarakoon et al. (2016) estimated that the crown node ages of Xylariaceae and Microdochiaceae were during the Late Mesozoic (66–100 Mya). Hongsanan et al. (2017) and Hyde et al. (2017) also concluded that the divergence times of familial ranks in Sordariomycetes should be around 50–150 Mya. Hyde et al. (2020) confirmed the familial status of Xylariaceae in the subclass Xylariomycetidae and estimated the divergence time for Xylariomycetidae at 278 Mya. Wijayawardene et al. (2018) listed 44 genera in Xylariaceae based on the updated phylogenetic relationships of Daranagama et al. (2018) and Wendt et al. (2018). Hyde et al. (2020) redefined the families of Sordariomycetes based on phylogenetic analyses and divergence estimates coupled with morphology. They accepted 32 genera for Xylariaceae, and this was followed by Wijayawardene et al. (2020).

Xylaria was introduced by Schrank (1789) as the generic type of Xylariaceae. *Xylaria* is the largest genus of Xylariaceae with *X. hypoxylon* as the type species (Greville 1824, Peršoh et al. 2009). *Xylaria* species are saprobes on dead wood and endophytes occurring in living plants and are sometimes associated with termites (Hsieh et al. 2010, Daranagama et al. 2018). The important characteristics of this genus are stromata that are extremely variable in size, colour, and shape; subglobose perithecia, immersed to slightly exposed in perithecia mounds; 8-spored asci that are unitunicate, cylindrical, long-pedicellate, with J+, apical ring and uniseriate ascospores, that are ellipsoid-inequilateral, medium to dark brown, containing two large guttules and with a germ slit. The asexual morph is geniculosporium-like, with hyaline-light brown, smooth, branched conidiophores bearing hyaline, roughened or smooth-walled, ellipsoidal conidia (Stadler et al. 2013, Maharachchikumbura et al. 2016, Daranagama et al. 2018).

Stilbohypoxylon was introduced by Hennings (1902) with the type species *S. moelleri*. The genus is characterized by globose to pulvinate black stromata, with scales or blunt spines on the surface, cylindrical asci, with a J+, apical ring, brown, ellipsoidal ascospores, often with a thin mucilaginous sheath, with a straight or spiral germ slit and geniculosporium-like asexual morphs (Hennings 1902, Rogers & Ju 1997, Petrini 2004, Daranagama et al. 2018). Rogers & Ju (1997) re-described the type species and introduced a new species, *S. samuelsii*. Hladki & Romero (2003) accommodated two new species in this genus viz. *S. macrosporum* and *S. minus*. A key to the species was provided by Petrini (2004). Recently, a new record of *S. quisquiliarum* was reported from Argentina (Esteban et al. 2013). DNA sequence data are available for only two species in

GenBank, *S. elaeidicola* and *S. quisquiliarum*. These two *Stilbohypoxylon* species did not resolve as a monophyletic group (Ju et al. 2007, Tang et al. 2007, 2009, Peláez et al. 2008, Hsieh et al. 2010, Daranagama et al. 2018, Wendt et al. 2018).

Both *Stilbohypoxylon* and *Xylaria* are unresolved lineages and much lumping and splitting of species has occurred over time. For example, Fröhlich & Hyde (2000) lumped numerous collections under *S. moelleri*, both from palms and dicotyledonous wood. Thus, researchers must strictly consider the type when comparing genera and species. However, since few types have sequence data and only few species have been epitypified, comparison of species is rather difficult. Phylogenetic studies indicated that *Stilbohypoxylon* and *Xylaria* do not form monophyletic groups, even though they clustered within Xylariaceae (Lee et al. 2000, Hsieh et al. 2010, Senanayake et al. 2015, Maharachchikumbura et al. 2016, Hongsanan et al. 2017, Daranagama et al. 2018, Wendt et al. 2018). Daranagama et al. (2018) and Wendt et al. (2018) discussed the phylogenetic affinities of xylariaceous genera based on morphology, phylogeny, and chemotaxonomic concepts. Wendt et al. (2018) found that *Xylaria* clustered in three main clades within Xylariaceae, while *Stilbohypoxylon* formed a clade with some *Xylaria* species and other genera viz. *Amphirosellinia*, *Astrocystis*, and *Collodiscula* but without statistical support. Daranagama et al. (2018) also confirmed that *Xylaria* is polyphyletic in Xylariaceae; for *Stilbohypoxylon*, *S. quisquiliarum* clustered within one subclade and *S. elaeidicola* clustered within another subclade.

This study is a continuation of the series on palmicolous fungi in Thailand (Konta et al. 2016, 2020). The combined sequence data of ITS, RPB2 and TUB2 is used to investigate the placement of *Neoxylaria* and *Stilbohypoxylon* and their phylogenetic relationships.

Materials & Methods

Collection, isolation, and identification

Dead palm materials were collected from two locations in Krabi and Phang-nga Provinces, Thailand, in 2014 (Fig. 1). Fungal isolates were obtained from dead petioles of palm and primary identification of the fungi was performed based on the presence of fruiting bodies, asci, and ascospores. Pure cultures were obtained using single spore isolation on a petri-dish containing malt extract agar (MEA) medium and incubated at 25–28°C overnight (Konta et al. 2016). Culture characteristics were recorded after incubation at 25–28°C for 14 days.

Morphological characteristics were examined using a Motic SMZ 168 series stereomicroscope and photographed using an Axio camera fitted on the Zeiss Discover V8 stereomicroscope. Micro-morphological structures were photographed using a Canon 600D camera on Nikon ECLIPSE 80i microscope. Distilled water, lactic acid and/or lacto glycerol were used as mounting agents, Meltzer's reagent was used for testing amyloid reaction of the apical ring structures. Fungal structures were measured using Image Framework software (IFW v. 0.9.7). Photo plates were processed using Adobe Photoshop CS6 (Adobe Systems, USA). The holotype specimens were deposited in the herbarium of Mae Fah Luang University (Herb. MFLU) and ex-type cultures in Mae Fah Luang Culture Collection (MFLUCC), Chiang Rai, Thailand. Facesoffungi and Index Fungorum numbers are registered as outlined in Jayasiri et al. (2015) and Index Fungorum (2020).

DNA extraction and PCR amplification

The DNA was extracted from the mycelia of 14 days old fungal cultures using the Biospin Fungus Genomic DNA Extraction Kit (BioFlux®, P.R. China) following the manufacturer's protocol. The internal transcribed spacer (ITS), partial RNA polymerase II second largest subunit (RPB2) and partial β-tubulin (TUB2) loci were subjected to PCR amplification and sequencing using specific primers and PCR conditions (Table 1). The total volume of PCR mixtures for amplifications were carried out in a 25 µl reaction volume containing, 8.5 µl of ddH$_2$O, 12.5 µl of 2× Easy Taq PCR Super Mix (mixture of Easy Taq TM DNA Polymerase, dNTPs and optimized buffer (Beijing Trans Gen Biotech Co., Chaoyang, Beijing, P.R. China), 2 µl of DNA template, and

1 µl of each forward and reverse primers (10 pM). The quality of PCR products was checked on 1% agarose gel electrophoresis stained with 4S green nucleic acid (Life Science Products & Services Cat. Songjiang, Shanghai, P.R. China). Purification and sequencing of PCR products were carried out by Sangon Biotech Co., Shanghai, China. Consensus sequences were generated using SeqMan software (DNASTAR). The newly generated sequences were deposited in GenBank (Table 2).
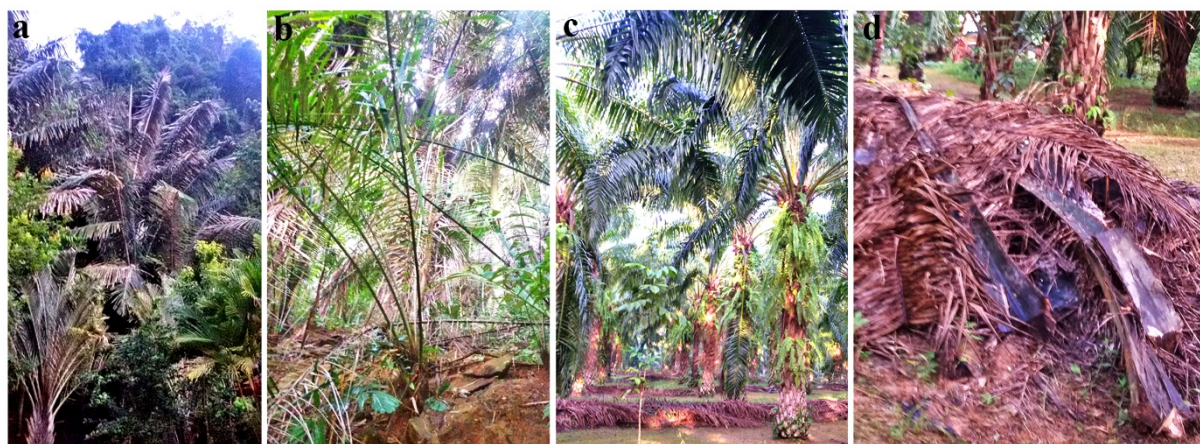

Figure 1 – a A forest in Phang-nga Province (the collection site of *Neoxylaria arengae*). b *Arenga pinnata* (Arecaceae). c An oil palm plantation in Krabi Province (the collection site of *Stilbohypoxylon elaeidis*). d Palm samples (*Elaeis guineensis*).

Table 1 Details of genes/loci with PCR primers and PCR conditions.

Genes/loci	Primers	PCR conditions	References
ITS	ITS5/ITS4	[a]; 95°C: 30 s, 55°C: 50 s, 72°C: 30 s (35 cycles); [c]	White et al. (1990)
RPB2	fRPB2-5f/fRPB2-7cR	[b]; 95°C: 1 min, 54°C: 2 min, 72°C: 1.5 min (35 cycles); [c]	Liu et al. (1999)
TUB2	T1/ T22	[b]; 94°C: 1 min, 52°C: 1 min, 72°C: 1.5 min; [c]	O'Donnell & Cigelnik (1997)

[a] Initiation step of 94°C: 3 min. [b] Initiation step of 95°C: 5 min. [c] Final elongation step of 72°C: 10 min and final hold at 4°C

Phylogenetic analyses

Consensus sequences were subjected to BLAST searches in the NCBI GenBank database (http://blast.ncbi.nlm.nih.gov/). Sequence data were retrieved from GenBank following recent studies (Hsieh et al. 2010, Daranagama et al. 2018, Ju et al. 2018, Wendt et al. 2018). Sequences of the ITS, RPB2 and TUB2 were analyzed individually and in combination. Alignments were processed with MAFFT v. 7.372 (Katoh et al. 2017) and manually improved where necessary. The sequence datasets were combined using MEGA7 (Kumar et al. 2016). Maximum likelihood analyses (ML) were performed with RAxMl GUI v.1.0. (Stamatakis 2006, Silvestro & Michalak 2012) and Bayesian inference (BI) analysis were performed with MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001). MrModeltest v. 2.2 (Nylander 2004) was used to estimate the best fit substitution model for each locus; which resulted in GTR+I+G (ITS, RPB2) and HKY+I+G (TUB2) substitution models under the Akaike Information Criterion (AIC). Bayesian posterior probabilities (BYPP) were determined by Markov Chain Monte Carlo sampling (MCMC) in MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001). Six simultaneous Markov chains were run for 3,000,000 generations and trees were sampled every 100th generation. MCMC heated chain was set with a "temperature" value of 0.20. All sampled topologies beneath the asymptote (25%) were discarded as part of a burn-in procedure; the remaining trees were used for calculating posterior probabilities

in the majority rule consensus tree. The phylogenetic tree was visualized in FigTree v1.4.0 (Rambaut 2006) and edited using Microsoft Office PowerPoint 2010 and Photoshop CS6. The alignments and respective phylogenetic tree were deposited in TreeBASE (submission number: 25775).

Table 2 GenBank accession numbers of the sequences used in phylogenetic analyses.

Species	Isolate No.	RPB2	TUB2	ITS	References
Amphirosellinia fushanensis	91111209 (HAST)	GQ848339	GQ495950	GU339496	Hsieh et al. 2010
Astrocystis bambusae	89021904 (HAST)	GQ844836	GQ495942	GU322449	Hsieh et al. 2010
Astrocystis concavispora	MFLUCC 14-0174	KP340532	KP406615	KP297404	Daranagama et al. 2015
Astrocystis mirabilis	94070803 (HAST)	GQ844835	GQ495941	GU322448	Hsieh et al. 2010
Astrocystis sublimbata	89032207 (HAST)	GQ844834	GQ495940	GU322447	Hsieh et al. 2010
Barrmaelia rappazii	CBS 142771	MF488998	MF489017	MF488989	Voglmayr et al. 2018
Barrmaelia rhamnicola	CBS 142772	MF488999	MF489018	MF488990	Voglmayr et al. 2018
Brunneiperidium gracilentum	MFLUCC 14-0011	KP340528	KP406611	KP297400	Daranagama et al. 2015
Brunneiperidium involucratum	MFLUCC 14-0009	KP340527	KP406610	KP297399	Daranagama et al. 2015
Clypeosphaeria mamillana	CBS 140735	MF489001	MH704637	KT949897	Jaklitsch et al. 2016, Voglmayr et al. 2018
Collodiscula bambusae	GZUH 0102	KP276675	KP276674	KP054279	Li et al. 2015b
Collodiscula fangjingshanensis	GZUH0109	KR002592	KR002589	KR002590	Li et al. 2015a
Collodiscula leigongshanensis	GZUH0107	KR002588	KR002587	-	Li et al. 2015a
Daldinia loculatoides	CBS 113279	KY624247	KX271246	MH862918	Wendt et al. 2018, Vu et al. 2019
Entoleuca mammata	100 JDR	GQ844782	GQ470230	GU300072	Hsieh et al. 2010
Entosordaria perfidiosa	EPE = CBS 142773	MF489003	MF489021	MF488993	Voglmayr et al. 2018
Euepixylon sphaeriostoma	261 JDR	GQ844774	GQ470224	GU292821	Hsieh et al. 2010
Hypocreodendron sanguineum	169 JDR	GQ844819	GQ487710	GU322433	Hsieh et al. 2010
Hypoxylon fragiforme	MUCL 51264	KM186296	KX271282	KC477229	Stadler et al. 2013, Daranagama et al. 2015, Wendt et al. 2018
Hypoxylon monticulosum	MUCL 54604	KY624305	KX271273	KY610404	Wendt et al. 2018
Kretzschmaria deusta	CBS 163.93	KY624227	KX271251	KC477237	Stadler et al. 2013
Kretzschmaria guyanensis	89062903 (HAST)	GQ844792	GQ478214	GU300079	Hsieh et al. 2010
Kretzschmariella culmorum	88 (JDR)	KX430045	KX430046	KX430043	Johnston et al. 2016
Nemania abortiva	467 BISH	GQ844768	GQ470219	GU292816	Hsieh et al. 2010
Nemania beaumontii	405 (HAST, JF)	GQ844772	GQ470222	GU292819	Hsieh et al. 2010
Nemania bipapillata	90080610 (HAST)	GQ844771	GQ470221	GU292818	Hsieh et al. 2010
Nemania primolutea	91102001 (HAST)	GQ844767	EF025607	EF026121	Ju et al. 2007, Hsieh et al. 2010
Nemania serpens	CBS 679.86	KU684284	KU684188	KU683765	U'Ren et al. 2016
Neoxylaria arengae	**MFLUCC 15-0292**	**MT502418**	-	**MT496747**	**This study**
Neoxylaria 'Xylaria' juruensis	92042501 (HAST)	GQ844825	GQ495932	GU322439	Hsieh et al. 2010

Table 2 Continued.

Species	Isolate No.	RPB2	TUB2	ITS	References
Podosordaria mexicana	176 WSP	GQ853039	GQ844840	GU324762	Hsieh et al. 2010
Podosordaria muli	167 WSP	GQ853038	GQ844839	GU324761	Hsieh et al. 2010
Poronia pileiformis	88113001 WSP	GQ853037	GQ502720	GU324760	Hsieh et al. 2010
Poronia punctata	CBS 656.78	-	KX271281	KT281904	Senanayake et al. 2015
Rosellinia aquila	MUCL 51703	KY624285	KX271253	KY610392	Wendt et al. 2018
Rosellinia buxi	99 JDR	GQ844780	GQ470228	GU300070	Hsieh et al. 2010
Rosellinia corticium	MUCL 51693	KY624229	KX271254	KY610393	Wendt et al. 2018
Rosellinia merrillii	89112601 (HAST)	GQ844781	GQ470229	GU300071	Hsieh et al. 2010
Rosellinia necatrix	CBS 349.36	-	KY624310	MH855818	Wendt et al. 2018, Vu et al. 2019
Sarcoxylon compunctum	CBS 359.61	KY624230	KX271255	KT281903	Senanayake et al. 2015
Stilbohypoxylon 'elaeidicola' elaeidis	JF-GUY-12-031	-	-	MF038896	Unpublished
Stilbohypoxylon elaeidis	**MFLUCC 15-0295a**	**MT502416**	**MT502420**	**MT496745**	**This study**
Stilbohypoxylon elaeidis	**MFLUCC 15-0295b**	**MT502417**	**MT502421**	**MT496746**	**This study**
Stilbohypoxylon elaeidicola	Y.M.J. 173	GQ844826	EF025616	EF026148	Ju et al. 2007, Hsieh et al. 2010
Stilbohypoxylon elaeidicola	94082615 (HAST)	GQ844827	GQ495933	GU322440	Hsieh et al. 2010
Stilbohypoxylon quisquiliarum	Y.M.J. 172	GQ853020	EF025605	EF026119	Ju et al. 2007, Hsieh et al. 2010
Stilbohypoxylon quisquiliarum	89091608 (HAST)	GQ853021	EF025606	EF026120	Ju et al. 2007, Hsieh et al. 2010
Stilbohypoxylon quisquiliarum	PR39	-	-	AY909023	Peláez et al. 2008
Xylaria acuminatilongissima	623 (HAST)	GQ853028	GQ502711	EU178738	Ju & Hsieh 2007, Hsieh et al. 2010
Xylaria adscendens	865 JDR	GQ844818	GQ487709	GU322432	Hsieh et al. 2010
Xylaria aethiopica	YMJ 1136	MH785222	MH785221	MH790445	Fournier et al. 2018b
Xylaria apoda	90080804 (HAST)	GQ844823	GQ495930	GU322437	Hsieh et al. 2010
Xylaria arbuscula	CBS 126415	KY624287	KX271257	MH864101	Wendt et al. 2018, Vu et al. 2019
Xylaria atrosphaerica	91111214 (HAST)	GQ848342	GQ495953	GU322459	Hsieh et al. 2010
Xylaria badia	95070101 (HAST)	GQ844833	GQ495939	GU322446	Hsieh et al. 2010
Xylaria bambusicola	162 JDR	GQ844801	GQ478223	GU300088	Hsieh et al. 2010
Xylaria berteri	90112623 (HAST)	GQ848362	AY951763	-	Hsieh et al. 2010, 2005
Xylaria brunneovinosa	720 (HAST)	GQ853023	GQ502706	EU179862	Ju & Hsieh 2007, Hsieh et al. 2010
Xylaria castorea	600 PDD	GQ853018	GQ502703	GU324751	Hsieh et al. 2010
Xylaria cf. *castorea*	91092303 (HAST)	GQ853019	GQ502704	GU324752	Hsieh et al. 2010
Xylaria cf. *glebulosa*	431 (HAST, JF)	GQ848345	GQ495956	GU322462	Hsieh et al. 2010
Xylaria cf. *heliscus*	88113010 (HAST)	GQ848355	GQ502691	GU324742	Hsieh et al. 2010
Xylaria crozonensis	398 (HAST, JF)	GQ848361	GQ502697	GU324748	Hsieh et al. 2010
Xylaria cubensis	159 GENT	GQ853017	GQ502702	-	Hsieh et al. 2010

Table 2 Continued.

Species	Isolate No.	RPB2	TUB2	ITS	References
Xylaria culleniae	189 JDR	GQ844829	GQ495935	GU322442	Hsieh et al. 2010
Xylaria curta	494 (HAST, JF)	GQ844831	GQ495937	GU322444	Hsieh et al. 2010
Xylaria digitata	919 (HAST)	GQ848338	GQ495949	GU322456	Hsieh et al. 2010
Xylaria discolor	Y.M.J. 1280	JQ087411	JQ087414	JQ087405	Ju et al. 2012
Xylaria enterogena	785 (HAST, JF)	GQ848349	GQ502685	GU324736	Hsieh et al. 2010
Xylaria feejeensis	91122401 (HAST)	GQ848353	GQ502689	GU324740	Hsieh et al. 2010
Xylaria frustulosa	92092010 (HAST)	GQ844838	GQ495944	GU322451	Hsieh et al. 2010
Xylaria globosa	775 (HAST, JF)	GQ848348	GQ502684	GU324735	Hsieh et al. 2010
Xylaria grammica	479 (HAST)	GQ844813	GQ487704	GU300097	Hsieh et al. 2010
Xylaria haemorrhoidalis	89041207 (HAST)	GQ848347	GQ502683	GU322464	Hsieh et al. 2010
Xylaria hypoxylon	CBS 122620	KY624231	KX271279	KY610407	Wendt et al. 2018
Xylaria ianthinovelutina	553 (HAST, JF)	GQ844828	GQ495934	GU322441	Hsieh et al. 2010
Xylaria intracolorata	90080402 (HAST)	GQ848354	GQ502690	GU324741	Hsieh et al. 2010
Xylaria karyophthora	DRH059	KY564216	-	KY564220	Husbands et al. 2018
Xylaria laevis	419 (HAST, JF)	GQ848359	GQ502695	GU324746	Hsieh et al. 2010
Xylaria luteostromata	508 (HAST, JF)	GQ848352	GQ502688	GU324739	Hsieh et al. 2010
Xylaria multiplex	580 (HAST, JF)	GQ844814	GQ487705	GU300098	Hsieh et al. 2010
Xylaria ophiopoda	93082805 (HAST)	GQ848344	GQ495955	GU322461	Hsieh et al. 2010
Xylaria oxyacanthae	859 JDR	GQ844820	GQ495927	GU322434	Hsieh et al. 2010
Xylaria palmicola	604 PDD	GQ844822	GQ495929	GU322436	Hsieh et al. 2010
Xylaria phyllocharis	528 (HAST, JF)	GQ844832	GQ495938	GU322445	Hsieh et al. 2010
Xylaria polymorpha	1012 JDR	GQ848343	GQ495954	GU322460	Hsieh et al. 2010
Xylaria reevesiae	HMH-2010g	GQ844821	GQ495928	GU322435	Hsieh et al. 2010
Xylaria regalis	92072001 (HAST)	GQ848357	GQ502693	GU324744	Hsieh et al. 2010
Xylaria schweinitzii	92092023 (HAST)	GQ848346	GQ495957	GU322463	Hsieh et al. 2010
Xylaria scruposa	497 (HAST, JF)	GQ848341	GQ495952	GU322458	Hsieh et al. 2010
Xylaria spinulosa	GZUCC13016	KM236098	KM236099	-	Li et al. 2015b
Xylaria telfairii	421 (HAST, JF)	GQ848350	GQ502686	GU324737	Hsieh et al. 2010
Xylaria vivantii	HMH-2010h	GQ844824	GQ495931	GU322438	Hsieh et al. 2010

*Newly generated strains are in bold.

Results

Phylogeny

The combined dataset (ITS, RPB2 and TUB2) comprised 93 taxa from selected species of Xylariaceae with 2,701 characters including gaps (ITS: 1−493, RPB2: 494−1,647, TUB2: 1,648−2,701). The RAxML analysis resulted in the best scoring likelihood tree selected with a final ML optimization likelihood value of −51211.148170, which is represented in Fig. 2. The final likelihood tree was evaluated and optimized under GAMMA model parameters: with 1,431 distinct alignment patterns and 10.27% of undetermined characters or gaps. Bayesian posterior probabilities from MCMC were evaluated with a final average standard deviation of split frequencies less than 0.01.

ITS-RPB2-TUB2 phylogeny shows that our strain MFLUCC 15-0292 clusters with "*Xylaria juruensis*" (92042501HAST), basal to *Stilbohypoxylon* clade II with high statistical support (100% ML, 1.00 BYPP). The strains MFLUCC 15-0295a and MFLUCC 15-0295b formed a clade with *Stilbohypoxylon* clade II as a sister to *S. elaeidicola* with high statistical support (95% ML, 0.99 BYPP). *Stilbohypoxylon quisquiliarum* (*Stilbohypoxylon* clade I) formed a separate clade and clustered with *Xylaria* "PO" clade II (58% ML, 0.95 BYPP, Fig. 2).

Xylaria is polyphyletic in Xylariaceae, which is in agreement with previous studies (Daranagama et al. 2018, Wendt et al. 2018). In this study, *Xylaria* can be separated into seven "PO" clades, two "HY" clades and a single "TE" clade. Delimitation of the *Xylaria* clades are mostly restricted to their morphological characteristics and habitats. *Xylaria* "HY" clades are represented by *X. hypoxylon* (*sensu stricto*, "HY" clade II) and taxa in these clades have pointed or sterile stromal apices. The *Xylaria* "PO" clades are represented by *X. polymorpha* where most taxa in these clades have blunt or fertile stromatal apices. The *Xylaria* "TE" clade is represented by taxa associated with termite nests.

Taxonomy

Neoxylaria Konta & K.D. Hyde, gen. nov.

Index Fungorum number: IF556650; Facesoffungi number: FoF06239

Etymology – In reference to the morphological resemblance to *Xylaria*

Saprobic on palms (Arecaceae). Sexual morph: *Stromata* erect, coriaceous, solitary, cylindrical, simple to branched from the base, arising separately or in small bundles, stipe (stem) with brown hairy-tomentose, fertile part, bearing exposed outlines, apex sterile with globose perithecia, free perithecia scattered along with a filiform stroma, arranged in zigzag or in rows, visible as black, thick, surface finely cracked, sterile apex attenuated conical. *Perithecia* immersed in stromatic tissues, globose, ostiolate with periphyses. *Peridium* thick-walled, composed of several layers, outwardly, comprising dark brown cells of *textura angularis* and inwardly, thick-walled, comprising hyaline to pale brown cells of *textura prismatica*. *Ostiole* hyaline, papillate, with a central periphyses ostiolar canal and brown to black surrounding disc appear on the surface. *Paraphyses* hyaline, filamentous, cylindrical, septate, unbranched. *Asci* 6–8-spored, unitunicate, cylindrical, long pedicellate, apically rounded, with a J+, apical ring, inverted hat-shaped. *Ascospores* uniseriate, hyaline to pale brown when immature, dark brown at maturity, broad fusoid, unicellular, a lot of small guttules when immature, two large guttules at maturity, smooth-walled, with a straight germ slit throughout ascospore-length. Asexual morph: Undetermined.

Type species – *Neoxylaria arengae* Konta & K.D. Hyde

Notes – Species of *Xylaria* cluster in ten subclades in the phylogenetic tree (Fig. 2) indicating that the genus is polyphyletic representing three major clades as *Xylaria* "HY", "PO" and "TE". The type species, *X. hypoxylon* clusters in *Xylaria* "HY" clade II which can be regarded as *Xylaria sensu stricto*. However, it is hard to justify the other clades (*Xylaria sensu lato*) as new genera without examining old types of these species or obtaining well-defined and identified fresh collections with molecular data.
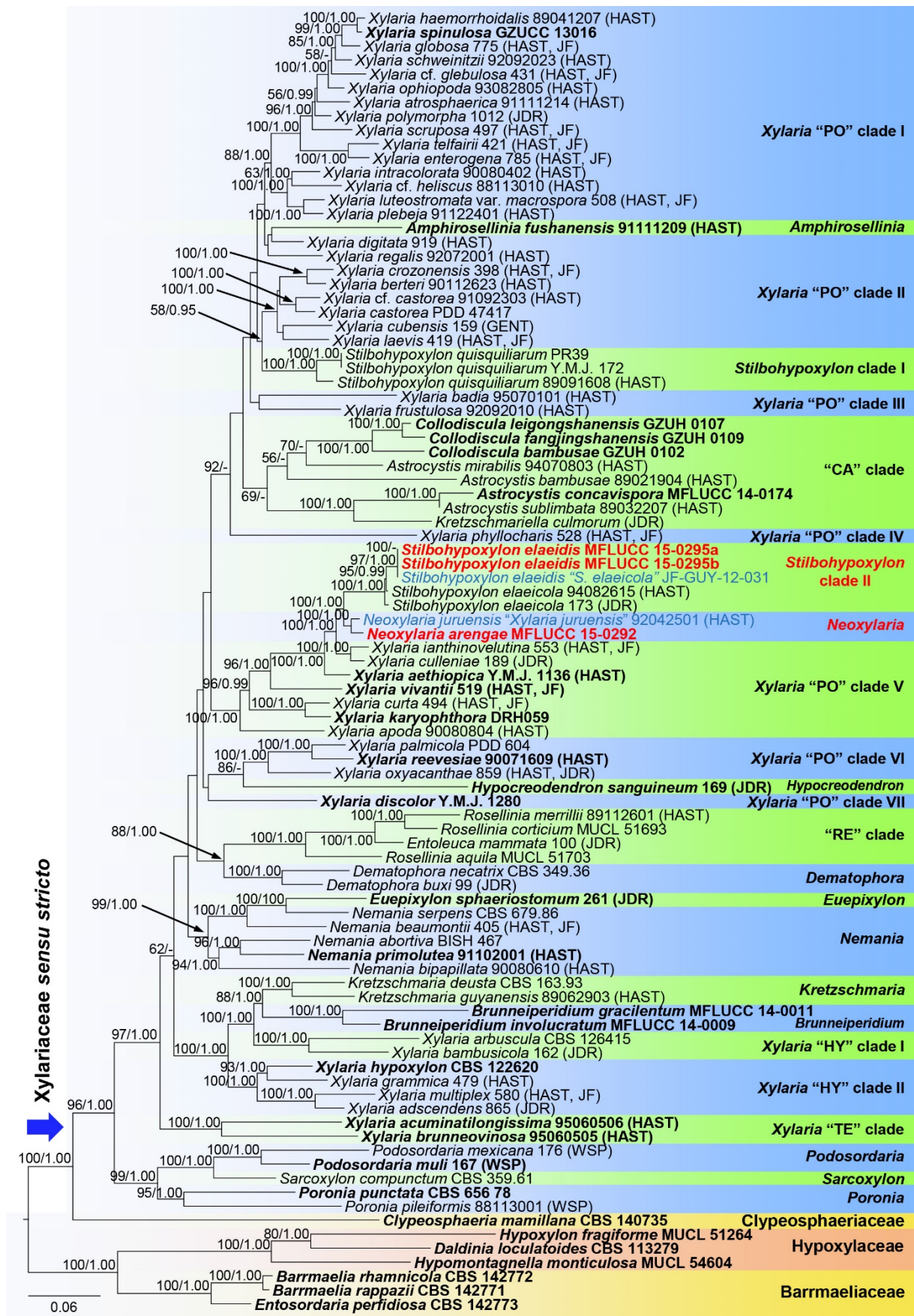
Figure 2 – RAxML tree based on analysis of a combined dataset of ITS-RPB2-TUB2 sequence dataset from selected species of Xylariaceae. Bootstrap support values for maximum likelihood (ML) greater than 50%, and Bayesian posterior probabilities (BYPP) greater than 0.90 are given at the nodes. Ex-type strains are in bold. Newly generated taxa are in red. The tree is rooted to

Daldinia loculatoides (CBS 113279), *Hypoxylon fragiforme* (MUCL 51264), *Hypomontagnella monticulosum* (MUCL 54604) (Hypoxylaceae), *Barrmaelia rappazii* (CBS 142771), *B. rhamnicola* (CBS 142772), and *Entosordaria perfidiosa* (CBS 142773) (Barrmaeliaceae).

The sexual morph of *Xylaria hypoxylon* comprises a stroma that is grey to dull black, cylindrical to narrowly fusiform to fan-shaped, with a long persistent white peeling outer layer and ostiolar papillae. The perithecia are immersed, brown to black, with a low conical papilla at center, asci are cylindrical with J+, apical ring, and ascospores are brown ellipsoid-inequilateral with a sinuous germ slit and cellular appendage (Peršoh et al. 2009, Daranagama et al. 2018). The new species collected in this study is clearly different from members of *Xylaria sensu stricto* based on host preferences and perithecia bulging from the long, but relatively small stromata.

Based on the morpho-molecular differences, we introduce a new genus *Neoxylaria* to accommodate *Neoxylaria arengae*. *Xylaria culleniae*, *X. ianthinovelutina*, *X. aethiopica* and *X. vivantii* (*Xylaria* "PO" clade V) also clustered with *Neoxylaria* and these species form conspicuously exposed perithecial contours under a narrowly striped outer layer, which is similar to *Neoxylaria*. Even though the morphological similarities exist, these species do not form a monophyletic clade. Therefore, we do not treat them under *Neoxylaria*. Further morpho-molecular studies are essential to clarify their generic boundaries.

Xylaria juruensis and *X. queenslandica* resemble *Neoxylaria arengae* in having cylindrical or narrowly fusiform, erect stroma, a brown hairy-tomentose stipe, immersed ascoma, cylindrical asci with inverted, hat-shaped, J+, apical ring, and brown ascospores with a straight germ slit which lacks a mucilaginous sheath. Thus, *X. juruensis* and *X. queenslandica* are transferred to *Neoxylaria* as *N. juruensis* and *N. queenslandica* comb. nov.

Neoxylaria arengae Konta & K.D. Hyde, sp. nov.   Fig. 3

Index Fungorum number: IF556651; Facesoffungi number: FoF03395
Etymology – Refers to the name of the host genus, *Arenga*
Holotype – MFLU 15-0267

Saprobic on dead petiole of *Arenga pinnata* (Arecaceae). Sexual morph: *Stromata* (1.6–)4–27(–30) × 0.5–1 mm ($\bar{x}$ = 13 × 0.7 mm, n = 30), erect, coriaceous, solitary, cylindrical, simple to branched from the base, unbranched when immature, branching from the base at maturity with 3(–5) branches, arising separately or in small bundles, stipes (stem) (1.7–)2.1–4.6(–7.1) × 0.4–1 mm ($\bar{x}$ = 3.2 × 0.7 mm, n = 20, up to 12 mm), cylindrical, longitudinally, black, with a hairy-tomentose broadened base, smooth to downy to hairy-tomentose above; tomentum black to dark brown, fertile part (1.7–)2.5–18(–25) mm ($\bar{x}$ = 9 mm, n = 20), bearing 29 to 35(–45) exposed perithecia, apex sterile, rarely find finely longitudinally furrowed delimiting narrow stripes, roughened with prominent ostiolar papillae, perithecia scattered along the stroma, arranged in a zigzag or in straight rows, without circumferential wrinkles isolating groups of perithecia, perithecial contours most often conspicuous, visible as black single or small fusiform ascoma, surface, outer crust, thick, coriaceous, cracked, interior solid, brown with white tissue surrounding perithecial layer, sterile apex attenuated conical, up to 1–2(–3) mm. *Perithecia* 400–620 × 260–570 µm ($\bar{x}$ = 493 × 464 µm, n = 10), pale brown, immersed in stromatic tissues, globose to subglobose, ostiolate, papillate, slightly conspicuous, with periphyses. *Peridium* 80–130 µm wide ($\bar{x}$ = 100 µm, n = 20), thick-walled, composed of several layers, outwardly, thick-walled, comprising dark brown cells of *textura angularis* and inwardly, thick-walled, comprising hyaline to pale brown cells of *textura prismatica*. *Ostiole* 150–215 × 150–285 µm ($\bar{x}$ = 180 × 210 µm, n = 5), raised-discoid, brown to black surrounding disc appear on the surface; hyaline, papillate, with a central periphyses. *Paraphyses* 3–5(–7) µm wide ($\bar{x}$ = 4 µm, n = 10), filamentous, cylindrical, septate, unbranched. *Asci* 74–160(–180) × 5–12 µm ($\bar{x}$ = 115 × 7 µm, n = 20), 6–8-spored, unitunicate, cylindrical, long pedicellate, apically rounded, with a J+, apical ring, inverted hat-shaped. *Ascospores* 10–18(–22) × 3.5–6(–7.5) µm ($\bar{x}$ = 15 × 5 µm, n = 20), uniseriate, hyaline to pale brown when immature, dark brown at maturity, broad fusoid, unicellular, a lot of small guttules when immature, two large

guttules at maturity, smooth-walled, with a straight, full length germ slit. Asexual morph: Undetermined. *Appressoria* 4–9 × 3–10 μm ($\bar{x}$ = 6 × 6 μm, n = 20), solitary, hyaline, mostly globose, irregular in shape, thick-walled.

Culture characteristics – Ascospores germinated on MEA within 24 hours and germ tube was produced from germ slit. Mycelium immersed in the medium, septate, branched, and smooth-walled hyphae. Colonies on MEA, medium dense, irregular in shape, flowered-like, surface slightly rough with curled margin, radiating outward colony, flat, slightly raised at the centre, hairy fluffy, initially white, becoming white at the margin, greyish white near the centre, with black and white curled, radiated near the centre; reverse zonate, yellow and white, curled with black radiating outward colony; not produced pigmentation on medium.

Material examined – THAILAND, Phang-nga Province, on dead petiole of *Arenga pinnata* (Wurmb) Merr. (Arecaceae), 5 December 2014, S. Konta, PHR03d (MFLU 15-0267, holotype; KUN-HKAS 100698, isotype), ex-type living culture, MFLUCC 15-0292.

Notes – *Neoxylaria arengae* resembles *N.* (syn. *Xylaria*) *juruensis*, but it has shorter stromata (fertile part) (1.6–)4–27(–30) mm vs 15–40 mm), forms branches at the base, smaller perithecia (0.4–0.6 diam. mm vs 0.7–0.9 diam. mm), slightly larger in asci (74–160 × 5–12 μm vs 100–120 × 4–6 μm) and ascospores overlapping in size (10–18(–22) × 3.5–6(–7.5) μm vs 12–17 × 4–5 μm). However, *N. arengae* was found on a dead part of *Arenga pinnata*, while *N. juruensis* was reported from a rotten palm frond and on *Arenga engleri* (Arecaceae) (Hennings 1904, Hsieh et al. 2010, Becerril-Navarrete et al. 2018).

Xylaria queenslandica is similar to *Neoxylaria* and is transferred in this paper. *Neoxylaria arengae* is similar to *X. tucumanensis* in the appearance of the stromata, but our new species has larger stromata (4–27 × 0.5–1 vs 12–15 × 0.5–0.6 mm), shorter stipes (2.1–4.6 × 0.4–1 vs 6–7 × 0.2–0.3 mm), forming 3(–5) branches at base, while *X. tucumanensis* form simple (unbranched), and larger numbers of perithecia (bearing 29–35 vs 9–17 perithecia per stroma) (Hladki & Romero 2010). *Neoxylaria arengae* also shares similar stomatal characters with *X. diminuta*, *X. enteroleuca*, *X. filiformioidea*, *X. himalayensis*, *X. mellissi*, and *X. subgracillima*, but differs in having branches at the base, of longer stromata (fertile part), and more perithecia per stromata than other species (Cooke 1883, Hennings 1904, Martin 1970, Narula et al. 1985, Hladki & Romero 2010, Huang et al. 2014). We also cross checked with *X. diminuta*, *X. enteroleuca*, *X. filiformioidea*, *X. himalayensis*, *X. mellissi* and *X. subgracillima*, but only *X. enteroleuca* has DNA sequence data, thus, we included *X. enteroleuca* in the phylogenic tree (not shown) and found that it did not form a branch close to *Stilbohypoxon* or *Neoxylaria*.

Neoxylaria juruensis (Henn.) Konta & K.D. Hyde, comb. nov.

Index Fungorum number: IF556652; Facesoffungi number*:* FoF06240

≡ *Xylaria juruensis* Henn., Hedwigia 43(4): 262 (1904)

Notes – *Xylaria juruensis* was introduced by Hennings (1904) from decayed palm material collected in Brazil. It similar to *Neoxylaria arengae* in having erect stromata, with prominent perithecia and a sterile apex. There is no sequence data for the type of *Xylaria juruensis*, but there is for a putatively named collection (92042501 HAST) from Taiwan (Hsieh et al. 2010). In the phylogenetic tree, the strain from Taiwan clustered together with *N. arenage* with strong support (100% ML, 1.00 BYPP, Fig. 2) and maybe the same genus, but is unlikely to be *Xylaria juruensis sensu stricto*, because of its location.

Neoxylaria queenslandica (Joanne E. Taylor, K.D. Hyde & E.B.G. Jones) Konta & K.D. Hyde, comb. nov.

Index Fungorum number: IF557765; Facesoffungi number*:* FoF08464

≡ *Xylaria queenslandica* Joanne E. Taylor, K.D. Hyde & E.B.G. Jones, in Taylor & Hyde, Fungal Diversity Res. Ser. 12: 236 (2003)

Notes – *Xylaria queenslandica* was also collected from a palm (*Archontophoenix alexandrae*) in Australia and is very similar to *Neoxylaria arengae* (Taylor & Hyde 2003). *Xylaria*

queenslandica differs from *N. arengae* in its average ascospore size (13 × 4.7 vs 10–18(–22) × 3.5–6(–7.5) µm) and mid red brown versus dark brown mature ascospores (Taylor & Hyde 2003).
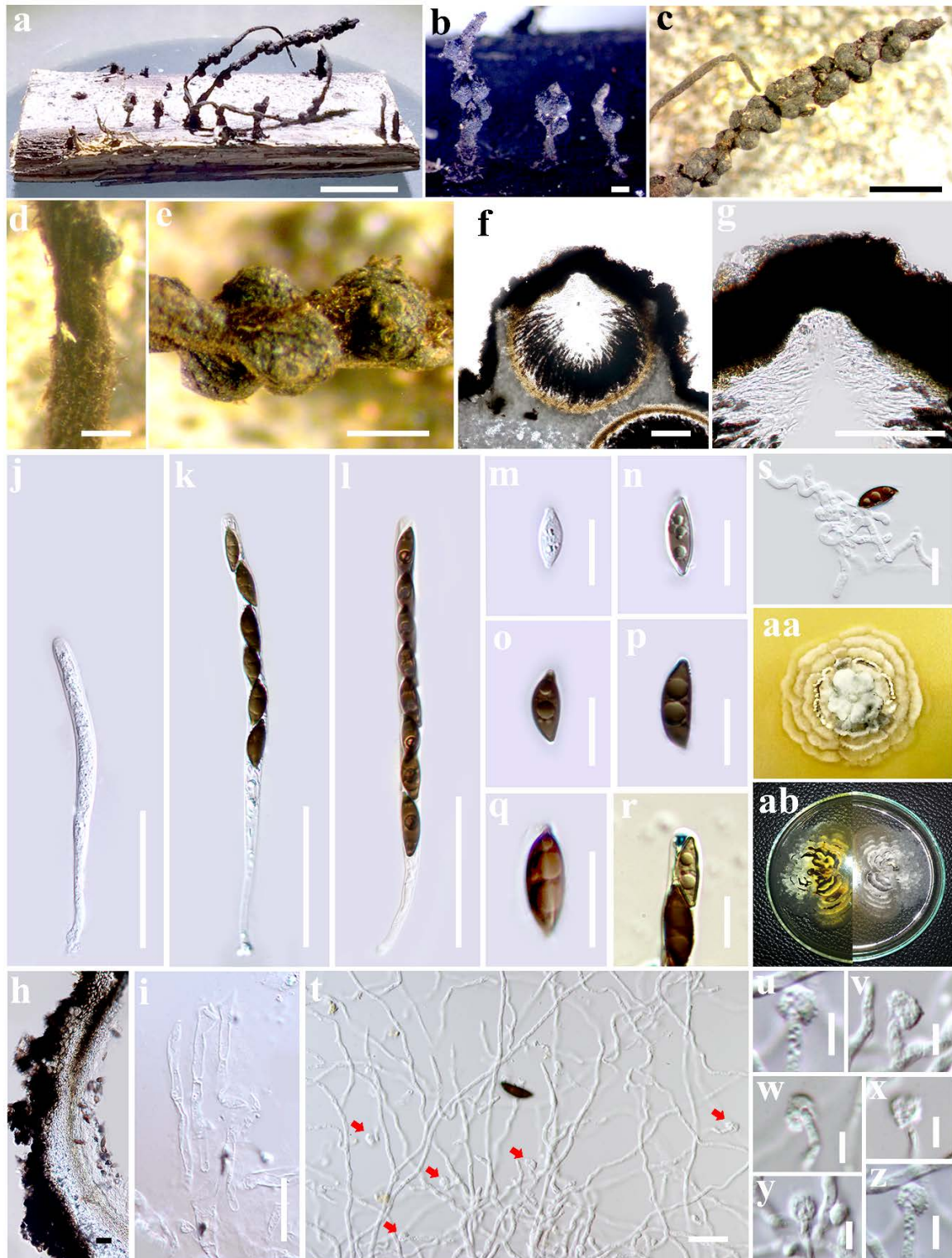

Figure 3 – *Neoxylaria arengae* (MFLU 15-0267, holotype). a–b Stromata on host substrate. c, e Perithecia and sterile apex strongly conical. d Stem with brown hair (Pubescent). f Section of a stroma. g Periphyses. h Peridium. i Paraphyses. j–l Asci. m–p Ascospores. q Ascospore with germ slit. r J+, apical ring in Melzer's reagent. s Germinated ascospore. t Germinated ascospore with appressoria-like structures. u–z Appressoria-like structures. aa, ab Colony on MEA. Scale Bars: a = 5 mm, b, d, e = 0.5 mm, c = 2 mm, f, g = 0.1 mm, h, i, t = 20 µm, j–l = 50 µm, m–s = 10 µm, u–z = 5 µm.

Stilbohypoxylon Henn., Hedwigia 41: 16 (1902)

Index Fungorum number: IF5264; Facesoffungi number: FoF06306

Saprobic on various hosts in tropical and subtropical regions. Sexual morph: *Stromata* superficial, carbonaceous perithecia, solitary to gregarious, lining in row or in groups, dark brown to black, smooth or rugulose or with cracks or warts or minute furrows, with or without conical to acicular synnematal remnants borne on mature stromata. *Ascomata* globose to pulvinate, ampulliform or mammiform, black carbonaceous, brittle, fragile, ostiolate, papillate, encircled with vaguely flattened area. *Synnemata* borne laterally on mature stromata or directly on wood, acicular to conical to somewhat cylindrical, light-brown or black, carbonaceous, brittle, fragile, sometimes covered by green-grey conidiophores at the base, or covered by yellow, greenish-yellow, or ochraceous scales, powdery or hyphae-like at early state. *Paraphyses* hyaline, filamentous, cylindrical, septate, unbranched, longer than asci. *Asci* 8-spored, unitunicate, cylindrical, pedicellate, apically rounded, with a J+, inverted hat-shaped, apical ring. *Ascospores* uniseriate, hyaline to pale brown when immature, dark brown at maturity, ellipsoidal to broad-fusoid, unicellular, with two large guttules, smooth-walled, with a straight germ slit over the whole spore length, surrounded by a thin mucilaginous sheath, with a pad of denser mucilage at each apex. Asexual morph: Hyphomycetous, geniculosporium-like. *Synnemata* green, scattered, acicular to conical, cylindrical, branched or unbranched. *Conidiophores* dense, dark brown palisades dichotomously branched several times from the bases. *Conidiogenous cells* terminal, cylindrical, hyaline, smooth, bearing lateral and terminal denticulate conidial secession scars. *Conidia* produced holoblastically in sympodial sequence, hyaline to pale yellow, yellowish to pale olivaceous, smooth, obovate, with a truncate base (adapted from Rogers & Ju 1997, Daranagama et al. 2018).

Type species – *Stilbohypoxylon moelleri* Henn.

Notes – *Stilbohypoxylon* contains 11 species, viz. *S. elaeidicola*, *S. hypoxylinum*, *S. ignobile*, *S. immundum*, *S. macrosporum*, *S. minus*, *S. moelleri* (type), *S. novae-zelandiae*, *S. quisquiliarum*, *S. samuelsii* and *S. theissenii* (Hyde et al. 2020, Index Fungorum 2020). All taxa are characterized by superficial, globose (sphaerical) stromata, with a smooth or delicately wrinkled surface that is usually overlain with yellow, greenish yellow or ochraceous scales at an early stage, unitunicate asci, unicellular ascospores with a straight germ slit, with or without mucilaginous sheath and a pad of denser mucilage at each end (Rogers & Ju 1997, Fröhlich & Hyde 2000, Hladki & Romero 2003, Petrini 2004, Daranagama et al. 2018).

According to Hsieh et al. (2010), Li et al. (2017), Daranagama et al. (2018) and Wendt et al. (2018), *Stilbohypoxylon* species clusters with *Xylaria* species in two subclades and it was mentioned that *Stilbohypoxylon* is polyphyletic. Currently, only *S. elaeidicola* and *S. quisquiliarum* have sequence data, while the generic type of *Stilbohypoxylon* (*S. moelleri*) has not yet been sequenced. Therefore, the phylogenetic affinity of *Stilbohypoxylon* is uncertain.

A lot of clumping has previously occurred in defining *Stilbohypoxylon* species (Fröhlich & Hyde 2000). Rogers & Ju (1997) revisited the genus and designated an epitype for the type species, *S. moelleri*, which was collected from a palm, *Euterpe* sp., in South America. We therefore follow Rogers & Ju (1997) and place the recent collections from palms in *Stilbohypoxylon sensu stricto*. *Stilbohypoxylon quisquiliarum* was collected in French Guiana on "wood" (Montagne 1840) and described in Miller (1961). Rogers & Ju (1997) have described the asexual morph of *S. quisquiliarum* and illustrated the ascospores with a spiral germ slit from an isotype specimen, which differentiates it from *Stilbohypoxylon sensu stricto*. *Stilbohypoxylon quisquiliarum* does not group with the clade comprising *S. elaeidis* and *S. elaeidicola* (*Stilbohypoxylon* clade II, Fig. 2). Therefore, we leave *S. quisquiliarum* as *Stilbohypoxylon sensu lato* (*Stilbohypoxylon* clade I, Fig. 2) until it is epitypified and described as a new genus. Unfortunately, the epitype specimen of *S. moelleri* has not yet been sequenced. Therefore, the congeneric status of the representative species (*S. elaeidis* and *S. elaeidicola*) with *S. moelleri* and the phylogenetic status of *Stilbohypoxylon sensu stricto* still need to be proven, however they all occur on decaying palm material.

The type species of *Stilbohypoxylon*, *S. moelleri* was detailed in Rogers & Ju (1997) and its lectotype was observed by Daranagama et al. (2018). *Stilbohypoxylon moelleri* is characterized by

sphaerical, gregarious, black, carbonaceous, fragile stromata, bearing 1–3-conical to acicular synnemata, cylindrical asci with apical ring bluing in Melzer's reagent, brown to dark brown ascospores and a geniculosporium-like asexual morph (Rogers & Ju 1997, Daranagama et al. 2018). A comparison of *S. moelleri* and *S. elaeidis* shows that *S. elaeidis* has solitary stroma with a smooth surface and lack of synnemata on stromata surface.

Stilbohypoxylon elaeidis Konta & K.D. Hyde, sp. nov.   Fig. 4

    Index Fungorum number: IF558007; Facesoffungi number: FoF05123

    Etymology – Refers to the name of the host genus, *Elaeis*

    Holotype – MFLU 15-0270

    Saprobic on dead petiole of *Elaeis guineensis* (Arecaceae). Sexual morph: *Stromata* superficial, visible as a black conical, or globose on the top view of host surface, solitary, or in groups, bearing conical to acicular synnematal remnants on mature stromata, carbonaceous, brittle, fragile, curved to straight. *Ascomata* 440–730 × 360–660 µm ($\bar{x}$ = 565 × 530 µm, n = 25), black, carbonaceous, brittle, conical to mammiform, 1 per stroma, glabrous, covered with remnants of host tissue, disappearing at maturity, with indistinct ostiolate. *Synnemata* 250–470 µm ($\bar{x}$ = 340 µm, n = 10), solitary, covered with yellow hyphae-like when immature, spine-like, wide at the base narrow towards the apex, black. *Peridium* 65–120(–130) µm wide ($\bar{x}$ = 90 µm, n = 25), thick-walled, composed of several layers, outwardly comprising dark brown to black cells 2–4 µm, of *textura angularis*. *Paraphyses* 2.3–3.7 µm wide ($\bar{x}$ = 3 µm, n = 20), filamentous, cylindrical, septate, unbranched, longer than asci. *Asci* 113–136 × 7–12 µm ($\bar{x}$ = 125 × 9 µm, n = 20), 6–8-spored, unitunicate, cylindrical, long pedicellate, apically rounded, with a J+, inverted, hat-shaped apical ring, 2–5 × 2–3 µm ($\bar{x}$ = 5 × 2 µm, n = 10). *Ascospores* 13–21 × 5–8 µm ($\bar{x}$ = 17 × 6 µm, n = 30), uniseriate, hyaline to pale brown when immature, dark brown at maturity, equilateral ellipsoidal to broadly fusoid, unicellular, with two large guttules, smooth-walled, with a straight germ slit over the whole spore length, surrounded by thin mucilaginous sheath, with a pad of denser mucilage at each apex. Asexual morph: Undetermined.

    Culture characteristics – Ascospores germinated on MEA within 24 hours and germ tube produced from germ slit. Mycelium immersed in media, mycelium at the center appears as grey to dark-green, mycelium towards margin appears white, hyphae, septate, branched, and smooth. Colonies on MEA, medium dense, irregular in shape, flowered-like, surface slightly rough with curled and undulate edge, radiating outward colony, flat, slightly raised at the centre, felty to cottonny, azonate, white at the margin, grey to dark grey near the centre, with black curled radiating towards the centre; reverse yellowish, curled with black radiating towards the centre; not produced pigmentation on medium.

    Material examined – THAILAND, Krabi Province, on a dead petiole of *Elaeis guineensis* Jacq. (Arecaceae), 3 December 2014, S. Konta, KBF01a (MFLU 15-0270, holotype), ex-type living cultures, MFLUCC 15-0295a, MFLUCC 15-0295b.

    Addition sequence data – LSU: MT496755, SSU: MT495460, TEF: MT495461 (MFLUCC 15-0295a); LSU: MT496756, SSU: MT495461 (MFLUCC 15-0295b).

    Notes – *Stilbohypoxylon elaeidis* is closely related to *S. elaeidicola* and both species are from palms. They form a well-separated branch with high statistical support in the combined ITS-RPB2-TUB2 phylogenetic analysis (Fig. 2). A comparison of ITS, RPB2 and TUB2 sequence data including gaps shows that *S. elaeidis* differs from *S. elaeidicola* (strains Y.M.J. 173 and 94082615 HAST) in 6 bp and 4 bp (1% and 0.68% of nucleotide base) for ITS; 7 bp and 3 bp (0.6% and 0.26% of nucleotide base) for RPB2; 53 bp and 42 bp (3.35% and 2.6% of nucleotide base) for TUB2. Furthermore, phylogenetic analysis showed that *S. elaeidis* clusters with *S. elaeidicola* strain JF-GUY-12-031 with good bootstrap support (97% ML, 1.00 BYPP, Fig. 2). However, this strain has no morphological description and only ITS sequence is available in GenBank database. Therefore, we rename this strain as *S. elaeidis*. Morphological comparison of *Stilbohypoxylon* species are detailed in Table 3.
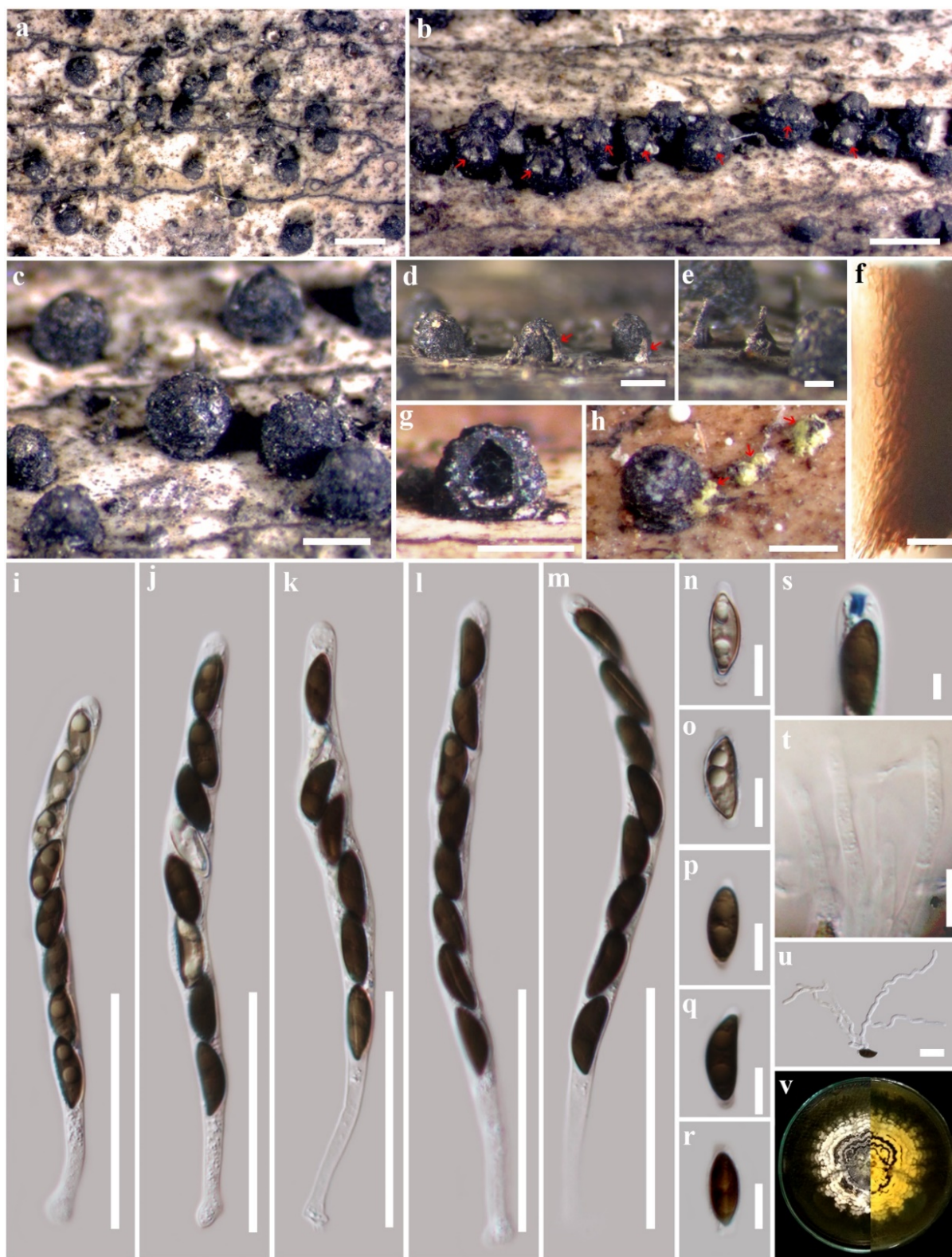
Figure 4 – *Stilbohypoxylon elaeidis* (MFLU 15-0270, holotype). a Immature and mature stromata on the host substrate from above. b Immature stromata covered with remnants of host material. c Close up of mature stromata. d Synnematal remnants. e Close up of synnematal remnants. f Peridium. g Section of stromata showing the perithecia. h Synnematal remnants covered by yellow hyphae-like. i–k Immature asci. l–m Mature asci. n, o Immature ascospores. p, q Mature ascospores. r Ascospore with germ slit. s J+, apical ring in Melzer's reagent. t Paraphyses. u Germinated ascospore. v Colony on MEA from above and below. Scale Bars: a, b = 1000 μm, c, d, g, h = 500 μm, e = 200 μm, f, n–t = 10 μm, i–m = 50 μm, u = 20 μm.

Table 3 Morphological comparison of species of *Stilbohypoxylon*.

Taxa	Stromata (μm)	Synnemata (μm)	Peridium (μm)	Asci (μm)	Apical ring (μm)	Ascospores (μm)	References
Stilbohypoxylon elaeidicola	(550–)813 ± 110(–1125) diam. × (400–)605 ± 80(–825) high, rough, rugose surface, sometimes with cracks, dull or shiny, sometimes covered by host material, sometimes 2–3 fused together	Up to 550 high	50–75	11–16 × 105–130	Upper 3–4, lower 2–3 × 2–4 high	(6–)7 ± 0.5(–8.5) diam. × (13–)16 ± 1.5(–22) high, straight germ slit, slimy cap at each end and on the flat side	Hennings 1895, Petrini 2004
S. elaeidis	367–664 diam. × 440–730 high ($\bar{x}$ = 527 × 565), globose, smooth, with cracks of the host on the surface, solitary, 1 ascoma per stroma, surrounded by synnematal remnants on host substrate	253–470 high, covered by yellow hyphae-like at early stage	65–120(–130), composed of *textura angularis*	7–12 × 113–136	2–3 × 2–5 high	5–8 diam. × 13–21 high ($\bar{x}$ = 6 × 17, n = 30) straight germ slit, thin mucilaginous sheath, with a pad mucilage at each apex	**This study**
S. hypoxylinum	375–450 wide × 450–700 high, globose to ampulliform, dull, powdery covered on stromata, solitary, synnemata	-	25	-	Upper 4–4.5, lower 3.5–4.5 × 4–4.5 high	(6.5–)8 ± 0.8(–9) diam. × (14–)17 ± 1.5(–21) high, straight germ slit	Petrini 2004
S. ignobile	625–800 wide × 750–925 high, cupulate with an elongate broad base, with cracks and warts on the surface, singly or 2–4 fused together, crowded, touching each other	-	25–50	-	-	4.5–5 diam. × 9–10.5 high (n = 3), straight germ slit	Petrini 2004
S. immundum	(625–)920 ± 190(–1250) diam. × (625–)930 ± 175(–1300) high, globose, subglobose, obovate to cupulate, surface warty, cylindrical synnemata, crowded, with perithecia closely adherent	-	Up to 125	-	Upper 4–7, lower 3.5–6 × 6–11 high	(8.5–)11 ± 1.5(–14) diam. × (27–)32 ± 3(–39) high, straight, rarely oblique germ slit	Petrini 2004
S. macrosporum	600–900 diam., globose or semi-globose, smooth, solitary or slightly fusionate, gregarious, with 1–2 synnemata on mature stromata, verrucose to rugulose	400–500 high	-	9–12 × 200–260	6.5 × 8–10.5 high	12–13 diam. × 30–40 high, spiral germ slit	Hladki & Romero 2003, Daranagama et al. 2018

Table 3 Continued.

Taxa	Stromata (µm)	Synnemata (µm)	Peridium (µm)	Asci (µm)	Apical ring (µm)	Ascospores (µm)	References
S. minus	400–600 diam., perithecioid, globose, rarely fusionate, gregarious, with 1 small synnema on immature stromata, shining, furfuraceous	100–200 high	-	13–14.5 × 165–185	6.5–7.8 × 5–6.5	12–13 × 23.5–26(–27.5), straight germ slit	Hladki & Romero 2003
S. moelleri (type species)	600–1000 diam., rough, overlain with yellow to greenish yellow scales at early stage, texture brittle	200–800 high	-	8–10 × 60–220	2.5–3.5 × 3–5	6–8 × 14.5–17, straight germ slit, enclosed by a thin hyaline sheath	Rogers & Ju 1997, Daranagama et al. 2018
S. novae-zelandiae	(400–)553 ± 82(–775) diam. × (350–)485 ± 70(–700) high, globose to subglobose, cupulate, rugose, with small cracks, solitary or densely crowded	-	≥ 25	-	Upper 2.4–3.8, lower 1.9–2.8 × (1.9–)2.3 ± 0.4(–3.3)	(5.8–)6.7(–8.2) × (9.6–)15.3 (–18.2) often with one cellular appendage, surrounded by a slimy sheath, sigmoid or straight germ slit	Petrini 2003
S. quisquiliarum	(600–)1020 ± 265(–1500) diam. × (575–)955 (–1600) high, globose to subglobose, ovoid, covered by yellow scales when young, later turning brown, surface warty, powdery, cracks, crowded, solitaryto 9 fused together with 1 synnemata on immature stromata	-	Up to 75	-	Upper 5–8, lower 4–7 × 6–10	(10–)13(–16) × (23–)28(–34), sigmoid to spiral germ slit	Rogers & Ju 1997, Esteban et al. 2013, Daranagama et al. 2018
S. samuelsii	700–1200 diam., spherical, gregarious, conical to acicular synnematal remnant, rugulose, sometimes overlain with ochraceous scales, texture hard	200–400 high		12–15.5 × 235–285(–315)	5.5–7 × 8–13	8.5–11(–13) × (27–)30–36(–40), straight germ slit	Rogers & Ju 1997, Petrini 2004
S. theissenii	750–1000 diam. × 750–1000 high, globose, subglobose, with a dull, rugose surface covered with fine cracks, conical synnemata	-	25–50	-	Upper 4–5.5, lower 3–5 × 6–7	(7–)8.5 (–11) × (22–)27(–33), large subglobose cellular appendage, straight to oblique germ slit	Petrini 2004

Stilbohypoxylon elaeidicola (Henn.) L.E. Petrini]as 'elaeicola'[, Sydowia 56(1): 55 (2004).

Index Fungorum number: IF631505; Facesoffungi number: FoF08465

≡ *Rosellinia elaeidicola* Henn. [as 'elaeicola'], Bot. Jb. 22: 77 (1895)

Notes – In our phylogenetic analysis based on DNA sequencedata from ITS region (data not shown) and combined sequence data of ITS, RPB2 and TUB2, *Stilbohypoxylon elaeidicola* clustered with *S. elaeidis* with high statistical support (Fig. 2). A comparison of *S. elaeidicola* with *S. elaeidis* shows they are different; *S. elaeidis* has solitary stromata (440–730 × 360–660 μm) with a smooth surface and forms synnemata remnants on the host, and covered the stroma when mature. *Stilbohypoxylon elaeidicola* has larger stromata (550–1,125 × 400–825 μm high), single or fused in clusters of 2–3, with rough to rugose walls, and with synnemata on the substrate or the stroma; while in *S. elaeidicola* asci and ascospores overlap in size with those of *S. elaeidis* (asci 105–130 × 11–16 μm vs 113–136 × 7–12 μm; ascospores 13–17 × 7–9 μm vs 13–21 × 5–8 μm) (Hennings 1895, Petrini 2004).

Discussion

There have been several taxonomic revisions of the larger Xylariaceae (*sensu* Daranagama et al. 2016) using traditional morphological concepts (e.g. Jaklitsch & Voglmayr 2012, Daranagama et al. 2015, Wendt et al. 2018, Lambert et al. 2019). In this paper, we introduce *Neoxylaria* which has a discrete morphology and is also phylogenetically distinct from *Xylaria sensu stricto*. Xylaria-like taxa have generally been lumped in a single genus pending an upcoming monograph (Stadler et al. pers. comm) and species/genera resolution has not advanced for numerous years. It is clear from the phylogenies generated in different studies (Hsieh et al. 2009, U'Ren et al. 2016, Daranagama et al. 2018, Wendt et al. 2018), that *Xylaria* is not monophyletic and should be spilt into several distinct genera. *Xylaria hypoxylon*, the type species is well-resolved and morphologically and phylogenetically characterized (Peršoh et al. 2009). Hsieh et al. (2010) and U'Ren et al. (2016) showed that there are three major *Xylaria* clades: *Xylaria* species associated with termite nests "TE clade" (including *X. nigripes*), *X. hypoxylon* (*Xylaria sensu stricto*) and closely related species "HY clade" and *X. polymorpha* and closely related species "PO clade". Several other xylaria-like species also cluster in different clades such as *Entoleuca*, *Euepixylon*, *Kretzmaria*, *Nemania*, *Podosordaria*, *Poronia* and *Rosellinia*. However, theoretically the HY clade (*Xylaria* "HY" clade II, Fig. 2) is the only acceptable cluster for strictly naming *Xylaria* species and other clades should represent other genera. Therefore, it is timely that xylaria-like taxa are resolved using both morphology and phylogeny.

This is not unique for *Xylaria*, but also similar for some other stromatic xylarialean taxa. Wendt et al. (2018) emphasized that ascal and ascospore characters have been the main discriminative criteria in traditional taxonomy and are artificial. Following a polyphasic taxonomic approach, Wendt et al. (2018) and Lambert et al. (2019) introduced several genera in Hypoxylaceae which were earlier placed in *Hypoxylon*. A similar approach should resolve the taxonomic confusion surrounding xylaria-like species. It is also not necessary to wait for a monograph as most of the old specimens cannot be sequenced and therefore, we can use fresh specimens to describe any new genera. Whether any old taxa are identical will be speculative, based on morphology and any combinations will be subjective (Dayarathne et al. 2016). Even though our new collection has superficial stromata similar to other *Xylaria* (*sensu stricto*) species, it is morphologically distinct in the palm host and perithecia which bulge from the stroma (as compared to immersed under a smooth stroma) and also phylogenetically distinct. The novel xylariacous genus, *Neoxylaria* is therefore introduced in this paper and will help to stabilize the classification of Xylariaceae. Phylogenetic analysis using three combined genes gave fair resolution for this order (Fig. 2).

Anthostomella-like species were also all clumped mostly under a single genus because they have immersed ascomata with or without a clypeus or a poorly or well-developed stroma, asci with a J+ or J- apical ring, dark unicellular ascospores (sometimes apiospores) with or without a germ-slit. Asci and ascospores were minute to large. Anthostomella-like taxa have now been shown to cluster in several different genera which are scattered in trees. Some authors used a single unique

character to separate anthostomella-like taxa into distinct genera, such as *Helicogermslita* (Hawksworth & Lodha 1983), which had spiral germ-slits but their introduction was subjective. One species that Duong et al. (2004) found was also anthostomella-like but introduced as a new genus *Emarcea* and eventually was shown to be sister to *Induratia* in a new family in Xylariales (Samarakoon et al. 2020). There are likely to be many other xylariaceous genera introduced in the future, just like as in *Anthostomella*.

We also introduced *Stilbohypoxylon elaeidis* as a new species confirmed by its phylogenetic placement. *Stilbohypoxylon* is polyphyletic and in this paper, we have defined *Stilbohypoxylon sensu stricto* and shows that *S. quisquiliarum* is distantly related and requires its own genus. Recent studies on tropical or poorly studied fungal genera have revealed an amazing diversity and numerous new species and this is likely to continue (Hyde et al. 2017, 2020). Thus, this study will help to resolve the naming and placement of the novel tropical taxa discoveries. Interestingly, *Stilbohypoxylon sensu stricto* (*S. elaeidis* and *S. elaeidicola*) occurred on the same host family, Arecaceae, with *Neoxylaria*, and they also share similar cultured characteristics. Both genera have cultured characteristics different from *Xylaria sensu stricto*, suggesting that both *Stilbohypoxylon* and *Neoxylaria* are likely ancient and related (but not the same genera) (Fig. 3 aa, ab, Fig. 4v).

Konta et al. (2016) reported appressoria formation in saprobic *Oxydothis* species. *Xylaria* species are mostly saprobes or endophytes and only a few species are pathogens (Miller & Nielsen 1957, Kodsueb et al. 2008, Okane et al. 2008, Karun & Sridhar 2015, Srihanant et al. 2015, Li et al. 2017, Adnan et al. 2018b, Chen et al. 2018, Debnath et al. 2018, Husbands & Aime 2018). *Xylaria* species can also form appressoria when they germinate (Daranagama, pers obs). In the case of *Neoxylaria arengae*, we observed appressoria-like structures produced at the tips of germinating hyphae on media (Fig. 3t–z). Thus, it is interesting that *Neoxylaria, Oxydothis* and *Xylaria* species collected from palms produce appressoria which indicate they may have different life modes.

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