



## Evolution of Xylariomycetidae (Ascomycota: Sordariomycetes)

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Samarakoon MC, Hyde KD, Promputtha I, Hongsanan S, Ariyawansa HA, Maharachchikumbura SSN, Daranagama DA, Stadler M, Mapook A. 2016 – Evolution of Xylariomycetidae (Ascomycota: Sordariomycetes). *Mycosphere* 7 (11), 1746–1761, Doi 10.5943/mycosphe/7/11/9

### Abstract

The class Sordariomycetes, which is the second largest class in the phylum Ascomycota, comprises highly diversified fungal groups, with relatively high substitution and evolutionary rates. In this preliminary study, divergence estimates of taxa of Xylariomycetidae are calculated using *Ophiocordyceps* fossil evidence and secondary data. The combination of fossil and secondary calibration can affect the divergence time estimates by pushing the ages towards the roots. The estimated divergence of Hypocreomycetidae, Lulworthiomycetidae and Xylariomycetidae occurred during the Early Mesozoic (201-252 Mya) and Diaporthomycetidae and Sordariomycetidae occurred later during the Late Mesozoic (145-252 Mya). Two characteristic divergence groups have evolved 168 and 147 Mya and probably provide additional evidence for continuation and species richness of the orders Amphisphaeriales and Xylariales. The early diversifications of the families in Xylariomycetidae have occurred during the Early Cretaceous (100-145 Mya).

**Key words** – divergence time–fossil–paleobiology–secondary data

### Introduction

Species in Sordariomycetes are endophytes, pathogens and saprobes (Zhang et al. 2006) and are characterized by perithecial ascomata, paraphyses, periphysate ostioles and unitunicate asci (Kirk et al. 2001, 2008). The species of hyphomycetes and coelomycetes linked to the Sordariomycetes have significant diversity (Zhang et al. 2006). Among the Ascomycota classes, Sordariomycetes shows a high substitution rate resulting from an acceleration of the speciation process over time, as compared to Dothideomycetes and Leotiomyces (Wang et al. 2010). Maharachchikumbura et al. (2016) estimated there were 1,331 genera in 105 families, 32 orders

and six subclasses in Sordariomycetes. The subclasses are Diaporthomycetidae, Hypocreomycetidae, Lulworthiomycetidae, Meliolomycetidae, Sordariomycetidae and Xylariomycetidae.

The subclass Xylariomycetidae, introduced by Eriksson & Winka (1997), mostly comprises species with large, conspicuous stromata, although there are also numerous, less well-studied microscopic forms (Daranagama et al. 2016a). Most taxa have asci with a J+, apical ring and brown, pigmented, unicellular ascospores, often with germ slits (Maharachchikumbura et al. 2015, Daranagama et al. 2016b). Members of Xylariomycetidae, as saprobic, pathogenic and endophytic species, have dynamic nutritional relationships with plants and animals (Zhang et al. 2006, Maharachchikumbura et al. 2016).

The subclass Xylariomycetidae were thought to comprise Amphisphaeriales and Xylariales, based on the morphological data and phylogenetic analysis of combined ITS and LSU sequence data (Smith et al. 2003, Tang et al. 2009, Senanayake et al. 2015). Senanayake et al (2015) resurrected Amphisphaeriales as a distinct order comprising the families Amphisphaeriaceae, Bartaliniaceae, Clypeosphaeriaceae, Discosiaceae (now Sporocadaceae), Pestalotiopsidaceae and Phlogicylindriaceae. The revised order Xylariales comprised the families Apiosporaceae, Cainiaceae, Coniocessiaceae, Diatrypaceae, Hyponectriaceae, Iodosphaeriaceae, Lopadostomataceae, Melogrammataceae, Pseudomassariaceae, Vialaeaceae and Xylariaceae. However, Amphisphaeriales was later considered as a synonym of Xylariales (Maharachchikumbura et al. 2016), because in the trees of Senanayake et al. (2015) there was poor statistical support for this separation. Maharachchikumbura et al. (2016) treated Xylariales with 22 well-established families, Amphisphaeriaceae, Apiosporaceae, Bartaliniaceae, Beltraniaceae, Cainiaceae, Clypeosphaeriaceae, Coniocessiaceae, Diatrypaceae, Hyponectriaceae, Iodosphaeriaceae, Lopadostomataceae, Melogrammataceae, Microdochiaceae, Myelospermataceae, Pestalotiopsidaceae, Phlogicylindriaceae, Pseudomassariaceae, Requiellaceae, Robillardaceae, Sporocadaceae (Discosiaceae), Vialaeaceae and Xylariaceae (“Hypoxyloideae” and “Xylarioideae”).

However, based on the phylogenetic placement of the generic type *Clypeosphaeria mamillana* within the family Xylariaceae, the family Clypeosphaeriaceae has been discontinued and treated as a synonym of Xylariaceae (Jaklitsch et al. 2016). Hence *Clypeosphaeria* is now accepted in Xylariaceae. A new family Oxydothidaceae was introduced in Xylariomycetidae (Konta et al. 2016) based on morphological data and evidence from phylogenetic analysis of LSU, SSU and ITS sequence data. Within the family Xylariaceae there is a traditional segregation (Ju & Rogers 1996) based on the asexual morph characters, which has been phylogenetically supported in several recent studies (Stadler et al. 2013, Daranagama et al. 2015, 2016a, b, c, Maharachchikumbura et al. 2015, 2016) as “Hypoxyloideae” and “Xylarioideae”. The classifications of orders, families and genera of Xylariomycetidae however, will need further refinement when type sequences or the authentic materials are available, with focus on collections, epitypification and molecular studies (Daranagama et al. 2015, 2016a, c, Maharachchikumbura et al. 2015, 2016, Senanayake et al. 2015).

Molecular timescales can provide insights into the history of organisms, taxonomic placements and are valuable for organisms with or without fossil records (Li et al. 2005, Vijaykrishna et al. 2006, Beimforde et al. 2014, Pérez-Ortega et al. 2016). Speciation events can provide valuable information concerning the genetic evolution and evolutionary history of taxon groups, through biochemical, selective pressure and population processes (Bromham & Penny 2003). Morphological and molecular characters of fossils and living samples are also important for determining evolutionary relationships (Kemp 2005). With fossil data for the calibration of node ages, patterns of phylogenetic prediction can be determined (Taylor & Berbee 2006). However, for the purpose of reasonable divergence time estimations, there is a need for clearly defined and dated fossils (Blair 2009).

This study focuses on the phylogenetic analyses and the application of fossil and non-fossil information for the estimation of divergence times for the subclasses within Sordariomycetes,

specifically Xylariomycetidae. The continuation of the order Amphisphaerales and Xylariales within the Xylariomycetidae is supported by the divergence time estimations. The diversification of Xylariomycetidae families and the provision of information for refining internal taxonomical classification are presented and described. The possibilities of using crown age dissimilarities as additional information for the differentiation of the internal groups are also discussed.

## Materials & Methods

### Taxon sampling, molecular data and phylogenetic analysis

A representative set of 175 sequences from 161 species of Sordariomycetes (including 21 families belonging to the subclass Xylariomycetidae) were selected. *Leotia lubrica*, *Coccomyces dentatus*, *Mollisia ventosa*, *M. cinerea* and *Thelebolus globosus* from the class Leotiomycetes were selected as out group taxa. Sequence data were obtained from GenBank based on previous literature (Table 1).

Initially, multiple sequence alignments were generated from three loci (LSU, SSU and rpb2) using MAFFT v. 7 (<http://mafft.cbrc.jp/alignment/server/index.html>) and manually corrected where necessary using BioEdit sequence alignment editor (Hall 1999) to minimize the uninformative gaps. The final alignment consisted of 3038 characters (nuLSU-907 bp, nuSSU-1084 bp and rpb2-1039 bp) and gaps were treated as missing data. The substitution models for each partition were performed using Akaike Information Criterion (AIC) implemented in jMODELTEST (Darriba et al. 2012). The GTR (LSU, RPB2 – GTR+I+G) and TN93 (SSU – TrN+I+G) were used as models of substitution for phylogenetic and divergence time estimation studies. The same multiple sequence alignment was used for phylogenetic and molecular clock estimations.

Phylogenies were generated using maximum likelihood and Bayesian inference analyses. Maximum likelihood analysis was performed with RAxMLGUI v.1.3 (Silvestro & Michalak 2012) using the ML+rapid bootstrap setting, GTRGAMMAI substitution model with 1000 replicates. The Bayesian tree was generated by using MCMC sampling in MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001, Zhaxybayeva & Gogarten 2002) for 7000000 MCMC generations using four chains and partition analysis with 100 sample frequencies which products 14,000 trees. The first 2,800 (20% from total) trees were the burn-in phase and were discarded, and remaining 11,200 trees were used to calculate the posterior probability. The resulting trees were viewed with FigTree v.1.4.0 (Rambaut 2006) and the final layout was done with CorelDRAW Graphics Suite X6.

**Table 1** Strains used in this study

Species	Culture collection no.	GenBank Accession no.		
		LSU	SSU	RPB2
<i>Adisciso yakushimense</i>	HHUF 29671	AB593721	AB593700	–
<i>Amphibambusa bambusicola</i>	MFLUCC 11-0617	KP744474	–	–
<i>Amphisphaeria sorbi</i>	MFLUCC 13-C0721	KP744475	–	–
<i>Amphisphaeria umbrina</i>	HKUCC 994	AF452029	AY083811	–
<i>Amphisphaeria umbrina</i>	AFTOL-ID 1229	FJ176863	FJ176809	–
<i>Annulohypoxyton multiforme</i>	CBS 119016	KT281893	–	–
<i>Annulohypoxyton stygium</i>	MFLUCC 12-0826	KJ940869	–	–
<i>Apiospora bambusa</i>	ICMP 6889	DQ368630	DQ368662	DQ368649
<i>Apiospora setosa</i>	ICMP 4207	DQ368631	DQ368661	–
<i>Arecophila bambusae</i>	HKUCC 4794	AF452038	AY083802	–
<i>Arthrinium arundinis</i>	AFTOL-ID 951	DQ471018	–	–
<i>Arthrinium hydei</i>	CBS 114990	KF144936	–	–
<i>Arthrinium phaeospermum</i>	HKUCC 3395	AY083832	AY083816	–
<i>Ascotaiwania lignicola</i>	NIL00005	HQ446364	HQ446284	HQ446419
<i>Ascotaiwania lignicola</i>	NIL00006	HQ446365	HQ446285	–
<i>Bartalinia robillardoides</i>	CBS 122705	KJ710438	–	–
<i>Beltrania pseudorhombica</i>	CBS 138003	KJ869215	–	–
<i>Beltraniella endiandrae</i>	CBS 137976	KJ869185	–	–
<i>Beltraniopsis neolitseae</i>	CBS 137974	KJ869183	–	–
<i>Biscogniauxia nummularia</i>	MUCL 51395	KT281894	–	–

Species	Culture collection no.	GenBank Accession no.		
		LSU	SSU	RPB2
<i>Bombardia bombardia</i>	AFTOL-ID 967	DQ470970	DQ471021	DQ470923
<i>Broomella vitalbae</i>	MFLUCC 14-1000	KP757750	KP757758	–
<i>Broomella vitalbae</i>	MFLUCC 15-0023	KP757751	KP757759	–
<i>Buergenerula spartinae</i>	ATCC 22848	DQ341492	DQ341471	–
<i>Cainia graminis</i>	MFLUCC 15-0540	KR092781	–	–
<i>Cainia graminis</i>	CBS 136.62	AF431949	AF431948	–
<i>Carpoligna pleurothecii</i>	CBS 114211	JQ429235	JQ429249	JQ429267
<i>Chaetosphaerella fusca</i>	GKML124N	FJ968967	–	–
<i>Chaetosphaerella phaeostroma</i>	SMH4257	AY695264	–	FJ968940
<i>Ciferriascosea fluctamurum</i>	MFLUCC 15-0541	KR092778	–	–
<i>Ciferriascosea rectamurum</i>	MFLUCC 15-0542	KR092776	–	–
<i>Ciliochorella mangiferae</i>	MFLUCC 12-0310	KF827445	KF827446	KF827479
<i>Clypeosphaeria uniceptata</i>	HKUCC 6349	AY083830	AY083812	–
<i>Clypeosphaeria uniseptata</i>	HKUCC Voucher	DQ810219	DQ810255	–
<i>Coccomyces dentatus</i>	AFTOL-ID 147	AY544657	AY544701	DQ247789
<i>Colletotrichum brevisporum</i>	MFLU<THA>:LC0600	JN940398	JN940357	–
<i>Colletotrichum fruticicola</i>	MFLU<THA>:LC0032	JN940418	JN940350	–
<i>Colletotrichum gloeosporioides</i>	CGMCC:LC0555	JN940412	JN940356	–
<i>Coniocessia anandra</i>	IRAN 1468C	GU553349	–	–
<i>Coniocessia cruciformis</i>	IRAN 1472C	GU553348	–	–
<i>Coniocessia maxima</i>	CBS 593.74	GU553344	–	–
<i>Coniocessia nodulisporioides</i>	CBS 281.77	GU553352	AJ875185	–
<i>Coniochaeta ligniaria</i>	C8	AY198388	–	–
<i>Coniochaeta luteoviridis</i>	CBS 206.38	FR691987	–	–
<i>Coniochaeta ostrea</i>	AFTOL-ID 915	DQ470959	DQ471007	–
<i>Conioscypha japonica</i>	CBS 387.84	AY484514	JQ437438	JQ429259
<i>Conioscypha lignicola</i>	CBS 335.93	AY484513	JQ437439	JQ429260
<i>Conioscyphascus varius</i>	CBS 113653	AY484512	–	–
<i>Cordyceps cardinalis</i>	OSC 93609	AY184962	NG013131	–
<i>Cordyceps irangiensis</i>	OSC 128578	DQ518770	DQ522556	DQ522445
<i>Cordyceps militaris</i>	OSC 93623	AY184966	AY184977	–
<i>Cosmospora coccinea</i>	AR2741	AY489734	AY489702	–
<i>Crassochaeta nigrita</i>	SMH2931	AY695266	–	–
<i>Creosphaeria sassafras</i>	ANM 1978	JN673042	–	–
<i>Creosphaeria sassafras</i>	CM AT-018	DQ840056	–	–
<i>Cryptosphaeria ligniota</i>	ATCC 46315	KT425299	–	–
<i>Cryptosphaeria multicontinentalis</i>	ARG03	KT425305	–	–
<i>Cumulospora marina</i>	MF46	GU252135	GU252136	–
<i>Daldinia bambusicola</i>	MFLUCC 11-0605	KU863143	–	KU940181
<i>Daldinia concentrica</i>	CBS 113277	KT281895	–	–
<i>Diaporthe eres</i>	AR 3519	AF362565	–	–
<i>Diatrype disciformis</i>	AFTOL-ID 927	DQ470964	DQ471012	DQ470915
<i>Diatrype palmicola</i>	MFLUCC 11-0020	KP744482	KP753950	–
<i>Diatrype whitmanensis</i>	ATCC MYA-4417	FJ430587	FJ430578	–
<i>Discosia brasiliensis</i>	MFLUCC 12-0431	KF827437	KF827441	KF827474
<i>Discosia pini</i>	MAFF 410149	AB593708	–	–
<i>Doratomyces stemonitis</i>	AFTOL-ID 1380	DQ836907	DQ836901	–
<i>Escovopsis weberi</i>	ATCC 64542	KF293281	KF293278	–
<i>Fragosphaeria purpurea</i>	CBS 133.34	AB189154	AF096176	–
<i>Gelasinospora tetrasperma</i>	AFTOL-ID 1287	DQ470980	DQ471032	DQ470932
<i>Gliocephalotrichum bulbilium</i>	ATCC 22228	AY489732	AY489700	–
<i>Glomerulispora mangrovis</i>	NBRC105264	GU252149	GU252150	–
<i>Harknessia australiensis</i>	CPC 15029	JQ706211	–	–
<i>Harknessia ellipsoidea</i>	CPC 17111	JQ706213	–	–
<i>Harknessia weresubiae</i>	CPC 17670	JQ706244	–	–
<i>Hyalotiella spartii</i>	MFLUCC 13-0397	KP757752	KP757760	–
<i>Hydea pygmaea</i>	NBRC 33069	GU252133	GU252134	–
<i>Hyponectria buxi</i>	UME 31430	AY083834	AF130976	–
<i>Hypoxylon fragiforme</i>	MUCL 51264	KM186295	–	KM186296
<i>Hypoxylon lenormandii</i>	MFLUCC 13-0311	KM039136	–	KM039137
<i>Hypoxylon monticulosum</i>	GZ AT-M050	DQ840067	–	–

Species	Culture collection no.	GenBank Accession no.		
		LSU	SSU	RPB2
<i>Idriella lunata</i>	CBS 204.56	KP858981	–	–
<i>Iodosphaeria tongrenensis</i>	GZUH0109=FJS8	KR095283	–	–
<i>Jobellisia fraterna</i>	SMH2863	AY346285	–	–
<i>Jobellisia guangdongensis</i>	GD14-4	JN936990	–	–
<i>Jobellisia luteola</i>	SMH2753	AY346286	–	–
<i>Jugulospora rotula</i>	ATCC 38359	AY346287	–	AY780178
<i>Koralionastes ellipticus</i>	JK5769	EU863585	EU863581	–
<i>Koralionastes ellipticus</i>	JK5771	EU863583	EU863580	–
<i>Kretzschmaria deusta</i>	CBS 163.93	KT281896	–	–
<i>Lasiosphaeria ovina</i>	SMH4605	AY436413	–	AY600284
<i>Leotia lubrica</i>	AFTOL-ID 1	NG027596	AY544687	DQ470876
<i>Lepteutypa cupressi</i>	IMI 052255	AF382379	AY083813	–
<i>Lindra thalassiae</i>	AFTOL-ID 413	DQ470947	DQ470994	DQ470897
<i>Lopadostoma turgidum</i>	LT1	KC774617	–	KC774562
<i>Lopadostoma turgidum</i>	LT	KC774616	–	KC774561
<i>Lopadostoma turgidum</i>	CBS 133207	KC774618	–	KC774563
<i>Lulworthia fucicola</i>	ATCC 64288	AY878965	AY879007	–
<i>Magnaporthe poae</i>	M47	JF414885	–	–
<i>Magnaporthe salvinii</i>	M21=ATCC 44754	JF414887	–	–
<i>Mazzantia napelli</i>	AR3498 = AFTOL-ID 2126	AF408368	DQ862051	EU219345
<i>Melanconis marginalis</i>	AR3442 = AFTOL-ID 2128	AF408373	DQ862053	EU219301
<i>Melanconis stilbostoma</i>	AR3501 = CBS 109778	AF408374	NG_013198	EU219299
<i>Melogramma campylosporum</i>	MBU	JF440978	–	–
<i>Microascus trigonosporus</i>	AFTOL-ID 914	DQ470958	DQ471006	–
<i>Microdochium bolleyi</i>	CBS 540.92	KP858946	–	KP859119
<i>Microdochium nivale</i>	CBS 116205	KP858944	AB586893	KP859117
<i>Microdochium phragmitis</i>	CBS 423.78	KP858948	–	KP859121
<i>Microdochium seminicola</i>	CBS 122707	KP858947	–	KP859120
<i>Microdochium trichocladiopsis</i>	CBS 623.77	KP858934	–	KP859107
<i>Mollisia cinerea</i>	AFTOL-ID 76	DQ470942	DQ470990	DQ470883
<i>Mollisia ventosa</i>	KUS-F52181	JN086700	–	JN086851
<i>Neonectria ramulariae</i>	CBS 151.29	HM042436	HQ840414	DQ789792
<i>Neopestalotiopsis clavispora</i>	CBS 447.73	KM116275	–	–
<i>Neopestalotiopsis foedans</i>	CGMCC 3.9144	JN940832	JN940799	–
<i>Neurospora crassa</i>	MUCL 19026	AF286411	X04971	–
<i>Ophioceras dolichostomum</i>	CBS 114926	JX134689	JX134663	–
<i>Ophiocordyceps gracilioides</i>	TSJ935	KJ130992	–	–
<i>Ophiocordyceps melolonthae</i>	TSJ679	KJ130990	–	–
<i>Ophiocordyceps sinensis</i>	YN09-64	JX968033	JX968028	JX968013
<i>Ophiidiaporthe cyatheae</i>	1364 (HAST)	JX570891	JX570890	JX570893
<i>Ophiostoma piliferum</i>	AFTOL-ID 910	DQ470955	DQ471003	–
<i>Oxydothis metroxylo-nicola</i>	MFLUCC 15-0281	KY206774	KY206769	KY206781
<i>Oxydothis palmicola</i>	MFLUCC 15-0806	KY206775	KY206771	–
<i>Oxydothis rhapsidicola</i>	MFLUCC 14-0616	KY206766	KY206772	–
<i>Parapleurotheciopsis inaequiseptata</i>	MUCL 41089	EU040235	–	–
<i>Pestalotiopsis adusta</i>	CGMCC 3.9103	JN940828	JN940796	–
<i>Petriella setifera</i>	AFTOL-ID 956	DQ470969	DQ471020	–
<i>Phlogicylindrium eucalyptorum</i>	CBS 111689	KF251708	–	–
<i>Phlogicylindrium eucalyptorum</i>	CBS 111680	KF251707	–	–
<i>Phlogicylindrium uniforme</i>	CBS 131312	JQ044445	–	–
<i>Pleurotheciella rivularia</i>	CBS 125238	JQ429232	JQ429244	JQ429263
<i>Pleurothecium semifecundum</i>	CBS 131271	JQ429240	JQ429254	JQ429270
<i>Podosordaria tulasnei</i>	CBS 128.80	KT281897	–	–
<i>Pseudobeltrania ocoteae</i>	CPC 26219	KT950870	–	–
<i>Pseudomassaria chondrospora</i>	PC1	JF440982	–	–
<i>Pseudomassaria chondrospora</i>	CBS 125600	JF440981	–	–
<i>Pseudomassaria sepincoliformis</i>	CBS 129022	JF440984	–	–
<i>Pseudopestalotiopsis theae</i>	SAJ 0021	JN940838	JN940785	–
<i>Requienella fraxini</i>	WU 33560	KT949909	–	–
<i>Requienella fraxini</i>	WU 33561	KT949910	–	–
<i>Requienella fraxini</i>	WU 33564	KT949911	–	–

Species	Culture collection no.	GenBank Accession no.		
		LSU	SSU	RPB2
<i>Requienella seminuda</i>	WU 33568	KT949912	–	–
<i>Requienella seminuda</i>	WU 33569	KT949913	–	–
<i>Robillarda africana</i>	CBS 122.75	KR873281	–	–
<i>Robillarda roystoneae</i>	CBS 115445	KR873282	–	–
<i>Robillarda sessilis</i>	CBS 101440	KR873283	–	–
<i>Robillarda sessilis</i>	CBS 114312	KR873284	–	–
<i>Robillarda terrae</i>	CBS 587.71	KJ710459	–	–
<i>Rosellinia limonisporea</i>	CBS 382.86	KF719211	–	–
<i>Rosellinia necatrix</i>	HKUCC 9037	AY083824	AY083805	–
<i>Rostrohypoxyton terebratum</i>	CBS 119137	DQ840069	–	DQ631954
<i>Sarcostroma restionis</i>	CBS 118154	DQ278924	–	–
<i>Savoryella lignicola</i>	NF00204	HQ446378	HQ446300	–
<i>Seimatosporium cornii</i>	MFLUCC 14-0467	KR559739	KR559741	–
<i>Seimatosporium lichenicola</i>	MFLUCC 14-0052	KT005514	–	–
<i>Seiridium phyllicae</i>	CPC 19962	NG_042759	–	–
<i>Selenodriella cubensis</i>	CBS 683.96	KP858990	–	–
<i>Selenodriella fertilis</i>	CBS 772.83	KP858992	–	–
<i>Seynesia erumpens</i>	SMH 1291	AF279410	AF279409	AY641073
<i>Sordaria fimicola</i>	CBS 508.50	AY681160	–	–
<i>Sporothrix stenoceras</i>	AFTOL-ID 1038	DQ836904	DQ836897	–
<i>Subramaniomyces fusisaprophyticus</i>	CBS 418.95	EU040241	–	–
<i>Thelebolus globosus</i>	AFTOL-ID 5016	FJ176905	FJ176851	–
<i>Tolypocladium capitatum</i>	OSC 71233	AY489721	AY489689	–
<i>Tolypocladium japonicum</i>	OSC 110991	DQ518761	DQ522547	DQ522428
<i>Torpedospora ambispinosa</i>	BCC16003	AY858949	AY858940	–
<i>Torpedospora radiata</i>	AFTOL-ID 751	DQ470951	DQ470999	DQ470902
<i>Torrubiella wallacei</i>	CBS 101237	AY184967	AY184978	EF469119
<i>Trichoderma citrinoviride</i>	CBS 258.85	AF399228	–	–
<i>Trichoderma viride</i>	GJS89-127	AY489726	–	–
<i>Truncatella spartii</i>	MFLUCC 15-0537	KR092782	–	–
<i>Vialaea insculpta</i>	AFTOL-ID 1302	KF511803	–	–
<i>Vialaea mangiferae</i>	MFLUCC 12-0808	KF724975	–	–
<i>Vialaea minutella</i>	BRIP 56960	KC181925	–	–
<i>Vialaea minutella</i>	BRIP 56959	KC181924	–	–
<i>Xylaria bambusicola</i>	MFLUCC 11-0606	KU863148	–	KU940183
<i>Xylaria grammica</i>	479 (HAST)	JQ862638	–	GQ844813
<i>Xylaria hypoxyton</i>	CBS122620	KM186301	–	KM186302
<i>Zetiasplozina acaciae</i>	CPC 23421	KJ869206	–	–

## Fossil calibration

In this study, we selected *Paleoophiocordyceps coccophagus* Sung et al., a fossil from the class Sordariomycetes (Hypocreomycetidae, Hypocreales) for calibrating the tree. Sung et al. (2008) investigated a fossilized male scale (Albicoccidae) insect parasitized by *P. coccophagus* from the Late Mesozoic (Upper Albian) period in Burmese amber, which was from lignitic seams in sandstone-limestone. It is the oldest fossil evidence recorded for the fungal-animal parasitism (Sung et al. 2008). Morphological characters of the fossil *P. coccophagus* are similar to the asexual characters of the extant *Hirsutella* and *Hymenostilbe* (Sung et al. 2008). The genera *Hirsutella* and *Hymenostilbe* are treated as synonyms of *Ophiocordyceps* (Ophiocordycipitaceae, Hypocreales; Quandt et al. 2014). The age of the fossil has been calculated around 99-105 Mya based on the geological timescale (Cruickshank & Ko 2003). Based on the geological time scale of Walker et al. (2012), the Albian period is demarcated as 100-113 Mya. In this study, the fossil data was used for the calibration of the crown node of the genus *Ophiocordyceps* (Exponential distribution, offset 100, mean 27.5, with 95% credibility interval of 182.4 Mya).

## Secondary calibration

Several studies have been conducted to estimate the crown age of Sordariomycetes. According to recent studies, the estimated crown ages of the class Sordariomycetes are 256 Mya

(202–306; Pérez-Ortega et al. 2016), 260 Mya (207–339; Beimforde et al. 2014) and 130 Mya (77–181; Prieto & Wedin 2013). The divergence time of Sordariomycetes studied by Pérez-Ortega et al. (2016) is comparatively closer to Beimforde et al. (2014). Generally, these two studies used similar fossil calibrations for the divergence time estimations (Beimforde et al. 2014, Pérez-Ortega et al. 2016). In this study, we used the mean crown age as 258 Mya (202–339) as the crown age for Sordariomycetes (normal distribution with the mean 258 and SD 35 with 95% credibility interval) of 315.6 Mya.

### **Molecular clock analysis**

Bayesian analysis was implemented for estimation of divergence times using data from multi-gene loci and accommodating fossil and secondary calibration nodes. Two scenarios for the divergence time estimations were implemented for calibrating the tree; scenario 1 with a combination of fossil data and secondary data; scenario 2 with only secondary data. Analyses were performed using the BEAST v1.8.0. The XML file was obtained including the partitioned alignment using the BEAUti (BEAST package). The GTR (LSU, RPB2 – GTR+I+G) and TN93 (SSU – TrN+I+G) were used as models of substitution. BEAST analyses were run for 100,000,000 generations, logging parameters and trees were obtained for every 10,000 generations. Effective sample sizes (ESS) of parameters were checked using Tracer v.1.6 (ESS>200). A burn-in of first 30% trees was removed from each analysis based on the ESS values using Tracer v1.6 (Rambaut et al. 2013). The remaining trees were used to generate a maximum clade credibility tree by using Logcombiner v1.8.0 and TreeAnnotator v1.8.0. The resulting trees were viewed with FigTree v.1.4.0 (Rambaut 2006) and the final layout was done with CorelDRAW Graphics Suite X6.

## **Results**

### **Topology of the Xylariomycetidae**

The results from RAXML and Bayesian analyses using LSU, SSU and rpb2 sequence data are shown in Fig. 1. The overall topology for the higher-level relationships is quite similar to those in previous phylogenetic analyses (Maharachchikumbura et al. 2015, 2016, Senanayake et al. 2015). The subclasses Diaporthomycetidae, Hypocreomycetidae, Lulworthiomycetidae, Sordariomycetidae and Xylariomycetidae cluster in Sordariomycetes (100 ML/1 PP). Lulworthiomycetidae and Hypocreomycetidae are sister clades (52 ML) as basal to the sister clade comprising Diaporthomycetidae, Sordariomycetidae and Xylariomycetidae. Diaporthomycetidae and Sordariomycetidae are sister clades (81 ML/0.99 PP) as basal to Xylariomycetidae. The 22 families of Xylariomycetidae clustered together (73 ML/0.98 PP). The subclass Meliolomycetidae is, however, not included in this study.

The family Iodosphaeriaceae diverges as a basal clade from other families of Xylariomycetidae. Microdochiaceae and Coniocessiaceae are sister families (88 ML/1 PP), forming a basal clade to other families. The families Amphisphaeriaceae, Apiosporaceae, Bartaliniaceae, Beltraniaceae, Hyponectriaceae, Melogrammataceae, Oxydothidaceae, Pestalotiopsisaceae, Phlogicylindriaceae, Pseudomassariaceae, Robillardaceae, Sporocadaceae and Vialaeaceae (Clade I, possible Amphisphaeriales), cluster sister to the families Cainiaceae, Diatrypaeae, Lopadostomataceae, Requinellaceae and Xylariaceae (“Hypoxyloideae” and “Xylarioideae”; as Clade II, possibly Xylariales *sensu stricto*).

### **Divergence time estimations with a combination of fossil and secondary calibration**

The comparable results (95% CI) from both scenarios 1 and 2 are listed in the Table 2. The divergence times estimated using a combination of fossil and secondary data (Scenario 1) are older than the divergence times estimated using only secondary data (Scenario 2). According to the estimates in Scenario 1, the class Sordariomycetes diverged from Leotiomycetes during the Paleozoic, around 343 Mya (264–446). The crown age of the class Sordariomycetes is around 300 Mya (249–359) during the Paleozoic. The subclasses Lulworthiomycetidae and Hypocreomycetidae

diverged approximately at 284 Mya (233-342) during the Late Paleozoic, while the crown ages of these two subclasses occurred during the Early Mesozoic; Lulworthiomycetidae 216 Mya (150-284), Hypocreomycetidae 245 Mya (199-301). The crown age of the clade comprising Sordariomycetidae, Diaporthomycetidae and Xylariomycetidae is around 274 Mya (216-337) during the Late Paleozoic and 228 Mya (169-290) for the split between Diaporthomycetidae and Sordariomycetidae during the Early Mesozoic. The earliest splits (crown ages) of the Sordariomycetidae (179 Mya), Diaporthomycetidae (197 Mya) and Xylariomycetidae (219 Mya) occurred during the Mesozoic. The crown age of the fossil in Hypocreales is around 163 Mya (129-200) with the stem age around 200 Mya (158-248) during the Middle of Mesozoic. The crown node ages of the families Microdochiaceae and Xylariaceae belong to the Late Mesozoic (66-100 Mya), while the majority of the families have diversified during the Cenozoic (66 Mya to present; see Fig 2). Divergence times of other families in Xylariomycetidae are shown in Fig. 2.

**Table 2** Comparison of the estimated divergence times (Mya) with 95% credibility intervals (CI) for Scenarios 1 and 2.

Node	Node age	Age (95% CI) Mya	
		Scenario 1	Scenario 2
1	Leotiomycetes-Sordariomycetes	347 (267-456)	270 (182-369)
2	Sordariomycetes crown group	308 (254-364)	243 (169-308)
3	Lulworthiomycetidae-Hypocreomycetidae	291 (237-348)	227 (159-294)
4	Lulworthiomycetidae crown group	219 (150-286)	164 (94-236)
5	Hypocreomycetidae crown group	252 (200-305)	186 (125-250)
6	Sordariomycetidae - Diaporthomycetidae-Xylariomycetidae	282 (221-340)	218 (147-287)
7	Diaporthomycetidae-Sordariomycetidae	236 (172-298)	178 (113-244)
8	Sordariomycetidae crown group	182 (121-251)	136 (70-199)
9	Diaporthomycetidae crown group	203 (141-266)	153 (94-214)
10	Xylariomycetidae crown group	235 (172-298)	173 (113-243)
11	Amphisphaeriales crown group	147 (103-199)	104 (66-152)
12	Xylariales crown group	168 (122-219)	119 (77-167)

## Discussion

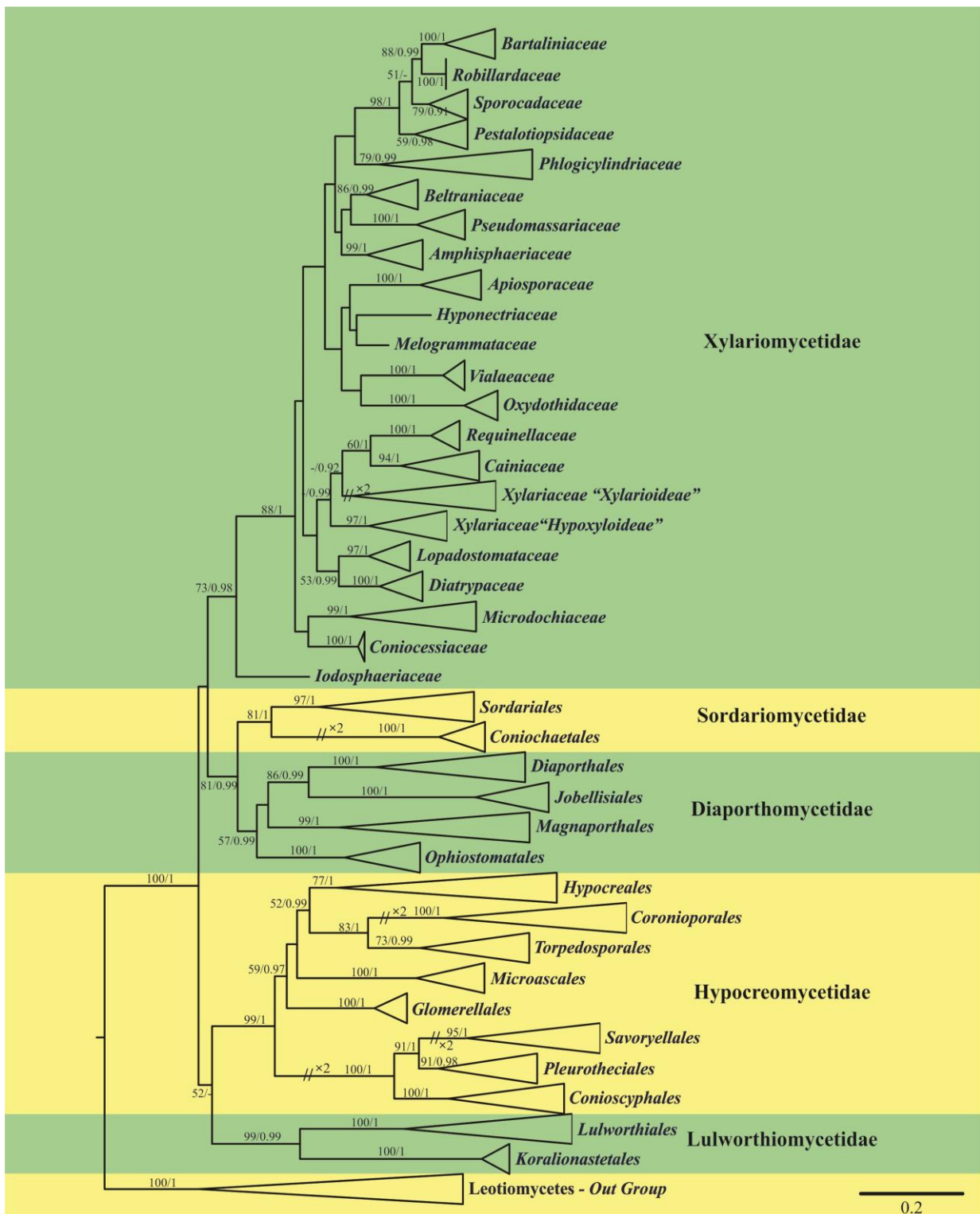
### Assigning calibration points

The *Paleoophiocordyceps coccophagushas* fossil appears to be similar to *Hirsutella* and *Hymenostilbe* species, which are now considered as the asexual morphs of *Ophiocordyceps* (Sung et al. 2008, Quandt et al. 2014). This provides additional evidence for the fossil calibration in the molecular clock analyses. The internal node calibration emphasizes the relationships among taxa (Ho & Phillips 2009). The fossil representing Hypocreomycetidae might provide acceptable divergence time estimates for taxa within Sordariomycetes. The known divergence dates from fossils (Mitchell-Olds & Bergelson 2000) and the availability of acceptable external calibration points (Lücking et al. 2009), can be used to estimate the divergence times. However, a combination of geological and molecular information, with appropriate selection of methods, with more representative fossil data, can provide reasonable lower (lower boundary) divergence times, but rarely realistic upper boundary of divergence times (Guicking et al. 2006, Eme et al. 2014, Magallón et al. 2015). The use of multiple calibration points can result in more comprehensive estimates than a single calibration point (Ho & Phillips 2009). Thus, the use of previous results as secondary calibrations (Beimforde et al. 2014, Pérez-Ortega et al. 2016), with an internal fossil, provides reasonable estimates; in addition, it avoids repetition of estimates. Hug & Roger (2007) suggested that the accumulation of the error in the original study might be a problem when using only secondary information.

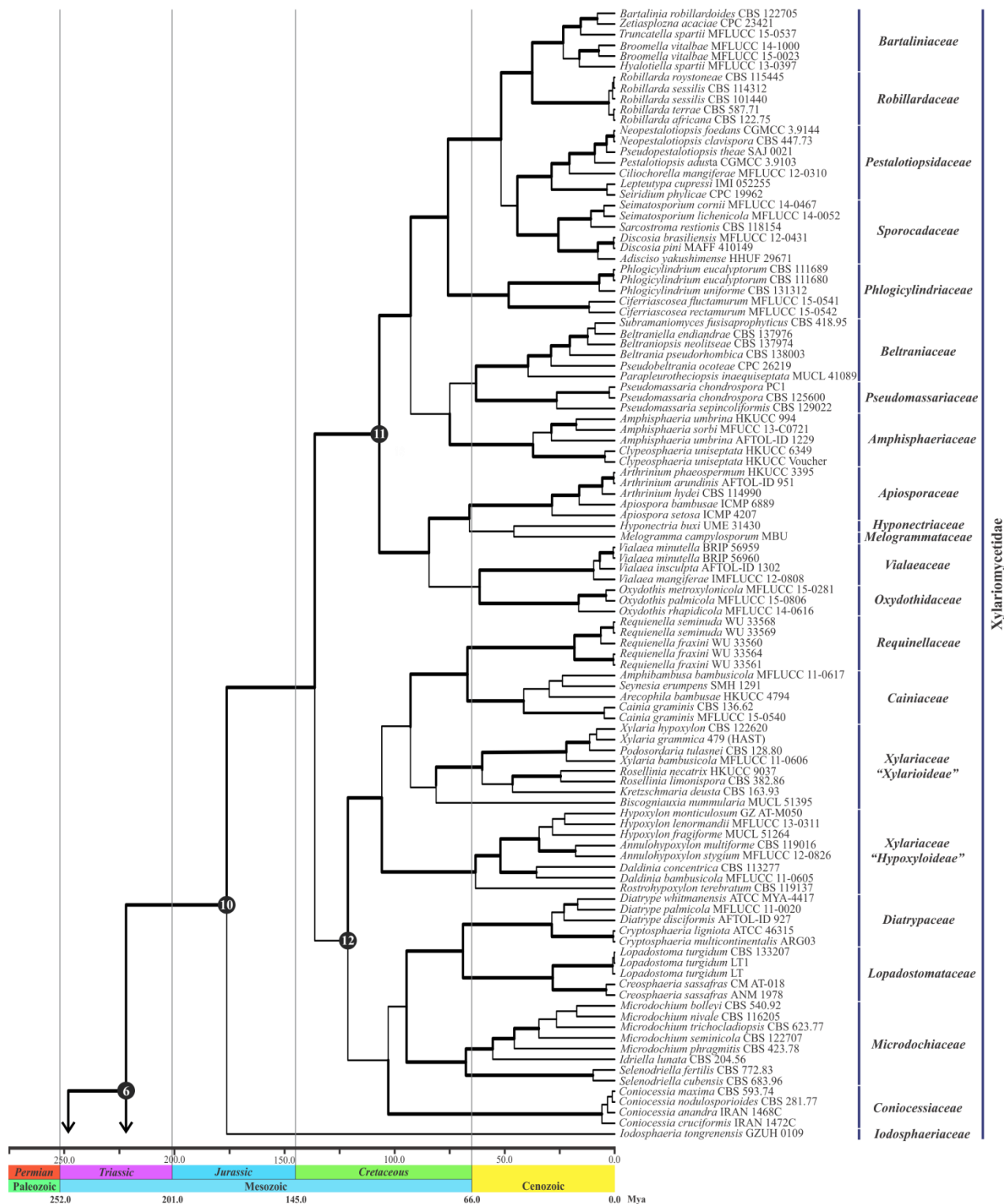


## The impact of calibrations

In most of the cases, the paleontological time estimations deviate from the molecular estimations (Hug & Roger 2007). This can result from model selection, sequence data and the



**Fig. 1** – Consensus tree resulting from a maximum likelihood analysis (compressed over view) of a combined LSU, SSU and RPB2 sequence alignment for taxa of Xylariomycetidae and other selected isolates of Sordariomycetes. RAxML bootstrap support values (ML above 50) and Bayesian posterior probabilities (PP above 0.9) are given at the nodes (ML/PP). The scale bar represents the expected number of changes per site. The tree is rooted to *Leotia lubrica*, *Coccoomyces dentatus*, *Mollisia ventosa*, *M. cinerea* and *Thelebolus globosus*.



**Fig. 2** – Xylariomycetidae divergence time tree (Scenario 2) estimated using lognormal relaxed clock mode (uncorrelated) in BEAST, with representative families. Numbers in the black circles indicate the median age and 95% highest posterior density (HPD) from Table 2. The yellow and red circles indicate the fossil (Scenario 1) and secondary (Scenarios 1 and 2) points respectively. Branches >0.9PP are in bold.

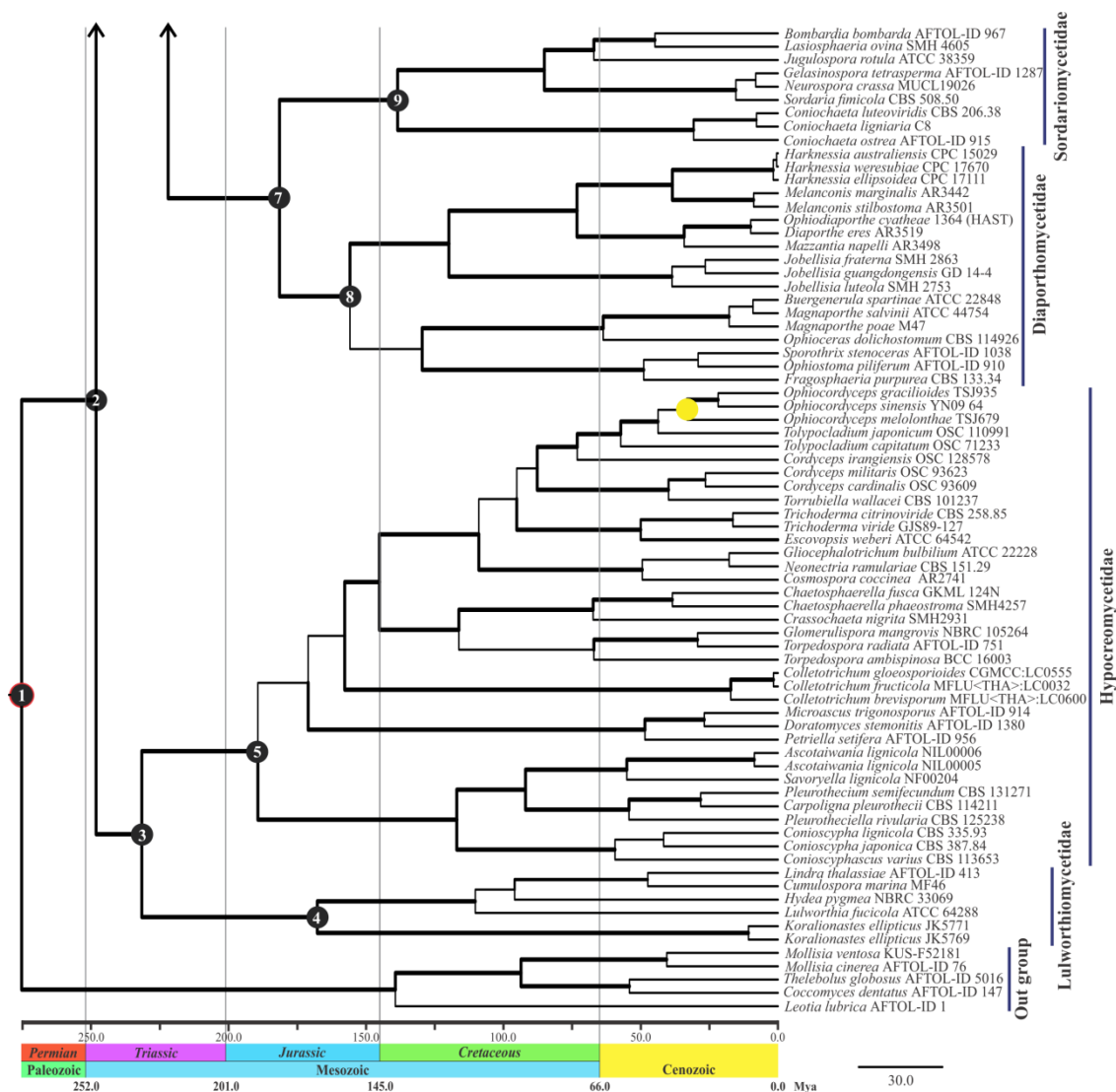


Fig. 2 – continued

calibration points (Hug & Roger 2007). Our sequence data set comprise a large number of species of Xylariomycetidae and Hypocreomycetidae. However, Hug & Roger (2007) suggested that the taxon sampling of the data set is less important for the age estimation. In addition, the use of single fossil for the calibration leads to unpredictable results (Hug & Roger 2007).

The estimated crown ages of Hypocreales are 167 Mya (Scenario 1) and 106 Mya (Scenario 2). Sung et al. (2008) estimated that the crown age of the Hypocreales as 193 Mya using the *Paleoophiocordyceps coccophagushas* fossil. Our results from Scenario 1 are similar to Sung et al. (2008). In this study, the combination of fossil and estimated mean divergence times as secondary information (Scenario 1) resulted in older divergence times, as compared to the secondary information alone (Scenario 2). In the first scenario, the fossil calibration might push the divergence times towards the bases. In the second scenario, there is no effect from terminal nodes to the bases. Because of the uncertainty of the estimated divergence times when using only secondary data for the calibration (Hug & Roger 2007) and the earlier divergence times of extant species, the results from Scenario 1 are considered more accurate and are discussed further.

### Evolution of major groups

The divergences of the subclasses in Sordariomycetes are discussed in this section based on the combined calibrations in Scenario 1 (see Table 2 and Fig. 2). The major clades are well-supported in both phylogenies and the divergence times, largely overlapping with previous studies (Beimforde et al. 2014, Pérez-Ortega et al. 2016). The Paleozoic divergence of Leotiomycetes and

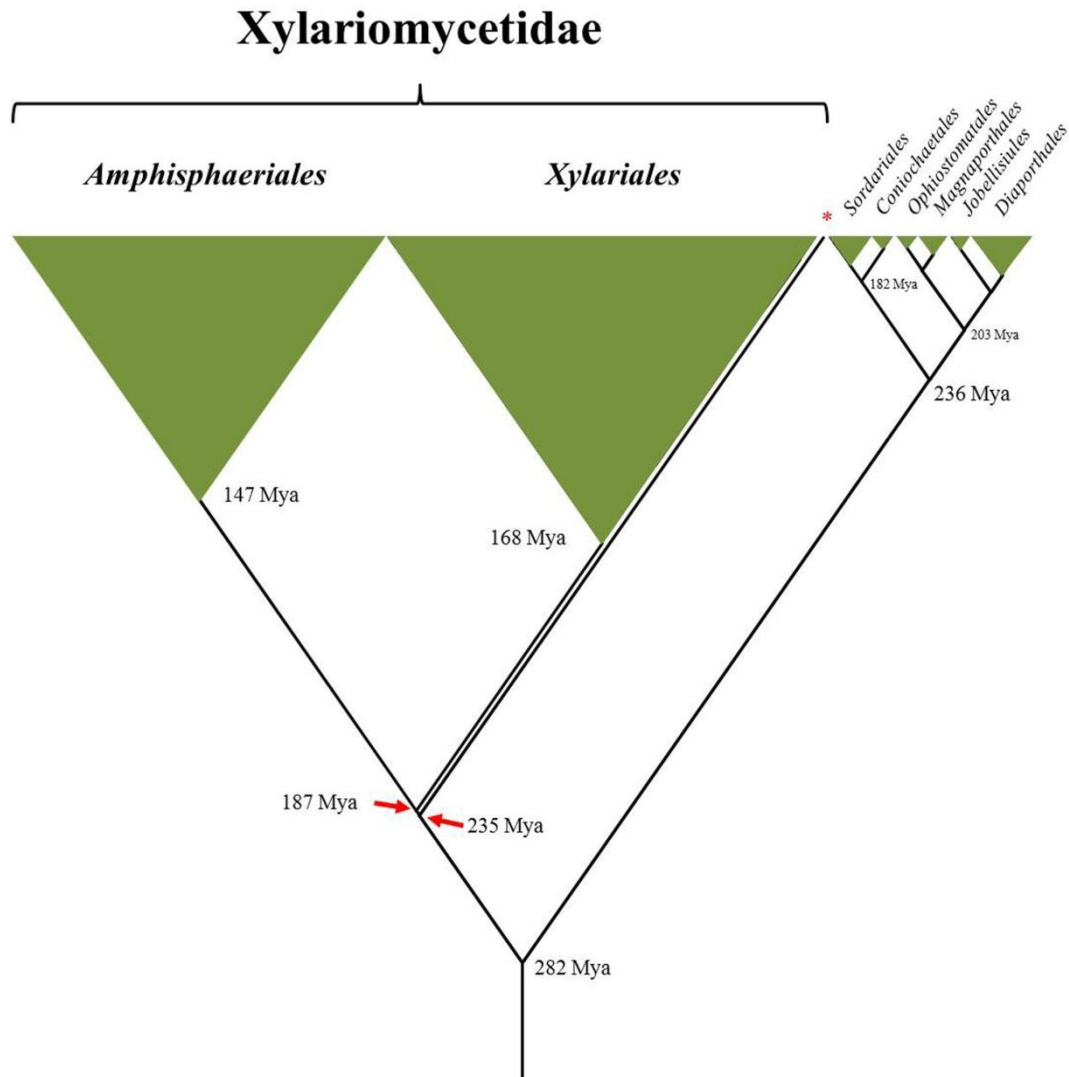
Sordariomycetes in our study (347 Mya), is similar to those in recent studies (317 Mya in Pérez-Ortega et al. 2016 and 309 Mya in Beimforde et al. 2014). Prieto & Wedin (2013) however gave a younger estimated age for the split between Leotiomycetes and Sordariomycetes at 247 Mya, during the Early Mesozoic. The Devonian to Late Paleozoic (290-380 Mya, Lücking et al. 2009), Permian 256 Mya (202-306, Pérez-Ortega et al. 2016) and 260 Mya (207-339, Beimforde et al. 2014) and Early Mesozoic 229 Mya (Gueidan et al. 2011) divergences of Sordariomycetes crown, have been reported in several studies. We also provide a reasonable age estimate for Sordariomycetes crown at 308 Mya, during the Late Paleozoic. Beimforde et al. (2014) suggested that the divergences of classes in Pezizomycotina started during the Ordovician (444-485 Mya). The classes Dothideomycetes and Sordariomycetes comprise a highly-diversified group, with saprobic, pathogenic, endophytic, epiphytic, fungicolous, lichenized or lichenicolous life styles, and are found in terrestrial, freshwater and marine habitats (Hyde et al. 2013, Jones et al. 2015, Maharachchikumbura et al. 2016). During the Paleozoic (252-541 Mya), it is thought that highly diversified plant-fungal interactions played a crucial role as the back bone of the ecosystem (Selosse et al. 2015). The divergence of Dothideomycetes crown group (290 Mya) occurred before Sordariomycetes (256 Mya) and the former class has a higher species richness (Pérez-Ortega et al. 2016). The high species richness in the Dothideomycetes might be a result of its early divergence or that species were better adapted to a range of environments. However, the relationship between early divergence and the species richness is still unclear (Magallón et al. 2015).

The phylogenies and divergent time tree provides support for five subclasses of Sordariomycetes. The subclasses Lulworthiomycetidae, Hypocreomycetidae, and Xylariomycetidae appear to have originated during the Early Mesozoic (201-252 Mya), while Sordariomycetidae and Diaporthomycetidae originated during the Middle of Mesozoic (145-201 Mya). The subclass Meliolomycetidae was not included in this study. The Late Paleozoic-Early Mesozoic mass extinction event is thought to have occurred around 251 Mya, and therefore it has been postulated that fungal species might have rapidly dominated terrestrial ecosystems during this time (Anon 2014, Eshet et al. 1995, Schubert & Bottjer 1995), or only shallow marine deposits (Wignall 1996), where dead biomass provided abundant organic matter for saprobes (Eschet et al. 1995). Lulworthiomycetidae (all aquatic and mostly marine), Hypocreomycetidae (mostly terrestrial, and insect fungi) and Xylariomycetidae (mostly terrestrial wood degraders) are mostly saprobes (Kirk et al. 2008, Boonyuen et al. 2011, Senanayake et al. 2015, Maharachchikumbura et al. 2015). Beimforde et al. (2014) suggested that ecological diversification of a few Ascomycota in each lineage might have protected them from mass extinction. Many species in Xylariomycetidae have large stromata and are saprobes, but there are also many microfungal representatives (Daranagama et al. 2016a).

### **Phylogeny of Xylariomycetidae**

In the phylogenies, there is lack of statistical support for the two main clusters within Xylariomycetidae in both maximum likelihood and Bayesian analysis when using LSU, SSU and rpb2 sequence data. These two main clades were used as evidence for the orders Amphisphaeriales and Xylariales as morphologically they can clearly be separated (Senanayake et al. 2015). Because of the poor phylogenetic support, Amphisphaeriales was placed under Xylariales in Jaklitsch et al. (2016) and Maharachchikumbura et al. (2016). These orders however, have different divergence estimates (147 Mya in Amphisphaeriales, versus 168 Mya in Xylariales Mya (Fig. 3) in the maximum clade credibility (MCC) tree and provides evidence for at least two distinct orders. The order Amphisphaeriales comprises Amphisphaeriaceae, Apiosporaceae, Bartaliniaceae, Beltraniaceae, Hyponectriaceae, Melogrammataceae, Oxydothidaceae, Pestalotiopsisaceae, Phlogicylindriaceae, Pseudomassariaceae, Robillardaceae, Sporocadaceae and Vialaeaceae, while Xylariales comprises Cainiaceae, Conioceciaceae, Diatrypaceae, “Hypoxyloideae”, Lopadostomataceae, Microdochiaceae, Requinellaceae and “Xylarioideae”. The divergence of Amphisphaeriales and Xylariales are similar to the common divergence trend of most of the fungal orders reported in Samarakoon et al. (2016) at 66-252 Mya. Therefore, we recommend that based

on the additional evidence provided here (Fig. 2), that the order Amphisphaeriales should be retained as a well-supported order.



**Fig. 3** – The major crown group of Xylariomycetidae (Amphisphaeriales – 147 Mya; Xylariales – 168 Mya). The \* denotes the family Iodosphaeriaceae in the subclass Xylariomycetidae

Iodosphaeriaceae is basal to all families in Amphisphaeriales and Xylariales and diverged 235 Mya. The evidence in the divergence tree (Fig. 2) therefore suggests that this family evolved early on in the subclass and may require its own order status. The life style (probably endophytic and then saprobic on leaves), morphology with unusual hairy, superficial ascomata (Hilber & Hilber 2002) and distinct phylogeny (Fig. 2) support this. Some other families in Amphisphaeriales and Xylariales also clustered as distinct groups. For example, *Diatrype* and *Lopadostoma* in Xylariales and *Oxydothis* and *Vialaeaceae* in Amphisphaeriales can be considered. However, the divergence estimates at 95 Mya for the split of *Diatrype* and *Lopadostoma* and 83 Mya for the split of *Oxydothis* and *Vialaea* may be too recent to warrant order status.

Most families in Xylariomycetidae originated during the Mesozoic (from 100 Mya); however, the exact crown ages are unclear due to limitations in available sequence data. Within the family Xylariaceae, there are two major clades represented by “Xylarioideae” and “Hypoxyloideae” with different stem ages (144 Mya and 127 Mya respectively). This provides additional evidence for the introduction of “Hypoxyloideae” as a new family. The phylogenetic relationships within Xylariomycetidae need further refining following the arrangements of Senanayake et al. (2015) and Maharachchikumbura et al. (2015, 2016). However, the lack of sequence data in most of the groups and several unresolved lineages within Xylariomycetidae that

need to be explored (Daranagama et al. 2016a) with the combination of the phylogeny, paleobiology and ecology.

## Conclusion

This is a preliminary study, for the application of divergence times on unresolved taxon groups. During the Late Paleozoic, the class Sordariomycetes became highly diversified, splitting into at least five subclasses during the Early Mesozoic and the Middle of Mesozoic. The wide range of nutritional modes and habitats in Sordariomycetes might have been advantageous for the survival and rapid domination in terrestrial, marine and freshwater habitats, even after the mass extinction that occurred during the Late Paleozoic-Early Mesozoic. The divergence age differences in the clusters of taxa in Xylariomycetidae, indicate that they diverged into numerous families of mostly saprobic taxa starting from Late Mesozoic (100 Mya).

## Acknowledgements

Kevin D. Hyde thanks the Chinese Academy of Sciences, project number 2013T2S0030, for the award of Visiting Professorship for Senior International Scientists at Kunming Institute of Botany. The authors extend gratitude to Dr. Martin Ryberg, Department of Organismal Biology, Evolutionary Biology Centre, Uppsala University, SE 75236 Uppsala, Sweden for his valuable comments and advice on this manuscript.

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